

# Systematics of *Hypanartia* (Lepidoptera: Nymphalidae: Nymphalinae), with a test for geographical speciation mechanisms in the Andes

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**Abstract.** A taxonomic review of the Neotropical nymphaline butterfly genus *Hypanartia* Hübner is presented, including notes on the taxonomy, biology and distribution of its component species, illustrations of all taxa and the male genitalia of all species, and the description of four new species and two new subspecies: *Hypanartia celestia* sp.n., *H. cinderella* sp.n., *H. dione disjuncta* ssp.n., *H. fassli* sp.n., *H. trimaculata* sp.n. and *H. trimaculata autumnna* ssp.n. *Hypanartia arcaei* (Salvin) is placed as a subspecies of *H. dione* (Latreille) (stat.n.) and lectotypes are designated for eight nominal taxa. Fourteen species are recognized, with the centre of diversity being in high Andean cloud forest habitats. A cladistic analysis was conducted, based on fifty-three illustrated characters of male genitalic and abdominal morphology, and external facies, to investigate phylogenetic relationships. The resulting phylogenetic hypothesis was used to test four different geographical mechanisms of speciation in the Andes: colonization from temperate latitudes, speciation across elevational gradients, radiation within the Andes and allopatric speciation between the Andes and other montane regions. There is evidence that speciation across an elevational gradient occurred twice, both times into elevations largely unoccupied by the genus, and in both cases followed by subsequent, elevationally sympatric, *in situ* radiation. Differentiation in allopatry between montane regions has apparently been of recent influence only, causing infraspecific variation in two species. These results parallel several recent studies of Andean bird speciation.

## Introduction

The last three decades have seen an explosion of interest in the species-level taxonomy of Neotropical butterflies, and many of the most phylogenetically distinctive and remarkable discoveries have been made in montane regions (e.g. Beutelspacher, 1975; Adams & Bernard, 1977, 1979, 1981; DeVries & Chacón, 1982; Adams, 1986; Johnson, 1992; Viloría & Pyrcz, 1994; Viloría, 1994; Hall & Willmott, 1995, 1998; Willmott & Hall, 1995). Although a large quantity of montane butterfly material exists in some collections, the great majority is

historical, collected during the pioneering years of biological exploration in the 1800s, and originates from a handful of well collected localities along ancient trading routes (Lamas, 1992). The high rates of faunal turnover (beta diversity) within and between montane regions, and along elevational gradients (Gentry, 1988; Bibby *et al.*, 1992), means that these few scattered collecting localities have seldom provided a representative picture of the true biotic diversity of montane habitats. Steep mountainous terrain, dense forests and almost perpetual cloud and rain have also combined to discourage the kind of basic faunistic inventories that are beginning to reveal the butterfly diversity of lowland Neotropical forests (e.g. de la Maza & de la Maza, 1985; Emmel & Austin, 1990; Lamas, 1994a,b; Robbins *et al.*, 1996).

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The rapidly accelerating degradation of montane habitats adds a special urgency to species-level taxonomic research on montane groups (Anon, 1995; Churchill *et al.*, 1995; Dinerstein *et al.*, 1995; Aldrich *et al.*, 1997). A resolved species-level taxonomy is not only essential for investigating the origins and evolution of montane faunas, but is also the basis for developing a firm understanding of spatial variation in species richness and endemism, as a precursor to conservation planning. Butterflies are widely believed to be one of the best taxonomically understood groups of tropical organisms (Daily & Ehrlich, 1995; Robbins & Opler, 1997), and this has been an important factor in their increasing use in assessing biodiversity and monitoring ecosystem health (Pyle *et al.*, 1981; Collins & Morris, 1985; Brown, 1991, 1996; Kremen, 1992; Beccaloni & Gaston, 1994; Daily & Ehrlich, 1995). However, despite this view, there are a number of Neotropical groups where detailed modern studies have illustrated surprising discrepancies between perceived and actual species-level diversity, even in supposedly well known, lowland nymphalid genera (Brévignon, 1996; Brower, 1996; Willmott & Hall, unpublished data). With the increasing accessibility of formerly remote and isolated mountain ranges and valleys, due to human expansion from overpopulated highland regions, the shortcomings in our taxonomic knowledge of many montane groups are becoming ever more apparent (e.g. Beutelspacher, 1976; Steinhäuser & Miller, 1977; Jenkins, 1986; Johnson, 1990; Attal & Crosson du Cormier, 1996; Torres *et al.*, 1996; Eitschberger & Racheli, 1998; Pycrz *et al.*, 1999; Willmott & Hall, 1999). This situation is well illustrated by *Hypanartia*, the subject of this paper.

*Hypanartia* is a medium-sized nymphalid genus whose members all have an orange, brown or reddish-brown dorsal surface, with a variable number of opaque, translucent or transparent forewing spots, an intricately patterned ventral surface and angular wing shapes, with a hindwing tail of variable length. The genus contains some of the most widespread and common butterfly species in the Neotropics, most of which were described before the middle of the nineteenth century. The last historical species description was by Rothschild (1903). Since then the taxonomy of the genus has remained static, as its species diversity was thought to have been fully elucidated. Some authors have regarded the genus as containing as few as six species (Smith *et al.*, 1994), but most have recognized eight (Seitz, 1914; DeVries, 1987). The discovery of a highly distinctive, undescribed species in the Peruvian Andes, along with the realization that the names *H. kefersteini* (Doubleday) and *H. lindigii* (C. & R. Felder), as applied by most authors, each included three distinct species, prompted us to review the entire genus. One species, *H. christophori* Jasiński, was recently described by Jasiński (1998), but the remaining four are described here, bringing the total number of recognized species in the genus to fourteen. These five recently discovered or recognized species are all from Andean cloud forest habitats, revealing that the true centre of diversity for the genus lies in these montane regions. The successful diversification of *Hypanartia* within such regions thus offers an unusual opportunity to test several distinct, but complementary, possible geographical modes of

speciation in Neotropical montane habitats, using a phylogenetic hypothesis for the genus.

We discuss the history of classification of the genus and present a revised, synonymic checklist. We present the results of a cladistic analysis conducted to investigate phylogenetic relationships between all known species and allow us to test several biogeographic hypotheses. An overview of the biology of the genus is presented, followed by more detailed reviews of the taxonomy of each species and a key to their identification, with supplementary notes on their biology, summarized from the literature and field observations by K.R.W. and J.P.W.H. in Ecuador and G.L. in Peru.

## Methods

### *Species taxonomy*

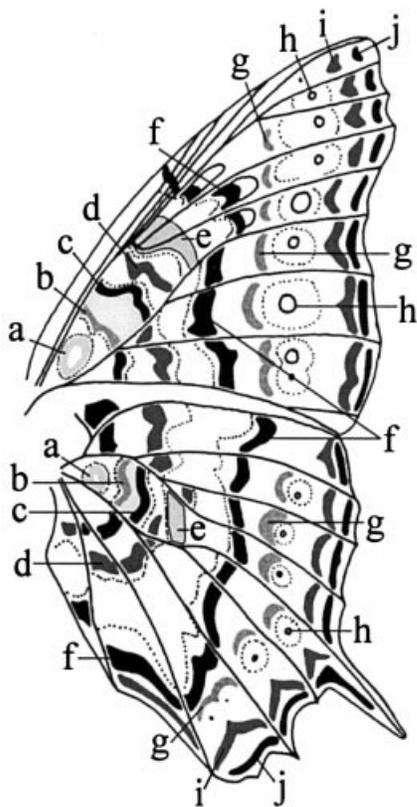
Adult *Hypanartia* specimens were studied in a number of public and private collections in Europe, South America and the U.S.A. to assess wing pattern variation and to record geographical and elevational ranges. The following acronyms are used throughout the text (collections not personally examined are marked with an asterisk): \*AJ, Artur Jasiński collection, Piastów, Poland; AME, Allyn Museum of Entomology, Sarasota, Florida, U.S.A.; AMNH, American Museum of Natural History, New York, New York, U.S.A.; AN, Andrew Neild collection, London, U.K.; \*AO, Andrés Orellana collection, Mérida, Venezuela; BMB, Booth Museum of Natural History, Brighton, U.K.; BMNH, The Natural History Museum, London, U.K. (M = main collection; R = Rothschild collection); \*BR, Basilio Rodríguez collection, Caracas, Venezuela; ESM, Ernesto W. Schmidt-Mumm collection, Bogotá, Colombia; FIML, Fundación e Instituto Miguel Lillo, Tucumán, Argentina; FSCA, Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, U.S.A.; JFL, Jean François Le Crom collection, Bogotá, Colombia; KWJH, Keith R. Willmott and Jason P. W. Hall collection, Bristol, U.K.; LMC, Luis M. Constantino collection, Cali, Colombia; \*MALUZ, Museo de Artrópodos Terrestres, La Universidad de Zulia, Venezuela; MECN, Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; MHNUC, Museo de Historia Natural, Universidad de Caldas, Manizales, Colombia; \*MIZA, Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela; MLP, Museo de la Plata, Universidad Nacional de la Plata, La Plata, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; \*MZUJ, Muzeum Zoologiczne Uniwersytetu Jagiellońskiego, Kraków, Poland; \*R, Romero family collection, Maracay, Venezuela; RSM, Royal Scottish Museum, Edinburgh, U.K.; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.; ZMHU, Zoologisches Museum, Humboldt Universität, Berlin, Germany.

Dissections were made using standard techniques, male abdomens being soaked in hot 10% KOH solution for

approximately 20 min and subsequently stored in glycerol. Drawings were made using a Wild M4A stereomicroscope at 30× magnification and a Wild camera lucida. Morphological terms for genitalia largely follow Klots (1970), and terminology for wing venation follows the widely used Comstock & Needham (1918) system (wing cells are referred to by their bounding veins). As all *Hypanartia* species have relatively unmodified wing patterns relative to the idealized nymphalid ground plan (Nijhout, 1991), we also apply Nijhout's (1991) terminology where it assists in the description of characters involving wing pattern elements (Fig. 1).

#### Phylogenetic analysis

Characters were derived from the study of adult male morphology of all fourteen *Hypanartia* species (see *History of classification* below). Female genitalic characters were not included because the females of the majority of *Hypanartia* species are very rare or, in several cases, unknown. Characters from the immature stages also were not included because these



**Fig. 1.** Elements of the *Hypanartia* wing pattern groundplan based on *H. paullus*, but also including elements not visible in this species but present in others. Terminology follows Nijhout (1991): a, wing root band; b,c, basal symmetry system; d, proximal band of central symmetry system; e, discal spot; f, distal band of central symmetry system; g (no name); h, border ocelli; i, parafocal element; j, submarginal band. Dotted lines represent pale marking.

are known for only four species. Wing pattern characters were analysed following determination of homologous pattern elements between taxa, based on their development from an idealized nymphalid wing pattern groundplan (Fig. 1).

Historically, systematists have regarded the African genus *Antanartia* Rothschild & Jordon as the closest relative of *Hypanartia*, suggesting that it might be the most suitable initial choice of outgroup (Watrous & Wheeler, 1981; Donoghue & Cantino, 1984), although Lyons-Weiler *et al.* (1998) dispute that this assumption is always valid. However, as there has been no cladistic analysis of Nymphalini, and its sister taxon within Nymphalidae remains unknown (Harvey, 1991), rigorous selection of the sister taxon to *Hypanartia* through cladistic methods is beyond the scope of this paper. To select an appropriate outgroup we examined wing pattern, male genitalia and other external and internal morphological characters of species in several genera in Nymphalini (*sensu* Harvey, 1991). These species included all those recognized by Howarth (1966) in his revision of *Antanartia*, and representatives of the genera *Nymphalis* Kluk, *Polygonia* Hübner, *Vanessa* Fabricius and *Symbrenthia* Hübner. Although the male genitalia of *Hypanartia* are slightly more similar to those of the Old World genus *Symbrenthia* than to other genera examined, *Hypanartia* wing pattern and shape most closely resemble those of species in *Antanartia* (in terms of shared character states; as noted above, a cladistic analysis was not conducted). We therefore polarized characters using species from three genera as outgroups: the type species of *Antanartia*, *A. delius* (Drury) (see Fig. 24 for illustration of male genitalia, and d'Abreu, 1980, for a colour illustration of the adult), *Symbrenthia hypatia* (Wallengren) and *Vanessa cardui* (Linnaeus).

The cladistic analysis was conducted with PAUP 4.0b4 (Swofford, 1999) using maximum parsimony as the optimality criterion. A heuristic search was performed using TBR branch swapping, and starting cladograms were obtained by random stepwise addition (10 000 replicates). All characters were unordered and equally weighted. To test the effect on cladogram topology of different character suites of potentially varying homoplasy, we also partitioned the data into external (1–36) and internal (37–53) character sets and analysed each separately. Although there are certain statistical objections (e.g. see Sanderson, 1995) to using bootstrap analysis to assess the strength of branch support (Felsenstein, 1985), it remains widely utilized, and branch support was partially estimated by means of 10 000 bootstrap replicates in PAUP. Additional branch support was estimated using decay indices, calculated using TreeRot 2 (Sorenson, 1999). Character evolution was studied using MacClade version 3.05 (Maddison & Maddison, 1995).

## Results

### Tree topology and support

A total of fifty-three characters were identified (Appendix 1) from the labial palpi (one character), wing shape and pattern (thirty-five characters) and male abdominal (three characters)

and genitalic (fourteen characters) morphology (see Appendix 2 for character matrix). Outgroup choice had no effect on the ingroup topology of the most parsimonious cladogram, with all three outgroup species or each species individually generating a single most parsimonious cladogram. With all three outgroup species, the resultant cladogram had 122 steps (CI=0.71, RI=0.83), whereas cladograms of length 100 and 101 steps were derived using only *Symbrenthia hypatia* and *Vanessa cardui*, respectively, as single outgroup taxa. The figured cladogram (Fig. 2) is that obtained using *Antanartia delius* only as an outgroup, and is of length 103 steps (CI=0.71, RI=0.83). As cladogram topology was unaffected by outgroup choice, we deemed it unnecessary to conduct more rigorous tests for the optimal outgroup (e.g. Lyons-Weiler *et al.*, 1998), and provide data and illustrations of character states for *A. delius* only. That taxon was also used as an outgroup for the analyses of partitioned characters. Universal synapomorphies for *Hypanartia* are given in Appendix 3. The evolution of other characters can be traced through examination of the character matrix (Appendix 2), whereas universal synapomorphies for individual clades are marked on appropriate nodes in Fig. 2.

The main pattern evident from this analysis is that the genus comprises two monophyletic clades, the 'paullus group' and the 'dione group'. The former has low bootstrap and Bremer support values, whereas the latter is highly supported by both measures. Several other clades are strongly supported, including *lethe/godmanii*, *fassli/christophori/lindigii* and *trimaculata/cinderella/kefersteini*. The total support index, a measure of cladogram stability, is 0.30, toward the upper end

of the range reviewed by Bremer (1994), whereas the proportional support index is 0.51 (Lee, 1999). The retrieval of identical cladograms with different outgroup taxa also gives confidence in the cladogram structure, and the overall consistency index represents an average value for the number of taxa studied (Sanderson & Donoghue, 1989). The latter is perhaps surprising given the high proportion of wing pattern characters, a character suite traditionally perceived as relatively homoplasious, and therefore often omitted from phylogenetic analyses of butterflies (e.g. DeVries *et al.*, 1985).

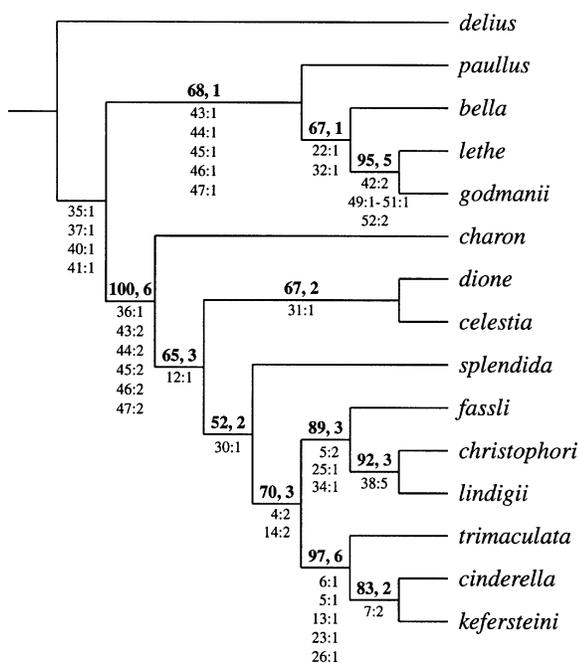
In the analysis of external characters only, four minimum length cladograms of 67 steps were generated (CI=0.66, RI=0.83). The strict consensus cladogram contains much of the structure evident in the most parsimonious cladogram derived from analysis of all characters, but did not support *paullus/bellalethe/godmanii* as a monophyletic group, with relationships between these four species unresolved at the base of the cladogram. The analysis of internal characters alone generated 1411 most parsimonious cladograms of length 32 steps (CI=0.91, RI=0.92). The strict consensus cladogram is completely unresolved with the exception of *godmanii* and *lethe* appearing as sister species.

#### Value of different character suites

Although strict consensus cladograms generated from each character suite do not contradict each other, it is clear that, although more homoplasious, *Hypanartia* wing pattern characters provide a great deal more phylogenetic information than internal morphology. Whether this information is reliable or not can only be ascertained through independent tests of the phylogenetic hypothesis; at least a hypothesis that is explicit is much more readily tested than one that is conservative and contains very little information (Miller *et al.*, 1997). It is also of interest that, whereas relationships among the more plesiomorphic species of the *paullus* group were unresolved when external characters alone were considered, only two changes in cladogram structure occurred in the more derived *dione* group, both involving the collapse of a node to produce a trichotomy. It therefore appears, as one might expect, that the intrinsic relatively high homoplasy of wing pattern characters is not only responsible for their relatively poor performance in resolving deep nodes, but is also responsible for their value in resolving relationships among closely related, more recently evolved taxa. With careful analysis of homologies, wing pattern characters may therefore be a very useful tool in any phylogenetic study of species-level taxa, even in genera where wing patterns have apparently been subjected to heavy selection for mimicry (Willmott, 2001).

