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A CONTRIBUTION TO RIODINID SYSTEMATICS

(LEPIDOPTERA: RIODINIDAE)

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A REVIEW OF THE GENUS *SAROTA* (LEPIDOPTERA: RIODINIDAE)

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ABSTRACT.— A review of the genus *Sarota* Westwood, 1851, is presented which includes a brief overview of the biology, biogeography and taxonomic history of its component species, a key to the identification of adults, illustrations of all known species and subspecies (including many type specimens) with accompanying taxonomic notes and the descriptions of five new species and two new subspecies: *Sarota chloropunctata* n. sp., *Sarota chocoensis* n. sp., *Sarota completa* n. sp., *Sarota harveyi* n. sp., *Sarota willmotti* n. sp., *Sarota estrada sabanilla* n. ssp., and *Sarota gamelia alba* n. ssp.. Twenty species are recognised. Neotypes are designated for *Sarota acantus* (Stoll, 1782) and *Sarota gyas* (Cramer, 1775). The tribe Sarotini (= Charitini Auctt.) is synonymised with the tribe Helicopini (n. syn.), and a cladogram based on a small character matrix is used to illustrate generic relationships within the more inclusive, newly conceived tribe.

KEY WORDS: Amazon, *Anteros*, Araceae, Argentina, behavior, biogeography, Bolivia, Brazil, *Callistium*, Central America, *Charis*, Charitini, *Charmona*, Chocó, cladistics, Colombia, *Comphotis*, Costa Rica, Ecuador, *Emesis*, Fabaceae, French Guiana, Guatemala, Guyana, Helicopini, *Helicopis*, Honduras, hostplants, *Hypochrysops*, Lejuniaceae, Lycaenidae, Mexico, Neotropical, *Nymphidium*, *Ourocnemis*, Panama, Peru, *Phaenochitonina*, pheromones, *Sarota chloropunctata* n. sp., *Sarota chocoensis* n. sp., *Sarota completa* n. sp., *Sarota harveyi* n. sp., *Sarota willmotti* n. sp., *Sarota estrada sabanilla* n. ssp., *Sarota gamelia alba* n. ssp., Sarotini, South America, Sterculiaceae, Surinam, taxonomy, *Theope*, Tiliaceae, Trinidad, Venezuela.

The bejewelled ventral wing patterns of *Sarota* species are spectacularly distinctive and rather reminiscent of those of the Oriental lycaenid genus *Hypochrysops* C. & R. Felder, 1860. The genus *Sarota* contains a well defined, relatively homogeneous, monophyletic group of species whose close phylogenetic relationship to the genera *Anteros* Hübner, [1819], and *Ourocnemis* Bethune-Baker, 1887, is well known (Stichel, 1911, 1930; Harvey, 1987). However, while the systematic position of the genus is reasonably well established, its alpha level taxonomy has remained poorly understood, no doubt because of the great phenotypic similarities between its species and their diminutive size, and previous authors have grossly underestimated its species diversity. Seitz (1916-18) figured a mere 6 species and both Stichel (1930) and Bridges (1994) list only 10 species, no significant additions being made to our taxonomic knowledge of the genus during that intervening period. D'Abbrera (1994) also misleadingly illustrates only a fraction of the diversity in *Sarota* with 6 species. For these reasons, coupled with the perpetual misidentification of species in published photographs and popular literature (see appendix) and the discovery of several new *Sarota* taxa in Ecuador during a comprehensive survey of the papilionoid fauna of that country, I decided to review the entire genus with a view to ending the aforementioned confusion and providing an illustrative benchmark against which potentially new taxa can be compared. To this end, the *Sarota* collections of the following institutions, whose acronyms are used throughout the text, were examined:

AME	Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, FL, USA
AMNH	American Museum of Natural History, New York, NY, USA
BMNH	Natural History Museum, London, England
FSCA	Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, FL, USA
GWB	George W. Busby collection, Boston, MA, USA
JHKW	Jason P. W. Hall and Keith R. Willmott collection, Gainesville, FL, USA
MNHN	Musée Nationale d'Histoire Naturelle, Paris, France
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
PJD	Philip J. DeVries collection, Dept. of Biology, University of Oregon, Eugene, OR, USA
RCB	Robert C. Busby collection, Boston, MA, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
ZMHU	Zoologische Museum, Humboldt Universität, Berlin, Germany

Characteristics of *Sarota*

All species in *Sarota* are essentially sexually monomorphic, typically small, often possess hindwing tails, and while usually having dull brown dorsal surfaces, have characteristic ventral surfaces. The ventral surface is predominantly shades of orange-brown with yellowish margins and all species have a double row of silver lines around the submargins of both wings, although the innermost forewing line is often broken into or inclusive of one or more proximally directed silver streaks; the basal portion of the wings consists of alternating transverse lines of small black spots and silver markings. Despite the remarkable resemblance of some *Sarota* species to certain *Anteros* species, most notably those of the "*carausius* Westwood, 1851, group" (see Hall and Willmott, 1998), the *Sarota* species can be distinguished by their less robust thoraces, typically more rounded or tailed hindwings and different genitalic structures. The male genitalia of *Sarota* are far more homogeneous than in *Anteros*, barely differing even between species groups; all species have a small serrate aedeagal cornutus that is not present in those *Anteros* species dissected and the valvae always consist of a long upper portion and typically a bluntly triangular lower portion, with a prominent basal lateral bulge, whereas in *Anteros* the lower portion is often as long as or longer than the upper portion. The upper valva arms in *Sarota* are also connected dorsally in a "V" shape by membranous tissue toward the tips whereas in *Anteros* they are joined towards the base, often by sclerotised rods that almost enclose the aedeagus.

The slight interspecific differences in wing pattern between many sympatric species, combined with the often significant intraspecific geographic or altitudinal variation and the seemingly endless combinations of the same basic ventral markings involved, can make identifications difficult, but the genus is at least readily separated into three distinct and roughly evenly sized groups on the basis of wing shape (see Fig. 1), as partially proposed by Stichel (1930). Members of the "*chrysus* group" are considerably larger than most species of the other groups, they have distinctive hindwing tails with a pointed tornus and two long tail elements at veins M_3 and Cu_2 either side of a shorter central one and typically white or cream spots on the dorsal forewing; with few exceptions, these species are also the only ones to have orange-brown tipped antennal clubs. Species identification characters include forewing shape, the pattern of spots on the dorsal forewing, the tone of the ventral orange-brown coloration, and the ventral silver

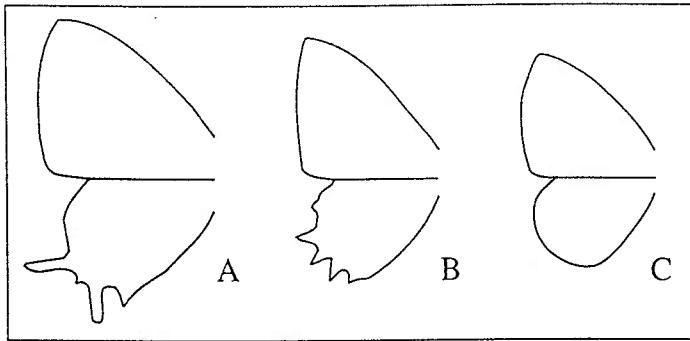


Fig. 1. Schematic drawings of *Sarota* wing shapes, highlighting hindwing differences between species groups: A) "*chrysus* group"; B) "*acanthoides* group"; C) "*gyas* group".

patterning. Members of the "*acanthoides* group" are smaller and have a pointed hindwing tornus with three smaller hindwing tail elements of roughly equal size at veins M_3 to Cu_2 , often with tiny points at veins M_2 and M_1 ; those of the "*gyas* group" are variably sized but typically small and do not have a pointed hindwing tornus or any hindwing tails. Identification characters for both latter groups include the pattern of silver markings in the submarginal and apical areas of the ventral forewing, the extent of ventral brown background coloration, the tone of the ventral orange-brown coloration, size, leg color and in females of the "*gyas* group", the presence/absence and extent of red-brown at the distal margin of the dorsal hindwing. The monophyly of these groups, in particular the "*gyas* group", is uncertain but their recognition allows the genus to be broken up into manageable portions.

