

**SYSTEMATICS OF THE RIODINID TRIBE SYMMACHIINI,
WITH THE DESCRIPTION OF A NEW GENUS AND
FIVE NEW SPECIES FROM ECUADOR, VENEZUELA AND BRAZIL
(Lepidoptera: Riodinidae)**

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Abstract: We preliminarily examine the systematics of the riodinid tribe Symmachiini Bates, 1859, and isolate an apparently monophyletic assemblage of species formerly included within the genera *Stichelia* and *Phaenochitonina*, which we describe as a new genus *Pirascca* **gen. nov.**. A summary of the taxa within the genera *Pirascca*, *Phaenochitonina*, *Stichelia* and *Pterographium* and a comparative table of their morphological differences are also presented, and four new species in the genera *Symmachia*, *Pirascca* and *Phaenochitonina* are described from western Ecuador, Venezuela and Brazil. We also describe a new species from eastern Ecuador in the genus *Comphotis*, which we hypothesise to be the ancestral genus to the tribe Symmachiini. We further discuss the taxonomic importance of the concealed androconial scales found on the abdominal tergites of all species in the tribe, first noted by HARVEY (1987).

Key-words: androconial scales, Brazil, Chocó, Colombia, *Comphotis apachita* sp. nov., Ecuador, endemism, *Esthemopsis*, foodplant, hilltopping, *Lucillella*, *Menander*, *Mesene*, *Mesenopsis*, Neotropical, Nymphidiini, Panama, *Panara*, perching behaviour, *Periplacis*, *Phaenochitonina gallardi* sp. nov., *Phaenochitonina pseudodebilis* sp. nov., *Pirascca* gen. nov., *Pirascca polemistes* sp. nov., *Pterographium*, Riodinini, *Stichelia*, *Symmachia hazelana* sp. nov., Symmachiini, Venezuela, *Xenandra*.

Introduction

The discovery of two phenotypically unusual new riodinid species from western Ecuador, in the tribe Symmachiini Bates, 1859, has prompted us to examine more closely the systematics of this tribe at the generic level. HARVEY (1987) defined the tribe Symmachiini by the presence of concealed androconial scales on the anterior margins of abdominal tergites 4 to 7 in males. The resulting group of genera closely corresponds to STICHEL's (1910-11, 1930) tribe Mesenini, except for the exclusion of the genus *Argyrogrammana* Strand, 1932, and inclusion of the genus *Lucillella* Strand, 1932. It should be noted that abdominal androconial scales also occur in the nymphidiine genera *Menander* Hemming, 1939, and *Periplacis* Geyer, 1837, but the position (tergites 5 to 7) and ultrastructure of these scales (which lack longitudinal ribs and acanthae [acellular projections] between the androconial scales), suggests that they have evolved independently (HARVEY, 1987).

The genera within the Symmachiini are often poorly defined, and taxonomic research is usually hindered by the rarity of most species and their consequently sparse representation in the world's entomological collections. The problem is particularly acute in the largest genus, *Symmachia* Hübner, [1819], but a full analysis of species group relationships in this genus is beyond the scope of this paper. Instead we attempt to create a generic framework for species formerly included in the phenotypically similar and historically confused genera *Phaenochitonina* Stichel,

1910, *Pterographium* Stichel, 1910, and *Stichelia* Zikán, 1949, and in the process describe the new genus *Pirascca* gen. nov.. In addition to describing the two new symmachiine species from western Ecuador, mentioned above, in the genera *Pirascca* and *Symmachia*, we take this opportunity to describe two unnamed species of *Phaenochitonina*, located in European museums, from Venezuela and Brazil. We also more fully elucidate the characters defining the genus *Comphotis*, transferring to it several species formerly placed in *Phaenochitonina* and describing a new species from eastern Ecuador, and hypothesise that it is immediately ancestral to *Phaenochitonina* and hence to the tribe Symmachiini.

***Symmachia hazelana* Hall & Willmott, sp. nov.** (Fig. 1 a-c; 4a-c).

Description: Male: forewing length 18mm. Dorsal surface: forewing ground colour dark iridescent blue (lighter blue at an oblique angle); thin black outer margin, thicker black costal margin thinning towards apex. Hindwing ground colour a similar dark iridescent blue; thin black anal and distal margins, black at apex; yellow along central half of anal margin and in a shallow semi-circle at costal margin (slightly darker at basal edge). Ventral surface: forewing ground colour dark brown; rich, broad yellow band vertically traversing middle of wing, tapering towards costal margin, outer edges broken and uneven; faint darker brown band immediately distal to yellow, and faint, thin darker brown submarginal line; two darker brown spots at base of wing; small section of white fringe at apex. Hindwing ground colour dark brown; rich, broad yellow band of even thickness traversing middle of wing, edges uneven; faint darker brown band immediately distal to yellow. Labial palpi black. Eyes brown and bare. Frons black. Antennae black with cream scales at the base of each segment, clubs slightly flattened and yellow. Thorax black; abdomen dorsal surface black, ventral surface yellow, yellow hairs at tip; single dense medium-sized patch of androconial scales on anterior margins of tergites 4 and 5 (see Table 3). Legs black. Genitalia (Fig. 4a-c): uncus angular; vinculum with a tiny central projection; valvae bifurcate with upper projection longer than lower projection; aedeagus short, large, pointed and open on dorsal side to expose two large internal scobinate patches; saccus short.

Female: unknown.

Types: Holotype ♂: Ecuador, *Esmeraldas Province*, km. 44 rd. Lita-San Lorenzo, La Punta, nr. El Durango, 300m, 21 June 1994 (K. R. Willmott). To be deposited in the Natural History Museum, London, England (BMNH).

Etymology: This species is named for my mother, Hazel WILLMOTT, who instilled in me an appreciation for the beauty of nature (KRW).

Diagnosis: *Symmachia hazelana* sp. nov. has a very distinctive and unique wing pattern that is only comparable to *Symmachia rita* Staudinger, 1887. Both species have dark blue dorsal iridescence, but in *S. rita* the blue on the forewing is restricted to the outer margin. *S. rita* is also smaller, has a more pointed wingshape, and lacks the yellow colouration on the dorsal surface of the hindwing and on both ventral wing surfaces.

Discussion: A single individual was found resting beneath a leaf with its wings outspread, around 5 metres above the ground. It was perching in a large forested ridgetop lightgap at approximately 7.30 a.m. in overcast conditions. We have not

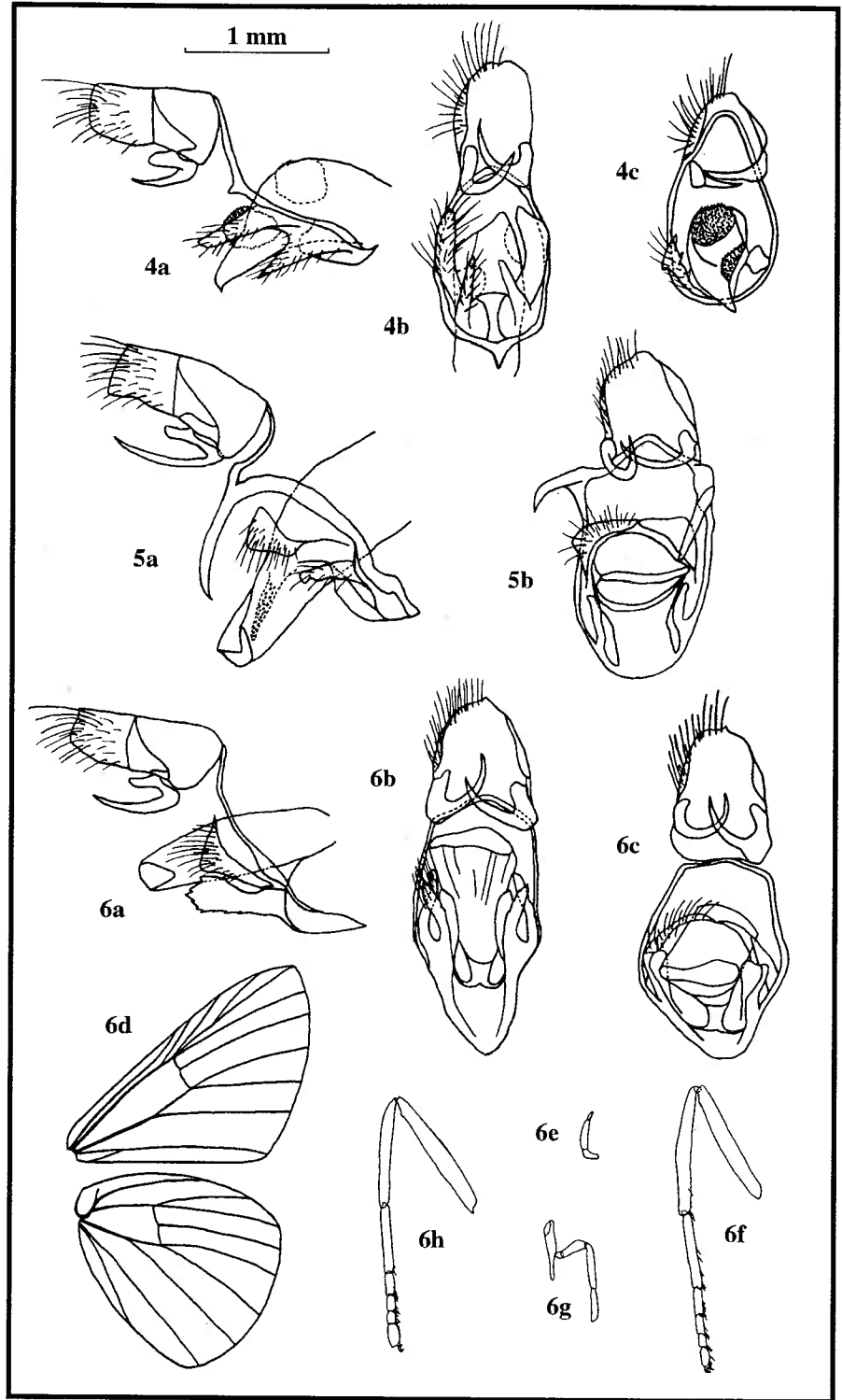
located any further specimens in major European or American museums and this extremely rare species is currently only known from the lowland pluvial forests of north-west Ecuador, although it will almost certainly be found in the Chocó region of west Colombia. Its rarity is no doubt due in part to the fact that this area has been seldom visited by lepidopterists, in addition to its behaviour of perching early in the morning.