#### Generic relationships and implications for other nymphaline genera

In the analysis including all three outgroups, *Antanartia delius* grouped with *Vanessa cardui* rather than *Hypanartia* as suggested by earlier authors. In fact, because Howarth (1966)



**Fig. 2.** The single most parsimonious cladogram generated for *Hypanartia*. Bootstrap values (left) and Bremer support indices (right) are given above branches, universal synapomorphies below branches.

defined genus *Antanartia* in comparison with *Hypanartia*, and most, if not all, of his defining character states are also present in *Vanessa*, the monophyly of both *Antanartia* or *Vanessa*, with respect to one another, may be open to question. More extensive phylogenetic analysis of the entire tribe is necessary before any firm conclusions may be drawn as to the true sister group of *Hypanartia*.

## Review of *Hypanartia*

*Hypanartia* Hübner, [1821]

*Hypanartia* Hübner, [1821]: Pl. [26]. Type species by monotypy: *Hypanartia demonica* Hübner, [1821].

*Eurema* Doubleday, [1845]: 83. Type species by selection of Hemming (1933: 223): *Papilio lethe* Fabricius, 1793: 80.

## History of classification

Hübner (1821) introduced genus *Hypanartia* for a single South American species, but all immediately subsequent authors ignored this name and described additional Neotropical species under the generic synonym *Eurema* Doubleday, [1845] (also a junior homonym of *Eurema* Hübner, [1819]). Rothschild & Jordan (1903b) later erected genus *Antanartia* to include several African species that had been ascribed to *Hypanartia* (Howarth, 1966; Ackery *et al.*, 1995), noting that *Hypanartia* was distinct in a number of male genitalic and abdominal characters, most notably the presence of a modified, heavily sclerotized 8th tergite (Figs 9–23), termed the superuncus by Kuznetsov (1915). Nevertheless, lingering doubts have still remained in the literature as to whether the two genera are distinct (Seitz, 1914; DeVries, 1987; Larsen, 1991). In fact, although the two genera share superficially similar wing patterns, the male genitalia of *Hypanartia* are rather homogeneous and very distinct from those of *Antanartia* species (all of which are illustrated by Howarth, 1966), which differ relatively little from other nymphalines we have dissected (see Methods, *Phylogenetic analysis*). Substantial anagenesis is evident in the male genitalic morphology of *Hypanartia*, masking its relationships within Nymphalini (*sensu* Harvey, 1991), and perhaps indicating that a relatively long period of time has elapsed since divergence from remaining nymphalines. Modern day distributions suggest that Nymphalini may be an ancient lineage, because its representative genera are widely distributed throughout the world in both temperate and tropical habitats, in contrast to a number of other diverse butterfly subfamilies (Heppner, 1991). The fossil butterfly *Prodryas persephone* Scudder, described by Scudder (1878) from the Oligocene Florissant shale beds in Colorado (Emmel *et al.*, 1992), differs little in wing pattern from modern members of *Hypanartia*, as noted by Brown & Heineman (1972). In fact, it is perhaps even more similar to extant species of *Antanartia*.

The only general treatments of *Hypanartia* are those of Seitz (1914) and d'Abrera (1987), where eight and ten species, respectively, were recognized, although the latter number

includes the recognition of *H. dione arcae* (Salvin) as a distinct species. A synonymic checklist for the genus, which includes fourteen species and seventeen taxa, is given in Table 1.

## Biology

*Hypanartia* species occur in a wide range of habitat, from primary forest to secondary growth and extensive areas of scrub, but the two main lineages within the genus exhibit different habitat preferences. Members of the *paullus* group typically occur in areas with extensive secondary growth, dry forest or along forest edges, whereas members of the *dione* group occur in more intact, humid forest habitats.

Males are generally more commonly encountered than females, particularly in the *dione* group, and are usually observed flying rapidly about roadsides, paths and rivers, stopping frequently to 'puddle'. Puddling behaviour involves the uptake of minerals through feeding at damp sand or mud, which provides males with sodium ions (Arms *et al.*, 1974), among other possible nutrients, which are important in reproduction (Dunlap-Pianka *et al.*, 1977; Boggs & Gilbert, 1979; Pivnick & McNeil, 1987; Boggs, 1990, 1995; Lederhouse *et al.*, 1990). Males are also attracted to dung and carrion, which probably provide similar nutrients to rotting fish (Downes, 1973; Hall & Willmott, 2000), and rotting fruits, which presumably provide carbohydrates. Both sexes occasionally nectar at a wide variety of flowers, especially those in the Asteraceae (DeVries, 1987; Schwartz, 1989). Solitary males are often encountered 'perching', a specific behaviour adapted for mate location, consisting of waiting at particular

**Table 1.** Synonymic checklist for *Hypanartia* Hübner, [1821]. '–' denotes a subspecies and '– –' a synonym

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<i>bella</i> (Fabricius, 1793)
– – <i>zabulina</i> (Godart, 1819)
– – <i>montana</i> Köhler, 1923
<i>celestia</i> Lamas, Willmott & Hall, sp.n.
<i>charon</i> (Hewitson, 1878)
<i>christophori</i> Jasiński, 1998
<i>cinderella</i> Lamas, Willmott & Hall, sp.n.
<i>dione</i> (Latreille, [1813])
– <i>arcae</i> (Salvin, 1871), stat.n.
– <i>disjuncta</i> Willmott, Hall & Lamas, ssp.n.
<i>fassli</i> Willmott, Hall & Lamas, sp.n.
<i>godmanii</i> (H. Bates, 1864)
– – <i>atropos</i> (C. & R. Felder, 1867)
<i>kefersteini</i> (Doubleday, [1847])
<i>lethe</i> (Fabricius, 1793)
– – <i>demonica</i> Hübner, [1821], stat.rev.
<i>lindigii</i> (C. & R. Felder, 1862)
<i>paullus</i> (Fabricius, 1793)
– – <i>tecmesia</i> Hübner, [1823]
<i>splendida</i> Rothschild, 1903
<i>trimaculata</i> Willmott, Hall & Lamas, sp.n.
– <i>autumna</i> Willmott, Hall & Lamas, ssp.n.

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topographic sites that are frequented by females (Scott, 1973, 1976). Such sites include large clearings or forest edges (in the case of *H. paullus* and *H. lethe*), more enclosed forest light gaps (in members of the *kefersteini* clade) or open highland vegetation (more primitive *dione* group members), particularly on ridgetops, and these areas are vigorously patrolled and defended against intruding males (Seitz, 1914; Schwartz, 1989; Smith *et al.*, 1994).

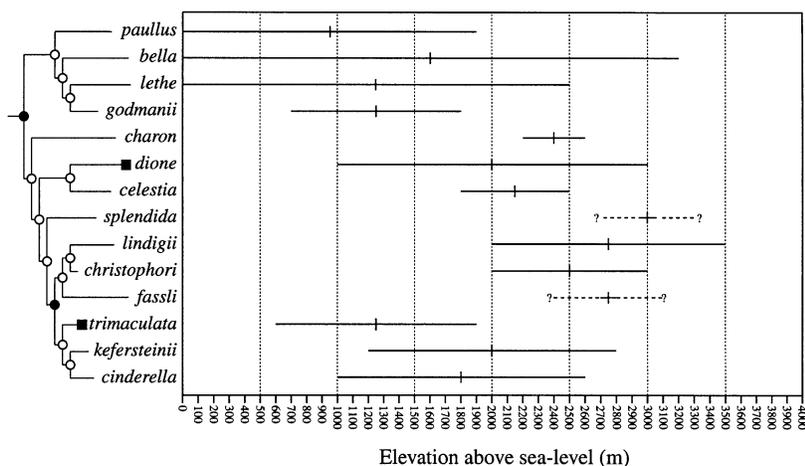
As is typical for Nymphalini, the majority of recorded foodplants for *Hypanartia* are among Urticaceae and Ulmaceae, but there is also a single report of Piperaceae (Alayo & Hernández, 1987). The white eggs are laid singly, the mature larvae are variable in colour and spiny, and the pupae are pale green with reflective silver markings (Seitz, 1914; Wolcott, 1924; Young, 1976; DeVries, 1987). The larvae are similar to those in *Vanessa* and *Anartia* Hübner, and sew hostplant leaves together with silk to make shelters in which they rest and even pupate (Seitz, 1914; DeVries, 1987).

### Biogeography

*Hypanartia* extends from the southern U.S.A. (Texas) and the Greater Antilles to northern Argentina, Paraguay and southeastern Brazil, encompassing the entire Neotropical Region. However, it is predominantly a montane genus, reaching its peak diversity in the Andean countries of Ecuador and Peru, which each harbour ten recorded (potentially twelve) species. Although three species occur at sea level, the majority are found from 1000 to 3500 m (Fig. 3), and regional species richness peaks from 2200 to 2500 m. Altitudinal records are based on many years of field work in Ecuador (K.R.W., J.P.W.H.) and Peru (G.L.), reliable museum specimen locality data and literature.

Although the evolution of the montane biota in the Neotropics has received some attention (e.g. Vuilleumier & Monasterio, 1986), there have been relatively few attempts to explicitly test biogeographic theories with species-level phylogenetic hypotheses (Lynch, 1986; Patton & Smith, 1992; Arctander & Fjeldså, 1994; Bates & Zink, 1994; García-Moreno *et al.*, 1998), and none, to our knowledge, for butterflies. This is probably due to the scarcity of species-level phylogenetic hypotheses for groups that occur in both lowland and montane habitats, for which there are accurate elevational data, and most studies have tended to be faunistic or floristic (e.g. Vuilleumier, 1986), or concentrate on higher level evolutionary patterns (e.g. Bleiweiss, 1998a,b). Lynch (1986) proposed two general scenarios for the evolution of montane species: speciation into an existing montane region with elevationally stable vegetation zones (static), and speciation contemporaneous with orogenic events (dynamic), influenced subsequently by elevationally fluctuating vegetation zones. We know little about the origins of *Hypanartia*, but it seems equally likely that they could be either allochthonous or autochthonous members of the South American fauna, and thus both of Lynch's scenarios could apply in terms of their evolution within the Andes. Nevertheless, there is substantial evidence for fluctuations in vegetation levels in the Andes (Van der Hammen, 1974; Hooghiemstra & Van der Hammen, 1998) and elements of the dynamic model are certain to be relevant. Under the dynamic model, at least four principal mechanisms of speciation are possible, and the well resolved phylogeny for *Hypanartia* presents a good opportunity to test the predictions and relative importance of each of these mechanisms.

Chapman (1917) proposed that Andean bird species were derived from three main sources: colonization from temperate latitudes with a similar climate to a given elevational zone, speciation from a neighbouring lower elevation species or

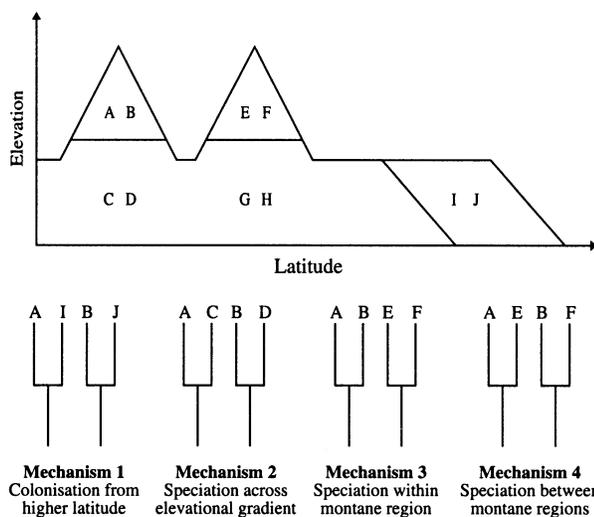


**Fig. 3.** Elevational ranges for *Hypanartia* species. On cladogram at left, ○ indicate a node where speciation has not been accompanied by a significant change in elevational range, ● indicate a node where speciation has been accompanied by a significant change in elevational range, and ■ indicate differentiation between isolated montane regions.

colonization from some other montane region (Fig. 4). He noted that a large number of montane species in Costa Rica and western Panama were closely related to Andean species, despite being isolated by wide expanses of lowland forest, and postulated the existence of former mountain chains connecting these areas and allowing faunal interchange, which must have subsequently subsided or been eroded away. Modern geological knowledge refutes the existence of these mountain 'bridges', but recent Pleistocene climatic fluctuations caused substantial changes in the elevational levels of vegetational zones, forming periodic connections between currently isolated montane forests (Van der Hammen, 1974; Hooghiemstra & Van der Hammen, 1998). Montane species in isolated regions may therefore be the result of expansion of a single species during a cool climatic period, followed by subsequent fragmentation leading to allopatric speciation. This mechanism was used by Adams (1985) to explain elevational patterns of related species in pronophiline satyrine butterflies in isolated Colombian cordilleras, and was proposed by Lynch (1986) as an important recent multiplier of species richness for Neotropical montane herpetofaunas.

Chapman (1917) also suggested that since higher elevations had been in existence for a shorter period of time than lower elevations, they would contain a larger proportion of species derived from temperate faunas of higher latitudes, an implicitly dynamic hypothesis. It also seems probable that once established within a montane zone, a colonizing species would experience an entirely novel habitat, presenting a potentially suitable situation for adaptive radiation, and thus providing a fourth possible mechanism for the origin of montane species.

These four mechanisms all produce different hypotheses about the phylogeographic relationships of species and species groups within a genus. Figure 4 illustrates a hypothetical genus comprised of ten species, A–J, of which four occur in two



**Fig. 4.** Geographic mechanisms of speciation in montane regions and predicted resultant phylogenetic relationships between sister taxa.

isolated montane areas (A,B,E,F), four occur in lowland areas adjacent to the mountains (C,D,G,H) and two occur at higher latitudes in lowland but temperate habitats (I,J). Making the major assumption that the current range of a species accurately reflects its area of origin (an assumption in most biogeographic analyses), we can derive a different set of sister-taxa relationships for each mechanism (Fig. 4).

There appears to be little evidence in *Hypanartia* for mechanism 1, colonization from temperate latitudes. Nevertheless, two of the more plesiomorphic species in the genus, *H. paullus* and *H. bella*, occur in peripheral areas of the Neotropics, down to sea level. If the mechanism was important in initial speciation in montane *Hypanartia*, its distributional signal has been obscured by extensive dispersal and extinction. Higher elevation Andean butterfly (Descimon, 1986), bird (Chapman, 1917; Vuilleumier, 1986; Bleiweiss, 1998b) and herpetological faunas (Lynch, 1986) all show evidence for colonization from higher latitudes.

There are significant differences in mean median altitudes (Fig. 3) between the two major lineages within *Hypanartia*: the *paullus* group occurs at a mean median altitude (MMA) of 1250 m, whereas members of the *dione* group occur at a MMA of 2250 m (Mann–Whitney *U*-test,  $P < 0.01$ ). Within the *dione* group, there is also a notable difference in the altitudinal ranges of the sister clades containing *H. kefersteini*, *H. trimaculata* and *H. cinderella*, and *H. lindigii*, *H. fassli* and *H. christophori*, the former clade being typical of lower montane forests at a MMA of 1700 m, the latter occurring in the uppermost montane forests at a MMA of 2650 m (Fig. 3). These elevational differences between sister clades fulfil the predictions of mechanism 2, speciation across an elevational gradient. However, in the absence of an additional basal member of the genus outside of the two principal clades, and with no certain knowledge of the sister taxon to *Hypanartia*, it is not possible to distinguish whether speciation occurred from lowland to montane habitats, or *vice versa*. Interestingly, the more primitive members of the *dione* group occur at higher elevations (e.g. *H. charon*, *H. celestia* and *H. splendida*), and the ancestor of the lower montane members of the *kefersteini/trimaculata/cinderella* clade, appears to have speciated from higher into lower elevations, a local reversal of Chapman's (1917) hypothesized direction of elevational speciation. García-Moreno *et al.* (1998) found a remarkably similar sequence of events in the evolution of a group of fourteen Andean bird species (chat-tyrants): sister groups to the chat-tyrants are lowland species characteristic of more open habitats (as is the *paullus* clade), the next most derived group occurs predominantly in open highland areas or elfin forest habitats (similar to several members of the *dione* group, such as *H. dione* and *H. lindigii*), and the most derived clade occurs in dense, humid, premontane rain and cloud forests (as in the *kefersteini* clade). Bates & Zink (1994) also tested Chapman's vertical speciation mechanism by deriving a cladogram for the four species of the Andean bird genus *Leptopogon*, whose members occur in three elevational zones, with the upper zone containing two allopatric species. They found that successively more derived species occurred at higher elevations, with the upper allopatric pair being sister species, and concluded that

speciation had occurred into successively higher elevations. However, the small number of taxa they sampled provides no support for directions of speciation, and their hypothesis is equally consistent with speciation from high to middle elevations (prior to allopatric divergence in the higher elevation pair). Nevertheless, the pattern of speciation exhibited by chat-tyrants, and possibly *Hypanartia*, may be rather unusual, and may be more dependent on the ecology of ancestral species. García-Moreno *et al.* (1998) hypothesized that a preference for open habitats in ancestral chat-tyrants predisposed them to invade open highland areas first, and this hypothesis could certainly also apply to *Hypanartia*.

In *Hypanartia*, there is no evidence of recent speciation across elevational gradients: no sister species occur in elevational parapatry or at significantly different elevations. Both Patton & Smith (1992) and Arctander & Fjeldså (1994) also found no evidence for sister-group relationships between elevationally parapatric Andean mice populations and tapaculo bird species, respectively. Instead, horizontally adjacent populations in the same elevational zone were sister taxa, fulfilling the predictions of mechanism 3, with para/allopatric differentiation. Nevertheless, both admitted that this did not rule out an initial speciation event across an elevational gradient.