Biology

Sarota species occur almost exclusively in wet forest habitats, but at least one species, *S. craspediodonta* (Dyar), appears to be tolerant of more xeric conditions. Most are found only below 1000m but a few occur as high as 1700m and one species, *S. myrtea* Godman & Salvin, flies as high as 2400m. The "*gyas* group" probably contains the largest number of more commonly encountered species while all members of the "*acanthoides* group" are uncommon to rare and, overall, most *Sarota* species are poorly represented in collections and only a few are likely ever to be seen in the field by the casual observer or collector.

Males of most species, particularly those in the "*acanthoides*" and "*gyas*" groups, perch in small groups, typically on low vegetation 2-5m high, along forest edges, on certain isolated trees or most commonly on streamside vegetation or in large clearings nearby. They are predominantly active on their perches in the early morning from about 0630h in some cases to about 1000h and are then only more sporadically encountered as solitary individuals in a wide range of forest microhabitats throughout the remainder of the day, but especially in the late afternoon. They frequently fly out to investigate passing objects with a fast, erratic flight and often engage in aerial spiralling with other male *Sarota*, factors that, combined with their small size, can make them difficult to see. They rest both beneath and on top of leaves with their wings shut but, like their close relatives, typically keep their hindwings slightly apart; they are sometimes observed to rub their hindwings together in a manner reminiscent of lycaenids (Robbins, 1986; pers. observ.). Occasionally, diverse perching communities are found with as many as five or more species co-occurring in the same small vicinity. While each species may be partitioned to some extent in space and time, to aid their reproductive isolation (Callaghan, 1983), this is not in my experience as rigid as is often reported in *Sarota* or riodinids in general (Callaghan, 1983; Brévignon and Gallard, 1995; DeVries, 1997). While the division of perching behavior into species specific windows of time and space is

clearly a characteristic phenomenon in riodinid butterflies, it is one that has large numbers of exceptions. Thus, several *Sarota* species may be found perching at the same time (although their mean activity time may be different) and on the same clump of leaves indicating the possibility that pheromonal chemistry plays a more important role in the reproductive isolation of riodinids than has previously been suggested.

Solitary females are encountered in the vicinity of male perching areas or flying low to the ground along forest edges in the understory and in lightgaps throughout most of the day. The females of two species, *S. acantus* (Stoll) (as *gyas*) and *S. chrysus* (Stoll), have been observed to oviposit on the leafy liverworts and mosses (Lejuniaceae) that grow as epiphylls on top of the old leaves of a variety of understory shrubs and these are thought to be the dominant foodplants for the genus (DeVries, 1988, 1997; DeVries *et al.*, 1994). The larvae of the only reared species, *S. acantus* (Fig. 2), are very similar to those of related genera (see DeVries, 1997; Brévignon and Gallard, 1998) in having very long dorsolateral tufts of downy white setae that may be moved in defense against ants and a cluster of bladder or balloon-like setae on the anterior edge of the prothoracic shield. Inside a rolled leaf, the long larval setae are used to surround the pupa to form a loose cocoon (DeVries, 1997).



Fig. 2. Fifth instar larva of *Sarota acantus* (photo by P. J. DeVries).

It is interesting to note that no *Sarota* species has been recorded feeding on rotting carrion, a behavior that is so pervasive in the closely related genera *Anteros* and *Ourocnemis* (Hall and Willmott, 1995, 1998, in prep.). This difference can be statistically correlated with wing area to thoracic volume ratio; in other words, slight bodied species, like those of *Sarota*, do not tend to feed on rotting carrion while larger bodied species, like those of *Anteros* and *Ourocnemis*, do, possibly because of differing nutrient requirements (Hall and Willmott, in prep.). Both sexes of at least one species have been recorded feeding on the flowers of *Croton* and *Alibertia* (DeVries, 1997) and several species are reported to visit the extrafloral nectaries of plants in a number of families, including the Araceae, Fabaceae, Sterculiaceae and Tiliaceae (DeVries, pers. comm.).

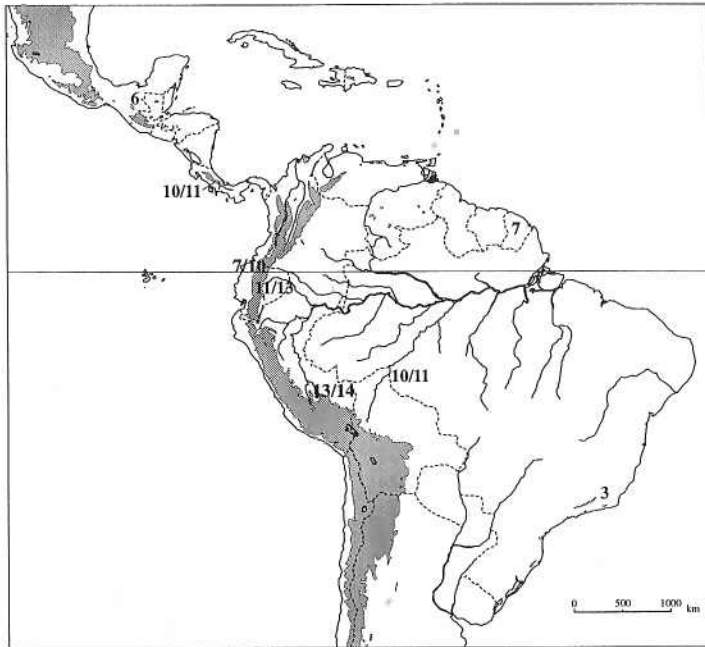


Fig. 3. Map of the Neotropical region showing *Sarota* diversity in selected areas. A single number or that to the left of a "/" is the number of recorded species, that to the right of a "/" is the expected number of species.

Biogeography

The genus *Sarota* is distributed from southern Mexico, through Central America to southwest Ecuador and throughout the Guianas and Amazon basin to southeast Brazil. Figure 3 shows the number of *Sarota* species known to occur in selected well-studied areas, indicating that the peak of diversity for the genus occurs along the base of the eastern Andes, where a single locality could theoretically harbor as many as 14 species (or 13 in the northern Andes where *S. harveyi* n. sp. probably does not occur). These data and those in Table 1 reflect with reasonable accuracy the distribution of overall riodinid diversity in the Andean countries, with Colombia and Ecuador sharing the highest species numbers (Hall, unpubl. data), but there are certain distributional anomalies in *Sarota*. Most notable of these is the high number of species from Costa Rica and neighbouring countries, a phenomenon explained by the diversity in the "chrysus group" west of the Andes; while five species in this group occur in the Transandean region, only a single representative occurs east of the Andes. This is in sharp contrast to the other two species groups in which about twice as many species occur east of the Andes as to the west. Mexico also has a slightly higher number of *Sarota* species than might be expected based on the distribution of overall riodinid diversity but conversely Brazil has slightly lower species numbers, no doubt because of the lack of lower Amazon and south-east Brazilian endemics.

Table 1. The number of recorded and expected *Sarota* species for selected Neotropical countries.