Although the wing pattern and, to a lesser extent the wing shape, of *S. hazelana* are not wholly typical of *Symmachia*, the male genitalia and abdominal androconial patch distribution (see Table 3) suggest that this species is best placed at present within this genus. However, a detailed phylogenetic analysis of the heterogeneous group of species currently included in *Symmachia* will no doubt highlight the existence of several lineages of generic worth. Since *S. hazelana* is morphologically quite distinct from the type species of the genus, *Symmachia probetor* (Cramer, 1782) (see D'ABRERA (1994: 1044) for an illustration), it may eventually need to be placed in a separate genus.

Pirascca Hall & Willmott, gen. nov. (Fig. 2a-d; 3a,b; 5a,b; 6a-h; 7a-c).

Type species: *Papilio sagaris* Cramer, 1775

Description: Male: Dorsal surface (Fig. 2c): ground colour entirely black, or with several slightly paler basal brown bands, sometimes with a dark blue sheen when viewed obliquely. Most species characterised by either having red/orange as a band oriented in a line joining forewing apex to hindwing anal margin or as a patch in the centre of the hindwing. Ventral surface (Fig. 2d): usually entirely black, often with a dark blue sheen when viewed obliquely, rarely with a similarly coloured mirror image of the dorsal red-orange markings, forewing anal margin paler grey-yellow. Venation (Fig. 6d): four forewing radial veins, R_1 , R_2 and R_{3-4} all arising basal to cell end. Eyes: bare and brown. Palpi (Fig. 6e): black; short, not projecting, closely pressed to head, third segment one third the length of the second. Frons: black. Antennae: usually black, rarely with sparse white scales at the base of each segment, slender and slightly laterally compressed at club; 36 (*sagaris* and *tyriotes*) - 40 (*iasis*) segments in length. Thorax and abdomen: black, some species with a red/orange dorsal abdominal stripe. Legs (Fig. 6f,g): hindleg and midleg with a single posterior tibial spur, and a series of spines along each tarsal segment; foreleg without spurs or spines. Genitalia (Fig. 5a,b; 6a-c): uncus often narrow and elongate, mid-point of posterior edge projecting slightly; vinculum often with a very small upper projection but occasionally with a projection that is longer than the falci; valve split into two distinct components, usually only joined by lightly sclerotised tissue: the upper triangular in shape and fused above aedeagus, the lower more heavily sclerotised, often lacking setae and usually modified with the edges serrate or bearing numerous small thick spines; aedeagus wide, widening posteriorly, with posterior tip vertically compressed to form a long, narrow opening; usually with small, simple internal sclerotised structures but occasionally with numerous long pectinate cornuti (e.g. *tyriotes*); saccus small. Secondary sexual structures: long, erectile androconial hairs located along a fold in the wing membrane mid-way between 1A+2A and Cu_2 (Fig. 7a); single wide, long and dense patch of androconial scales on anterior margins of abdominal tergites 4 and 5 (Fig. 7b,c), usually greater in extent on tergite 5.



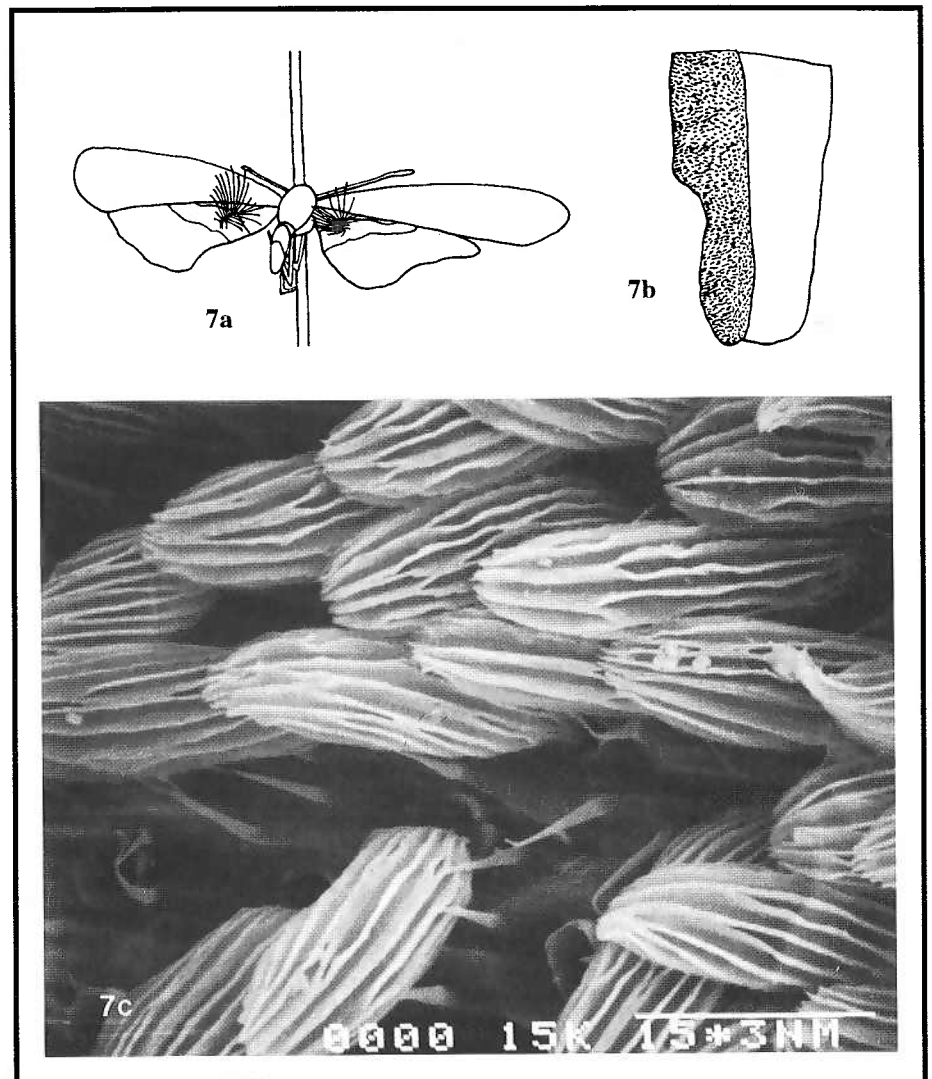


Fig. 7. (above) **Male secondary sexual characters.** a) An oblique view of *Pirascca tyriotes* (Godman & Salvin, 1878), showing the position of the erectile androconial hairs on the hindwing; b) arrangement of androconial scales on the anterior portion of the tergite of abdominal segment 5 in male *Pirascca sagaris* (Cramer, 1775); c) a scanning electron micrograph (SEM) of the androconial scales illustrated in (b) with the acanthae (acellular projections) also visible (x 2100).

Fig. 4-6 (left). Morphology. 4. *Symmachia hazelana* sp. nov., holotype ♂ genitalia: a) lateral view; b,c) ventral views. 5. *Pirascca polemistes* sp. nov., holotype ♂ genitalia: a) lateral view; b) ventral view. 6. *Pirascca sagaris* (Cramer, 1775) ♂: a) genitalia, lateral view; b,c) genitalia, ventral views; d) wing venation; e) palpus; f) hindleg; g) foreleg. ♀: h) foreleg.

Female: Differs from the male as follows: Dorsal surface (Fig. 2a): usually unicolourous dark brown to black, occasionally with darker basal markings on both wings, usually with an oblique orange-yellow band extending from costa to tornus on forewing and sometimes also on hindwing. Ventral surface (Fig. 2b): similar to dorsal surface except very slightly paler. Thorax and abdomen: always dark brown to black. Legs (Fig. 6h): foreleg with tarsal spines on all except terminal segment, without tibial spur. Also lacks long hindwing androconial hairs and abdominal androconial scales.

Etymology: The name is derived from the Inca term "pirascca", meaning "striped with blood", and refers to the typical male dorsal wing pattern of species in this genus. It is considered masculine.

Diagnosis: The possession of a pedicel in the male genitalia places *Pirascca* gen. nov. in the subfamily Riordininae Grote, 1895 (*sensu* Harvey, 1987), and the presence of concealed androconial scales (with longitudinal ribs) on the anterior margins of certain abdominal tergites in males places it in the tribe Symmachiini Bates, 1859 (*sensu* Harvey, 1987). Species placed here in *Pirascca* are phenotypically most similar to and have previously been included in the genera *Phaenochitonia*, *Stichelia*, and *Pterographium*; these four genera may be distinguished by the series of characters given in Table 1. The characters highlighted in bold type do not occur elsewhere within the tribe Symmachiini or, to our knowledge, outside of the tribe, and they appear to represent synapomorphies for *Pirascca*. Thus, these characters, in addition to the distinctive wing pattern, hindwing androconial hairs and distribution of abdominal androconial scales, also serve to distinguish *Pirascca* from the remaining genera in the Symmachiini.

Discussion: The species in the genus *Pirascca* have generally had confused taxonomic histories and were originally described in a diverse array of genera, including *Mesene* Doubleday, 1847, *Symmachia* Hübner, [1819], and *Charis* Hübner, [1819]. Stichel (1910) described the genus *Phaenochitonia* and subsequently (1910, 1930) divided it into two species groups ("Cohors"); the "Cinguliformes", which included species placed here in *Phaenochitonia* and *Comphotis* (see later discussion), and the "Sagariformes", which included an equally heterogeneous group of species placed here in *Pirascca*, *Stichelia* and *Symmachia* (see Table 2).

