

# A phylogenetic reassessment of *Hyalenna* Forbes and *Dircenna* Doubleday, with a revision of *Hyalenna* (Lepidoptera: Nymphalidae: Ithomiinae)

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**Abstract.** A morphological study of adults and immature stages and a cladistic analysis were conducted to clarify the relationships amongst members of the sister nymphalid butterfly genera *Dircenna* Doubleday and *Hyalenna* Forbes. Two species formerly included in *Dircenna*, *Ithomia paradoxa* Staudinger and *Dircenna hugia* Schaus, clustered with *Ithomia perasippa*, the type species of *Hyalenna*. Therefore, the first two species are transferred from *Dircenna* to *Hyalenna* (**comb.n.**). *Hyalenna* and *Dircenna* as now conceived are both monophyletic and well supported by morphological apomorphies and branch support measures. The taxonomy and classification of *Hyalenna* are reviewed and seven species and twenty-four taxa are recognized, including one new species, *Hyalenna buckleyi* **sp.n.**, and eleven new subspecies: *Hyalenna paradoxa incachaca* **ssp.n.**, *H. perasippa valencia* **ssp.n.**, *H. perasippa ortygiosa* **ssp.n.**, *H. perasippa solitaria* **ssp.n.**, *H. buckleyi pomacocha* **ssp.n.**, *H. alidella exsulans* **ssp.n.**, *H. alidella cinereola* **ssp.n.**, *H. alidella vesca* **ssp.n.**, *H. sulmona balsamica* **ssp.n.**, *H. sulmona hyalina* **ssp.n.** and *H. sulmona tersa* **ssp.n.** A key for the identification of all taxa, and illustrations of male and female genitalia for all species and adult specimens of all taxa (where known), are presented. The natural history of each species is summarized and the immature stages of *H. paradoxa* and *H. sulmona* are described for the first time.

## Introduction

The systematics of the neotropical nymphalid butterfly subfamily Ithomiinae have been relatively well studied, at least in comparison with other Nymphalidae. Fox (1956, 1960, 1967) and Fox & Real (1971) partially revised the ithomiine genera, completing only about 105 of the *c.* 360 species (Lamas, 2004). Other workers further refined Fox's taxonomy (e.g. Brown, 1977, 1980; Lamas, 1979, 1988), so that our knowledge of these genera is relatively good, despite some notable recent discoveries (e.g. Willmott &

Lamas, 2004). However, the remainder of the subfamily, mostly within the three largest tribes, the Oleriini, Dircennini and Godyridini, and dominated by largely 'transparent' species inhabiting Andean cloud forests, has received little attention since Haensch's review nearly 100 years ago (Haensch, 1909–10). Therefore, this paper is the first of a series of taxonomic revisions treating the genera and species of these ithomiine tribes.

The small genus *Hyalenna* Forbes, 1942 contains some of the rarest species of the subfamily and exemplifies the taxonomic problems to be found amongst the larger 'transparent' genera. The first species description did not appear until 1869 (Hewitson, 1869) and, even today, *Hyalenna* material in many collections consists of fewer than five specimens, often placed uncertainly in an accession drawer or scattered randomly throughout the collection. The relationships between *Hyalenna* taxa and the true diversity of the genus have thus remained uncertain, in part as a result of this rarity. More

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significantly, intergrades between allopatric taxa are virtually unknown, because of the strong selection which maintains narrow hybrid zones between marked geographical races in mimetic butterflies (Mallet & Barton, 1989). Most taxa therefore have been treated as distinct species, but modern distributional data and clear morphological characters argue for the merging of some to create polytypic species (Lamas, 2004).

Hewitson (1869, 1877) placed the three species that he described in the genus *Ithomia* Hübner, 1816, his destination for virtually all transparent ithomiines, but subsequent authors placed the various species usually in *Episcada* Godman & Salvin, 1879, *Pteronymia* Butler & H. Druce, 1872 or *Dircenna* Doubleday, 1847, based on the similar hindwing venation (e.g. Haensch, 1909–10; Bryk, 1937). Forbes (1942) noted a distinctive character of the forewing venation which united several species in the *Dircennini*. Based on this character, he described the genus *Hyalenna*, with *Ithomia perasippa* Hewitson, 1877 as type species. Even so, Forbes included in the genus only five of the eight taxa known at that time with this venation character, with some confusion as to what names should be applied to them. The remaining three taxa eventually were transferred into *Hyalenna* by subsequent authors, including Brown & D'Almeida (1970), Lewis (1973), Mielke & Brown (1979) and D'Abbrera (1984).

To date, Forbes' forewing venation character has been regarded as a strong synapomorphy for *Hyalenna*, but cladistic analyses of the Ithomiinae (K. R. Willmott & A. V. L. Freitas, unpublished data) suggest that *Hyalenna* and its sister *Dircenna*, as formerly conceived, might not be monophyletic genera. Here, we conduct a cladistic analysis to revise the limits of these two genera and review the taxonomy of *Hyalenna*, describing one new species and eleven new subspecies, and summarize the little that is known of *Hyalenna* natural history.