Country/ Region	Recorded no. of species	Predicted no. of species
Mexico	6	6
Costa Rica	10	11
Panama	8	11
Venezuela	6	14
Colombia	13	17
Ecuador	15	17
Peru	13	14
Bolivia	4	14
Brazil	11	11
Guianas	7	7

Taxonomy

Acceptance of the generic name *Sarota* has been patchy since its description by Westwood (1851) nearly 150 years ago, probably because it was only initially given subgeneric status. Before and after that publication, the species now placed in *Sarota* were most frequently regarded as belonging to the genera *Charis* Hübner, [1819] and *Anteros*, and it was not until the work of Godman & Salvin (1886) that their names were again used in combination with *Sarota*. Stichel (1910, 1911, 1930) further complicated matters by again disregarding the validity of the name *Sarota*. He placed its component species into the genus *Charis*, which he erroneously believed had the taxon *gyas* as its type species, and placed the taxon *auisus* Cramer, 1776, and relatives, which currently constitute the genus *Charis*, into the invalid genus *Charmona* Stichel, 1910. Hemming (1967) recognised these errors and finally validated *Sarota* as the only available name for the group of species reviewed in this paper.

Stichel (1911) erected the tribe Charitini for *Sarota* (as *Charis*), *Anteros*, *Ourocnemis* and *Callistium* Stichel, 1911, on the basis that all shared a posterior projection from the dorsum of the uncus in the male genitalia. However, this character is found elsewhere in the family (e.g., *Comphotis* Stichel, 1910, and *Phaenochitonina* Stichel, 1910; see Hall and Willmott, 1996) and Harvey (1987) redefined the tribe on the basis that females possess spatulate scales surrounding the ovipositor lobes. Since the single member of *Callistium*, *C. cleadas* (Hewitson, 1866), lacks this character, Harvey (1987) transferred it to an *incertae sedis* section (four forewing radial veins). The tribal name Charitini has been extensively used since its erection, but as it is based on a misidentified type genus it is nomenclaturally invalid. Bridges (1988) provided the tribal name Sarotini (as an infratribe) as a replacement; however, it has largely been overlooked by subsequent authors.

Harvey (1987) used the presence of tails at veins M_1 and Cu_2 to define his sister tribe Helicopini, citing their different position and extreme development to distinguish them from those of, for example, *Sarota*. However, the tails of the two genera are not in different positions but merely developed to different extremes along different veins, a phenomenon that occurs within the clearly monophyletic genus *Sarota*, which of course even has members lacking tails altogether. I propose that the morphological differences between members of the tribe Sarotini and those of the Helicopini Reuter, 1897 (= Helicopidi Stichel, 1928, and Helicopini Clench, 1955), are insufficient to warrant their sustained separation and I synonymise the tribe Sarotini into the Helicopini (n. syn.). The more inclusive tribe, as informally used by Brown (1993) (as a subtribe), contains *Helicopsis* Fabricius, 1807, *Sarota*, *Anteros* and *Ourocnemis*, and can be defined by the known larvae of its members possessing yellow or white bladder-like setae on the anterior edge of the prothoracic shield

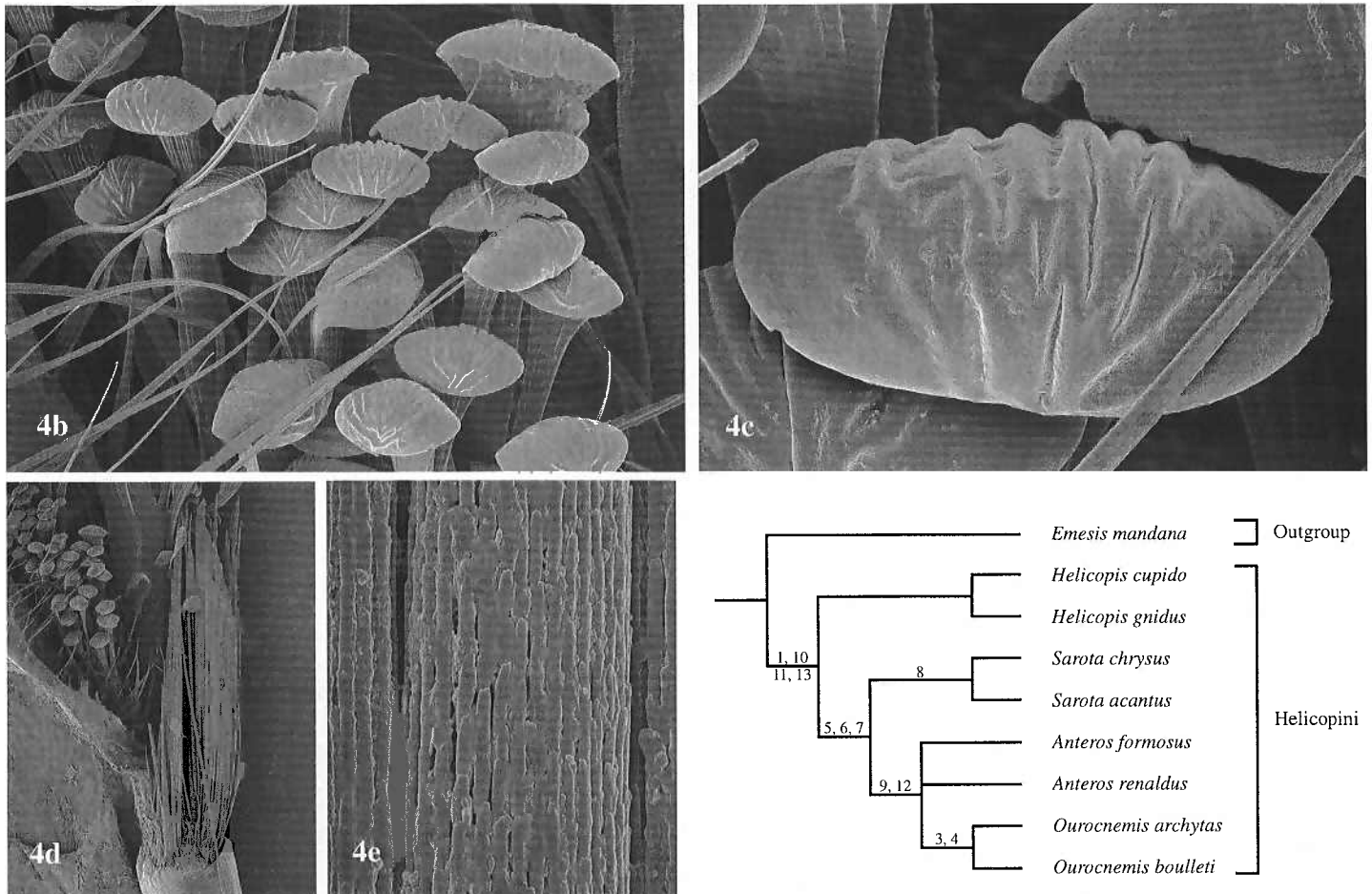


Fig. 4a (lower right). A cladogram showing generic relationships within the tribe Helicopini. The numbers at the nodes represent the characters (the derived character state in each case) that support each in-group clade.

Fig. 4b-e. Scanning electron micrographs of female genitalic morphology for *Sarota chrysus*. 4b,c. Spatulate scales surrounding the papillae anales (b: x400; c: x2000). 4d,e. Long spine-like setae between the papillae anales and ostium bursae (d: x90; e: x6000).

(Harvey, 1987; DeVries, 1988, 1997). These setae differ in fine structural details from those found on the larvae of certain species in the tribe Nymphidiini (e.g. *Theope* Doubleday, 1847, and *Nymphidium* Fabricius, 1807) and are deemed to have arisen independently (Harvey, 1987). Behavioral characters, such as hindwing rubbing, not seen elsewhere in the Riodinidae (Robbins, 1986; pers. observ.), and resting with wings shut instead of open, not seen in any closely related genera, also support the newly proposed tribal arrangement.