ZIKÁN (1949) attempted to split STICHEL'S "Sagariformes" into more natural groups, based largely on the form of the male hindwing androconial hairs, but unfortunately only discussed species from south-east Brazil. He described a new genus *Stichelia* to include species that possessed simple "odoriferous hairs" at the anal margin of the hindwing, and placed the remaining species into the genus *Pterographium* Stichel, 1910, on the basis of their "odoriferous erectile hair pencils". In this latter genus he included *aphaniodes* Stichel, 1910 (= *sicora* Hewitson, 1875 - see Table 2), a new species *similatum* Zikán, 1949 (= *semiota* Bates, 1868 - see Table 2), and *satnius* Dalman, 1823. The taxon *satnius* is a south-east Brazilian subspecies of *sagaris* Cramer, 1775, but ZIKÁN regarded the two taxa as separate species, since he only had female specimens of what he believed to be typical *sagaris*. He thus placed the species *sagaris* into two genera; males (as *satnius*) into *Pterographium*, on the basis of hindwing hair pencils, and females (as *sagaris*) into *Stichelia*, due to the presence of dark spots at the base of the wings on the ventral surface (a poor generic character). This mistake has led to subsequent confusion as to whether species in Stichel's "Sagariformes" should correctly be placed in the genera *Stichelia*, *Pterographium* or the earliest established genus *Phaenochitonia* (LEWIS, 1973;

BIEZANKO *et al.*, [1979]; CALLAGHAN, 1985, 1989; BRIDGES, 1988; BROWN, 1993; D'ABRERA, 1994).

ZIKÁN (1949) correctly noted that the hindwing androconial hairs of *sagaris* (as *satnius*) were of the same form as those in *Pterographium sicora* (as *aphaniodes*). However, *sagaris* and its closest relatives also share a number of characters of wing pattern and morphology that distinguish them from *Pterographium* (see Table 1), and they appear to form a monophyletic group worthy of generic recognition. Thus we divide the species of Stichel's "Sagariformes" between the two genera *Stichelia* and *Pirascca* (additionally placing a single species in the genus *Symmachia*), and we present a summary of the taxa in these genera and in *Phaenochitonina* and *Pterographium* in Table 2.

The species in *Pirascca* range throughout Central and South America, and are most diverse in the lowland Amazon basin, although some species also occur in cloud forest habitats (e.g. *P. pluto*, *P. iasis*, *P. tyriotes*). All the species are uncommon to very rare and the females of several species are still unknown. They are usually encountered as solitary individuals, although males of certain species may be locally common (e.g. *P. sagaris* - SEITZ, 1917; BARCANT, 1970), especially on hilltops and ridgetops (e.g. *P. iasis* - pers. obs.), as is typical for members of the tribe (CALLAGHAN, 1983; BRÉVIGNON & GALLARD, 1992; HALL & WILLMOTT, 1995a). The only taxon with any published information on its early stages is *P. sagaris satnius*; Callaghan (1989) describes the larval morphology and behaviour, and reports the foodplant as being in the Melastomataceae.

***Pirascca polemistis* Hall & Willmott, sp. nov.** (Fig. 3a,b; 5a,b)

Description: Male: forewing length 18mm. **Dorsal surface:** forewing ground colour dark brown; slightly paler brown basally with a few faint darker spots at base of anal margin. Hindwing ground colour dark brown; three darker brown spots in discal cell; large light orange patch at outer margin extending from tornus to near apex, tapering slightly toward apex, proximal edge uneven, thin black distal margin. **Ventral surface:** forewing ground colour black with a faint and subtle dark blue iridescence; pale brown at anal margin, fringe with tiny white section at apex. Hindwing ground colour black with a faint dark blue iridescence; large dark orange patch at outer margin whose shape and position mirrors that of dorsal surface. Labial palpi brown, tips black. Eyes brown and bare. Frons black. Antennae black with cream scales at the base of each segment, clubs black. Thorax and abdomen black; single dense, long and wide patch of androconial scales on anterior margins of abdominal tergites 4 and 5 (see Table 3), greater in extent on tergite 5. Legs black. **Genitalia** (Fig. 5a,b): uncus long and slender with posterior ventral angle square; falci long and thin; vinculum with a long, thin downward-pointing upper projection; valvae split into two distinct components and joined only by very lightly sclerotised tissue: an upper triangular shaped part fused above the aedeagus, a lower, slightly serrate, more heavily sclerotised part; aedeagus wider and compressed vertically at tip, only a few very small internal sclerotised structures on the surface of the vesica; saccus very short.

Female: unknown.

Types: Holotype ♂: Ecuador, *Esmeraldas Province*, Río San Miguel, nr. San Miguel, 100m, 11 June 1994 (J. P. W. Hall). To be deposited in the BMNH.

Paratypes: 2 ♂♂: Panama, Panama Province. 1 ♂ Cerro Jefe, 900m, 29 April 1977 (G. B. Small); 1 ♂ Altos de Pacora, April 1975 (G. B. Small). Both in the United States National Museum, Washington, USA (USNM).

Etymology: The name is derived from the Greek for "warrior", with reference to the sharp, sword-shaped upper projection of the vinculum of the male genitalia.

Diagnosis: The hindwing orange patch of *Pirascia polemistes* sp. nov. is much larger than that of any other species in the genus and its placement at the distal margin is unique. This orange patch is also mirrored on the ventral surface, a character that is shared only with the otherwise phenotypically different *Pirascia apolecta* (Bates, 1868) and *Pirascia pluto* (Stichel, 1910).

Discussion: A single individual was captured in flat lowland pluvial forest. It was observed to fly slowly into a lightgap adjoining a trail at 3.30 p.m. and come to rest beneath a leaf with its wings outspread. The discovery of this species and *Symmachia hazelana*, described above, further highlights how much there is still to learn about the butterfly fauna of the forests of north-west Ecuador (see also WILLMOTT & HALL, 1994; HALL & WILLMOTT, 1995a), and how important research is in this area where the remaining natural vegetation is being so rapidly cleared for agriculture (DODSON & GENTRY, 1991; PARKER & CARR, 1992).

***Phaenochitonía gallardi* Hall & Willmott, sp. nov.** (Fig. 9a-d; 14a-c).

Description: Male: forewing length 10.5mm. Dorsal surface: forewing entirely black. Hindwing black except for an elongate ovoid blood red patch at the costal margin, extending from base to near apex. Ventral surface: forewing ground color brown; four dark brown spots in discal cell, one marking cell end; two spots below cell; dark brown postdiscal transverse line that curves around cell end and moves inwards to reach the anal margin; indistinct, broader, more distal postdiscal dark brown band; faint dark brown ocelli at outer margin encircled by paler brown/grey; two faint apical, one medial and one tornal section of white fringe. Hindwing ground colour brown, faint red area mirroring red patch on dorsal surface; five dark brown spots in discal cell, one marking cell end; two spots above and below cell; dark brown postdiscal transverse line that curves around cell end creating a semi-circular area between the cell end and postdiscal lines; indistinct, broader, more distal postdiscal dark brown band; faint dark brown ocelli at outer margin encircled by paler brown/grey. Labial palpi pale yellow, tips brown. Eyes brown and bare. Frons brown with yellow scaling in basal half. Antennae brown with cream scales at the base of each segment, clubs brown. Thorax black; abdomen black with paler scaling along the ventral surface; single long, thin and sparse patch of androconial scales on anterior margins of tergites 4 and 5 (see Table 3). Legs brown. Genitalia (Fig. 14a-c): mid-point of posterior edge of uncus projecting and pointed downwards; valvae dorsoventrally compressed and heavily sclerotised with a single upper rounded projection that curves slightly inwards, less sclerotised tissue joins the valvae above the aedeagus; aedeagus cylindrical and split at the apex along the dorsal side; saccus long and thin.

Female: unknown.

Types: Holotype ♂: Venezuela, no specific locality, 1923 (Mayol Gusol). In the "Old Collection" (drawer no. 31) of the Muséum National d'Histoire Naturelle, Paris, France (MNHN).

Paratypes: 1 ♂: Venezuela, Amazonas, Río Orinoco, Maipures [nr. Puerto Ayacucho], December 1898 (Cherrie). In the BMNH.

Etymology: This species is named for Jean-Yves GALLARD, who, with Christian BRÉVIGNON, has contributed so much to our knowledge of French Guianan riodinid systematics and ecology.

Diagnosis: The dorsal colour pattern of *Phaenochitonina gallardi* sp. nov. is shared by several other symmachiines, including *Xenandra helius* (Cramer, 1779), *Symmachia probetor* (Cramer, 1782), to a lesser extent *Symmachia threissa* Hewitson, 1870, and *Mesene boyi* Stichel, 1925, and by the euselasiine *Euselasia gelon* (Stoll, 1787). However, none of these species exhibit the small size, rounded wing shape, and characteristic "signature" pattern of ventral markings of *Phaenochitonina* (see Fig. 8a). Within the genus *Phaenochitonina*, *P. gallardi* is unique in possessing an ovoid red patch at the costal margin of the hindwing dorsal surface. It is probably most closely related to *P. fuliginea* (Bates, 1868) which has a very similar ventral colour pattern, a completely black dorsal surface and very similar male genitalia that differ only by having a more angular shaped valve that is slightly shorter and broader.

***Phaenochitonina pseudodebilis* Hall & Willmott, sp. nov.** (Fig. 10a,b; 15a-c).

Description: Male: forewing length 9mm. Dorsal surface: forewing ground colour dark brown; small triangle of red at the centre of the anal margin that is slightly curved inwards at its tip to touch the cell end. Hindwing ground colour dark brown; thick red band diagonally traverses basal half of the wing, leaving a small dark brown area at the wing base. Ventral surface: forewing ground color brown; four dark brown spots in discal cell, one marking cell end; two spots below cell; dark brown postdiscal transverse line that curves around cell end and moves inwards to reach the anal margin, small orange-red patch distal to this line at the anal margin; indistinct, broader, more distal postdiscal dark brown band; dark brown ocelli at outer margin encircled by paler brown (or grey towards the tornus); two apical, one medial and one tornal section of white fringe. Hindwing ground colour brown, faint orange-red area at wing base mirroring red marking on dorsal surface; five dark brown spots in discal cell, one marking cell end; two spots above and below cell; dark brown postdiscal transverse line that curves around cell end creating a semi-circular area between the cell end and postdiscal lines; indistinct, broader, more distal postdiscal dark brown band; dark brown ocelli at outer margin encircled by paler brown (or grey towards the tornus). Labial palpi pale yellow, tips brown. Eyes brown and bare. Frons a mixture of brown and yellow scaling. Antennae brown with cream scales at the base of each segment, clubs brown. Thorax black; abdomen red on dorsal surface yellow-brown on ventral surface; single long, thin and sparse patch of androconial scales on anterior margins of tergites 4 and 5 (see Table 3). Legs missing. Genitalia (Fig. 15a-c): mid-point of posterior edge of uncus projecting and pointed downwards; valvae dorsoventrally compressed and heavily sclerotised with a long upper flattened projection that curves slightly inwards, less sclerotised tissue joins the valvae above the aedeagus; aedeagus cylindrical with a cluster of small pencilate cornuti towards the tip; saccus long and broad.