*Hypanartia* species richness is disproportionately high in the Andean mountain chain, with only two species extending into montane regions outside the Andes (*H. dione* and *H. trimaculata*). It therefore seems highly probable that the *dione* group has speciated entirely within the Andes, and as eight of the nine nodes within this group are associated with little notable change in elevational range between resultant sister taxa (Fig. 3), there is strong support for mechanism 3. Speciation within a single montane region could occur in sympatry, parapatry or allopatry. Each of these three processes produces different patterns of distribution between species: sympatry would be supported by the range of one species being entirely contained within that of another, and para- or allopatry by closely abutting or widely separated range limits. Only the range of *H. celestia* is entirely contained within that of its sister species, *H. dione*, but the numerous phenotypic differences between these species suggest that substantial time has elapsed since their speciation, during which time significant range expansion or contraction could have taken place. Remaining species are typically broadly sympatric with their sister taxa, and the mode of speciation is unclear. Lynch (1986) concluded that *in situ* speciation in the Andean herpetofauna had been substantial, with approximately 80% of species being most closely related to other Andean species.

No montane species of *Hypanartia* occurs exclusively outside the Andean region, suggesting that mechanism 4 has had little influence on the species diversity of the genus. However, two species, *H. dione* and *H. trimaculata*, have phenotypically differentiated populations in isolated montane regions of Central America. It thus seems that expansion and fragmentation of montane ranges, abetted by cooler past climatic periods, has had an effect only at the subspecific level in *Hypanartia*. Van der Hammen (1974) concluded that vegetation zones in the northern Andes may have been up to

1200–1500 m lower in past glacial periods, and it may be significant that no *Hypanartia* with a lower range limit of more than 1200 m occurs in more than one isolated montane region. *Hypanartia trimaculata* occurs at the lowest elevations of any species in the *dione* group, as low as 600 m, and it is perhaps not surprising that it has colonized several isolated montane areas. Similarly, *H. dione* also has one of the lowest elevational ranges of the *dione* group, although both *H. kefersteini* and *H. cinderella* do not occur substantially higher. An additional factor may be that *H. dione*, a more primitive species, has had longer and therefore a higher chance to colonize adjacent montane areas. In the nymphalid butterfly genus *Adelpha*, the only upper montane clade to occur in several montane regions is also one of the most primitive in the genus (Willmott, 2000).

In conclusion, the distributional patterns and phylogenetic hypothesis for *Hypanartia* presented here offer support for three possible geographical mechanisms of differentiation between montane faunas. Perhaps of greatest interest are the relative frequencies and possible evolutionary sequence of the three mechanisms. Invasion and speciation into a different elevational zone has apparently occurred twice, in both cases into an elevational zone that was formerly largely unoccupied by other members of the genus, and most notably early in the evolution of the genus. However, the most phenotypically similar (and therefore probably most recently derived) species are elevationally sympatric and appear to have speciated within a single montane region, a pattern suggestive of adaptive radiation and representing the most common mechanism. Fragmentation of populations through climatic fluctuations has probably been of recent influence only, and has only produced differentiation at the subspecific level.

In *Adelpha*, speciation across elevational gradients also seems to largely precede differentiation within or between montane regions. In pairs of closely related lowland/montane species or clades, the montane species/clade is almost always widely distributed throughout several isolated montane regions and has undergone subsequent subspecific or specific differentiation within a single elevational zone (Willmott, 2000). Speciation within an elevational zone also seems to dominate that between zones in other taxa (e.g. Lynch, 1986; Roy, 1997). Bleiweiss (1998b) found that approximately six major lineages of hummingbirds had colonized the Andes from the lowlands, producing around 130 species. Speciation across an elevational gradient thus appears to be relatively difficult and may happen only infrequently, and is more typical of the early evolutionary history of a clade. In addition, other workers have concluded that the large eco-climatic fluctuations of the Pleistocene (Hooghiemstra & Van der Hammen, 1998) have had less influence on modern day species diversity than previously supposed (Klicka & Zink, 1997; Bleiweiss, 1998a; García-Moreno *et al.*, 1998; but see Roy, 1997), and that many species and genera may date back to the Mio-Pliocene. There are thus broad areas of agreement between evolution in montane *Hypanartia* and other groups, and investigating whether these sequences of mechanism dominance are a general pattern in additional taxa would be of great evolutionary interest.

Key to the species of *Hypanartia*

1. Dorsal hindwing predominantly orange-brown or red-brown ..... 4  
 – Dorsal hindwing shades of plain brown ..... 2
- 2(1). Dorsal forewing with white/transparent spot in cell Cu2-Cu1 ..... 3  
 – Dorsal forewing without white/transparent spot in cell Cu2-Cu1 ..... *charon*
- 3(2). Dorsal forewing with spot in cell Cu2-Cu1 small and narrow, cells 2 A-Cu2 and Cu1-M3 without white spots ..... *dione*  
 – Dorsal forewing with spot in cell Cu2-Cu1 very large and round, cells 2 A-Cu2 and Cu1-M3 with additional postdiscal white spots ..... *celestia*
- 4(1). Dorsal hindwing predominantly red-brown ..... 9  
 – Dorsal hindwing predominantly orange-brown ..... 5
- 5(4). Dorsal forewing without transparent spot in cell Cu2-Cu1 ..... 6  
 – Dorsal forewing with transparent spot in cell Cu2-Cu1 ..... *splendida*
- 6(5). Dorsal forewing with white or orange marks in postdiscal area ..... 7  
 – Dorsal forewing with postdiscal area entirely black...  
 ..... *godmanii*
- 7(6). Dorsal forewing with orange discal band separated from orange-brown basal area by black band, hindwing tail at vein M3 short and triangular ..... 8  
 – Dorsal forewing with basal half almost entirely orange, hindwing tail at vein M3 long, thin and pointed *paullus*
- 8(7). Dorsal forewing with postdiscal and subapical markings orange, orange discal band extending almost to distal margin in cell Cu2-Cu1, forewing distal margin mildly concave ..... *lethe*  
 – Dorsal forewing with postdiscal and subapical markings white, orange discal band only in basal half of cell Cu2-Cu1, forewing distal margin strongly concave ..... *bella*
- 9(4). Dorsal forewing with 2 or 3 black markings surrounded by orange in discal cell, red-brown at tornus extending into cell 2 A-Cu2 or Cu2-Cu1 ..... 12  
 – Dorsal forewing with a single black bar extending right across discal cell, red-brown at tornus extending into cell Cu1-M3 ..... 10
- 10(9). Ventral hindwing with dark postdiscal line (element f; Fig. 1) approximately straight ..... 11  
 – Ventral hindwing with dark postdiscal line (element f; Fig. 1) markedly disjointed at vein M3 ..... *fassli*
- 11(10). Ventral hindwing with thick dark brown scaling proximal to inner submarginal ocelli in cells Cu2-Cu1 and Cu1-M3 (element g present; Fig. 1), dorsal forewing with relatively broad transparent spot in cell Cu2-Cu1 ..... *lindigii*  
 – Ventral hindwing with no dark brown scaling proximal to inner submarginal ocelli in cells Cu2-Cu1 and Cu1-M3 (element g absent; Fig. 1), dorsal forewing with relatively thin transparent spot in cell Cu2-Cu1 .....  
 ..... *christophori*
- 12(9). Dorsal forewing with 2 relatively small white postdiscal spots in cells M3-M2 to M1-R5, that in cell M3-M2 reduced or absent, and no purplish shading proximal to inner submarginal ocelli (border ocelli, element h; Fig. 1) on ventral hindwing ..... 13  
 – Dorsal forewing with 3 large white postdiscal spots in cells M3-M2 to M1-R5 surrounded by blue scaling (not in Venezuelan specimens) or purplish shading, or both, proximal to inner submarginal ocelli (border ocelli, element h; Fig. 1) on ventral hindwing (not in Central American specimens) ..... *trimaculata*
- 13(12). Ventral hindwing with dark brown postdiscal line (element f; Fig. 1) in cell 2 A-Cu2 approximately straight, distal edge of forewing white postdiscal spot in cell Cu2-Cu1 slightly concave, hindwing tail at vein M3 relatively short ..... *cinderella*  
 – Ventral hindwing with dark brown postdiscal line (element f; Fig. 1) in cell 2 A-Cu2 sharply kinked at middle, distal edge of forewing white postdiscal spot in cell Cu2-Cu1 straight, hindwing tail at vein M3 relatively long ..... *kefersteini*

***paullus* group*****Hypanartia paullus* (Fabricius, 1793)** (Figs 5A; 9A–C)

*Papilio paullus* Fabricius, 1793: 63. Type locality: Jamaica. Types unknown.

*Hypanartia tecmesia* Hübner, [1823]: Pl. [27]. Type locality: not stated. Types probably lost.

*Identification and taxonomy.* Typical FW length 29 mm ('typical' forewing lengths are intended as an indication of size only, to assist in identification, and do not represent mean values). *Hypanartia paullus* has a straighter and better defined postdiscal line on the ventral hindwing compared to other *paullus* group species, and is readily distinguished from all other *Hypanartia* by having two pointed hindwing tails.

Wetherbee (1991b) considered that the female specimen of *paullus* (wrongly emended by him to '*paulla*') illustrated by Daubenton (1765) as 'le souchet de St. Domingue' could have been used as the basis for Fabricius's description of the species, and regarded Daubenton's specimen as 'lectotypic.' However, Fabricius explicitly refers his description to a specimen (or specimens) from Jamaica, belonging to William Jones, and illustrated by the latter in Plate 78, Fig. 2, of volume 5 of his unpublished 'Icones' (Waterhouse, 1938). Examination of Plate 78 of Jones' 'Icones' reveals that a male (not a female) specimen is depicted there, and that specimen (which might still be extant in the Macleay Museum at the University of Sydney, Australia) should be regarded as a syntype of *paullus*. Thus, Wetherbee was wrong in assuming that '...Jones copied the same figure of Daubenton that Fabricius had in front of him in 1775' and that the type locality of *paullus* is Haiti. The syntypes of *tecmesia* came probably from Cuba and appear to be lost.

**Biology.** The ecology of *H. paullus* is the best known of any species in the genus, and extensive biological notes are given by Riley (1975), Schwartz (1989), Smith *et al.* (1994), Wetherbee (1991a) and Wetherbee & Schwartz (1996). It occurs in a wide variety of wooded habitats from sea level to 1900 m but is most common in the upper portion of this elevational range. It is most frequently encountered perching along the forest edge on the tops of leaves with its wings half open or nectaring on a variety of flowers, including *Eupatorium*, *Daucus*, *Palicourea*, *Tournefortia*, *Urera*, *Senecio* and *Canna*. It appears to be present throughout the year but is most abundant between June and August (Schwartz, 1989; Smith *et al.*, 1994). Wolcott (1924) reared *H. paullus* on *Trema micrantha* (Ulmaceae) in Puerto Rico, describing the larva and pupa, and Alayo & Hernández (1987) report rearing it on *Piper* (Piperaceae) in Cuba. Torres (1992) reports defoliation of *Trema* by *H. paullus* larvae during successional changes caused by hurricane damage.

**Distribution.** Greater Antilles (Cuba, Jamaica, Hispaniola, Puerto Rico).

#### ***Hypanartia bella* (Fabricius, 1793)** (Figs 5B; 10A–E)

*Papilio bella* Fabricius, 1793: 79. Type locality: 'Indiis'. Types unknown.

*Vanessa zabolina* Godart, 1819, in Latreille & Godart, 1819: 301. Type locality: Brazil. Lectotype ♂ (here designated by G.L.), MNHN (examined).

*Hypanartia bella* f. *montana* Köhler, 1923: 23, Pl. 2, Fig. 11. Type locality: Argentina, Córdoba, Sierra de Córdoba. Lectotype ♂ (here designated by G.L.), MLP (examined).

**Identification and taxonomy.** Typical FW length 26 mm. *Hypanartia bella* is most similar to *H. lethe* but has a more produced forewing apex, more pronouncedly scalloped distal wing margins, a more diagonal orange discal band on the dorsal forewing, largely white instead of orange subapical markings on the dorsal forewing that are reduced in number, and a different, darker ventral pattern. Peruvian specimens have a somewhat wider orange discal band on the dorsal forewing, and the postdiscal band is largely orange (it is largely white in southeastern Brazilian specimens), except the spot in cell M2-M1, which is white in both populations. However, the geographical variation in *H. bella* appears to be rather variable and clinal, and no subspecies are recognized here.

The lectotype of *zabolina* bears the following labels: 'Brésil/Delalande', 'Eurema/zabolina, God.', 'MUSEUM PARIS/Bresil/Delalande' and 'SYN-/TYPE'. One possible syntype of *zabolina* has been mentioned by Grimshaw (1897) as being

found in the RSM. The lectotype of *montana* bears the following labels: 'REP. ARGENTINA/A. BREYER', 'Tipus', '3168', 'f. Montana Khlr./type' and 'LECTOTYPUS male/G. Lamas des. '92'.

**Biology.** This species occurs up to 3200 m in southeastern Peru (Ayacucho, Apurímac and Cuzco, being very common at Machu Picchu), along the margins of cloud and montane forests. Males frequently puddle at damp mud, and the species also nectars on flowers of Asteraceae. The food plant of *H. bella* is reported as *Celtis* (Ulmaceae) by Biezanko (1949) and as *Trema* (Ulmaceae) and *Urtica* (Urticaceae) by Hayward (1969). Toledo (1973) reared the species on *Phenax* and *Parietaria* (Urticaceae) in northwestern Argentina, and gave an almost complete life history (no eggs were found).

**Distribution.** Southern Peru to northern Argentina, Brazil (eastern and southeastern), Uruguay and Paraguay.

#### ***Hypanartia lethe* (Fabricius, 1793)** (Figs 5C; 11A–E)

*Papilio lethe* Fabricius, 1793: 80. Type locality: 'Indiis'. Types unknown.

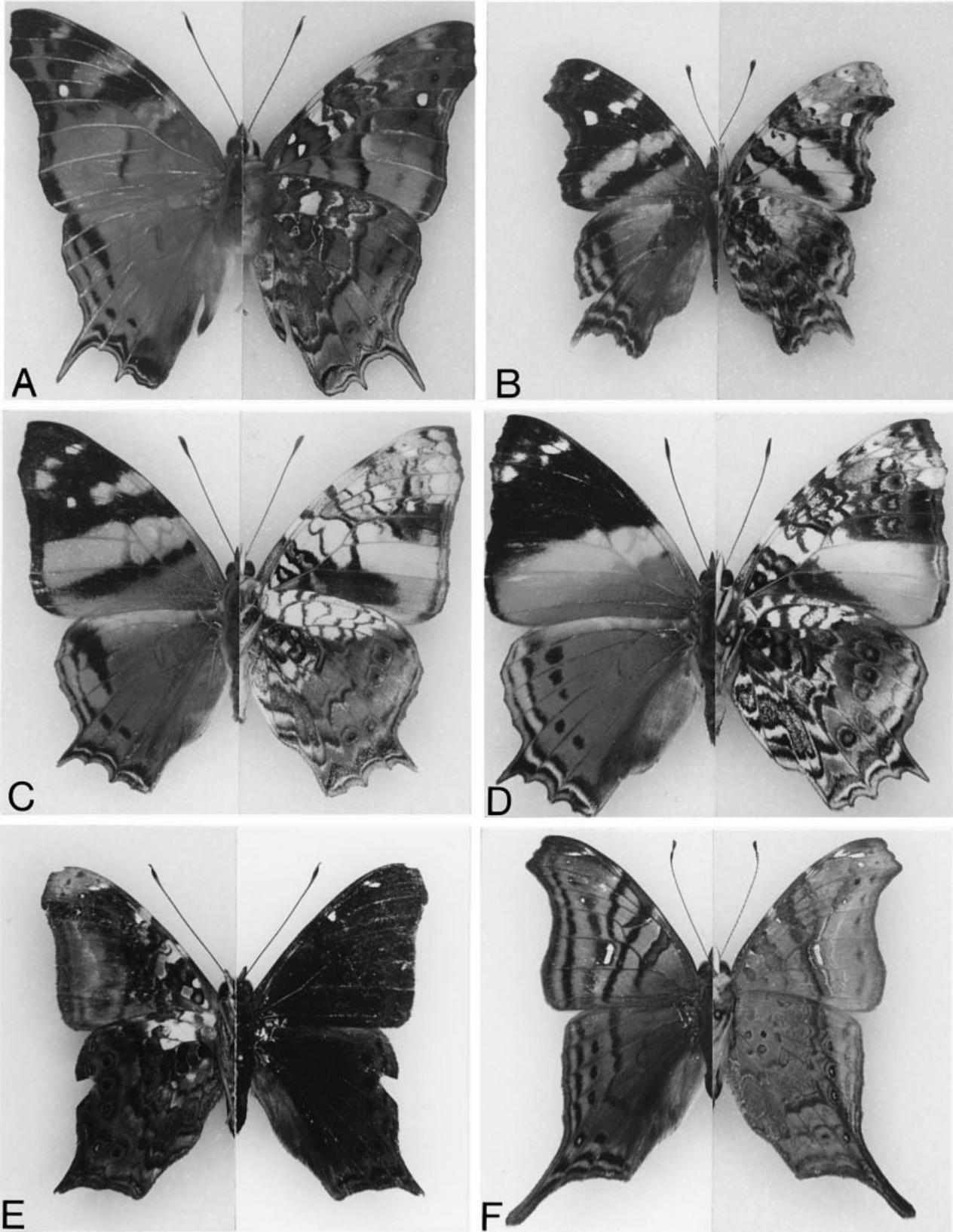
*Hypanartia demonica* Hübner, [1821]: Pl. [26]. Type locality: Brazil. Lectotype ♂ (designated by Hemming, 1964), probably lost. Stat.rev.