Preliminary phylogenetic analyses were performed with PAUP version 3.0s (Swofford, 1991) to illustrate generic relationships within the Helicopini, using *Emesis mandana* (Cramer, 1780) as an outgroup and the type species plus one other of each in-group genus. The following list of 13 binary characters used encompasses wing pattern, adult behavior, and the morphology of larvae, male and female genitalia and adult appendages. All characters are equally weighted. Using an exhaustive search, one most parsimonious tree was generated (Fig. 4a) of 15 steps (consistency index = 0.867) upon which supporting characters for each in-group clade are marked.

List of characters employed in cladistic analysis (see Table 2):

1. Silver ventral markings absent (0); present (1).
2. Hindwing tails absent (0); present (1).
3. Ventral surface of antennae black with some white scaling (0); red-brown (1).

4. Setae on palpi, and tibia and tarsi of forelegs not densely layered (0); very densely layered (1).
5. Spatulate scales surrounding the papillae anales of the female genitalia absent (0); present (1) (Fig. 4b,c). The assignment of character state (1) to *O. archytas* is based on data in Harvey (1987).
6. Long spine-like setae between the papillae anales and ostium bursae of the female genitalia absent (0); present (1) (Fig. 4d,e).
7. Posterior projection from the dorsum of the uncus in the male genitalia absent (0); present (1).
8. Lateral bulge at the base of the valvae in the male genitalia not prominent (0); prominent (1).
9. Valvae of the male genitalia join dorsally towards tip (0); towards base (1).
10. Adults rest with wings spread open (0); with wings closed over the body (1).
11. Adults do not rub hindwings together (0); do rub hindwings together (1). Character state (1) is expected to occur in most if not all in-group taxa.
12. Adult males have not been recorded as attracted to rotting fish (0); have been recorded as attracted to rotting fish (1).
13. Larvae without a cluster of bladder-like setae on the anterior edge of the prothoracic shield (0); larvae with bladder-like setae (1). The assignment of character state (1) is based on data in Harvey (1987) and DeVries (1988, 1997). Character state (1) is expected to occur in all in-group taxa.

Table 2. A binary character matrix for selected taxa in the tribe Helicopini, including *Emesis mandana* as an outgroup.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Helicopsis cupido</i> Linn.	1	1	0	0	0	0	0	0	0	1	1	0	1
<i>Helicopsis gnidus</i> Fab.	1	1	0	0	0	0	0	0	0	1	?	0	?
<i>Sarota chrysus</i> Stoll	1	1	0	0	1	1	1	1	0	1	1	0	?
<i>Sarota acantus</i> Stoll	1	0	0	0	1	1	1	1	0	1	1	0	1
<i>Anteros formosus</i> Cr.	1	0	0	0	1	1	1	0	1	1	1	1	1
<i>Anteros renaldus</i> Stoll	1	0	0	0	1	1	1	0	1	1	1	1	?
<i>Ourocnemis archytas</i> Stoll	1	0	1	1	1	?	1	0	1	1	?	1	?
<i>Ourocnemis bouletti</i> Le C.	1	0	1	1	?	?	1	0	1	1	?	1	?
<i>Emesis mandana</i> Cr.	0	0	0	0	0	0	0	0	0	0	0	1	0

Helicopsis, characterised by having clustered, yellow, bladder-like setae on the prothoracic shield of the pupa (Harvey, 1987), a unique foodplant association (in the Riodinidae) with the semi-aquatic Araceae (Kaye, 1921; Barcant, 1970; Mallet in Harvey, 1987; DeVries et al., 1994), and extreme hindwing tail development in the adults with the longest tail on vein Cu₁, is the most plesiomorphic genus in the tribe. The remaining clade is well supported by the presence of stiff spatulate scales around the female ovipositor lobes and long spine-like setae between them and the ostium bursae. Interestingly, morphologically very similar spatulate scales have been independently derived in certain tortricid and geometrid moths (Pellmyr, 1980); in these moths they are known to be used for scraping dirt over eggs after they have been deposited (Scoble, 1991) but observations on their function in helicopine riodinids are lacking. The majority of species in this clade also possess a posterior projection from the dorsum of the uncus in the male genitalia, although this is lacking in certain "gyas group" species of *Sarota*; whether its absence in these species represents a plesiomorphic condition for the clade or a secondary loss is not clear at present because of a conflict with the character polarity of, for example, the presence of hindwing tails. Within the clade previously conceived as the Sarotini, *Sarota* would appear to be the most basal genus, defined by its characteristic male genitalic valvae, which invariably consist of a long upper arm connected dorsally in a "V" shape by membranous tissue toward their tips, often a bluntly triangular lower projection, and a prominent basal, lateral bulge, and unique foodplant association (in the Riodinidae) with the epiphylls of old leaves. The most derived group within the tribe appears to be *Anteros* + *Ourocnemis*, but while the latter genus is clearly monophyletic, defined by the red-brown ventral surface to the antennae and the clubbed and densely setose palpi, I could find no character in this preliminary analysis to characterise *Anteros* exclusive of *Ourocnemis* and there is a distinct possibility that the former genus is paraphyletic with respect to the latter.

Key to the Species of *Sarota*

- 1. - Hindwing with distinct tails 2
- Hindwing without tails (or vestigial) 12
- 2(1) - Hindwing with three tails: two long and rounded outer ones and a shorter and more pointed central one (Fig. 1A) 3
- Hindwing with several short and pointed tails (Fig. 1B) 7
- 3(2). - Pale areas of discal cell on both ventral wing surfaces whitish-silver or white, two black spots at base of ventral hindwing costa, dorsal forewing spots white *subtessellata*
- Pale areas of discal cell on both ventral wing surfaces silver, one black spot at base of ventral hindwing costa, dorsal forewing spots cream 4
- 4(3). - Ventral forewing with strongly marked white spots in the apex and in cell Cu₂ *chrysus*
- Ventral forewing without such strongly marked white spots 5
- 5(4). - Ventral forewing with a fragmented postmedial silver line that has more than two proximally directed silver streaks *turrialbensis*
- Ventral forewing with a continuous postmedial silver line that has two proximally directed silver streaks in the apex 6