Female: unknown.

Character	<i>Pirasca</i> gen. nov.	<i>Phaenochitonina</i>	<i>Stichelia</i>	<i>Pterographium</i>
Male dorsal wing surface	black/dark brown, either with red/orange as a band oriented in a line joining FW apex to HW anal margin or as a patch on the hindwing; occasionally with dark blue iridescence or dark brown basal markings	black/dark brown, usually with red markings that traverse both wings in a band or are restricted to the inner margins of the HW	black/dark brown often with darker brown markings basally, with oblique orange/red band(s) from costa to distal or anal margin, on only FW or on both wings	black/dark brown, with oblique dark orange FW band from costa to distal margin; type species with dark blue iridescence
Male ventral wing surface	almost uniform black/dark brown ground colour, usually with dark blue iridescence; sometimes dorsal red/orange HW patch is also visible on ventral surface	brown, rarely with orange along FW anal margin, always with a characteristic pattern of darker brown basal spots (see fig. 8a), submarginal ocelli encircled by pale brown	same as dorsal surface but paler	same as dorsal surface but paler and lacking blue iridescence
Female dorsal wing surface	very different from male; black/dark brown, often with darker brown basal spots, and usually with an oblique orange band from costa to tornus on FW, sometimes also on HW	the few known females are very different from males; black/dark brown with transverse orange/red bands on only FW or on both wings	similar to male but paler	similar to male but paler, and lacking any blue iridescence
Wing fringe	FW usually with an apical white section and sometimes with a tornal section	FW with two apical, one medial and sometimes one tornal section of white	FW apex sometimes white; entire HW margin white in type species	entirely black
Male wingshape	FW costa straight, distal margin slightly convex, apex acute; HW tornus pointed	FW costa and distal margin more strongly convex, HW rounded	FW costa straight, distal margin slightly convex; HW slightly rounded	FW costa straight, distal margin slightly convex, apex acute; HW tornus pointed
Hindwing androconial hairs	long erectile hairs on HW densely packed along a short line mid-way between 1A+2A and Cu ₂	hairs extremely sparse or absent	evenly scattered shorter hairs on posterior half of HW	long erectile hairs on HW densely packed along a short line mid-way between 1A+2A and Cu ₂
Collar	black	black	red or black	black
Dorsal surface of abdomen	black or with a red/orange stripe	black or with a red/orange stripe	black	black

Character	<i>Pirasca</i> gen. nov.	<i>Phaenochiton</i>	<i>Stichelia</i>	<i>Pterographium</i>
Male genitalia: Uncus	usually relatively narrow and elongate, mid-point of posterior edge slightly projecting and rounded	medium width and length, mid-point of posterior edge projecting and pointed (usually slightly curved downwards)	broader and shorter, mid-point of posterior edge slightly projecting and rounded, posterior ventral angle lobed	broader and shorter, mid-point of posterior edge slightly projecting and rounded, posterior ventral angle lobed
Vinculum	often with upper projection, occasionally longer than falci	without projections	without projections	without projections
Valve	split into two distinct components, usually only joined by lightly sclerotised tissue: an upper triangular shaped part fused above aedeagus; a lower more heavily sclerotised part, usually lacking setae, often serrate or spinose	a single component fused above the aedeagus that is dorso-ventrally flattened and heavily sclerotised	a single dorso-ventrally flattened and quite heavily sclerotised component fused above aedeagus	a single component, joined by long section of soft, unsclerotised tissue above aedeagus
Saccus	usually short, occasionally medium	long	short	medium
Aedeagus	posterior tip the widest point and vertically compressed into a long, thin opening; internal sclerotised structures usually small and simple, occasionally numerous	cylindrical and occasionally split along the dorsal side at the apex, usually with small internal sclerotised structures	internal pectinate cornuti	cylindrical, small internal sclerotised structures
Pedicel	simple and "strap-like"	simple and "strap-like"	with a large posteriorly projecting spike	simple and "strap-like"
Abdominal androconial scales (on anterior margins of tergites)	1 wide and dense patch on tergites 4 and 5	1 thin and sparse patch on tergites 4 and 5	2 patches on tergites 4 and 5 of medium width and with an uneven posterior edge	1 wide patch on tergites 4 and 5

Table 1. A morphological comparison of the genera *Pirasca*, *Phaenochiton*, *Stichelia* and *Pterographium*. Characters highlighted in bold type indicate apparent synapomorphies for *Pirasca*.

Types: Holotype ♂: Brazil, Mato Grosso, River System Cuiabá-Corumbá. In the MNHN.

Etymology: This species is named for its remarkable resemblance to *Comphotis debilis* (Bates, 1868).

Symbols: "-" designates a subspecies and "--" designates a synonym; * indicates the type species for the genus; † indicates that we have not seen any specimens of this species; f indicates species that were described from and are only known to us from female specimens and whose definitive generic placement depends upon a future examination of the male morphology. Having not seen any specimens of *cuneifascia* we retain that species in the genus in which it was described. However, based on female specimens in the MNHN (Paris) of the taxon *vittata* which exhibit white forewing fringe elements, basal brown spotting and large size characteristic of the known *Pirascca* females, we transfer the species *suapure* (the nominate differs in the type illustration by having thinner transverse orange bands) from *Stichelia* to *Pirascca*. It is not known whether *suapure* is referable to a described or an undescribed male.

Notes:

1) the type illustration of the taxon *pygmaea* in Cramer (1775) depicts a small butterfly with very elongate and rounded wings, a central vertically positioned red stripe traversing two-thirds the length of the hindwing and one-third the length of the forewing, and a series of curved grey lines on both wings paralleling the outer margins. Although the illustration does resemble certain species in the genus *Pirascca*, its stylistic form means that *pygmaea* can not be matched to any particular extant taxon and thus we exclude it from our classification.

2) the taxon *basilissa* Bates, 1868, was described as a *Mesene* and subsequently moved into *Phaenochitonina* by Stichel (1911), but its pointed wing shape, ventral spotting pattern and male genitalia do not place it in that genus or any other in Table 2. Instead, although *basilissa* is slightly atypical for the genus (like *hazelana* n. sp.), it is more properly placed in *Symmachia* (comb. nov.) as it is currently broadly conceived, until its precise phylogenetic placement can be established (see final remarks section).

3) the taxa *histrica*, *simpla* and *eanides* were all described from female specimens, the first two as full species and the third as a subspecies of *P. pyrsoles*; each is a subjective synonym of *P. arbuscula*, *P. sagaris sagaris* and *P. ignipicta* respectively.

4) The taxon *semiota* was described by Bates (1868) in the genus *Limnas* and is currently treated in the genus *Melanis* (Bridges, 1994), but a comparison of the type illustration of *Pterographium simlatum* Zikán, 1949, with the type specimen of *semiota* clearly indicates that the two taxa are conspecific. We therefore synonymise *simlatum* with *semiota* and, since *semiota* has the same long erectile androconial hairs on the hindwing as *sicora* and a very similar phenotype, we place *semiota* in the genus *Pterographium*. Hewitson (1875) described the taxon *sicora* as a species in the riodinine genus *Panara* and Stichel (1930) synonymised it with *Panara phereclus* (Linnaeus, 1758). However, the presence of androconial scales on certain abdominal tergites in the male of *sicora* (see Table 3), that are not present in *phereclus*, places it in the tribe Symmachiini. Since the taxa *aphaniodes*, described by Stichel (1910) in the new genus *Pterographium*, and *ambigua*, described by d'Almeida (1932) in the genus *Aricoris* are synonymous with *sicora* (the latter synonym being noticed by Zikán (1949), but not recorded by Bridges (1994)), we place *sicora* in combination with *Pterographium* and return it to specific rank.

5) The taxa *clarissa*, *debilis*, *eanes*, *ignicauda* and *sophistes* have been moved to the genus *Comphotis* (see Table 4 and ensuing discussion).

Table 2. A summary of the taxa in the genera *Pirascia*, *Phaenochitonina*, *Stichelia*, and *Pterographium*.