**Identification and taxonomy.** Typical FW length 28 mm. The wing pattern of *H. lethe* most closely resembles *H. bella*, but the male genitalia show it unequivocally to be the sister species of *H. godmanii*. It is distinguished from each of these species in their respective accounts.

West (1996) stated that *H. lethe* showed evidence of subspeciation, and resurrected Hübner's name *demonica* to represent the populations found throughout eastern Brazil, south to northeastern Argentina. However, Fabricius' specimen of *H. lethe* probably came from southeastern Brazil, as Jones' illustration of it clearly shows the 'white posterior spot on the forewing subapical fascia' mentioned by West as diagnostic of the southern population, and it is thus identical to the lectotype of *demonica* (based by Hemming solely on Hübner's illustration). The types of *lethe* might be found in the Macleay Museum, Sydney, but the lectotype of *demonica* is probably lost. Although it is true that specimens of *H. lethe* from southeastern Brazil typically differ from specimens from elsewhere in the range in being smaller, having a paler ventral surface and the white spot on the dorsal forewing, all of these characters are slight and variable, and show extensive clinal variation through northern Argentina, Paraguay and Mato Grosso, Brazil. We therefore do not believe that such populations deserve subspecific recognition.

The few known specimens of *H. lethe* from the Venezuelan tepui region, almost certainly geographically isolated from

**Fig. 5.** Wings of males (dorsal surface on left; ventral surface on right, except E where reversed). A, *Hypanartia paullus*, Jarabacoa, Jamaica (FSCA); B, *H. bella*, Joinville, Brazil (SC) (FSCA); C, *H. lethe*, Salto de Napac, western Ecuador (KWJH); D, *H. godmanii*, Salto de Napac, western Ecuador (KWJH); E, *H. charon*, Tulcán-La Bonita Rd, eastern Ecuador (KWJH); F, *H. dione dione*, Río Machay, eastern Ecuador (KWJH).



remaining *H. lethe* populations, differ from Andean *H. lethe* on the dorsal forewing in having more extensive orange in the basal half and a reduced orange subapical spot in cell M2-M1, with that in cell M1-R5 absent. Whether this population merits subspecific status is under investigation by A. Neild (personal communication).

**Biology.** This species is very common in a wide variety of habitats, ranging from wet primary forest to semi-deciduous dry forest, but is most typical of disturbed secondary growth habitats. It is most abundant from sea level to 2000 m, but rarely may occur as high as 2500 m. Both sexes are attracted to rotting fruits and weedy flowers, and males also puddle. Males perch on secondary growth vegetation 1–2 m above the ground in large clearings and along forest edges. Recorded foodplants for *H. lethe* include *Boehmeria* (Müller, 1886), *Phenax* (DeVries, 1986) (both Urticaceae), *Sponia* (d'Almeida, 1922), *Celtis* (Biezanko, 1949) and *Trema micrantha* (Janzen, in DeVries, 1986) (all Ulmaceae). DeVries (1987) describes the egg, larva and pupa.

**Distribution.** Southern U.S.A. (Texas) to northwestern Peru, Venezuela (Andes and tepui region; A. Neild, personal communication) to northern Argentina, Paraguay, Uruguay, Brazil (southern and southeastern) and Trinidad.

#### ***Hypanartia godmanii* (H. Bates, 1864)** (Figs 5D; 12A–C)

*Eurema godmanii* H. Bates, 1864: 85. Type locality: Guatemala, central valleys. Lectotype ♂ (here designated by G.L.), BMNH (examined).

*Eurema atropos* C. & R. Felder, 1867: 397, Pl. 51, Figs 5, 6. Type locality: Mexico. Lectotype ♂ (here designated by G.L.), BMNH (examined).

**Identification and taxonomy.** Typical FW length 30 mm. This species is most closely related to *H. lethe*, as evidenced by several shared characters in the male genitalia, including a broad and angular tip to the uncus, a long, straight aedeagus with small lateral projections from the posterior tip, and a weakly sclerotized juxta that is densely setose. *Hypanartia godmanii* is easily distinguished from *H. lethe* on the dorsal forewing by having the orange discal band fused with the basal orange-brown area, by lacking a yellow postdiscal mark and by having white instead of yellow subapical spots.

The lectotype of *godmanii* bears the following labels: 'Centr. Valleys./Guatemala/F.D.G. & O.S.', 'Guatemala/interior', 'B.C.A. Lep. Rhop./Eurema/godmanii./Bates/Godman-Salvin/Coll. 1915:3.', 'Type/H.T.', 'SYN-/TYPE', 'male', 'SYNTYPE/Eurema/godmanii/Bates./det. S. M. North. 1984.' and 'B.M. TYPE/No.Rh8643/Eurema/godmanii/Bates'. The lectotype of *atropos* bears the following

labels: 'Mexico/Sallé', 'Atropos n.', 'FELDER/COLLn.' and 'SYN-/TYPE'.

**Biology.** In Central America, this species occurs in cloud forest habitats from 900 to 1800 m (DeVries, 1987) where, judging from material in collections, it is not uncommon. In the Andes, however, the species is local and very uncommon, especially on the eastern slope where only two *bona fide* records are known to the authors, from southern Colombia (Salazar, 1995) and extreme northern Ecuador (Willmott & Hall, unpublished data). In Ecuador, the species has been recorded from 700 to 1200 m. Both sexes are encountered as solitary individuals along rivers and forest edges, and males 'puddle' at wet sand.

**Distribution.** Mexico to western Ecuador, Venezuela to northeastern Ecuador.

#### ***dione* group**

#### ***Hypanartia charon* (Hewitson, 1878)** (Figs 5E; 13A–D)

*Eurema charon* Hewitson, 1878: 151. Type locality: Ecuador. Lectotype ♂ (here designated by G.L.), BMNH (examined).

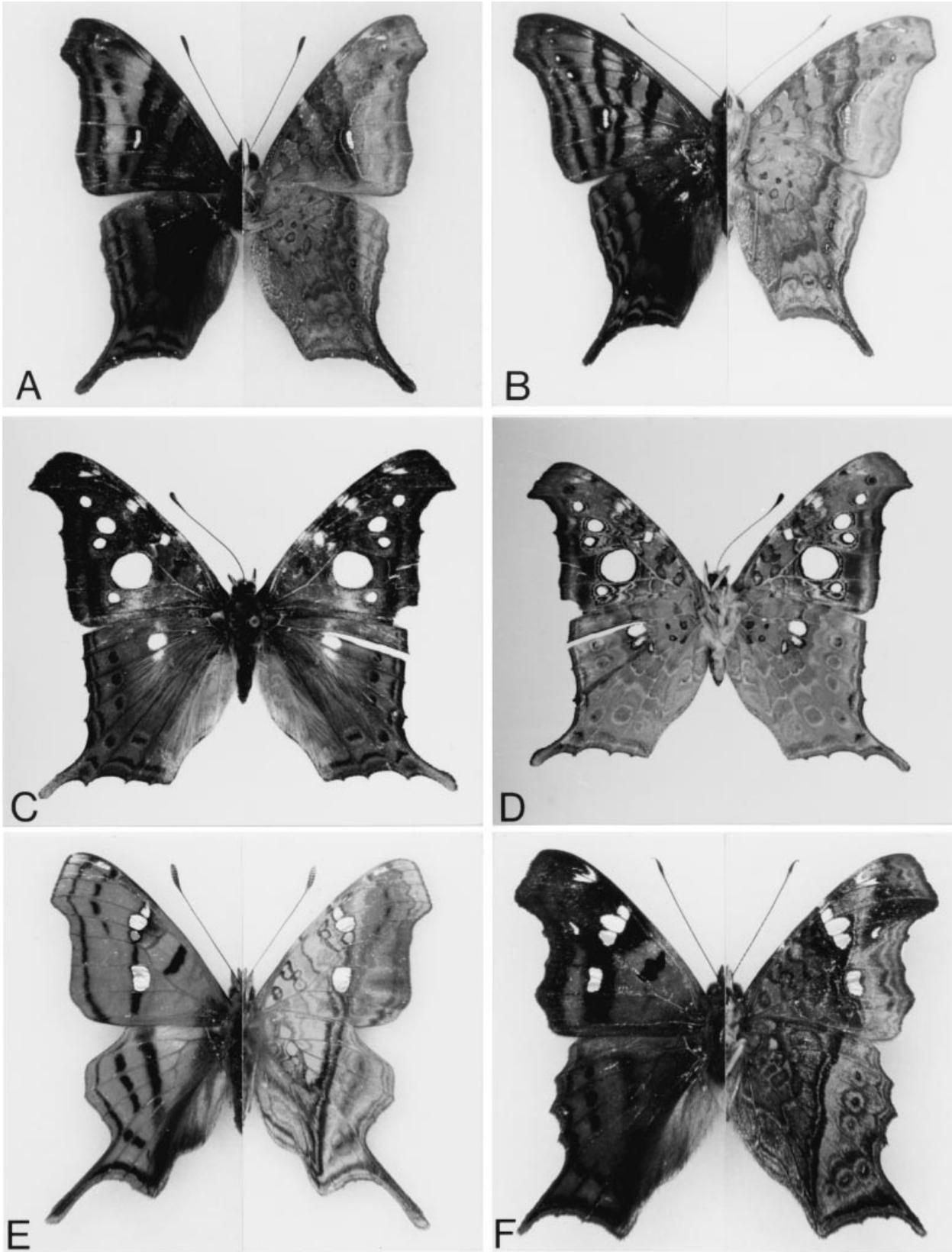
**Identification and taxonomy.** Typical FW length 23 mm. This species is readily distinguished by its evenly rounded forewing shape, uniform, almost entirely black dorsal surface and extensive yellow colouration on the ventral hindwing.

The lectotype bears the following labels: 'Ecuador/Hewitson Coll./79–69./Eurema/charon. 1.', 'Type', 'SYN-/TYPE', 'B.M. TYPE/No.Rh. 8639/Eurema/charon/male Hew.' and 'SYNTYPE/Eurema/charon/Hewitson./det. S. M. North. 1984.'

**Biology.** This species is perhaps the rarest in the genus, with only five male specimens known to the authors, and it appears not to have been collected during the century following its description, thus remaining unknown to some early workers (Seitz, 1914). It has reliably been recorded only from the east Andean slope in Ecuador, but one of two specimens in the MIZA (A. Neild, personal communication), and one in the AME, collected by commercial dealers and labelled Niebli and El Nono (both Pichincha Province), respectively, suggest that the species may also occur on the west Andean slope in Ecuador. However, the altitudinal data accompanying these specimens of 3750 m and 3500 m are almost certainly erroneous, and the species has only reliably been recorded from 2200 to 2600 m. A solitary male was encountered puddling at a stream near primary cloud forest in northeastern Ecuador, implying its almost certain occurrence in Colombia.

**Distribution.** Eastern (and western?) Ecuador.

**Fig. 6.** Wings of males (dorsal surface on left; ventral surface on right). A, *Hypanartia dione arcaei*, Cerro de la Muerte, Costa Rica (FSCA); B, *H. dione disjuncta* ssp.n., holotype; C,D, *H. celestia* sp.n., holotype; E, *H. splendida*, Huancabamba, Peru (BMNH(M)); F, *H. lindigii*, Tulcán-La Bonita Rd, eastern Ecuador (KWJH).



***Hypanartia dione dione* (Latreille, [1813])** (Figs 5F; 14A–C)

*Vanessa dione* Latreille, [1813], in Humboldt & Bonpland, 1813: 87, Pl. 37, Figs 1,2. Type locality: Not stated. Holotype not located (BMNH?).

**Identification and taxonomy.** Typical FW length 27 mm. This species is readily distinguished by its entirely or predominantly brown dorsal surface, with prominent darker brown transverse lines, its pale brown ventral surface and long hindwing tails. However, there is some difficulty distinguishing the Andean and northern Central American populations and determining which of these represents the nominotypical subspecies. The original description of *H. dione* contains a colour illustration of both wing surfaces, which have an almost uniformly pale brown ground colour and bear fine, dark brown transverse postdiscal lines, characteristic of the Andean population. Boisduval (1870) stated that he possessed the [holo]type of this taxon, which had been flattened inside a book (presumably by Humboldt or Bonpland) and was consequently much rubbed, as evidenced by the poor quality of the original figure. This specimen should be in the BMNH (ex collection Boisduval, via collection Oberthür), but, despite extensive searching, we have been unable to locate it. Notwithstanding this, we are convinced that Latreille's type represents the Andean subspecies, and was probably obtained in northern Colombia.

**Biology.** This subspecies is common and widespread from 1000 to 3000 m, and although occasionally males may be encountered perching high on forested hilltops or along forest edges, they are more often observed in degraded habitats puddling along roadsides and field margins.

**Distribution.** Venezuela to Ecuador (both Andean slopes), to northern Argentina (eastern slopes).

***Hypanartia dione arcae* (Salvin, 1871), stat.n.** (Fig. 6A)

*Eurema arcae* Salvin, 1871: 415. Type locality: Panama, Chiriquí volcano. Holotype ♂, BMNH (examined).

**Identification and taxonomy.** Typical FW length 27 mm. This taxon was described, and has typically been treated, as a full species (d'Abbrera, 1987; DeVries, 1987; Lamas & Small, 1992), but the closely allopatric occurrence of *dione*, *arcae* and the taxon described below, the minor differences in wing pattern and essentially identical male genitalic and tergal morphology, suggest that they should be conservatively regarded as a single species. This subspecies differs from the nominotypical subspecies and the subspecies described below by having a broad orange submarginal band on the dorsal

forewing. Specimens from eastern Panama (Darién) show a somewhat reduced orange submarginal band on the forewing, and are clearly transitional to *H. d. dione*.

**Biology.** DeVries (1987) reported that *H. d. arcae* in Costa Rica occurs in wet cloud forest habitats from 1200 m to over 2000 m, where it perches on vegetation overhanging rivers, puddles, or occasionally visits flowers of *Senecio* and other Compositae. It is possible that the divergent dorsal pattern of this subspecies could be explained by mimicry of the common cloud forest species *Adelpha tracta* (Butler, 1872), with which it shares a similar geographical range and dorsal wing pattern.

**Distribution.** Costa Rica and Panama.

***Hypanartia dione disjuncta* Willmott, Hall & Lamas, ssp.n.** (Fig. 6B)

Both sexes differ consistently from the nominotypical subspecies in the following respects.

**Dorsal surface:** Ground colour of both wings slightly darker brown, especially in basal half of hindwing, all transverse markings slightly broader and darker brown, with increased shading between spots of inner submarginal line.

**Type material.** *Holotype*, ♂, GUATEMALA: Baja Verapaz, Purulá (Champion). (BMNH(M)). *Paratypes*, GUATEMALA: 1 ♂, same data as holotype (BMNH(M)); Quezaltenango, 2 ♂, 1 ♀, Volcán de Santa María (Richardson) (BMNH(M)); Alta Verapaz, 2 ♂, Chiacám (Champion) (BMNH(M)). MEXICO: Puebla, 1 ♂, Tequezuitla, 625 m, 10 Aug 1981 (L. González-Cota) (MUSM); Chiapas, 1 ♂, Municipio Independencia, San Antonio Buenavista, 1500 m, 30 Aug 1982 (L. González-Cota) (MUSM).

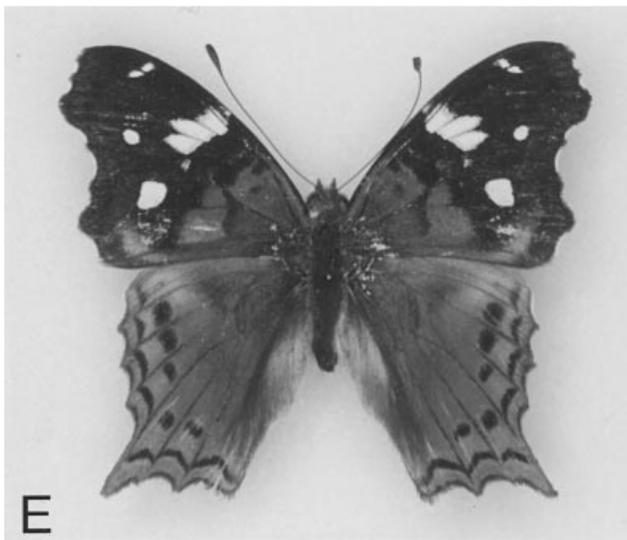
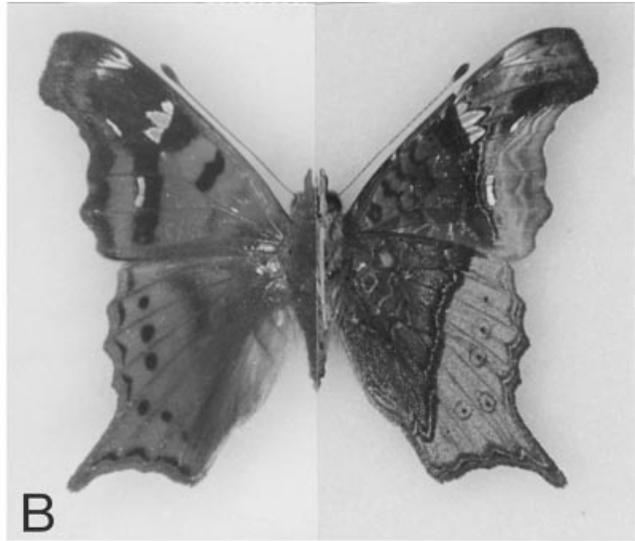
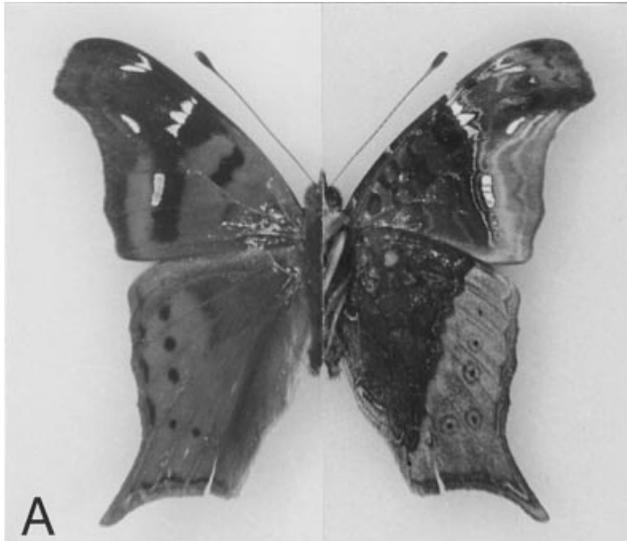
**Etymology.** The name is derived from its disjunct geographical distribution in relation to the phenotypically similar nominotypical subspecies.