- 6(5). - Ventral surface richly colored, dorsal forewing with only two prominent cream spots in the apex *neglecta*
- Ventral surface pale, dorsal forewing with one spot in the apex and one in cell Cu₂ *chocoensis*
- 7(2). - Ventral surface heavily dusted with white scaling *psaros*
- Ventral surface without extensive white scaling 8
- 8(7). - Silver in cell Cu₁ of the postmedial silver line on both ventral wing surfaces displaced proximally by a large black spot *craspediodonta*
- Postmedial silver line on both ventral wing surfaces even 9
- 9(8). - Ventral surface very dark, forelegs black *spicata*
- Ventral surface paler, forelegs shades of yellow 10
- 10(9). - Postmedial silver line on ventral forewing has only one proximally directed silver streak at its apex, male forewing pointed *willmotti*
- Postmedial silver line on ventral forewing has two proximally directed silver streaks at its apex, male forewing rather rounded 11
- 11(10). - Proximally directed silver streak in cell M₂ complete, relatively small area of brown background color visible on both ventral wing surfaces *acanthoides*
- Proximally directed silver streak in cell M₂ partially (male) or completely (female) divided, relatively large area of grainy brown background color visible on both ventral wing surfaces *harveyi*
- 12(1) - Hindwing without tails (Fig. 1C); other characters different -13
- Hindwing intermediate between those in Fig. 1B and 1C, without white fringe elements; forelegs black; both wings ventrally with extensive black distal to postmedial silver lines; ventral hindwing with postmedial silver line incomplete *chloropuncta*
- 13(12). - Ventral forewing with a postmedial silver line that has no long proximally directed silver streaks 14
- Ventral forewing with a postmedial silver line that has two or more proximally directed silver streaks 15
- 14(13). - Central and basal black spots on both ventral wing surfaces encapsulated by orange-brown coloration, apex of forewing postmedial silver line divided into two silver spots *completa*
- Central and basal black spots on both ventral wing surfaces typically not encapsulated by orange-brown coloration, apex of forewing postmedial silver line divided into three silver spots *lasciva*
- 15(13) - Ventral forewing with a postmedial silver line that has two proximally directed silver streaks 16
- Ventral forewing with a postmedial silver line that has more than two proximally directed silver streaks 19
- 16(15). - Outer forewing margin uneven with sections of white fringe in cells 1A+2A and Cu₂, more extensive ventral brown background coloration, proximally directed silver streaks in apex of ventral forewing short and of equal size *myrtea*
- Outer forewing margin even without any sections of white fringe, less extensive ventral brown background coloration, proximally directed silver streaks in apex of ventral forewing not of equal size or longer 17
- 17(16). - Discal cell of ventral hindwing contains single large black square, black spot at base of ventral forewing absent, male forelegs yellow *acantus*
- Discal cell of ventral hindwing contains two smaller black marks, black spot at base of ventral forewing present, male forelegs blackish 18
- 18(17). - Proximally directed silver streak in cell M₁ of ventral forewing typically divided, black scaling distal to postmedial silver line on ventral forewing minimal, distal forewing margin of male typically straight *gyas*
- Proximally directed silver streak in cell M₁ of ventral forewing undivided, black scaling distal to postmedial silver line on ventral forewing extensive, distal forewing margin of male typically convex *miranda*

- 19(15). - Average forewing length 14mm, postmedial silver line on ventral hindwing broken, legs predominantly brown *estrada*
 - Average forewing length 12mm, postmedial silver line on ventral hindwing complete, legs predominantly yellow *gamelia*

SAROTA Westwood, 1851

Sarota Westwood, 1851. In: Doubleday, *Gen. Diurn. Lep.* (2):424. Type species by selection by Scudder (1875, *Proc. Amer. Acad. Arts Sci.*, Boston 10:265): *Papilio chrysus* Stoll, 1782.

SAROTA Westwood, 1851 (20 species)

("-" denotes a subspecies and "--" a synonym)

- acanthoides* (Herrich-Schäffer, [1853])
acantus (Stoll, 1782)
chloropunctata Hall, n. sp.
chocoensis Hall, n. sp.
chrysus (Stoll, 1782)
 --*polypoecila* (Stichel, 1910)
 --*dematria* (Westwood, 1851)
completa Hall, n. sp.
craspediodonta (Dyar, 1918)
estrada Schaus, 1928
 -*sabanilla* Hall, n. ssp.
gamelia Godman & Salvin, 1886
 -*alba* Hall, n. ssp.
gyas (Cramer, 1775)
harveyi Hall, n. sp.
lasciva (Stichel, 1911), n. stat.
 --*flavicincta* (Lathy, 1932), n. syn.
 --*atlantica* Brévignon & Gallard, 1998, n. syn.
miranda Brévignon, 1998
myrtea Godman & Salvin, 1886, stat. rev.
neglecta Stichel, 1910, n. stat.
 --*alacer* (Stichel, 1929), n. syn.
psaros Godman & Salvin, 1886
 -*albidisca* (Lathy, 1932)
 -*psaronius* (Stichel, 1911)
spicata (Staudinger, 1888), stat. rev.
subtessellata (Schaus, 1913)
turrialbensis (Schaus, 1913)
willmotti Hall n. sp.

"chrysus group" (Chrysiiformes of Stichel (1930))***Sarota subtessellata*** (Schaus, 1913)

Fig. 5a-d; 25a,b

Charis subtessellata Schaus, 1913, *Proc. Zool. Soc. Lond.* 3:351, pl. 53, fig. 11. TL: Carrillo, Costa Rica. Holotype male USNM [Examined] (Fig. 5a,b).

Identification and taxonomy: Average FW length 16mm.

This is the largest species of *Sarota* and it can only really be confused with the much more common *S. chrysus*. Both sexes differ from that species by having a more pointed forewing, a darker dorsal surface, white instead of cream dorsal forewing spots, and a ventral surface with more whitish-silver markings, basal red-brown markings in the discal forewing cell that are non-convergent, broken apical forewing silver streaks that, in part, form two characteristic isolated whitish-silver marks at the costa, and typically more red-brown at the base of the hindwing with two black costal spots instead of one.

Biology: *S. subtessellata* is sparsely represented in collections, most specimens originating from Costa Rica and Panama from sea-level to about 1000m. DeVries (1997) states that in Costa Rica:

"The males are encountered as solitary individuals perching from 2 to 5 meters above the ground along forest edges and in light gaps between 12:30 and 13:30 hrs. The females are most frequently found in the shaded forest understory between 12:00 and 14:00 hrs".

Distribution: Costa Rica to west Colombia and probably west Ecuador, although it has yet to be recorded there.

Sarota chrysus (Stoll, 1782)

Fig. 6a-f; 26

Papilio chrysus Stoll, 1782, in Cramer, *Uitl. Kapellen* 4 (32):178, pl. 380, fig. D, E. TL: Surinam. Types unknown, figures [Examined].

= *Charis chrysus* f. *polypoecila* Stichel, 1910, *Berl. Ent. Zeit.* 55(1/2):27. TL: Bugaba, Panama. Holotype female ZMHU [Examined].

= *Helicopsis dematria* Westwood, 1851, in Doubleday, *Gen. Diurn. Lepid.* 2:424, pl. 71, fig. 10. TL: Honduras. Syntype female BMNH [Examined].

Identification and taxonomy: Average FW length 15mm.

There is no extant type specimen for this species, but since the type illustration in Cramer (1775-82) (Fig. 6a) is reasonably accurate and no other "chrysus group" species occur in the type locality, Surinam, there is no problem identifying it and I deem a neotype designation to be unnecessary. It is distinguished from *S. subtessellata* as outlined in that species account and from *S. neglecta* and *S. chocoensis* n. sp. (described below) by having four spots on the dorsal forewing, a broken postmedial silver line on the ventral forewing and more prominent white coloration at the base of both ventral wing surfaces, and in the apex and cell Cu₂ of the ventral forewing.

The species is quite variable over its wide geographic range, the most distinct populations being those occurring from Mexico to Honduras, named by Westwood (1851) as a full species, *dematria* (see Fig. 6f). I recognise as a heretofore unlabelled syntype a female specimen in the BMNH from Honduras with a handwritten label saying "*Helicopsis dematria*". Both sexes of this taxon tend to have darker ventral pattern elements, reduced white markings in the apex of the ventral forewing, where there are also more elongate black marks in cells Cu₁ and M₃, and a complete row of postdiscal black spots on the ventral hindwing. I considered recognising *dematria* as a subspecies of *chrysus* but the observed variation is clinal, the most extreme forms occurring in Mexico. The female type of the form *polypoecila* has unusually prominently marked dorsal forewing spots but is otherwise typical. On a nomenclatural note, it is worth mentioning that in the paper in which *polypoecila* was described, although Stichel (1910) was confusingly using the generic headings of *Sarota* and *Charis* interchangeably in the text, *polypoecila* was clearly described under the heading of "*C. chrysus*". Thus, contrary to the assertions of Stichel (1930) and Lamas *et al.* (1995), *polypoecila* was not described in *Sarota*, parentheses therefore being required around its author's name.