<i>Pirascia</i> Hall & Willmott gen. nov.	<i>Phaenochitonina</i> Stichel, 1910	<i>Stichelia</i> Zikán, 1949	<i>Pterographium</i> Stichel, 1910
<i>apolecta</i> (Bates, 1868) comb. n.	* <i>cingulus</i> (Stoll, 1790)	† <i>almeidai</i> (Zikán, 1946)	<i>semiota</i> (Bates, 1868) comb. n.
<i>arbuscula</i> (Möschler, 1883) comb. n.	-- <i>aerope</i> (Westwood, 1851)	* <i>boechoris</i> (Hewitson, 1876)	-- <i>similatum</i> Zikán, 1949 syn. n.
-- <i>histrica</i> (Stichel, 1910) comb. n., syn. n.	-- <i>trucidata</i> (Butler, 1877)	- <i>suavis</i> (Stichel, 1911)	<i>sicora</i> (Hewitson, 1875) comb. n., stat. rev.
- <i>mandosa</i> (H. H. Druce, 1904) comb. n.	<i>fuliginea</i> (Bates, 1868)	† <i>cuneifascia</i> (Zikán, 1946)	-- * <i>aphaniodes</i> Stichel, 1910 syn. n.
<i>crocostigma</i> (Bates, 1868) comb. n.	<i>gallardi</i> Hall & Willmott sp. n.	<i>dukinfieldia</i> (Schaus, 1902)	-- <i>ambiguosa</i> (d'Almeida, 1932)
<i>iasis</i> (Godman, 1903) comb. n.	<i>ignipicta</i> Schaus, 1913	<i>pelotensis</i> Biezanko et al., [1979]	
<i>interrupta</i> (Lathy, 1932) comb. n.	-- <i>eanides</i> Stichel, 1929 syn. n.		
<i>phoenicura</i> (Godman & Salvin, 1886) comb. n.	<i>pseudodebilis</i> Hall & Willmott sp. n.		
-- <i>noctis</i> (Staudinger, 1887) comb. n.	<i>pyrsodes</i> (Bates, 1868)		
<i>pluto</i> (Stichel, 1910) comb. n.	-- <i>pyrophlegia</i> Stichel, 1923		
<i>polemistes</i> Hall & Willmott sp. n.			
* <i>sagaris</i> (Cramer, 1775) comb. n.			
-- <i>simpla</i> (Kaye, 1914) comb. n., syn. n.			
- <i>amazonica</i> (Stichel, 1925) comb. n.			
- <i>phrygiana</i> (Stichel, 1916) comb. n.			
- <i>reducta</i> (Lathy, 1932) comb. n.			
- <i>sarnius</i> (Dalman, 1823) comb. n.			
-- <i>majorina</i> (Stichel, 1910) comb. n.			
<i>sticheli</i> (Lathy, 1932) comb. n.			
† <i>suapure</i> (Weeks, 1906) comb. n.			
- <i>vitata</i> (Stichel, 1910) comb. n.			
<i>tyrtotes</i> (Godman & Salvin, 1878) comb. n.			

Table 3. Distribution of concealed androconial scales on the anterior margins of abdominal tergites in male *Symmachiini* (Riodinidae)

Androconial patches on the following abdominal segments were either absent (0), a continuous patch (1), or mesially divided into two patches (2). Ref: a) data taken from Harvey (1987); b) data first presented in Harvey (1987) and verified in this study; c) data from Willmott & Hall (1994); d) data from Hall & Willmott (1995a); e) data presented for the first time in this study. The male genitalia have been examined for species with refs b-e.

Abdominal segment number:	4	5	6	7	Ref
Taxon:					
<i>Lucillella camissa</i> (Hewitson, 1870)	2	2	2	0	b
<i>Esthemopsis alicia</i> (Bates, 1864)	2	2	2	0	a
<i>Esthemopsis clonia</i> Felder & Felder, 1865	2	2	2	0	a
<i>Esthemopsis colaxes</i> (Hewitson, 1870) ¹	2	2	2	0	e
<i>Esthemopsis celina</i> (Bates, 1868)	1	1	1	0	e
<i>Esthemopsis sericina</i> (Bates, 1867)	1	1	1	0	a
<i>Esthemopsis inaria</i> (Westwood, 1851)	2	2	0	0	a
<i>Xenandra caeruleata</i> (Godman & Salvin, 1878)	2	2	2	0	b
<i>Xenandra desora</i> Schaus, 1928	1	1	0	0	b
<i>Xenandra heliodes</i> Felder & Felder, 1865	1	1	0	0	a
<i>Xenandra helius</i> (Cramer, 1779)	1	?	0	0	a
<i>Chimastrum argenteum</i> (Bates, 1866)	1	1	1	0	b
<i>Mesene babosa</i> Hall & Willmott, 1995	1	1	1	0	e
<i>Mesene citrinella</i> Hall & Willmott, 1995	1	1	1	0	e
<i>Mesene croceella</i> Bates, 1864	1	1	1	0	e
<i>Mesene cyneas</i> (Hewitson, 1874)	1	1	1	0	d
<i>Mesene martha</i> Schaus, 1902	1	1	1	0	b
<i>Mesene monostigma hya</i> Westwood, 1851 ²	1	1	1	0	b
<i>Mesene nola</i> Herrich-Schäffer, 1850	1	1	1	0	e
<i>Mesene phareus</i> (Cramer, 1777)	1	1	1	0	b
<i>Mesene silaris</i> Godman & Salvin, 1878	1	1	1	0	b
<i>Mesene margareta</i> (White, 1843)	1	1	0	0	a
<i>Mesenopsis pulchella</i> Godman, 1903	1	1	1	1	a
<i>Mesenopsis briseis</i> Godman & Salvin, 1886	1	1	0	0	b
<i>Mesenopsis bryaxis</i> (Hewitson, 1870)	1	1	0	0	a
" <i>Panara</i> " <i>elegans</i> Schaus, 1920	2	2	0	0	b
<i>Stichelia bocchoris</i> (Hewitson, 1876)	2	2	0	0	b
<i>Stichelia pelotensis</i> Biezanko <i>et al.</i> , [1979]	2	2	0	0	e
<i>Symmachia phaedra asclepia</i> Hewitson, 1870 ³	2	2	0	0	e
<i>Symmachia rubrica</i> (Stichel, 1929) ⁴	2	2	0	0	c
<i>Symmachia xypete</i> (Hewitson, 1870) ³	2	2	0	0	b
<i>Symmachia accusatrix</i> Westwood, 1851	1	1	0	0	b
<i>Symmachia basilissa</i> (Bates, 1868)	1	1	0	0	e
<i>Symmachia batesi</i> (Staudinger, 1887)	1	1	0	0	e
<i>Symmachia calligrapha</i> Hewitson, 1867	1	1	0	0	e
<i>Symmachia fassli</i> Hall & Willmott, 1995	1	1	0	0	e
<i>Symmachia hazelana</i> Hall & Willmott sp. n.	1	1	0	0	e
<i>Symmachia jugurtha</i> Staudinger, 1887	1	1	0	0	e
<i>Symmachia maeonius</i> Staudinger, 1888	1	1	0	0	e
<i>Symmachia probetor</i> (Cramer, 1782)	1	1	0	0	b
<i>Symmachia rubina</i> Bates, 1866	1	1	0	0	a
<i>Symmachia suevia</i> Hewitson, 1877	1	1	0	0	e
<i>Symmachia technema</i> Stichel, 1910	1	1	0	0	a
<i>Symmachia titiana</i> Hewitson, 1870	1	1	0	0	a
<i>Symmachia triangularis</i> (Thieme, 1907)	1	1	0	0	e
<i>Symmachia tricolor</i> Hewitson, 1867	1	1	0	0	b
<i>Symmachia leena harmodius</i> Godman & Salvin, 1886	0	1	0	0	e
<i>Xynias lithosina</i> Bates, 1868	1	1	0	0	a
<i>Pterographium sicora</i> (Hewitson, 1875)	1	1	0	0	b
<i>Phaenochitonina cingulus</i> (Stoll, 1790)	1	1	?	0	a
<i>Phaenochitonina fuliginea</i> (Bates, 1868)	1	1	0	0	e
<i>Phaenochitonina gallardi</i> Hall & Willmott sp. n.	1	1	0	0	e
<i>Phaenochitonina pseudodebilis</i> Hall & Willmott sp. n.	1	1	0	0	e
<i>Phaenochitonina pyrsoles</i> (Bates, 1868)	1	1	0	0	e
<i>Pirascca arbuscula</i> (Möschler, 1883)	1	1	0	0	e
<i>Pirascca crocostigma</i> (Bates, 1868)	1	1	0	0	e
<i>Pirascca iasis</i> (Godman, 1903)	1	1	0	0	e
<i>Pirascca interrupta</i> (Lathy, 1932)	1	1	0	0	e
<i>Pirascca phoenicura</i> (Godman & Salvin, 1886)	1	1	0	0	e
<i>Pirascca polemistes</i> Hall & Willmott sp. n.	1	1	0	0	e
<i>Pirascca sagaris</i> (Cramer, 1775)	1	1	0	0	b
<i>Pirascca tyriotes</i> (Godman & Salvin, 1878)	1	1	0	0	e

¹The taxon *colaxes* was correctly described in the genus *Esthemopsis* by Hewitson (1870) but subsequently moved to *Brachyglenis* (tribe Riodinini) by Stichel (1910). On the basis of shared morphological characters with *E. clonia* (type species for the genus), we place *colaxes* back in *Esthemopsis* (**comb. rev.**); *Esthemopsis linearis* Godman & Salvin, 1880, is a synonym of *Esthemopsis colaxes* (**syn. nov.**).

²Examination of long museum series shows *Mesene hya* to be only a geographic phenotype, from more westerly Amazon localities, of *Mesene monostigma* (Erichson, 1848) and we place the former as a subspecies of the latter (**stat. nov.**).

³Stichel (1930) regarded the taxon *xypete* as a subspecies of *asclepia* but the wing facies and male genitalia show that *xypete* is a distinct species (**stat. rev.**) and that *asclepia* is a subspecies of *phaedra* (**stat. nov.**).

⁴Stichel (1929) described *rubrica* in the genus *Polystictis* and it is currently placed in the genus *Calospila* (Bridges, 1994), but the wing facies, male genitalia and presence of androconial scales on certain abdominal tergites clearly place it in *Symmachia* (**comb. nov.**); *Symmachia wiltoni* Willmott & Hall, 1994, is a synonym of *rubrica* (**syn. nov.**).

Diagnosis: *Phaenochitonina pseudodebilis* sp. nov. most closely resembles *Comphotis debilis* (Fig. 11a,b) and in fact it was curated as such in the MNHN. However, despite their very similar dorsal surfaces (*pseudodebilis* differs only by having red instead of orange markings, a slightly smaller forewing patch and a slightly wider hindwing band), the ventral surfaces, although also similar, diagnose their differing generic placements and these differences are highlighted in the schematic drawings of Figure 8. The dorsal surface of the abdomen of *pseudodebilis* is also entirely red while that of *debilis* is orange on the basal two-thirds and black on the distal third. Morphologically, *pseudodebilis* differs by possessing androconial scales on tergites 4 and 5 (placing it in a different tribe - see discussion below on the systematics of *Comphotis*) and very different male genitalia (see Fig. 15a-c; 17a,b).