**Discussion.** This taxon, which occurs from Mexico to Honduras, has always been treated as nominotypical *H. dione*, but given the intervening occurrence of the phenotypically very distinct *H. d. arcae* in Costa Rica and Panama, and slight but consistent wing pattern differences, we believe it requires subspecific recognition. Although this population and *H. d. arcae* are currently confined to isolated montane 'islands', and intermediate phenotypes are unknown, the male genitalia do not differ significantly between the two taxa and we believe they are best treated as conspecific.

***Hypanartia celestia* Lamas, Willmott & Hall, sp.n.** (Figs 6C,D; 15A–C)

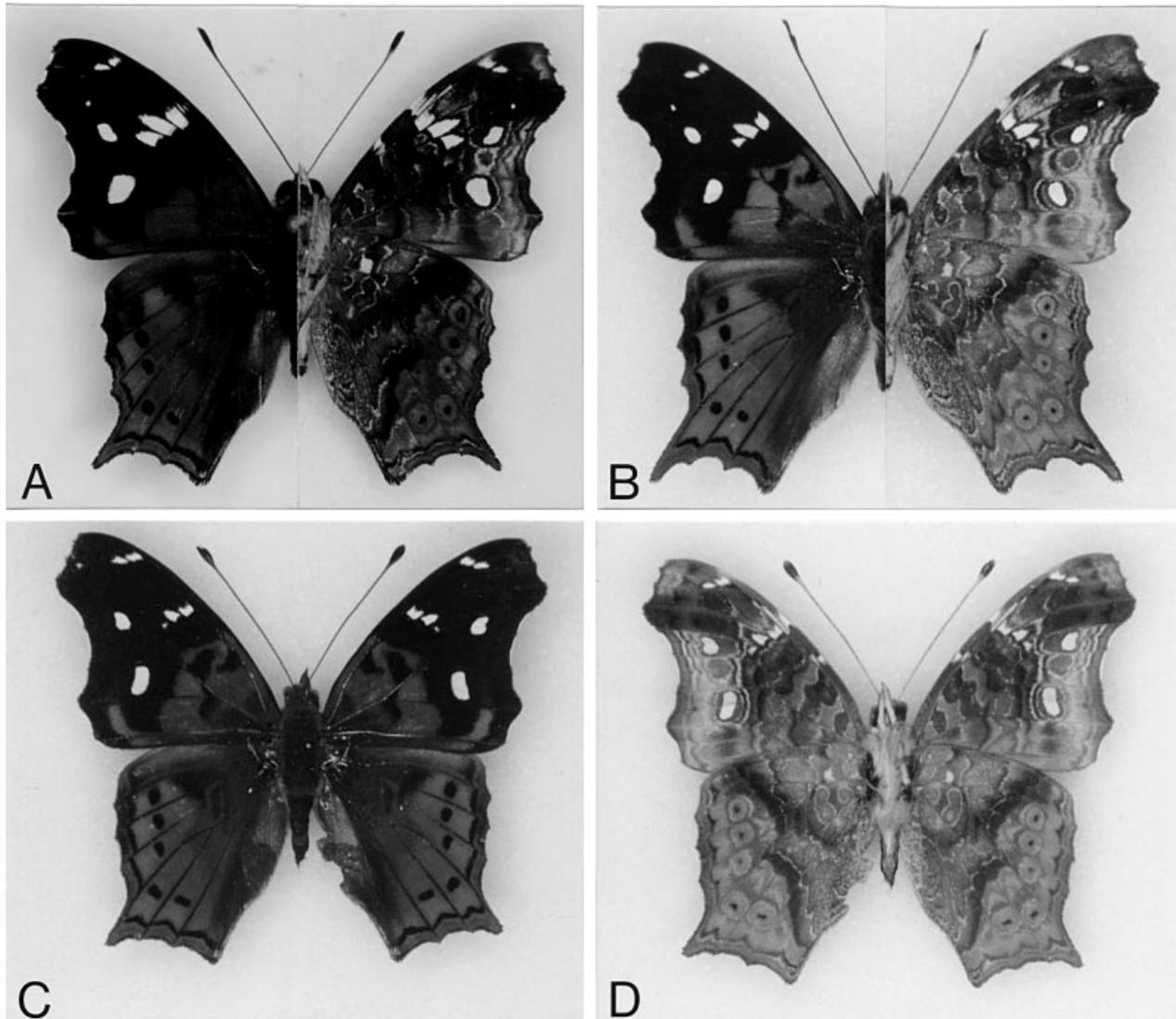
**Male.** Forewing length 32 mm. Forewing apex sharply produced at vein M1, remainder of distal margin straight except slight point at end of vein M3; hindwing squarish with

**Fig. 7.** Wings of males (dorsal surface on left; ventral surface on right). A, *Hypanartia christophori*, Huancabamba, northern Peru (BMNH(R)); B, *H. christophori*, Marcapata, southern Peru (BMNH(R)); C,D, *H. fassli* sp.n., holotype; E,F, *H. trimaculata* sp.n., holotype.



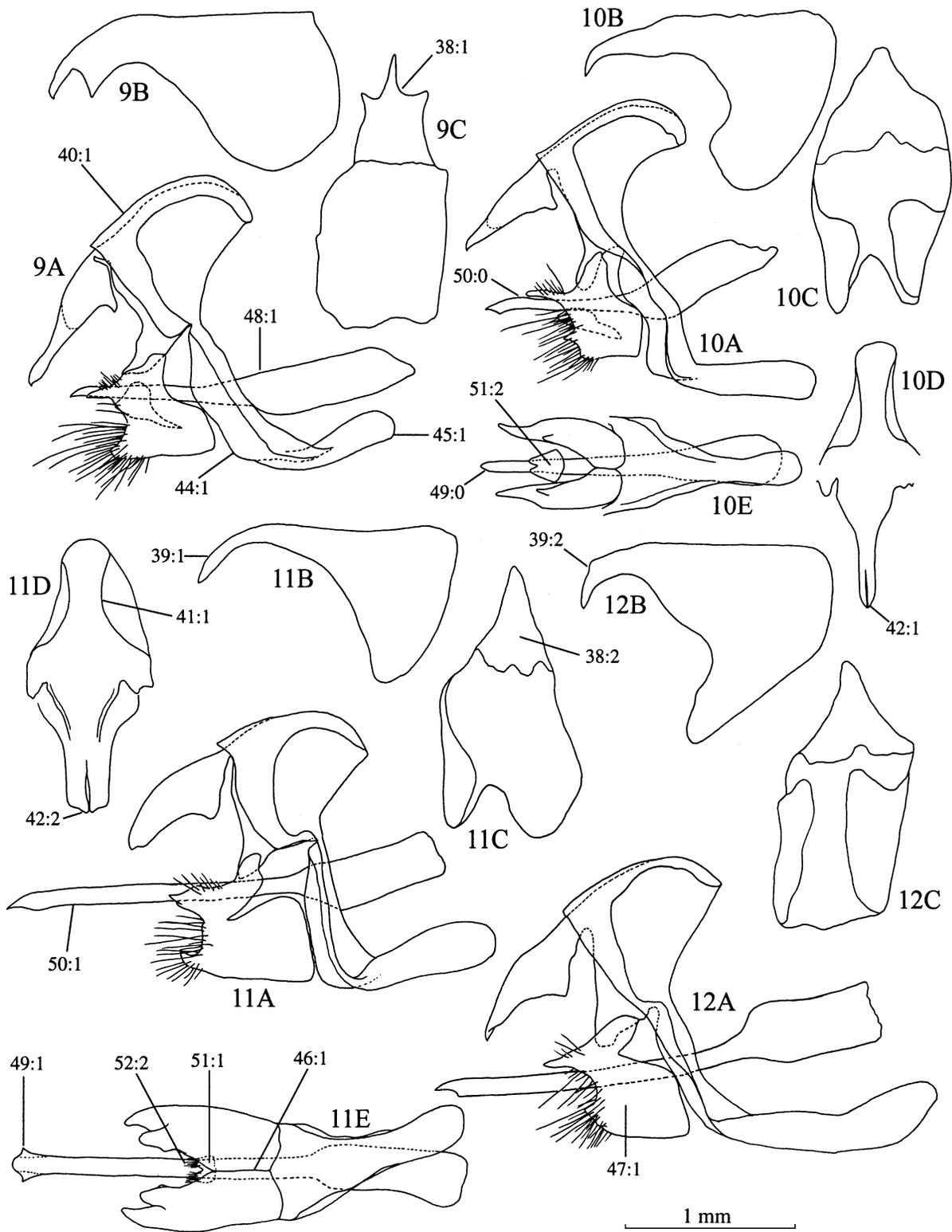
sharply angled apex, straight distal margin to a long, rounded tail at vein M3, then slightly scalloped to tornus. *Dorsal surface*: Forewing ground colour dark brown; discal cell with an indistinct, uneven, darker brown bar representing basal symmetry system (elements b,c), a white spot followed posteriorly by a white dash at cell end; white postdiscal dashes at costa anterior of vein M1, faint white scales in cell M2-M1; uneven line of seven postdiscal to submarginal white

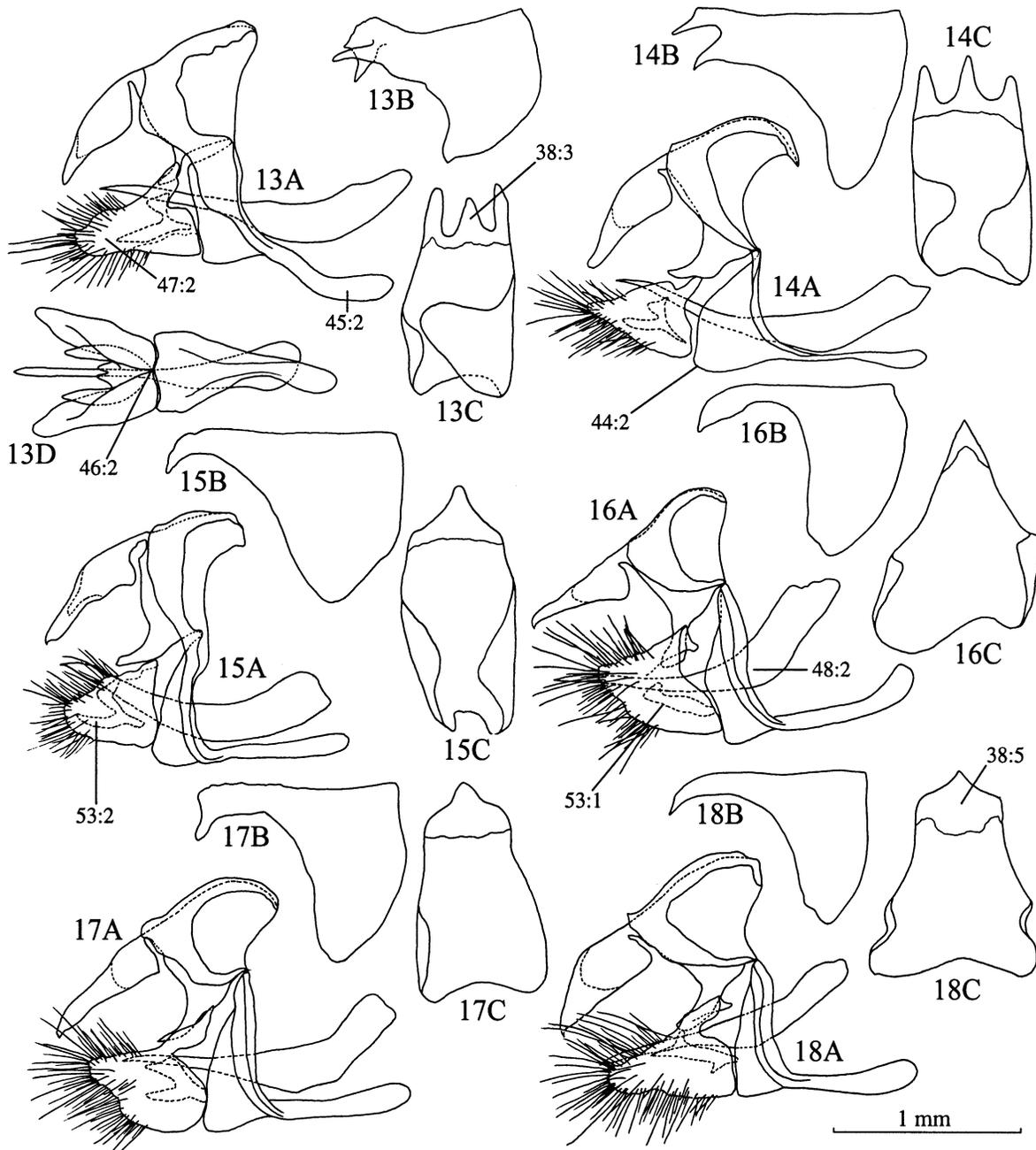
spots (border ocelli, element h) in cells 2 A-Cu2 to R4-R3 (none in cell M1-R5), largest in cell Cu2-Cu1 extending right across cell and deforming base of vein Cu1, remainder smaller, those in R5-R3 sagittate; diffuse, pale greyish scaling basal to spot in cell 2 A-Cu2 extending from anal margin into cell Cu2-Cu1; 2 darker brown submarginal bands (elements i,j); fringe brown. Hindwing ground colour brown, paler along anal margin; long, grey-brown hairs in discal cell and anal margin;



**Fig. 8.** Wings of males (dorsal surface on left; ventral surface on right). A, *Hypanartia trimaculata autumnna* ssp.n., holotype; B, *H. kefersteini*, Reserva Las Golondrinas, western Ecuador (KWJH); C,D, *H. cinderella* sp.n., Chanchamayo, Peru, paratype (BMNH(M)).

**Figs 9–12.** Male terminalia. A, Genitalia, lateral view; B, last abdominal tergite, lateral view; C, last abdominal tergite, ventral view; D, tegumen and uncus, dorsal view; E, valvae, saccus and aedeagus, ventral view. Character states from Appendix 1 are indicated where appropriate. 9, *Hypanartia paullus*, Jarabacoa, Jamaica (FSCA); 10, *H. bella*, Rio do Julio, Brazil (SC) (FSCA); 11, *H. lethe*, Río Tanti, western Ecuador (KWJH); 12, *H. godmanii*, Salto de Napac, western Ecuador (KWJH).





**Figs 13–18.** Male terminalia. A, Genitalia, lateral view; B, last abdominal tergite, lateral view; C, last abdominal tergite, ventral view; D, valvae, saccus and aedeagus, ventral view. Character states from Appendix 1 are indicated where appropriate. 13, *Hypanartia charon*, Tulcán-La Bonita Rd, eastern Ecuador (KWJH); 14, *H. dione dione*, Río Machay, eastern Ecuador (KWJH); 15, *H. celestia* sp.n., nr Pomacochas, Peru, paratype (MUSM); 16, *H. splendida*, Huancabamba, Peru (BMNH(M)); 17, *H. lindigii*, Aloag-Sto. Domingo Rd, western Ecuador (KWJH); 18, *H. christophori*, Huancabamba, Peru (BMNH(R)).

grey scaling along anal margin to tornus; oval, white postdiscal spot extending across cell M1-Rs, bordered by smaller spot in cell M2-M1; round, darker brown submarginal spots (border ocelli, element h) in cells Cu2-Cu1 to M1-Rs, each surrounded

by slightly paler brown ocellus, indistinct, paler brown ocellus in anterior half cell 2 A-Cu2; continuous line of darker brown submarginal crescent-shaped marks (element i); darker brown marginal border except at tail, which is dusted with

pale brown scales; fringe brown. *Ventral surface*: Forewing ground colour pale brown; discal cell with darker brown wing root band and basal symmetry system, white mark at costa at end of discal cell continuing as a dash posteriorly across cell, bordered basally by thin dark brown line (element d); costa dark brown to distal edge of dark band, then whitish, then dark brown; white postdiscal and subapical spots reflecting dorsal surface, each ringed with thin pale greyish lines in cells 2A-Cu2 to M2-M1, and an additional 3 similar lines in basal half cell 2A-Cu2; black subapical spot (element h) with yellow ring in cell M1-R5; darker brown submarginal band bordering distal edge of white postdiscal spots, then pale brown submarginal line with indistinct pale grey scaling, then darker brown margin; fringe dark brown. Hindwing ground colour pale brown; 3 dark brown circles in basal half of discal cell (contracted basal symmetry system), white spot at discocellulars; base cell Rs-Sc+R1 red brown (element d); central symmetry system broad, uneven, slightly paler brown; row of submarginal pale yellowish ocelli (element h) in cells 2A-Cu2 to M1-Rs; thin, pale greyish submarginal line, with indistinct, darker crescent-shaped markings (element i) basally. *Head*: Ventral surface of labial palpi pale greyish white with sparse, long black hairs, dorsal surface dark brown. Eyes brown and densely setose, margins with cream scaling. Frons orange-brown. Antennal segments orange-brown with some white scaling ventrally; clubs dark brown, tips orange-brown. *Body*: Dorsal surface of thorax dark brown with long hairs dark green at certain angles, ventral surface pale brown; dorsal surface of abdomen dark brown, ventral surface pale brown. Forelegs pale brown; femur of mid- and hindlegs pale brown, remainder brown. *Genitalia and terminal tergite* (Fig. 15A–C): Valvae roundly triangular; juxta with 2 prominent ventral processes; vinculum broadening ventrally; saccus narrow and of even width; tegumen high and narrow, uncus in posterior view deeply cleft with 2 small, sharp points at distal tip; terminal tergite in lateral view gradually tapering, tip smoothly curved; tip in ventral view broadly triangular.