Biology: *S. chrysus* is one of the most widespread and commonly encountered species in the genus, occurring in primary and secondary growth habitats from sea-level to 1350m. Both sexes are typically seen as solitary individuals along open forest trails, forest edges and streamsides, although females are the most commonly encountered sex. A male was once observed puddling on a forest path in the late afternoon. Both sexes visit flowers of *Croton* and *Alibertia* (DeVries, 1997). Females have been observed to oviposit on mosses and liverworts (Lejuniaceae) that grow as epiphylls on old leaves and are assumed to be the larval hostplant (DeVries 1988, 1997; DeVries *et al.*, 1994).

Distribution: Mexico to west Ecuador, Venezuela to Bolivia, Brazil (Amazon, Mato Grosso and southeast), Guianas, Trinidad.

Sarota neglecta Stichel, 1910, n. stat.

Fig. 7a-d; 27

Sarota chrysus neglecta Stichel, 1910, *Berl. Ent. Zeit.* 55(1/2):27. TL: Río San Juan, W. Colombia. Syntype males and females ZMHU [Examined].

= *Charis chrysus neglecta* f. *alacer* Stichel, 1929, *Dtsch. Ent. Zeit.* 1929:205. TL: Río Dagua, W. Colombia. Holotype female ZMHU [Examined], n. syn.

Identification and taxonomy: Average FW length 14.5mm.

This taxon was described as a subspecies of *S. chrysus*, but as the two taxa occur sympatrically and show numerous phenotypic differences, I raise *S. neglecta* to specific status. The species was described from a conspecific series of two males and three females, all from the same locality, and as such no lectotype designation is necessary. The female type of form *alacer* has a more prominently marked dorsal surface than any of the aforementioned syntype females but it falls within the normal range of variation for *S. neglecta* into which I synonymise it. *S. neglecta* has a very similar wing shape and ventral pattern to that of *S. chocoensis* n. sp. (described below) and the diagnostic differences are discussed in that species account.

Biology: Throughout most of its range, *S. neglecta* tends to be the most commonly encountered of the "chrysus group" species and it is thus frequently misidentified in museum collections, published photographs and books (see appendix) as *S. chrysus*. It occurs in primary and secondary forest habitats from sea-level to approximately 1400m where both sexes, but more commonly females, are found resting low to the ground both on top of and beneath large leaves along forest edges, streamsides and ridgetops. Males especially are most active in the early to late morning and then again in the mid to late afternoon.

Distribution: Costa Rica to west Ecuador and northwest Venezuela.

***Sarota chocoensis* Hall, new sp.**

Fig. 8a-d; 28

Description.— MALE: forewing length 14.5mm. Forewing costa slightly convex towards apex, distal margin smoothly convex; hindwing tornus pointed, three tails at middle of distal margin, two long ones at end of veins Cu_2 and M_3 , one very small central one at end of vein Cu_2 . **Dorsal surface:** forewing ground color brown; a large, ovoid cream spot in middle of cells Cu_2 and M_2 ; fringe orange-brown. Hindwing ground color brown, paler at anal margin; a submarginal orange-brown square in cells 1A+2A to Cu_2 ; margin and tails between veins 1A+2A and M_2 pale yellow brown with black, then white, then a thin layer of black scales distally forming fringe, fringe at margin of cell M_2 white. **Ventral surface:** forewing ground color pale yellow-brown, paler at anal margin; black line at discal cell end surrounded by orange-brown with silver mark above, pale yellow-brown triangle surrounded by silver towards discal cell end, orange-brown "U" shape extends from vein 1A+2A to costal edge of discal cell and back with internal black scaling especially below discal cell, orange-brown surrounds costal edge of discal cell, remainder of discal cell silver, silver at base of costa; uneven, orange-brown postdiscal line extends from costa to vein 1A+2A, contains black spots, is largely black below vein Cu_2 , has an uneven silver line proximally that is broken above vein M_1 , and dark silver marks distally in cells Cu_1 and M_3 ; a parallel silver line in each of cells M_2 and M_1 that parallel costa, former pale yellow-brown in proximal half with vertical, pale silver line extending from near distal edge to vein 1A+2A, some darker orange-brown scaling proximally; orange-brown at costal and distal margins, latter divided by thin submarginal silver line that extends from near apex to vein 1A+2A; fringe orange-brown. Hindwing ground color pale yellow-brown; orange-brown band at base lined by silver contains small black spot at costa; postdiscal orange-brown band lined on both sides with black and containing black spots extends from costa, curving inwards to vein Cu_1 , kinking inwards in cell Cu_2 , then continuing to anal margin; another similar, more proximal, parallel band extends from near costa at vein Sc+R₁ to vein M_3 with silver inbetween; more proximal, uneven triangle of orange-brown containing black spots in left and upper apices, lined on both sides with black and encircled by and encircling silver, extends from anal margin to cell 1A+2A to costal edge of discal cell and back; orange-brown at submargin extends from apex to tornus, contains black spot in cell Cu_1 , has silver proximally, except in cells M_3 and M_2 , and distally below vein M_1 ; margin and tails between veins 1A+2A and M_2 pale yellow brown with black, then white, then a thin layer of black scales distally forming fringe, fringe at margin of cell M_2 white. **Head:** labial palpi yellow-brown with some hairs that are tipped with black. Eyes brown and bare, margins with yellow-brown scaling. Frons yellow-brown with some black hairs. Antennal segments black with white

scaling at base, that increases immediately before clubs, then small bare brown patch laterally and ventrally; clubs black, bare tips orange-brown. **Body:** dorsal surface of thorax and abdomen brown, ventral surface pale brown. Forelegs yellow-brown, mid and hindlegs yellow-brown with black banded tarsi. **Genitalia** (Fig. 28): uncus rounded, small posteriorly projecting point from dorsal edge; vinculum evenly thin; valvae have basal, lateral bulge, long upper portion that is of even width and slightly upturned at tip, and connected by membranous tissue dorsally, and small triangular point at lower posterior edge; aedeagus narrow and pointed at tip, tiny cornutus at base; pedicel long.

FEMALE: differs from HT in the following respects: forewing length 13mm. A small cream mark at discal cell end of dorsal forewing, more pronounced postmedial cream markings on dorsal hindwing, an extra black spot, in cell Cu_2 , in the submarginal orange-brown of the ventral hindwing. All of these characters are also present in certain male specimens.

Types.— **Holotype male:** ECUADOR.— *El Oro* Prov.: Zaruma, 1891 (M. de Mathan) (diss. # 4423); in the BMNH.

Allotype female: ECUADOR.— *Pichincha* Prov.: Tinalandia, Río Tanti, 750m, 8 May 1994 (J. P. W. Hall); in the coll. of JHKW.

Paratypes: ECUADOR.— *Pichincha* Prov.: same locality data as AT, 3 ♀: 2 Aug 1993, 1 ♀ (J. P. W. Hall); 26 June 1993, 2 ♀ (K. R. Willmott); all in the coll. of JHKW. Tinalandia, 700m, 20 Sep 1975, 1 ♀ (S. S. Nicolay); in the coll. of D. Ahrenholz, St. Paul, MN. *Manabí* Prov.: nr. Pedernales, Cerro Pata de Pájaro, 750m, 11 Aug 1996, 2 ♂ (K. R. Willmott); in the coll. of JHKW. *El Oro* Prov.: same data as HT, 1 ♂ (BMNH). *Chimborazo* Prov.: Chimbo, 1000ft, Aug 1897, 1 ♀ (Rosenberg) (BMNH). COLOMBIA.— *Chocó:* Río San Juan, San Pablo, 1 ♀ (ex Staudinger coll.) (BMNH). PANAMA.— *Coclé:* El Valle, 26 Aug 70, 1 ♂ (H. L. King) (FSCA).

Etymology.— This species is named after the Chocó region to which, as defined in its broadest sense, it currently appears to be largely confined.