Systematics of the genera *Phaenochitonina* and *Comphotis*

While dissecting species in the genus *Phaenochitonina* for this study, we discovered that the taxon *sophistes* lacked concealed androconial scales on the anterior margins of its abdominal tergites thereby excluding it from the tribe Symmachiini. The phenotypic similarity of *sophistes* to *Comphotis irroratum* (type species for the genus) is very evident, especially in specimens from the western Amazon that have a slightly more rounded wing shape (these specimens may represent a distinct subspecies, although the male genitalia do not differ from typical *sophistes* from the lower Amazon) and the former only differs by possessing a thin transverse orange line across the centre of both wings. The male genitalia of *sophistes* differs from that of *irroratum* only by having a small projection at the base of the valve.

The dissection of additional species in "*Phaenochitonina*" revealed the existence of three other species (*debilis*, *eanes* and *ignicauda*) that lacked concealed androconial scales and had very similar male genitalia to *C. irroratum* (the genitalia of *debilis* [Fig. 17a,b] is almost identical to that of *irroratum*). The specimens in question also exhibit subtle but clear differences in their ventral patterns to true *Phaenochitonina* species (see Fig. 8) that do possess concealed androconial scales and whose male genitalia are rather different (see Fig. 14a-c, 15a-c). Additionally these specimens have forewing vein Sc fused to R₁, while true *Phaenochitonina* species do not. Based on the above morphological and phenotypic differences we place *sophistes*, *debilis*, *eanes* and *ignicauda* in the genus *Comphotis* (see Table 4 below). STICHEL (1930) regarded *eanes* as a form of *pyrsodes*, no doubt based on their superficial phenotypic similarity, but as outlined above their morphology places them in different genera (and even tribes) and we return *eanes* to full specific rank.

Comphotis Stichel, 1910

apachita Hall & Willmott sp. n.

clarissa (E. Sharpe, 1890) comb. n.

debilis (Bates, 1868) comb. n.

eanes (Godman, 1903) comb. n., stat. rev.

ignicauda (Godman & Salvin, 1878) comb. n.

* *irroratum* (Godman, 1903)

sophistes (Bates, 1868) comb. n.

Table 4. A summary of the taxa in the genus *Comphotis*. Symbols: * indicates the type species for the genus.

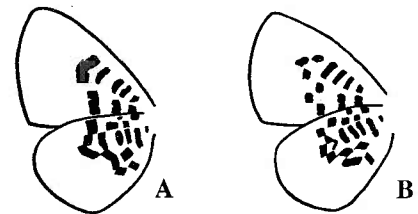


Fig. 8. Schematic drawings indicating the differences in the basal ventral patterns of species in the genera *Phaenochitonina* (A) and *Comphotis* (B).

The taxon *clarissa* was described from and is only known to us from the female holotype and we place it in *Comphotis* on the basis of its venation and ventral patterning, and *apachita* is a new species that we describe below. Two taxa placed in the genus *Comphotis* in BRIDGES (1994) are excluded from our classification.

The first of these is *delicia* Rebillard, 1958, described from a female from Rio Umary, Brazil. In the original description, REBILLARD erroneously states that *hippea* Herrich-Schäffer, [1853], is the type species for *Comphotis* and it is upon this basis that he described *delicia* in *Comphotis*. From the type illustration, it can clearly be seen that the taxon *delicia* is indeed closely related to *hippea* but this latter species is currently (and was at that time (STICHEL, 1930)) placed in the genus *Symmachia* and this is where *delicia* more appropriately belongs (**comb. nov.**). It is phenotypically very similar to the female type of *Symmachia norina* Hewitson, 1867 (TL: Pará, Brazil), but since the whereabouts of the type specimen of *delicia* is unknown (it is not listed in CALLAGHAN (1995) nor was it located during a search of the MNHN by the authors) no synonymy is made.

The second taxon included in *Comphotis* by BRIDGES (1994) is *sinuata* Stichel, 1925, described from Manicoré, Brazil. The male type specimen of *sinuata* differs from that of *Theope drepana* Bates, 1868 (TL: Ega, W. Brazil), only by having a darker ventral surface, slightly more pale scaling in the apex of the ventral forewing and slightly less black at the outer margin of the dorsal forewing, and we synonymise *sinuata* with *drepana* (**syn. nov.**). This species undoubtedly does not belong in the genus *Theope* Doubleday, 1847, and although the ventral pattern of markings does superficially resemble that of *Comphotis*, the wing shape (falcate forewing and angular hindwing), ventral colour pattern (orange-brown basal maculae and tiny submarginal black spots) and blue dorsal colouration suggest a different generic placement. Once its morphology has been carefully examined, *drepana*, along with an undescribed probable sister species from Panama in the USNM, may need to be placed in a new genus.

HARVEY (1987) provisionally placed the genus *Comphotis* in the tribe Riodinini Grote, 1895, defined by the presence of a deeply indented notch at the anterior margin of the tegumen of the male genitalia. However, he had not been able to examine the genitalic morphology of the genus, and we believe that *Comphotis* is better placed in HARVEY's (1987) *incertae sedis* section (four forewing radial veins), as it does not possess the synapomorphic characters of any existing tribe. However, several lines of evidence suggest that *Comphotis* may be immediately ancestral to *Phaenochitonia* and hence a plausible ancestor to the tribe Symmachiini.

As outlined above, the two genera have, until the present time, been largely confused, with most *Comphotis* species having been considered members of *Phaenochitonia* (STICHEL, 1930; BRIDGES, 1994) and this is understandable considering the great phenotypic similarity between the two genera. It is this similarity that provides the first superficial clue that the two genera may be closely related and an examination of the male genitalia (see Fig. 14-18) and forewing venation further strengthens this idea. Interestingly, the existence of remarkable dorsal wing pattern similarities between the largely sympatric species pairs *P. pseudodebilis*/*C. debilis*, *P. pyrsoles*/*C. apachita* or *eanes*, and *P. ignipicta*/*C. ignicauda* strongly suggests convergent evolution by means of atavism.

In support of the above hypothesis of relatedness, the taxon *apachita*, described below, appears to have characters intermediate between species of the two genera and in fact before dissection had been mistakenly identified as a *Phaenochitonia* on account of its rather typical "*Phaenochitonia*-like" ventral pattern (as illustrated in Fig. 8a). However, upon closer examination, the extent of the grey

scaling on the hindwing, especially distal to the postdiscal line of spots, is rather more typical of *Comphotis*. The forewing vein Sc of *apachita* is joined to R₁, over a distance of approximately 0.3mm while in typical *Comphotis* species it is actually fused for a distance of approximately 0.4mm and in *Phaenochitonina* species the veins run very close to each other but are not joined. The male genitalia also seem to have begun to develop some character states typical of *Phaenochitonina* species such as a longer downwardly pointing projection from the centre of the posterior edge of the uncus, and a more pointed upper valve section that extends beyond the aedeagus. The male genitalic valve shape of the taxon *pyrsodes* is not dissimilar to that of *apachita* and is intermediate between that species and *P. gallardi*, potentially indicating the ancestral position of *pyrsodes* in the genus *Phaenochitonina*.

Despite the similarities between *apachita* and members of *Phaenochitonina*, its lack of concealed androconial scales on all abdominal tergites places it outside of the tribe Symmachiini and it is thus most appropriately placed in the genus *Comphotis* with which it shares the most characters. In accordance with the theory that *Phaenochitonina* is a more ancestral member of the tribe Symmachiini, its species have very thin and sparse concealed androconial scale patches on their abdominal tergites in contrast to species in, for example, *Pirascia*, that have very wide and dense patches of scales which may be hypothesised to represent a more derived state.

***Comphotis apachita* Hall & Willmott, sp. nov.** (Fig. 12a,b; 16a-c).

Description: Male: forewing length 11.5mm. **Dorsal surface:** forewing ground colour black; a large triangular red patch at the centre of the anal margin that extends from near the wing base to near the tornus to a point just distal to the cell end, a thick red line then angles inwards to mark the cell end. Hindwing ground colour black; a large triangular red patch in the basal half of the wing that extends from the wing base to a point two-thirds of the way along the anal margin, leaving a thin strip of black at the margin, and then to a point just distal of and below the upper corner of the discal cell end, two small black indentations in the centre of the costal edge of the triangle. **Ventral surface:** forewing ground color brown, a triangular orange patch at the centre of the anal margin mirroring the red dorsal one; four black spots in discal cell, three ringed by light grey, one marking cell end, one immediately before cell end particularly large and round; two spots below cell, basal one ringed by light grey, upper half of distal one black, lower half dark orange; black postdiscal line, column of three spots below cell end, upper one black, lower two dark orange, central one displaced slightly distally; indistinct, broader, more distal postdiscal dark brown band; faint dark brown ocelli at outer margin encircled by pale grey that forms pointed triangles proximally, especially near tornus; fringe not discernible. Hindwing ground colour brown, faint orange/red basal area mirroring red patch on dorsal surface; five dark brown spots in discal cell, three ringed by light grey, one marking cell end, one immediately before cell end particularly large and round; two spots above and below cell ringed with pale grey; undulating black postdiscal transverse line, with pale grey scaling distally, that curves around cell end creating a semi-circular area between the cell end and postdiscal lines; indistinct, broader, more distal postdiscal dark brown band; triangular dark brown ocelli at outer margin that are enlarged at apex and encircled by pale grey that also forms pointed triangles distally. Labial palpi pale yellow, tips brown. Eyes brown and bare. Frons yellow with some brown scaling. Antennae brown with cream scales at the base of each segment, clubs brown. Thorax black; basal two-thirds of dorsal surface of abdomen red, distal two-thirds black, ventral surface grey/brown. Legs pale yellow. **Venation:** Forewing vein Sc joined (but not completely fused) to R₁, for

approximately 0.3mm. **Genitalia** (Fig. 16a-c): mid-point of posterior edge of uncus projecting and pointed downwards; valvae narrow with a small lower angular projection, fused above the aedeagus; aedeagus cylindrical and split at the apex along the dorsal side; saccus of medium length.

Female: unknown.

Types: Holotype ♂: Ecuador, *Napo Province*, km. 12 Tena-Puyo, Finca San Carlo, 600m, 23 February 1995 (K. R. Willmott). To be deposited in the BMNH.