*Female*. Unknown.

*Type material*. *Holotype*, ♂, PERU: Junín, Puente Yanango, [11°13'S, 77°29'W 2000 m], 27 Oct 1965 (P. Hocking) (MUSM). *Paratypes*, PERU: Junín, 1♂, Río Tarma, Huacapistana 1800 m, 1 Mar 1943 (W. Weyrauch) (FIML); Amazonas, 1♂, 5 km W of Pomacochas, Quebrada Chiro, 05°50'S, 78°00'W, 2300–2500 m, 24 Aug 1998 (G. Lamas) (MUSM); 1♂, same locality data as preceding, 2200 m, 8 July 1998 (J. Wojtusiak) (AJ); 1♂, same locality as preceding, 17 Aug 1998 (T. Pyrcz) (MUSM).

*Etymology*. This species name is derived from the Latin *celestia*, meaning heavenly, with reference to the dorsal pattern of white orbs on a dark background reminiscent of the night sky.

*Discussion*. *Hypanartia celestia* is most closely related to *H. dione*, but bears little resemblance to that, or indeed any other, species of *Hypanartia*. The greatly enlarged white spot in cell Cu2-Cu1 on the dorsal forewing, which results in the distortion of vein Cu1, and the white postdiscal spots on the dorsal hindwing are unique to this species. A specimen from central Peru lacking precise locality data differs from typical speci-

mens in having a much straighter forewing distal margin (A. Jasiński, personal communication). *Hypanartia celestia* was known to us until recently only from the holotype collected in 1965. One of us (G.L.) found another male in the FIML, collected in 1943, only a few kilometres downriver from the type locality, and recently captured a male in northern Peru. This individual was puddling, moving sluggishly with its wings outspread and looking somewhat like a moth. The species has thus far been recorded only from Peru, from 1800 to 2500 m, but it may also occur in extreme southern Ecuador.

***Hypanartia splendida* (Rothschild, 1903)** (Figs 6E; 16A–C)

*Hypanartia splendida* Rothschild, 1903: 309. Type locality: Peru. Lectotype ♂ (here designated by G.L.), BMNH (examined).

*Identification and taxonomy*. Typical FW length 26 mm. The combination of the bright orange dorsal coloration, long hindwing tails and distinctive wing shape render this species, as the name suggests, unmistakable. The lectotype (illustrated in Rothschild & Jordan, 1903a) bears the following labels: 'Peru', 'Hypanartia/splendida. R./Nov. Zool. 1903/Type', 'Type', 'SYN-TYPE', 'NOV. ZOOL. 1903/PL. XI. FIG. 8' and 'SYNTYPE/Hypanartia/splendida/Rothschild./det. S. M. North. 1984.'

*Biology*. *Hypanartia splendida* is one of the rarest species in the genus and nothing is known of its biology.

*Distribution*. To date, this species is known with certainty from central Peru only. Specimens in the BMNH labelled 'Huancabamba, N. Peru' come from the Huancabamba in Pasco Department (central Peru), not Piura (north Peru) (see Lamas, 1976). There is a single specimen in the BMB with the label data 'Bolivia, Ernst A. Bottcher, Berlin, e coll. Thieme 1910', but other specimens in that collection that appear to be Peruvian and mislabelled from Bolivia (e.g. typical *H. christophori*) make confirmation of this record desirable.

***Hypanartia lindigii* (C. & R. Felder, 1862)** (Figs 6F; 17A–C)

*Eurema lindigii* C. & R. Felder, 1862: 420. Type locality: Colombia, Bogotá. Lectotype ♂ (here designated by G.L.), BMNH (examined).

*Identification and taxonomy*. Typical FW length 25 mm. This species is distinguished from its closest relatives, *H. christophori* and *H. fassli*, in those species accounts. The lectotype bears the following labels: 'Bogota/Lindig/Type', 'Lindigii n.', 'FELDER/COLLn.', 'Type', 'SYN-/TYPE' and 'SYNTYPE/Eurema/lindigii/Felder & Felder/det. S. M. North. 1984'.

*Biology*. This species is local and uncommon from 2000 to 3500 m in cloud forest habitats, but appears to be especially scarce in the southern portion of its range. Males are

encountered hilltopping, perching on low bushes or puddling along roads and rivers, and are occasionally attracted to traps baited with rotting fish. The very rare female is only known from a handful of specimens in collections.

*Distribution.* Northern Colombia (central and western cordilleras) to Ecuador (both slopes) and southern Peru.

***Hypanartia christophori* (Jasiński, 1998)** (Figs 7A,B; 18A–C)

*Hypanartia christophori* Jasiński, 1998: 406, Figs 1–3. Type locality: Ecuador, Zamora-Chinchipec, Cordillera de Sabanilla (= Cordillera de Zamora), north of Valladolid, 2500 m. Holotype ♂, AJ (holotype illustration examined).

*Identification and taxonomy.* Typical FW length 25 mm. This species is most closely related to *H. lindigii* and *H. fassli* (described below), but can readily be distinguished from *H. fassli* by the straight postdiscal line (element f) on the ventral hindwing and by the last abdominal tergite being rectangular instead of tapering at the distal tip in dorsal view. These two characters unite *H. christophori* and *H. lindigii*, which appear to be sister species. *Hypanartia christophori* consistently differs from *H. lindigii* by having a narrower transparent spot in cell Cu2-Cu1 of the forewing, with a consequently straighter purple-blue proximal line, and by lacking darker brown shading on the ventral hindwing proximal to the inner submarginal spots (element g) and in the tail.

*Hypanartia christophori* is variable over its geographical range, specimens from southern Peru and Bolivia (Fig. 7B) differing from the typical illustrated specimen (Fig. 7A) by having slightly larger postdiscal spots on the forewing, which are also transparent, a straighter postdiscal line on the ventral hindwing, and more scalloped distal margins on both wings, in all these respects more closely approaching *H. lindigii*. Although specimens from southern Ecuador to central Peru appear to be phenotypically quite constant, those from southern Peru and Bolivia are rather variable, and as the extent of clinal variation is not understood due to the lack of specimens from intervening areas, we feel it is unwise to recognize subspecies at present.

*Biology.* This species is local but apparently not uncommon, and is known from about 2000 m to 3000 m in primary cloud forest localities, where males are encountered puddling along roadsides and feeding on dung during periods of bright sun (Jasiński, 1998).

*Distribution.* Southern Ecuador to Bolivia.

***Hypanartia fassli* Willmott, Hall & Lamas, sp.n.**  
(Figs 7C,D; 19A–C)

*Male.* Forewing length 25 mm. Distal margin of forewing scalloped, produced at end of vein Cu2 into small rounded point and at apex into long angular extension; distal margin of

hindwing scalloped, tornus angular, long tail centred on cell Cu1-M3. *Dorsal surface:* Forewing ground colour black; basal half of wing dark red-brown (darker at very base), with uneven black discal cell bar filling space between elements c and d; dark red-brown submarginal line from anal margin to cell Cu1-M3; 3 small elongate, postdiscal white spots in cells M3-M2 to M1-R5; narrowly elongate, slightly concave, transparent white mark in middle of cell Cu2-Cu1, small white fleck in distal half of cell M3-M2, 2 small subapical white marks in cells R5-R4 and R4-R3; fringe brown with some white scaling in middle of all cells except Cu2-Cu1, M2-M1 and M1-R5. Hindwing dark red-brown (darker at very base) except for brown along anal margin (grey hairs at distal margin), costal margin and in apex, and indistinct black postdiscal band (element f) in cells M3-M2 to M1-Rs, black, angular, submarginal spots (border ocelli, element h) in cells 2 A-Cu2 to M1-Rs and a continuous line of black, submarginal crescent-shaped marks (element i) with a very thin, fainter black line distally; long brown hairs at anal margin; fringe brown with white scaling in middle of cells M1-Rs and Rs-Sc + R1. *Ventral surface:* Forewing ground colour orange-brown in basal half, dark brown in anterior distal half and pale brown in posterior distal half; elements a–d visible in discal cell as dark red-brown lines, white mark at costa towards end of discal cell; distal white marks as on dorsal surface; thin, purplish line between elements f and g from costa to anal margin, curving in cell Cu2-Cu1; slightly paler brown scaling in subapex leaving 2 sagittate darker markings (element i); border ocellus a purple spot in cell M1-Rs; a thin, concave pale purple submarginal line extending from vein M2 to vein 2 A; 2 undulating, submarginal bands (elements i,j), j straighter. Hindwing ground colour dark brown in basal half and at tornus, brown in remainder of distal half; dark brown postdiscal band (element f) extending in a concave arc from costa (at a point three-quarters distance from base to tornus) to discal cell end, then as another slightly concave arc to anal margin, lined proximally throughout with a thin faint blue line then thin dark brown; proximal half of wing very faintly powdered with pale blue scaling with darker elements a-d in discal cell and a small yellow spot at base of cell Rs-Sc + R1; a series of brown submarginal ocelli (element h), with black and pale blue pupils surrounded by a thin line of dark brown, forming a diagonal line in cells 2 A-Cu2 to Cu1-M3 and an almost vertical line in cells M3-M2 to M1-Rs, dark brown scaling (element g) proximal to all but less in cells 2 A-Cu2 and M1-Rs, where spots are also smaller; 2 uneven dark brown submarginal lines (elements i,j) with purple-blue between, lines in cell Cu1-M3 extending into tail. *Head:* Ventral surface of labial palpi greyish white, dorsal surface dark red-brown. Eyes brown and densely setose, margins with greyish white scaling. Frons orange-brown. Antennal segments brown with white scaling ventrally; clubs black, tips orange-brown. *Body:* Dorsal surface of thorax dark brown with long hairs which are dark green at certain angles, ventral surface pale orange-brown; dorsal surface of abdomen dark orange-brown, ventral surface pale brown. Forelegs pale brown; femur of mid- and hindlegs brown, remainder pale brown. *Genitalia and terminal tergite* (Fig. 19A–C): Valvae triangular, slightly upturned at

tip; juxta with 2 small ventral processes; vinculum broadening ventrally; saccus narrow and of even width; tegumen broad, uncus in posterior view shallowly cleft; terminal tergite in lateral view sharply tapering at middle, tip long, narrow and smoothly curved; tip in ventral view evenly tapering and pointed.

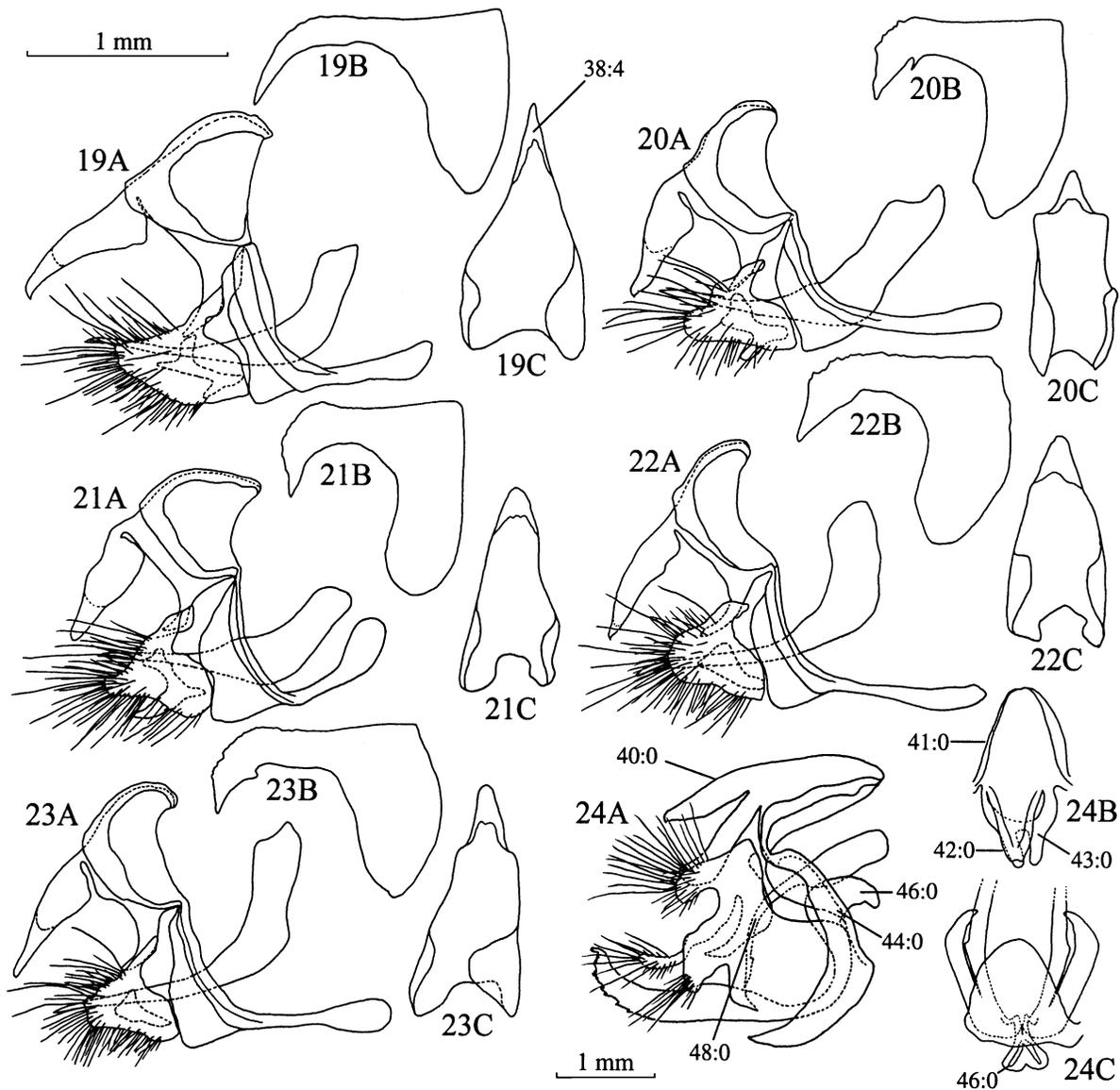
*Female.* Unknown.

*Type material.* *Holotype*, ♂, COLOMBIA: Huila, above San José de Isnos, 2750 m, 9 Aug 1982 (M. Adams) (BMNH, Adams & Bernard coll.). *Paratypes*, COLOMBIA: Quindío, 1 ♂, Salento, Reserva Natural 'Acaime', 2700 m, 12 Jan 1989

(J. H. Vélez) (MHNUC); Tolima, 1 ♂, Monte Tolima, 3500 m, Feb 1910 (A. H. Fassl) (BMNH(R)); Nariño, 1 ♂, Piedranca 1700 m, Dec 1945 (AMNH). ECUADOR: Sucumbíos, 1 ♂, El Calvario-La Alegría Rd, 2800 m, 11 Nov 1997 (K. R. Willmott) (KWJH).

*Etymology.* This species is named for the German explorer and entomologist Anton Hermann Fassl, who to our knowledge collected the first known specimen.

*Discussion.* *Hypanartia fassli* is most similar to *H. lindigii* and *H. christophori*, but can readily be distinguished from both by having a postdiscal line on the ventral hindwing that



**Figs 19–24.** Male terminalia. A, Genitalia, lateral view; B, last abdominal tergite, lateral view; C, last abdominal tergite, ventral view (Figs 19–23). Upper scale bar applies to Figs 19–23, lower scale bar to Fig. 24. Character states from Appendix 1 are indicated where appropriate. 19, *Hypanartia fassli* sp.n., holotype; 20, *H. trimaculata* sp.n., holotype; 21, *H. trimaculata autumnna* ssp.n., holotype; 22, *H. kefersteini*, nr Saraguro, western Ecuador (KWJH); 23, *H. cinderella* sp.n., Chanchamayo, Peru, paratype (BMNH(M)); 24, *Antanartia delius*, 'Central Africa' (FSCA).

consists of two concave elements instead of a single scalloped line, and a tapering instead of rectangular tip to the last male abdominal tergite in dorsal view. *Hypanartia fassli* shares a number of distinct wing pattern characters with both *H. lindigii* and *H. christophori*, but can be additionally distinguished from *H. lindigii* by having entirely black antennal clubs without an orange-brown tip, smaller postdiscal forewing spots that are not as transparent, a narrower transparent spot in cell Cu2-Cu1 of the forewing, a darker ventral ground colour and a ridge on the upper instead of middle inner edge of the valvae in the male genitalia; and from *H. christophori* by having a slightly broader transparent spot in cell Cu2-Cu1 of the forewing, dark brown scaling on the ventral hindwing distal to the inner submarginal spots and in the tail, spots in ventral hindwing cells Cu1-M3 and M3-M2 that are further apart, a more angular hindwing tornus with a more pronouncedly concave region between the tornus and tail, and less elongate valvae and a more slender uncus in the male genitalia in lateral view.

*Hypanartia fassli* is currently known from central Colombia (both slopes of the Cordillera Central) to extreme northeastern Ecuador, and reliable, recent locality data indicate that it occurs from 2700 to 2800 m, although its true altitudinal range is undoubtedly broader. The only known Ecuadorian specimen was encountered puddling along a road at the edge of primary cloud forest. It appears to be sympatric with *H. lindigii* over its entire range.