Diagnosis.— *Sarota chocoensis* n. sp. has an almost identical ventral pattern to that of *S. neglecta*, but in both sexes the yellow-brown and orange-brown pattern elements are paler, the black markings less prominent, the pale yellow-brown on the lower of the two forewing apical silver streaks is proximally instead of centrally positioned, the silver at the discal cell end of the hindwing lacks a white spot and, most diagnostic of all, it has a pure yellow-brown basal band on the hindwing instead of a broken silver one that contains a white spot near the costa. On the dorsal surface, *S. chocoensis* also has two prominent cream spots in cells Cu_2 and M_2 of the forewing, positioned one above the other, whereas *S. neglecta* has an additional tiny spot towards the base of cell M_1 , both of those in the subapex are smaller and that in cell Cu_2 is virtually absent in males, present as a prominent spot only in females. The male genitalia of the two species differ very little from each other, as do all those in the "chrysus group", but the lower portion of the valvae in *S. chocoensis* is slightly less produced.

Discussion.— This species is currently known from central Panama to west Ecuador, but it may also occur in eastern Costa Rica. The majority of locality data indicate that *S. chocoensis* predominantly inhabits lower premontane forests between 700 and 1300m, although one historic record suggests that it may occur as low as 350m. At one well collected locality, Tinalandia, situated at about 750m, *S. chocoensis* has been found sympatrically with *S. neglecta* and *S. chrysus*. Solitary males of *S. chocoensis* have been observed perching low to the ground in hilltop lightgaps in the early morning and again in the late afternoon. The more common females can be found resting beneath large, low leaves along streamsides, forest edges and in secondary growth areas throughout much of the day.

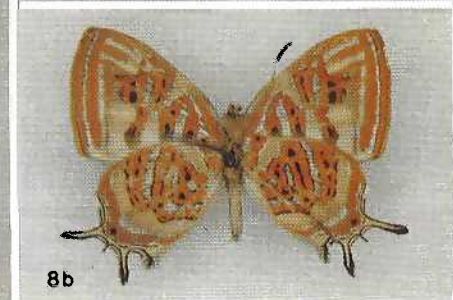
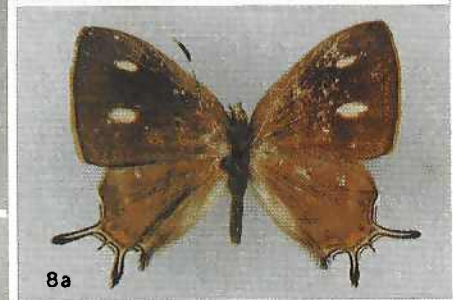
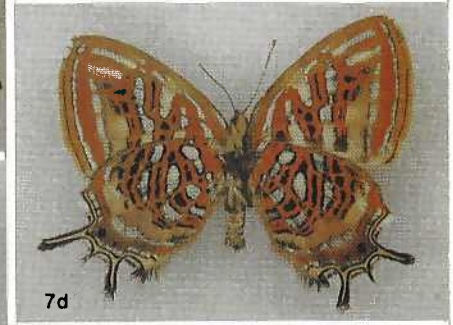
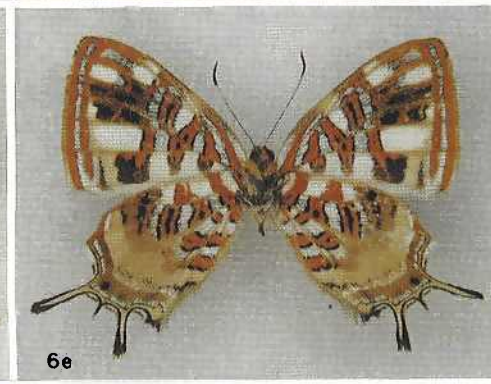
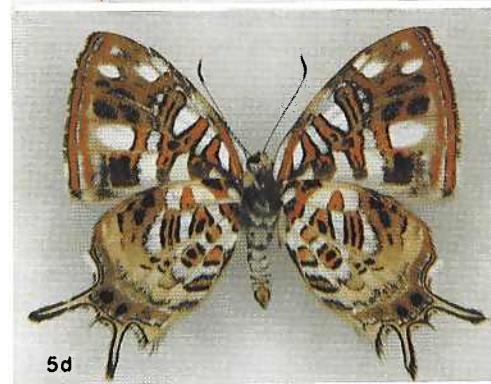
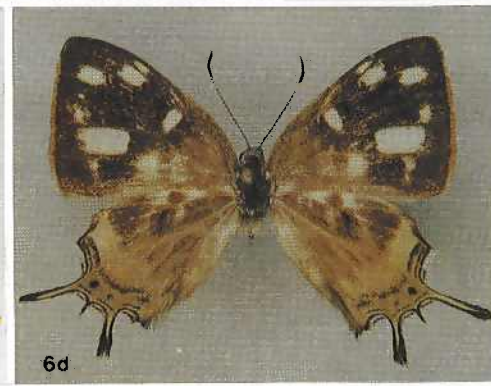
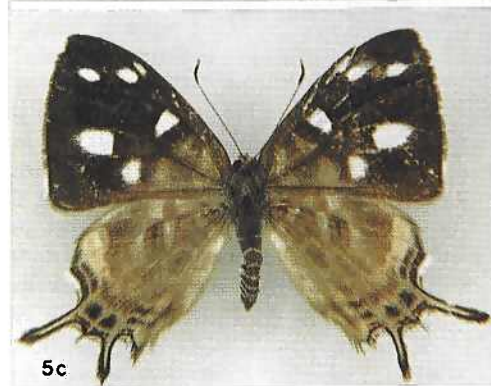
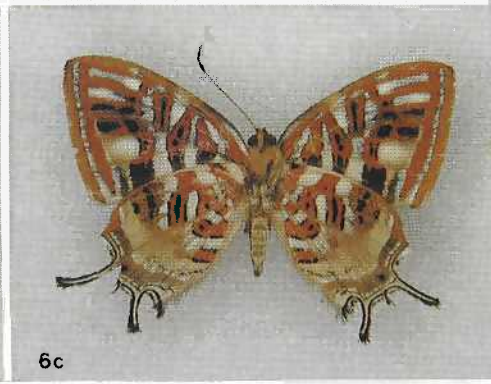
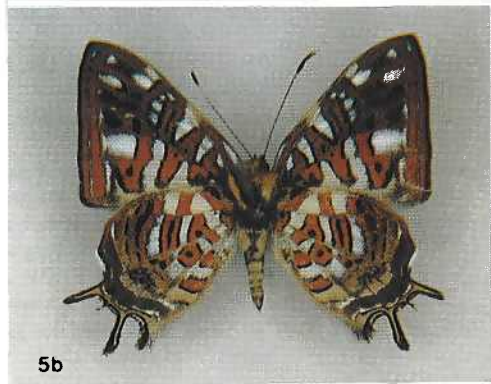
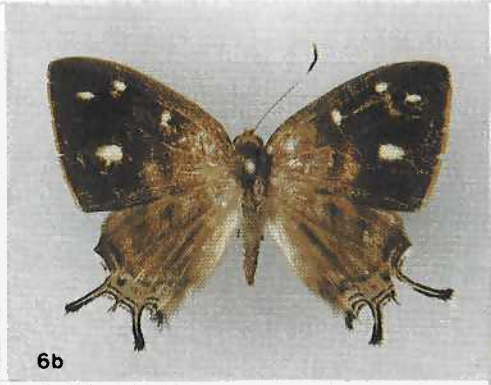
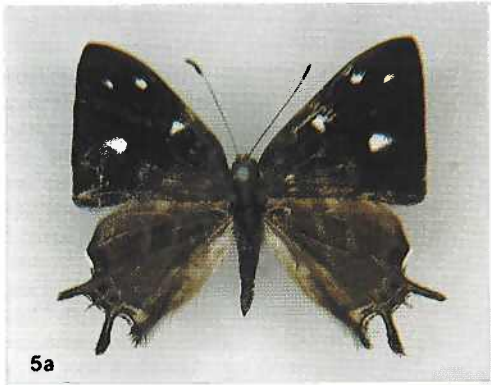
***Sarota turrialbensis* (Schaus, 1913)**

Fig. 9a,b

Charis turrialbensis Schaus, 1913, *Proc. Zool. Soc. Lond.* 3:352, pl. 53, fig. 13. TL: Turrialba, Costa Rica. Holotype male USNM [Examined] (Fig. 9a,b).