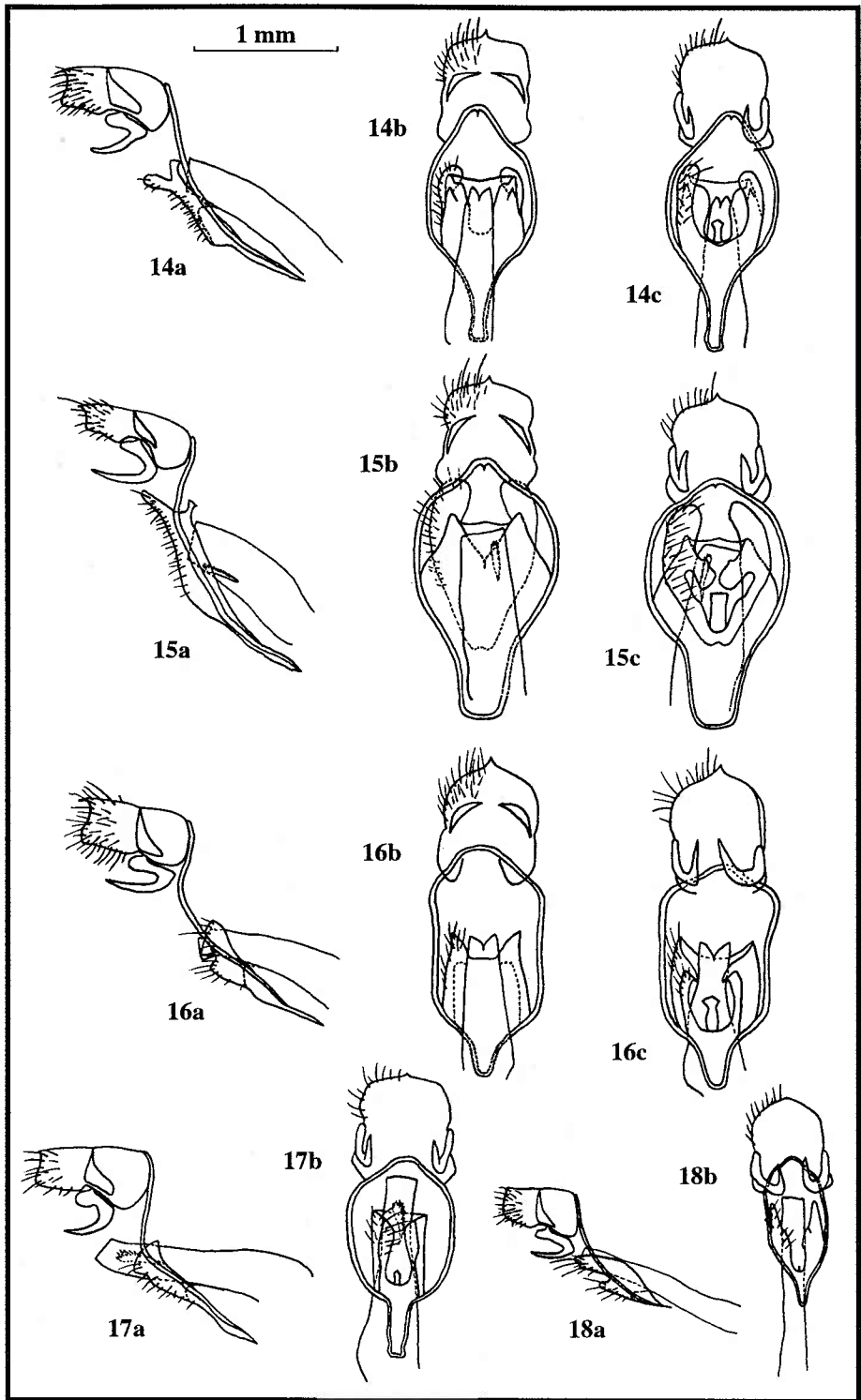
Etymology: This species is named after the Quichua word "apachita", meaning "a high place or hilltop along a road", in reference to its capture locality.

Diagnosis: *Comphotis apachita* sp. nov. very closely resembles *Comphotis eanes*, especially on the dorsal surface. It differs on the dorsal surface by having a wider black margin at the base of the forewing costa, with no red in the discal cell, and a hindwing red patch that extends further towards the anal margin. The ventral surface of *apachita* has an orange triangle at the centre of the anal margin of the forewing and a pattern of basal spots more like that of a species in the genus *Phaenochitonia* (see Fig. 8 and discussion above concerning the phylogenetically intermediate position of *apachita*), the differences between the two species being most apparent in the postdiscal forewing line of spots. The male genitalia of *eanes* (Fig. 18a,b) differs primarily from that of *apachita* by not having a projection from the mid-point of the posterior edge of the uncus, by having a more cylindrical aedeagus and markedly bifurcate valvae that are only joined across the top of the aedeagus by soft instead of sclerotised tissue and in a more anterior position.

Phaenochitonia pyrsodes, with which the taxon *eanes* has for so long been regarded a form, is also similar especially on the ventral surface. *P. pyrsodes* is most quickly distinguished by having a black instead of red dorsal surface to the abdomen, and on the dorsal wing surface by having a less pointed forewing triangular patch and a hindwing red patch that extends all the way to the costal margin. The male genitalia are rather similar but *pyrsodes* has a cluster of small pencilate cornuti towards the tip of the aedeagus and a longer saccus.

Discussion: This species is only known from a single male specimen and no others have been located in the world's major museums. It was found perching in a hilltop lightgap (where several other new riodinid discoveries have recently been made (HALL & WILLMOTT 1995b, 1996)) at 3.15 p.m., resting beneath a leaf with its wings outspread. See the above section on the systematics of *Phaenochitonia* and *Comphotis* for a discussion of the phylogenetic position of *C. apachita*.

Fig. 14-18. Male genitalia. 14. *Phaenochitonia gallardi* sp. nov., holotype ♂: a) lateral view; b) dorsal view; c) ventral view. 15. *Phaenochitonia pseudodebilis* sp. nov., holotype ♂: a) lateral view; b) dorsal view; c) ventral view. 16. *Comphotis apachita* sp. nov., holotype ♂: a) lateral view; b) dorsal view; c) ventral view. 17. *Comphotis debilis* (Bates, 1868) Brazilian male (MNHN): a) lateral view; b) ventral view. 18. *Comphotis eanes* (Godman, 1903) Brazilian male (MNHN): a) lateral view; b) ventral view.



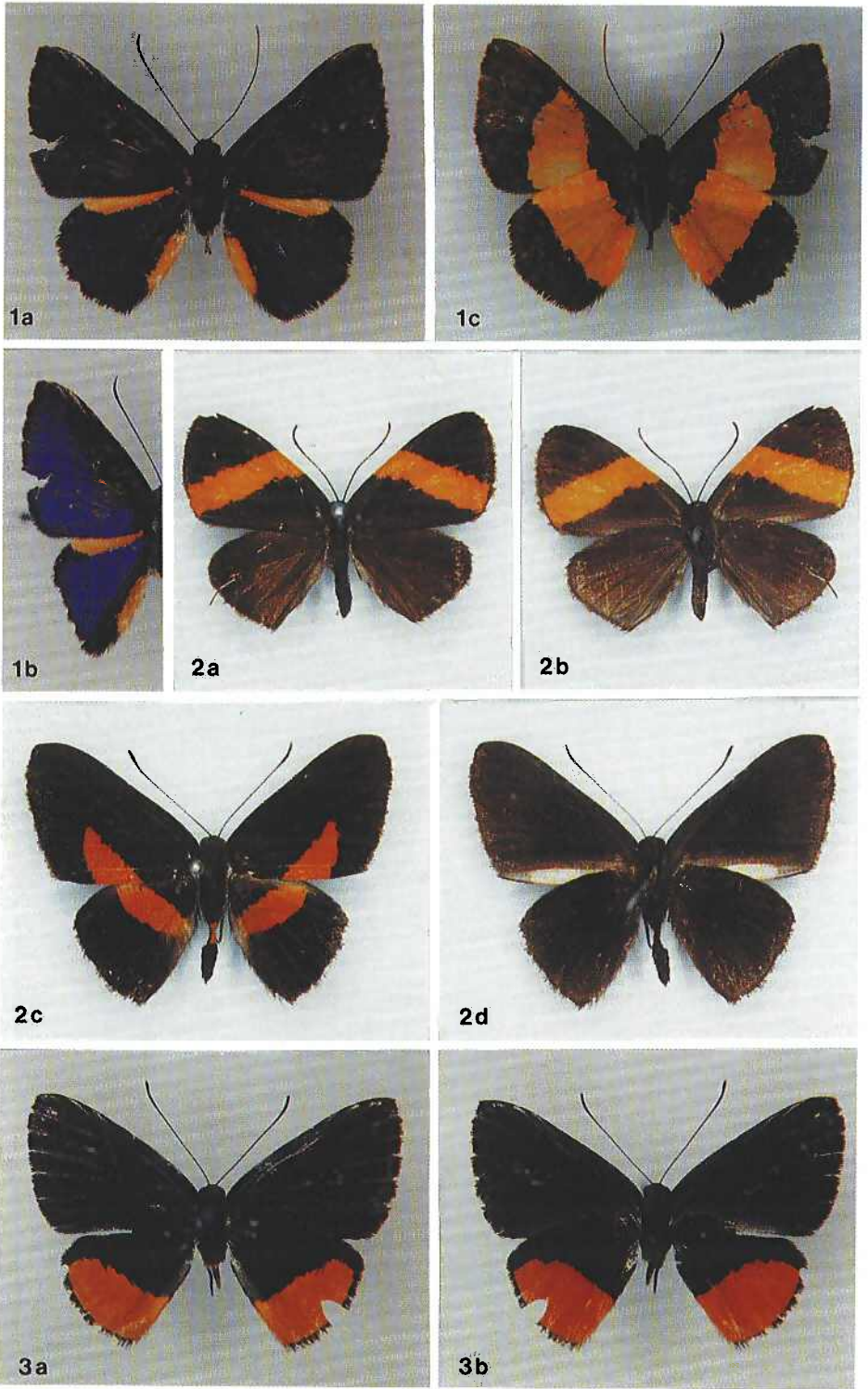


Fig. 1-3. Type specimens. 1 *Symmachia hazelana* Hall & Willmott sp. nov., holotype ♂: a) dorsal surface; b) dorsal surface viewed at an oblique angle; c) ventral surface. 2. *Pirascia sagaris* (Cramer, 1775), type species for the genus, Brazilian female: a) dorsal surface; b) ventral surface. Brazilian male: c) dorsal surface; d) ventral surface. 3. *Pirascia polemistes* Hall & Willmott sp. nov., holotype ♂: a) dorsal surface; b) ventral surface.