***Hypanartia trimaculata* Willmott, Hall & Lamas, sp.n.**  
(Figs 7E,F; 20A–C)

**Male.** Forewing length 25 mm. Distal margin of forewing scalloped, produced at end of vein Cu2 into small rounded point and at apex into angular extension; distal margin of hindwing scalloped, short triangular tail centred on cell Cu1-M3. **Dorsal surface:** Forewing ground colour black; basal third of wing dark red-brown (darker at very base), except for 2 small black spots in discal cell in area of basal symmetry system, an undulating, black transverse line posterior to discal cell (element d) and a large black block towards distal edge of red-brown area in cell 2A-Cu2; 3 elongate, postdiscal white spots in cells M3-M2 to M1-R5, surrounded by traces of blue scaling; large rounded white square in middle of cell Cu2-Cu1, small round white spot in distal half of cell M3-M2, 2 small subapical white marks in cells R5-R4 and R4-R3; fringe brown with white scaling in middle of all cells except Cu2-Cu1 and M2-M1. Hindwing dark red-brown (darker at very base) except for brown along anal margin (grey hairs at distal margin), costal margin, in apex and a brown mark at end of discal cell (discal spot), and round black submarginal spots (border ocelli, element h) in cells Cu2-Cu1 to M1-Rs and a continuous line of black submarginal crescent-shaped marks (element i); long brown hairs at anal margin; fringe brown with white scaling in middle of cells M1-Rs and Rs-Sc+R1. **Ventral surface:** Forewing ground colour brown, paler at anal margin; discal cell with element a and basal symmetry system red-brown, lined with pale blue, white mark at costa between elements c and d, central symmetry system red-brown edged with black

with 2 central, thin pale blue lines; distal white marks as on dorsal surface but no blue scaling present; 2 small blue-pupilled black ocelli (element h) in cells M2-M1 and M1-R5; all submarginal spots posterior to cell M3-M2 and equivalent space in cell 2A-Cu2 surrounded by large, yellow-scaled rings with a line of purple-blue scaling proximally; purplish submarginal markings from vein M2 to anal margin, yellowish subapical marks in cells M1-R4 between elements i and j. Hindwing ground colour brown; dark, uneven red-brown postdiscal band (element f), lined proximally throughout with thin blue then thin dark brown; proximal half of wing powdered with pale blue scaling; discal cell with darker element a and basal symmetry system, both lined with pale blue, and a yellow square at posterior base of cell Rs-Sc+R1; a series of large submarginal ocelli (element h) with dark brown element g basally, with a black and blue pupil in cells Cu2-Cu1 to M1-Rs, purple-blue scaling proximal to element g; uneven, dark brown submarginal line (element i), containing some purple scaling towards apex and tornus, with purple-blue distally, brighter at tornus. **Head:** Ventral surface of labial palpi greyish white with short black hairs, dorsal surface dark red-brown. Eyes brown and densely setose, margins with cream scaling. Frons orange-brown. Antennal segments orange-brown with some white scaling ventrally; clubs dark brown, tips orange-brown. **Body:** Dorsal surface of thorax dark brown with long hairs that are dark green at certain angles, ventral surface pale orange-brown; dorsal surface of abdomen dark orange-brown, ventral surface dirty cream. Forelegs pale brown; femur of mid- and hindlegs pale brown, remainder brown. **Genitalia and terminal tergite** (Fig. 20A–C): Valvae constricted at posterior tip in lateral view; juxta with 2 long ventral processes projecting beyond ventral edge of valvae; vinculum broadening ventrally; saccus narrow and of even width; tegumen relatively narrow, uncus in posterior view moderately cleft; terminal tergite in lateral view angular, tip sharply hooked ventrally with 2 small lateral projections; tip in ventral view evenly tapering and pointed.

**Female.** Differs from the male in the following respects: wing shape broader, hindwing slightly more angular.

**Type material.** *Holotype*, ♂, COLOMBIA: Cundinamarca, Bogotá (Child) (BMNH(R)). *Paratypes*, COLOMBIA: Risaralda, 2♂, Distrito de Pereira 1886 (R. M. Valencia) (BMNH(M)); 1♂, Qbda. Río Negro, cerca a Pueblo Rico, 1550 m, 18 Aug 1984 (P. Valdés) (MHNUC); 1♀, Tapartó, Municipio Pueblo Rico, 700 m, 14 Jan 1982 (J. H. Vélez) (MHNUC); Boyacá, 1♂, Otanche, Oct 1985 (J. Urbina) (JFL); 1♂, same data as preceding except Mar 1986 (JFL); Cauca, 2♂, Tambito Forest Reserve, 1500 m, 2–5 May 1997 (J. Wojtusiak) (AJ); Valle del Cauca: 2♂, Juntas, fin 1897-Jan 1898 (M. de Mathan) (BMNH(M)); 1♂, Lago Calima, 1300 m, 12 Oct 1984 (ESM); 1♂, km 55 via a Queremal, 19 Dec 1984 (J. Salazar) (MHNUC); 1♂, Río San Juan, Queremal, km 57, 28 Jul 1985 (L. M. Constantino) (LMC); 1♂, same data as preceding except km 85, 10 Jul 1983 (LMC); 1♂, between Queremal and Buenaventura, 3500–4000 ft, 7 Feb 1935 (E. I. Huntington) (AMNH). ECUADOR: Imbabura, 1♂, nr Lita, Jul 1997 (I. A. Villafuerte) (AJ); 2♂, Cachaco, ridge to south, nr Lita, 1300 m, 13 Jul 1999 (K. R. Willmott) (1 in KWJH, 1 in

MECN); Pichincha, 1♂, Palmito Pamba, km 5 Nanegal-García Moreno Rd, 1500 m, 11 Jul 1998 (K. R. Willmott) (KWJH); Chimborazo, 1♂, Chimborazo (Spruce) (BMNH(M)); Tungurahua, 1♂, Río Machay 1700 m, 4–5 Jul 1993 (C. Velástegui) (KWJH). PERU: Junín, 1♀, Río Ipoki, Ipokiarí, May 1979 (H. Rojas) (MUSM); Huánuco, 1♂, Parque Nacional de Tingo María, Cueva de las Lechuzas, 4 km N Tingo María, 28 Mar 1991 (J. Y. Miller) (AME); 1♂, Tingo María, 30 July 1980 (D. & J. Jenkins) (AME); 4♂, Tingo María (M. Rojas) (MIZA).

*Etymology.* The species name refers to the prominent, diagnostic three white postdiscal spots on the forewing.

*Discussion.* *Hypanartia trimaculata* is most closely related to and has long been confused with *H. kefersteini* and *H. cinderella* (described below). It is readily distinguished from both by having a slightly broader wing shape, larger postdiscal white spots on the forewing surrounded by blue scaling on the dorsal surface (except in Venezuelan specimens, see below), a slightly broader spot in forewing cell Cu<sub>2</sub>-Cu<sub>1</sub>, no dark red-brown scaling at the discal cell end on the dorsal forewing and well defined yellow-brown apical markings on the ventral forewing. The nominotypical subspecies additionally differs by having pale purplish shading proximal to the inner submarginal ocelli on the ventral hindwing. The male genitalia differ from those of both *H. kefersteini* and *H. cinderella* by having much longer ventral projections from the juxta, which extend beyond the ventral edge of the valvae, and valvae that are constricted at the posterior tip in lateral view.

The nominotypical subspecies is uncommon in lower Andean cloud forest habitats from 600 to 1700 m, this altitudinal range being noticeably lower than that of its close relatives *H. kefersteini* and *H. cinderella*. The majority of known specimens are from the western slopes in Colombia and Ecuador, but the species also occurs in the eastern Andes. Specimens from eastern Ecuador and Peru do not differ appreciably from western specimens, but the few specimens we have seen from the eastern slopes of the Venezuelan Mérida range have reduced white postdiscal spots at the dorsal forewing costa and more yellowish labial palpi, and additional material may show this population to represent a distinct subspecies. In Ecuador, males have been encountered perching from 6 to 8 m above the ground on the tips of leaves, in large light gaps or clearings on hilltops during sunny periods in the middle of the day. Males are also attracted to traps baited with rotting fish in primary forest light gaps along ridgetops. Females have been observed searching for oviposition sites along forest edges.

***Hypanartia trimaculata autumnata* Willmott, Hall & Lamas, ssp.n.** (Figs 8A; 21A–C)

Both sexes differ consistently from the nominotypical subspecies in the following respects. *Dorsal surface:* Border ocellus (element h) typically expressed as a tiny white spot in cell M<sub>2</sub>-M<sub>1</sub> of forewing. *Ventral surface:* Ground colour darker, more orange-brown on hindwing, especially in distal

half, pale purplish scaling proximal to element g on hindwing absent; postdiscal hindwing line (element f) of more even thickness and more heavily lined with red-brown. *Head:* Ventral surface of labial palpi yellowish. *Male genitalia and terminal tergite* (Fig. 21A–C): The two specimens dissected (the holotype and one from Guatemala) show two slight genitalic and abdominal tergite differences: valvae narrower at posterior tip and no small lateral projections just before tip of ventral tergite. Deeper tegumen, apparent in illustrated genitalia of this subspecies, not a consistent difference.

*Type material.* *Holotype*, ♂, COSTA RICA: San José, Parque [Braulio] Carrillo, 30 Jun 1980 (G. B. Small) (USNM). *Paratypes*, PANAMA: Chiriquí, 1♀, Cerro Colorado, 1450 m, 10 Aug 1979 (G. B. Small) (USNM). MEXICO: Chiapas, 1♂, Santa Rosa Comitán, Apr 1959 (T. Escalante) (AME); San Luis Potosí, 1♀, El Salto Falls, 20 Oct 1970 (H. L. King) (FSCA); Veracruz, 1♂, Fortín de las Flores, Planta de la Cervecería, Ing. Daniel Rabago Res., 2500–3000 ft, 20 May 1965 (H. V. Weems, Jr) (FSCA); Puebla, 3♂, 1♀, Tequezuitla, 625 m, 13 Sep 1981 (L. González-Cota) (MUSM); 1♂, same data, 10 Aug 1981 (MUSM). GUATEMALA: Baja Verapaz, 2♂, Purulá (Champion) (BMNH(M)). COSTA RICA: San José, Cerro de la Muerte, 1600 m, 6 Dec 1971 (H. L. King) (FSCA). PANAMA: Chiriquí, 1♂, Cerro Punta, El Volcán Chiriquí, 4 Mar 1936 (W. J. Gertsch) (AMNH); 1♂, Potrerillos, 3600 ft, 1 Jan 1973 (H. L. King) (FSCA).

*Etymology.* The name is derived from the Latin *autumnus*, meaning autumnal, with reference to the rich yellow and red ventral colours which characterize this subspecies.

*Discussion.* *Hypanartia trimaculata autumnata* ranges from Mexico to Panama, and in eastern Panama individuals with wing patterns transitional to the nominotypical subspecies occur (the labial palpi are also greyish white). Nevertheless, both the nominotypical subspecies and this subspecies are phenotypically stable over virtually their entire known ranges, and given the close similarity of members of the *H. kefersteini* species group and probable low gene flow between the Andes and montane Central America, we believe that both phenotypes merit taxonomic recognition. DeVries (1987) reported that this taxon (as *H. kefersteini*) occurs in cloud forest habitats from 800 m to 1900 m in Costa Rica, typically near rivers. He stated: ‘males visit water seepage at landslips and along riverbanks, and during the morning they perch high in the forest canopy’. Young (1976) reared this taxon on *Pilea* (Urticaceae), and described the egg, larva and pupa (as *H. kefersteini*).

***Hypanartia kefersteini* (Doubleday, [1847])** (Figs 8B; 22A–C)

*Eurema kefersteini* Doubleday, [1847]: Pl. 24, Fig. 4. Type locality: Venezuela. Lectotype ♂ (here designated by G.L.), BMNH (examined).

*Identification and taxonomy.* Typical FW length 24 mm. *Hypanartia kefersteini* is most similar to *H. cinderella* and

*H. trimaculata* (described here), and it is distinguished in those species accounts. Its ventral pattern is one of the most variable in the genus; in particular, the distal half of the hindwing varies from dull brown to rich orange-brown (throughout the range of the species). Although the postdiscal hindwing line typically narrows towards the tornus, it may also rarely be of even width throughout (in some Venezuelan specimens).

The lectotype bears the following labels: 'SYNTYPE/Eurema kefersteini/Doubleday/det. S. M. North. 1984.', 'B.M. TYPE/No. Rh.8641/Eurema kefersteini/male D. & H.', 'Venezuela/49-9./Purch. from. Dyson.', 'kefersteini, D. & H./Agrees with/Figure. 4/pl. xxiv. Gen. Diurn. Lep.', 'Type' and 'SYN-TYPE', '47/9'.

**Biology.** This species is common from 1200 to 2800 m in the vicinity of primary cloud forest. Males are typically encountered flying swiftly along rivers, forest edges and roadsides or puddling, and may be attracted to rotting fish in forest light gaps.

**Distribution.** Venezuela to Ecuador (both Andean slopes) and Bolivia (east Andean slopes).

***Hypanartia cinderella* Lamas, Willmott & Hall, sp.n.**  
(Figs 8C,D; 23A–C)

**Male.** Forewing length 24.5 mm. Distal margin of forewing scalloped, produced at end of vein Cu2 into small rounded point and at apex into very angular extension; distal margin of hindwing scalloped, short triangular tail centred on cell Cu1-M3. **Dorsal surface:** Forewing ground colour black; basal third of wing dark red-brown (darker at very base), except for 2 large black blocks in discal cell (one in anterior half between elements b and c, one in posterior half between elements c and d) and a black line in cell 2A-Cu2 opposite base vein Cu2 (element d); red-brown submarginal dash in cell 2A-Cu2; 3 small postdiscal white spots in cells M3-M2 to M1-R5; large elongate, slightly concave, white mark in middle of cell Cu2-Cu1, small slightly concave white spot in distal half of cell M3-M2, 2 small subapical white marks in cells R5-R4 and R4-R3; fringe brown with white scaling in middle of all cells except Cu2-Cu1 and M2-M1. Hindwing dark red-brown (darker at very base) except for brown along anal margin (grey hairs at distal margin), costal margin, in apex and a brown mark at end of discal cell (discal spot), angular black submarginal spots (border ocelli, element h) in cells Cu2-Cu1 to M1-Rs and a continuous line of submarginal black crescent-shaped marks (element i); long brown hairs at anal margin; fringe brown with white scaling in middle of cells M1-Rs and Rs-Sc + R1. **Ventral surface:** Forewing ground colour brown, paler at anal margin; discal cell with element a and basal symmetry system red-brown, lined with pale blue; white mark at costa towards end of discal cell; distal white marks as on dorsal surface but purple-blue in costal mark; 2 small blue-pupilled black spots in cells M2-M1, M1-R5 (element h), all border ocelli posterior to cell M3-M2 and equivalent space in cell 2A-Cu2 surrounded by large yellow rings with a line of purple-blue scaling proximally; purple-blue submarginal markings between anal margin and vein M2, slight yellowish scaling in subapex between elements i

and j. Hindwing ground colour brown; dark brown postdiscal band (element f), lined proximally throughout with thin blue then thin dark brown; proximal half of wing faintly powdered with pale blue scaling; discal cell with element a and basal symmetry system orange brown, lined with pale blue; a small yellow square in posterior half at base of cell Rs-Sc + R1; distal half of wing orange-brown with a series of large submarginal black-pupilled ocelli (element h), element g darker orange-brown; uneven dark brown submarginal line (element i) with purple-blue distally in apex and tornus, brighter at tornus. **Head:** Ventral surface of labial palpi greyish white with short black hairs, dorsal surface dark red-brown. Eyes brown and densely setose, margins with cream scaling. Frons orange-brown. Antennal segments orange-brown with white scaling ventrally; clubs black, tips orange-brown. **Body:** Dorsal surface of thorax dark brown with long hairs which are dark green at certain angles, ventral surface pale orange-brown; dorsal surface of abdomen dark orange-brown, ventral surface dirty cream. Forelegs pale brown; femur of mid- and hindlegs pale brown, remainder brown. **Genitalia and terminal tergite** (Fig. 23A–C): Valvae bluntly triangular; juxta lacking prominent ventral processes (although small processes are present in some specimens, their size is continuously variable); vinculum broadening ventrally; saccus narrow; tegumen high and narrow, uncus in posterior view moderately cleft; terminal tergite in lateral view angular, tip sharply hooked ventrally; tip in ventral view evenly tapering and pointed.