Identification and taxonomy: FW length 13.5mm.

S. turrialbensis is the smallest "chrysus group" species and easily



distinguished from all others by lacking dorsal forewing spots. In this regard and by having more than two proximally directed postmedial silver streaks and small hindwing tails, it would appear to be somewhat intermediate towards species of the "*acanthoides* group".

Biology: The unique specimen of *S. turrialbensis* forms part of the Schaus material in the USNM and is labelled "Turrialba, 5800ft". Nothing is known of its biology, but given its apparent rarity, the lack of associated females and its intriguing phylogenetic position within the genus, any information would be worth publishing.

Distribution: Costa Rica.

"*acanthoides* group" (in part, Gyadiformes of Stichel (1930))

Sarota craspediodonta (Dyar, 1918)

Fig. 10a-d; 29

Charis craspediodonta (Dyar, 1918), *Proc. U. S. Natl. Mus.* 54:335. TL: Presidio, Mexico. Holotype female USNM [Examined] (Fig. 10c,d).

Identification and taxonomy: Average FW length 10.5mm.

The dark ventral surface of this species is reminiscent of *S. spicata* but the hindwing margin is dark orange-brown instead of yellow, there is an enlarged black spot in the submargin of cell Cu₁ on both wings, additional silver spots distal to the postdiscal forewing line of black spots in the apex and the male has white legs while that of *S. spicata* has black forelegs and black mid and hindlegs with partially white tibia and white tarsi.

Biology: Nothing is known about the biology of this species but, from locality data, it would appear to predominantly occur in or at least be tolerant of drier semi-deciduous habitats, a phenomenon that does not occur elsewhere in the genus. It is very rare in collections.

Distribution: Mexico and Guatemala.

Sarota spicata (Staudinger, 1888), *stat. rev.*

Fig. 11a-d; 30

Anteros acanthoides var. *spicata* Staudinger, 1888, *Exot. Schmett.* 1:252. TL: Pebas, Peru. Lectotype male ZMHU [Designated] (Fig. 11a,b).

Identification and taxonomy: Average FW length 10.5mm.

This species was described from two males (Pebas and Iquitos) and one female (Pebas) but as the female belongs to a separate species, *S. willmotti* n. sp. (described below), I designate the male from Pebas (the type locality stipulated in the original description) as a lectotype (Fig. 11a,b) to avoid confusion. It bears the following three labels: "*Anteros* sp.?, near, *A. acanthoides*, H-Sch., (G&S)", "Pebas, Hhl" and "Origin".

Although *spicata* was described as a variety of *S. acanthoides* the sympatry of the two taxa and their numerous phenotypic differences clearly show them to be distinct species and I return *spicata* to the full species status that it was once accorded by Stichel (1910) (the species status accorded to it by DeVries (1997) was based on an error of identification; see appendix). *S. spicata* has the darkest ventral patterning of all the sympatric Amazonian "*acanthoides* group" species and is distinguished from most by not having elongate, proximally directed silver streaks in the apex of the ventral forewing. It somewhat resembles *S. willmotti* n. sp., especially in the female, but has an even smaller final apical silver streak on the ventral forewing, broken postmedial silver lines on both ventral wing surfaces with heavy distal black, a much darker ventral ground color and largely black legs (part of the tibia and tarsi are white) instead of largely orange ones. The last character also separates *S. spicata* from its most

similar species *S. craspediodonta* which is additionally distinguished in that species account.

Biology: This uncommon species is confined to primary forest and its immediate environs below 600m. Males perch as solitary individuals or in small groups on low bushes in large lightgaps along forest edges or more commonly near streambanks from 0645-1100h and then again more sporadically in the late afternoon. Females are encountered as solitary individuals throughout much of the day in similar microhabitats. DeVries (pers. comm.) reports finding *S. spicata* in Ecuador feeding from the extrafloral nectary of a *Montrichardia* species (Araceae) and also at a light at night.

Distribution: Colombia to Peru, west Brazil.

Sarota willmotti Hall, new sp.

Fig. 12a-d; 31

Description. - MALE: forewing length 11mm. Forewing pointed, distal margin straight; hindwing apex and tornus produced into small points, three roughly equally sized tails at middle of distal margin. *Dorsal surface:* ground color of both wings brown; faint, darker brown discal, postdiscal and postmedial hindwing markings; fringe brown on forewing, white then dark brown on hindwing. *Ventral surface:* forewing ground color brown, paler at anal margin; black line surrounded by orange-brown with silver streak above and silver distally at discal cell end and towards cell end with a vertical black line, that is surrounded by orange-brown and has silver distally, in cells below; small black spot surrounded by triangle of orange-brown towards base of discal cell with silver distally and proximally and black square in cell below, orange-brown surrounds base of costal edge of discal cell, silver at base of costa; orange-brown postdiscal line containing black spots extends from cell M₃ to cell 1A+2A curving slightly outwards in upper half, a small black spot surrounded by orange-brown with silver streak distally toward base of cell R₃; slightly broken, postmedial silver line edged proximally with black gradually increases in width from cell M₂ to cell 1A+2A, broader proximally directed silver streak in cell M₁; remainder of costa and submargin orange-brown, margin yellow-orange, thin submarginal silver line extends from apex to vein 1A+2A; fringe brown. Hindwing ground color brown with a light scattering of pale brown scales; orange-brown band at base lined distally and proximally by silver contains two small black spots towards costa, a tiny silver spot at middle; postdiscal orange-brown band containing black spots extends from costa, curving inwards to vein M₃, kinking inwards in cells Cu₁ and Cu₂, then continuing to anal margin, kinking inwards below vein 1A+2A, disjunct silver proximally at costa, discal cell end and towards anal margin; black mark surrounded by orange-brown at discal cell end and in middle of discal cell with silver inbetween, similarly marked band extends below latter silver patch to anal margin, and above and below medial discal mark to the costal and anal margins respectively; uneven, postmedial silver line with thin layer of black scaling distally curves sharply inwards at costal and anal margins and thins in cells M₃ and M₂; orange-brown at submargin extends from apex to tornus and has a thin silver line distally below vein M₁; margin and tails between tornus and vein M₁ yellow with black, then white, then a thin layer of black scales distally forming fringe, fringe at apex brown. *Head:* labial palpi yellow-orange. Eyes brown and bare, margins with brown scaling. Frons brown with some yellow hairs. Antennal segments black with white scaling at base that increases laterally and towards clubs; clubs black, bare tips dark brown. *Body:* both surfaces of thorax dark brown; dorsal surface of abdomen dark brown, ventral surface cream. Forelegs yellow-orange, femur of mid and hindlegs brown, remainder yellow-orange except tarsi brown banded. *Genitalia* (Fig. 31): uncus rounded, small posteriorly projecting point from dorsal edge; vinculum evenly thin; valvae have basal, lateral bulge, long upper portion that narrows slightly towards tip and is connected by membranous tissue dorsally, and small bluntly rounded lower posterior edge; aedeagus narrow and pointed at tip, tiny cornutus at base; pedicel long.

FEMALE: differs from male in the following respects: forewing length