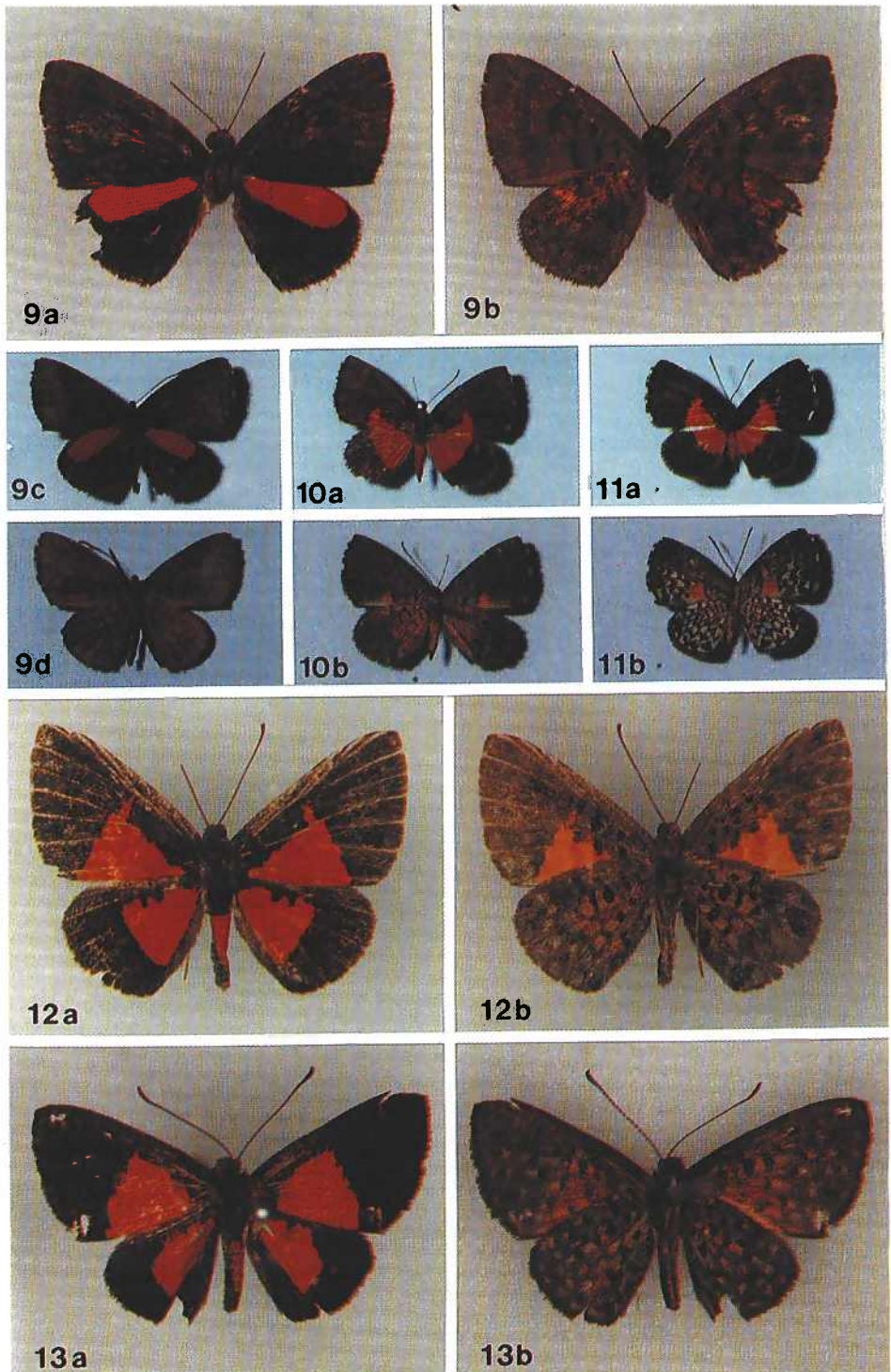


Fig. 9-13. Type and comparative specimens. 9. *Phaenochitonina gallardi* Hall & Willmott sp. nov., paratype ♂: a) dorsal surface; b) ventral surface. Holotype ♂: c) dorsal surface; d) ventral surface. 10. *Phaenochitonina pseudodebilis* Hall & Willmott sp. nov., holotype ♂: a) dorsal surface; b) ventral surface. 11. *Comphotis debilis* (Bates, 1868) Brazilian ♂ (MNHN): a) dorsal surface; b) ventral surface. 12. *Comphotis apachita* Hall & Willmott sp. nov., holotype ♂: a) dorsal surface; b) ventral surface. 13. *Comphotis eanes* (Godman, 1903) Guyanan ♂ (BMNH): a) dorsal surface; b) ventral surface.

Remarks on the systematic importance of concealed androconial scales in the remaining genera of the Symmachiini

HARVEY (1987) was the first to note the systematic importance of the arrangement of androconial scales on the anterior margins of particular male abdominal tergites, the possession of which (in conjunction with acanthae) defines the tribe Symmachiini. In Table 3 we present information on the distribution of these scales for 62 symmachiine species in 12 existing genera (representing approximately half of the species in the tribe and all of the genera), including data taken from HARVEY (1987).

In a case opposite to that outlined earlier for certain *Phaenochitonina* species, the possession of two patches of androconial scales on tergites 4 and 5 in the taxon *Panara elegans* Schaus, 1920, places it in the tribe Symmachiini and thus excludes it from the genus *Panara* Doubleday, 1847, which is in the tribe Riadini (HARVEY, 1987). The phylogenetic relationships of this species remain unclear however, for while it has a similar wing pattern and hindwing androconial hair-pencil arrangement to *Pterographium sicora*, it differs in the genitalia and distribution of abdominal androconial scales and may be best placed in a monotypic genus.

While certain genera exhibit relatively consistent patterns of androconial scale distribution, such as *Mesene* Doubleday, 1847, and *Pirasecca* gen. nov., others, such as *Mesenopsis* Godman & Salvin, 1886, *Esthemopsis* Felder & Felder, 1865, *Xenandra* Felder & Felder, 1865, and *Symmachia* Hübner, [1819] show a variety of patterns (see Table 3). As noted by HARVEY (1987), it is not surprising that a classification of probably mimetic species based on wing pattern similarity often proves to be unnatural. For example, *Mesenopsis* contains species that appear outwardly similar, but *M. pulchella* differs from *M. briseis* and *M. bryaxis* in having additional androconial scales on tergites 6 and 7. Similarly, *Esthemopsis sericina*, which resembles *E. clonia*, *E. alicia* and *E. colaxes*, differs from them by having a single, undivided androconial patch on each tergite. However, as might be expected, those species that are phenotypically atypical for a genus often also have different androconial scale distributions. For example, the phenotypically unusual taxa *inaria* and *caeruleata* have quite different scale distributions to species typical of the genera *Esthemopsis* and *Xenandra* respectively and *caeruleata* may prove to be better placed in *Esthemopsis*.

For the species examined in this study, the abdominal androconial scale distribution in the large genus *Symmachia* indicates the existence of at least three species groups, although it is not clear at present which scale arrangements are derived and which are ancestral. The majority of species possess a single patch of scales on tergites 4 and 5, but appear to have no other immediately obvious shared morphological characters, suggesting that this group may not be monophyletic; however, two other distinctive groups emerge that may be. *S. leena* Hewitson, 1870, is unique among the species examined in possessing androconial scales on only a single tergite and moreover has a very dense and localised cluster of long androconial hairs near the anal margin of the hindwing. If these androconial hairs function to more effectively disseminate sex pheromones, they might be expected to be positioned opposite those abdominal tergites that have androconial scales, and this appears largely to be the case in this species, other symmachiines and in the nymphidiine genus *Menander*. In *S. leena* the presence of androconial scales on only a single tergite may explain its unusually dense concentration of hindwing androconial hairs. We predict that other *Symmachia* species which share similar wing pattern characters and such dense hindwing androconial hairs, for example *S. aconia* Hewitson, 1876, *S. pardalia* Stichel, 1924, and *S. punctata* Butler, 1877,

will also have the same unusual arrangement of abdominal androconial scales. *S. phaedra* (Bates, 1868), *S. rubrica* (Stichel, 1929) and *S. xypete* (Hewitson, 1870) differ from other *Symmachia* species in having the androconial scales on tergites 4 and 5 reduced to a single, small, ovoid patch on each side of the tergite, and in addition they share similar wing shapes, wing patterns and male genitalia, forming a cohesive group. We suggest that the taxon *splendida*, described by Salazar and Constantino (1993) from north Colombia, does not belong in *Calospila*, in which it was originally placed, but in *Symmachia*, specifically in the "*phaedra* group". This is based on the wing shape, ventral spotting pattern and presence of numerous pencillate cornuti in the aedeagus of the male genitalia, and we predict that *Symmachia splendida* **comb. nov.** will also possess the same pattern of androconial scales found in species of the "*phaedra* group".

As mentioned in the introduction, the fact that many symmachiine species are known from only a handful of specimens, scattered widely among the world's museums, has greatly complicated phylogenetic studies in this tribe. The above observations, we hope, have highlighted some of the more confused areas of systematics which are most in need of future research and shown that the arrangement of abdominal androconial scales can and should be used, in conjunction with other characters, to make new generic combinations and/or create new genera in order to more accurately reflect phylogenetic relationships within the Symmachiini. Through a reassessment of the species relationships within a portion of the tribe, it has been our intention to begin this process of creating more natural generic groupings.

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