**Female.** Differs from the male in the following respects: wing shape broader, hindwing slightly more angular.

**Type material.** *Holotype*, ♂, PERU: Amazonas: Cordillera del Cóndor, PV3 (Alfonso Ugarte), 1000–1200 m, 03°55'S, 78°26'W, 18 Jul 1994 (G. Lamas) (MUSM). *Paratypes*, VENEZUELA: Táchira, 1♀, Funda Piedra Blanca, Qbda. La Florida, above San Vicente, Parque Nacional El Tamá 2000–2350 m, 10 Apr 1995 (F. Rey) (AN); 1♀, same data as preceding, 30 Sep 1998 (AN); 1♂, Umuquena, 1300 m (J. Joly, J. Salcedo & J. Clavijo) (MIZA); Mérida, 1♂, Chorreras de las Gonzalez, via Jají, 1700 m, 5 Sep 1997 (A. Orellana) (AO); 1♀, same data as preceding except 1675 m (AO); 1♂, La Carbonera, S de La Azulita, 20 Feb 1978 (E. Inciarte M.) (MALUZ); 1♂, Río La Lejía, via La Mesa, 19 Aug 1978 (J.B. Rodríguez) (BR); Barinas, 1♂, Barinitas, 1000 m 16 Dec 1968 (C.P. Bermudez) (R). COLOMBIA: Boyacá, 1♂, Muzo (BMNH(M)); Huila, 1♂, Garzón, Mar 1987 (J. Urbina) (JFL); Caldas, 1♂, Manizales, Bosque Municipal, Mar 1980 (J. H. Vélez) (MUSM); Valle del Cauca, 7♂, Cali, 1000 m, 15 Jun 1972, 18 and 29 Aug 1973, 29 Aug 1976 (L. Denhez) (MIZA). ECUADOR: Pichincha, 1♂, Reserva El Pahuma, km 13 Nanegalito-Quito Rd, 1900 m, 31 Aug 1996 (K. R. Willmott) (KWJH); Cotopaxi, 1♂, Qbda. Milagro, Latacunga-Quevedo Rd, 1000 m, 6–7 Aug 1996 (K. R. Willmott) (KWJH); 2♂, Río Mulatos, 2600 m, 19–20 Mar 1972 (S. E. Velástegui) (MIZA); Sucumbíos, 1♂, Río Sucio, nr La Bonita, 1800 m, 20–22 Nov 1996 (K. R. Willmott) (KWJH); Napo, 1♂, 33 km N Tena, 27 km E on Loreto Rd, 3600 ft, 2 Nov 1988 (J. S. Miller) (AMNH); 2♂, Misahuallí, 650 m, Mar 1975 (S. E. Velástegui) (MIZA); Tungurahua, 1♂, Río Negro, 4000 ft, 7 Jan 1980 (C. M. Stevens) (FSCA); 1♂,

Río Machay 1700 m, 12 Sep 1993 (J. P. W. Hall) (KWJH); 1 ♂, Río Topo, 1200 m, 19 Feb 1974 (S. E. Velástegui) (MIZA); Morona-Santiago, 1 ♂, Cordillera del Cóndor, Camp Achupalla, 15 km E Gualaquiza, 2100–2200 m, 03°27'S, 78°21'W, 23 Jul 1993 (T. A. Parker) (MUSM); Zamora-Chinchipe, 1 ♂, Qbda. San Ramón, Zamora-Loja Rd, 1700 m, 27–29 Oct 1997 (K. R. Willmott) (KWJH); 4 ♂, Zamora, 3–4000 ft (O. T. Baron) (BMNH(R)). PERU: Amazonas, 1 ♂, Huambo, IV<sup>c</sup> Trim, 1889 (M. de Mathan) (BMNH(M)); 2 ♂, same locality data as holotype, 21 Jul 1994 (MUSM); 1 ♂, entre Buenos Aires y Yamborasbamba, 28 Oct 1977 (A. Luscombe) (MUSM); 1 ♂, Mendoza, 1500 m (B. Calderón) (MUSM); San Martín, 1 ♂, Parque Nacional Abiseo, Huicungo, Macedonio, 2400–2600 m, 3 Aug 1990 (M. Medina) (MUSM); Huánuco, 1 ♂, 13 km S of Tingo María, Tambillo Chico Canyon, 14 Jun 1982 (P. J. Eliazar) (FSCA); 1 ♂, Chinchao, 1900 m, 2 May 1978 (G. Lamas) (MUSM); 1 ♂, Tingo María, 28 Aug 1969 (Y. Villena) (MUSM); 2 ♂, Tingo María (MUSM); 5 ♂, Tingo María (M. Rojas) (MIZA); 1 ♂, Tingo María, 30 July 1980 (D. & J. Jenkins) (AME); Pasco, 1 ♂, Pozuzo (AME); 1 ♂, Oxapampa (MUSM); Junín, 1 ♂, Chanchamayo (K. L. E. Ford) (B.M. 1958–338) (BMNH(M)); 1 ♂, San Luis de Shuaro, Apr 1930 (MUSM); 1 ♂, same locality data as preceding, Aug 1944 (C. A. Ridoutt) (MUSM); Cuzco, 1 ♂, Río Cosñipata, Yanamayo 2000 m, 6–11 Feb 1975 (G. Lamas) (MUSM); 2 ♂, Río Cosñipata, 0–7 km E. Buenos Aires, 2–2300 m, 6 Dec 1979 (G. Lamas) (MUSM); 1 ♂, Pillahuata, 2500 m, 15 Aug 1982 (M. Matthews) (MUSM); Puno, 1 ♂, Río Inambari to Limbani, Feb 1904 (G. Ockenden) (BMNH(R)). BOLIVIA: Cochabamba, 5 ♂, Yungas del Espíritu Santo, 1888–89 (P. Germain) (BMNH(M)); 6 ♂, Chapare, Alto Palmar, 1100 m (F. Steinbach) (MIZA); 1 ♂, Chapare, Alto Palmar, 1100 m, 17°04'S, 65°18'W, Nov 1965 (F. Steinbach) (MUSM); La Paz, 1 ♂, Caranavi, 1200 m, Feb 1989 (C. Tello) (MUSM).

*Etymology.* This species is named after the fairy tale character Cinderella, who, like this species, was a long neglected and overlooked sister.

*Discussion.* *Hypanartia cinderella* has long been confused with the very similar *H. kefersteini*. It consistently differs from that species by having slightly less pronounced scalloping at the distal margins of both wings, a shorter hindwing tail, slightly concave distal white spots in cells Cu2-Cu1 and M3-M2 of the forewing, and an even instead of scalloped postdiscal line below vein Cu2 on the ventral hindwing. The entire postdiscal line on the ventral hindwing of *H. cinderella* is generally of a more even thickness than it is in *H. kefersteini*, although this character does not apply to some specimens of the latter species, including one of the paralectotypes. *Hypanartia cinderella* also consistently has a rich orange-brown distal half to the ventral hindwing, whereas in *H. kefersteini* this region varies from a similar orange-brown to a dull pale brown. The two species exhibit no consistent male genitalic differences; whereas some specimens of *H. cinderella* have ventral projections on the juxta, their size is variable and they may be entirely absent.

*Hypanartia cinderella* occurs commonly from Venezuela to Bolivia between 1000 m and 2600 m, typically in equal

abundance and sympatry with its sister species *H. kefersteini*. Its habits are the same as that species.

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**Appendix 1.** Characters used in phylogenetic analysis.*Appendages*

1. *Ventral surface of labial palpi*: (0) yellowish; (1) whitish grey.

*Wing shape* (Figs 5–8)

2. *Pronounced tail on vein Cu2 of hindwing*: (0) present; (1) absent.
3. *Hindwing tail on vein M3*: (0) generally short, triangular and pointed; (1) long and rounded at tip.

*Dorsal forewing pattern* (Figs 5–8)

4. *Pattern*: (0) predominantly orange; (1) various shades of brown and black; (2) predominantly red-brown.
5. *If dorsal surface predominantly red-brown (4:2), red-brown coloration in tornal submargin of DFW extends*: (0) –; (1) as far as vein Cu2, sometimes faintly into cell Cu2-Cu1; (2) prominently into cell Cu1-M3.
6. *Black scaling in discal cell of DFW opposite base of vein Cu2*: (0) present filling entire area between 2 elements of basal symmetry system (b,c); (1) present as spot near costa only; (2) absent.
7. *Black scaling in discal cell of DFW opposite middle of cell Cu2-Cul, between distal element of basal symmetry system (c) and proximal band of central symmetry system (d)*: (0) absent; (1) present as a complete band across cell; (2) present as a band truncated by red-brown scaling near costa.
8. *Pale postdiscal spots at costa of DFW, at distal edge of distal band of central symmetry system (f)*: (0) present; (1) absent.
9. *If pale postdiscal spots present at costa of DFW (8:0)*: (0) spots not arranged in a line, that in cell M2-M1 displaced distally with respect to remainder; (1) spots arranged in a line, with a straight basal edge.
10. *If postdiscal spots at costa of DFW present (8:0), spots*: (0) pure white; (1) orange or pale orange.
11. *If postdiscal spots at costa of DFW present (8:0), spots*: (0) opaque; (1) transparent.
12. *Pale postdiscal spot in cell Cu2-Cul of DFW, corresponding to border ocelli (h)*: (0) absent; (1) present.
13. *If pale postdiscal spot in cell Cu2-Cul of DFW present (12:1), spot*: (0) –; (1) opaque; (2) transparent.
14. *If pale postdiscal spot in cell Cu2-Cul of DFW present (12:1), spot positioned towards*: (0) –; (1) base of cell; (2) middle of cell.

*Dorsal hindwing pattern* (Figs 5–8)

15. *DHW anterior of vein Sc+R1*: (0) with some orange colouration; (1) entirely dark brown.

16. *Dark brown postdiscal band on DFW, corresponding to distal band of central symmetry system (f)*: (0) absent or faint, not extending into cell Cu2-Cu1; (1) prominent, extending into cell 2A-Cu2.
17. *Submarginal black spots on DHW in cells M3-M2 to M1-R5, corresponding to border ocelli (h)*: (0) isolated; (1) fused to form a wedge.
18. *If submarginal spots on DHW in cells M3-M2 to M1-R5 isolated (17:0), spots*: (0) circular; (1) oval or rectangular.
19. *Dark submarginal ocellus in cell 2A-Cu2 on DHW, corresponding to border ocelli (h)*: (0) absent; (1) present.
20. *Black submarginal line between tornus and vein M3 on DHW (element j, submarginal band)*: (0) pronounced and equal in width to immediately basal submarginal line (element i, parafoveal element); (1) reduced or absent.

*Ventral forewing pattern* (Figs 5–8)

21. *Pale marking at VFW costa, between elements c and d*: (0) wide and yellowish; (1) narrow and whitish.
22. *Distal (f) and proximal (d) bands of central symmetry system on VFW*: (0) separate and distinct in cell 2A-Cu2; (1) fused in cell 2A-Cu2 to form a diagonal black band with basal symmetry system in discal cell.
23. *Pale postdiscal line in cell 2A-Cu2 of VFW, bordering basal edge of element g*: (0) absent; (1) pale purplish, indistinct and uneven; (2) bluish purple, thin, sharply defined and straight; (3) pale whitish grey and uneven.
24. *Submarginal ocellus (element h) in cell M3-M2 of VFW*: (0) substantially larger than that in cell M2-M1; (1) absent, of similar size, or slightly larger than that in cell M2-M1.
25. *If submarginal ocellus (element h) in cell M3-M2 of VFW substantially larger than that in cell M2-M1 (24:0), ocellus*: (0) rounded; (1) a thin dash.
26. *Submarginal ocellus in cell Cu1-M3 of VFW (border ocelli, h) of males*: (0) present, with a central pupil; (1) present, circular and yellow, without a pupil; (2) absent.
27. *Thin dark submarginal markings in cells M2-M1 to R4-R3 of VFW apex (element i, parafoveal element)*: (0) form a continuous and jagged line; (1) isolated in each cell.
28. *Pale yellowish scaling between elements i and j in VFW apex*: (0) present; (1) absent.

*Ventral hindwing pattern* (Figs 5–8)

29. *Pale yellowish or whitish scaling anterior of vein Sc+R1 on VHW*: (0) present; (1) absent.
30. *Second dark bar from base in cell Rs-Sc+R1 of VHW (element d)*: (0) approximately straight, sloping towards wing apex, or vertical, bordered basally by pale scaling extending across most of cell; (1) sharply angled and sloping towards wing base, fusing with element c alongside vein Rs to enclose a small yellow block in posterior half of cell.

31. *Bar in middle of discal cell of VHW (basal symmetry system, b,c)*: (0) entire or 2 touching circles; (1) 2 isolated spots.
32. *Dark postdiscal line on VHW (distal band of central symmetry system, element f)*: (0) entire; (1) reduced or absent in cells M2-MI to M1-R5.
33. *Dark postdiscal line on FHW (distal band of central symmetry system, element f)*: (0) uneven; (1) straight.
34. *Ground colour on VFW*: (0) matte brown distal of central symmetry system (element f), with or without orange scaling; (1) shining, steely grey-brown.
35. *Submarginal ocelli (border ocelli, h) on VHW*: (0) arranged in a smoothly curving line; (1) disjointed at vein M3.
36. *Greenish-grey scaling at submargin of VHW tornus, at distal edge of parafoveal elements (i)*: (0) prominent; (1) thin or absent.

#### Male abdomen (Figs 9–23)

37. *Last male tergite*: (0) simple, similar to remaining tergites; (1) modified, terminating with a strongly sclerotized, sharp point (a superuncus) (e.g. Fig. 9B).
38. *If superuncus present (37:1), in ventral view*: (0) – ; (1) with a single, sharp terminal projection with angular lateral projections (Fig. 9C); (2) smoothly triangular with straight basal edge (e.g. Fig. 11C); (3) with 3 approximately equal terminal projections (e.g. Fig. 13C); (4) sharply triangular with an indented basal edge (e.g. Fig. 19C); (5) squared at tip with a small central point and straight basal edge (e.g. Fig. 18C).
39. *If superuncus present (37:1), tip in lateral view*: (0) – ; (1) smoothly tapering (e.g. Fig. 11B); (2) triangular, with a dorsal ‘hump’ just before tip (e.g. Fig. 12B).

#### Male genitalia (Figs 9–24)

40. *Tissue connecting uncus to last tergite*: (0) weakly sclerotized (Fig. 24A); (1) more heavily sclerotized and tightly folded back over tegumen (e.g. Fig. 9A).

41. *Tegumen*: (0) gradually tapering anteriorly in dorsal view (Fig. 24A); (1) sharply laterally constricted (e.g. Fig. 11D).
42. *Uncus in posterior view*: (0) broad with shallow indent (Fig. 24B); (1) bifurcate with tips pointed or rounded (Fig. 10D); (2) blunt and angular (Fig. 11D).
43. *Gnathos*: (0) heavily sclerotized, forming 2 long, posteriorly pointing projections (Fig. 24B); (1) a simple ‘U’-shape, with projections connected by soft tissue; (2) joined and continuously sclerotized.
44. *Vinculum in lateral view*: (0) narrowest at base of saccus (Fig. 24A); (1) of approximately even width (e.g. Fig. 9A); (2) broadest at base of saccus (e.g. Fig. 14A).
45. *Saccus*: (0) absent; (1) present, anterior tip broad (e.g. Fig. 9A); (2) present, anterior tip narrow or of medium width (e.g. Fig. 13A).
46. *Ventral base of valvae*: (0) join anterior of vinculum, forming a support for aedeagus (Fig. 24A,C); (1) simple and closely appressed posterior of vinculum (e.g. Fig. 11E); (2) simple and separate (Fig. 13D).
47. *Valvae in lateral view*: (0) with four projections of varying length (Fig. 24A); (1) with short upper and lower projections (e.g. Fig. 12A); (2) approximately triangular (e.g. Fig. 13A).
48. *Aedeagus in lateral view*: (0) curved ventrally (Fig. 24A); (1) straight or mildly curved dorsally (e.g. Fig. 9A); (2) strongly curved dorsally (e.g. Fig. 16A).
49. *Tip of aedeagus in dorsal view*: (0) smoothly tapering (e.g. Fig. 10E); (1) with 2 lateral projections (Fig. 11E).
50. *Thin, distal portion of aedeagus*: (0) similar length to broader basal portion (e.g. Fig. 10A); (1) substantially longer than broader basal portion (e.g. Fig. 11A).
51. *Juxta*: (0) absent or unsclerotized soft tissue; (1) a thin, weakly sclerotized ‘ribbon’ (Fig. 11E); (2) a broad, well sclerotized plate (e.g. Fig. 10E).
52. *If juxta present (51: 1 and 2), posteriorly pointing hairs on juxta*: (0) – ; (1) absent or sparse; (2) dense (Fig. 11E).
53. *If juxta present (51: 1 and 2), paired ventral projections on juxta*: (0) – ; (1) absent or weak (e.g. Fig. 16A); (2) pronounced (e.g. Fig. 15A).

**Appendix 2.** Character matrix for *Hypanartia* and outgroup *Antanartia delius*. Non-applicable and polymorphic characters are coded with a ‘?’.

	1	1 2	2 3	3 4	4 5	
	5 0	5 0	5 0	5 0	5 0	
<i>delius</i>	000000000	000000000	000000000	000000000	000000000	000
<i>paullus</i>	000002001	0000001?00	000000000	0000101111	1111111100	211
<i>bella</i>	010000001	0000001?00	010000000	0100101211	1111111200	211
<i>lethe</i>	010000001	0000001?00	010000000	0100101221	1211111111	121
<i>godmanii</i>	01000201??	?000000000	0101?00000	0100101211	1211111111	121
<i>charon</i>	11010000??	?000100001	0001?20100	0000111321	1122222200	212
<i>dione</i>	01110001??	?121110110	1021?21110	1000111321	1122222200	212
<i>celestia</i>	1111000010	0121100011	1031001100	1000111211	1122222200	212
<i>splendida</i>	1110021010	1121010111	0001?20001	0010111411	1122222200	211
<i>fassli</i>	1112221010	0122100011	1020121011	0001111411	1122222200	212
<i>christophori</i>	1112221010	1122100011	1020121011	0011111511	1122222200	212
<i>lindigh</i>	1112221010	1122100011	1020121011	0011111511	1122222200	212
<i>frimaculata</i>	?102111010	0112100001	1010010011	0000111421	1122222200	212
<i>kefersteinii</i>	1102112010	0112100001	1010010011	0000111421	1122222200	211
<i>cinderella</i>	1102112010	0112100001	1010010011	0000111421	1122222200	211

**Appendix 3.** Universal synapomorphies for *Hypanartia*.

1. The inner submarginal line of ocelli on the ventral hindwing is disjointed at vein M3 (this also occurs in certain other nymphaline genera, such as *Polygonia*).
2. The eighth male abdominal tergite is heavily sclerotized and modified to form a ‘superuncus’. A superuncus also occurs in certain genera in the butterfly families Papilionidae (e.g. *Ornithoptera* Boisduval) and Pieridae (e.g. *Colias* Fabricius and *Zerene* Hübner) (Kuznetsov, 1915; personal observation), but in *Colias* and *Zerene*, at least, it consists only of the posterior margin of the tergite being folded to form a blunt lobe, which is no more heavily sclerotized than the remaining tergites. In *Hypanartia*, the tip is heavily sclerotized and bears long setae.
3. The tissue connecting the eighth male abdominal tergite to the genitalia is heavily sclerotized and tightly folded back over the tegumen.
4. The tegumen is laterally (not dorsally) compressed.