## Materials and methods

### *Museum and field study*

Specimens were examined in major public and private collections in Europe and North and South America to record distributional data, study morphological variation, assess taxonomic diversity and locate type specimens. Six lectotypes are designated to ensure nomenclatural stability. The following collection codens and abbreviations are used in the text:

AFEN Andrew F. E. Neild collection, London, U.K.  
 AMNH American Museum of Natural History, New York, New York, U.S.A.  
 AS Andrei Sourakov collection, Gainesville, Florida, U.S.A.  
 AVLF André V. L. Freitas collection, Campinas, Brazil.  
 BMB Booth Museum of Natural History, Brighton, U.K.  
 BMN The Natural History Museum, London, U.K.

FV Fabio Vitale collection, Lecce, Italy.  
 GR Gabriel Rodríguez collection, Envigado, Colombia.  
 GTB Gerrit ten Broek collection, Krommenie, Holland.  
 IAVH Instituto Alexander von Humboldt, Villa de Leyva, Colombia.  
 ICNB Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia.  
 JFL Jean F. Le Crom collection, Bogotá, Colombia.  
 KSB Keith S. Brown, Jr. collection, Campinas, São Paulo, Brazil.  
 KWJH Keith Willmott & Jason Hall collection, Gainesville, Florida, U.S.A.  
 LMC Luis M. Constantino collection, Cali, Colombia.  
 MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.  
 MECN Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador.  
 MGCL McGuire Center for Lepidoptera and Biodiversity, University of Florida, Gainesville, Florida, U.S.A. (contains former Allyn Museum of Entomology).  
 MHNUC Museo de Historia Natural, Universidad de Caldas, Manizales, Colombia.  
 MNRJ Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil.  
 MUSM Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru.  
 MZSP Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.  
 OD Olivier Duviols collection, Provence, France.  
 OHM Olaf H. H. Mielke collection, Curitiba, Brazil.  
 PB Pierre Boyer collection, Le Puy Sainte Réparate, France.  
 SMF Senckenberg Museum, Frankfurt-am-Main, Germany.  
 SMTD Staatliches Museum für Tierkunde, Dresden, Germany.  
 UFP Universidade Federal do Paraná, Curitiba, Brazil.  
 USNM National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A.  
 ZMHU Museum für Naturkunde, Naturhistorisches Forschungsinstitut, Zentralinstitut der Humboldt Universität zu Berlin, Berlin, Germany.  
 ZSBS Zoologische Sammlung des Bayerischen Staates, Munich, Germany.  
 (D)FW (dorsal) forewing.  
 (V)HW (ventral) hindwing.

Morphology was studied using standard techniques, with the adult abdomen being soaked in hot 10% KOH for 10–15 min, dissected and subsequently stored in glycerol. Body morphology, dissections and immature stage material were studied using a binocular microscope at up to 50× magnification. Wing venation was drawn from wings cleared with bleach as well as from uncleared specimens. Hindwing androconial scales and other wing scales were examined *in situ*, after removal of the right forewing, using a binocular microscope at 50× magnification. Male androconial scales

were further examined in *Episcada apuleia* (Hewitson, 1868), *Dircenna jemina* (Geyer, 1837), *Hyalenna paradoxa*, *H. persippa* and *H. pascua*, as well as various other ithomiine species, using a Hitachi S2500 scanning electron microscope (Hitachi, Tokyo, Japan) at magnifications of up to 5000 $\times$ . Wing sections for examination were mounted on stubs with white glue and coated with a 20-nm layer of gold/palladium (95%/5%) using a Cressington Sputter Coater (Cressington Scientific Instruments, Valencia, PA, U.S.A.).

Field observations on the natural history of *Hyalenna* have been made by both authors in Colombia, Ecuador and Peru over the last two decades. Fieldwork consisted mainly of sampling ithomiine faunas in little-known regions, elevations or habitats to provide better distributional data, as well as making observations of adult behaviour. In some cases, dried *Heliotropium* (Boraginaceae) was used as a bait for sampling ithomiines, but no *Hyalenna* individuals were recorded by us at such baits. During a 10-week study of ithomiine immature stages in Ecuador, the immature stages of *H. paradoxa* and *H. sulmona* were located and reared (see descriptions below). During this study, Solanaceae plants encountered at sites between 1000 and 2700 m in two areas of eastern Ecuador (Loja-Zamora road, Zamora-Chinchipec and La Bonita-Lumbaquí road, Sucumbíos) were searched for ithomiine eggs and larvae. Solanaceae are larval host plants of most Ithomiinae, including known *Hyalenna* and all closely related genera (Drummond & Brown, 1987; Willmott & Mallet, 2004). Immature stages were collected and reared in plastic bags, with fresh leaves of the natural host plant provided every 2–3 days. Leaf material was removed from the bag just prior to pupation to permit the pupa to form freely. Photographs were taken of each instar, and cast larval skins, head capsules and specimens of larvae and pupae were preserved, where possible, in ethanol.

#### Cladistic analysis

The cladistic analysis included all thirteen currently recognized species in *Hyalenna* and *Dircenna* (see Lamas, 2004) (Appendix 1). In addition, approximately 100 representative ithomiine species from all genera were examined as part of a higher level phylogenetic analysis of the subfamily (K. R. Willmott & A. V. L. Freitas, unpublished data). This analysis demonstrates *Dircenna* and *Hyalenna* to form a clade that is sister to the remaining Dircennini, with the exception of *Callithomia* Bates, 1862. We chose *Episcada apuleia* as outgroup because its immature stages are known and because it has many plesiomorphic character states (unlike *Callithomia* and many *Pteronymia*, for example).

Characters were identified from both adult morphology (colour pattern, size, genital and abdominal structure and wing venation of both sexes, and male androconial scales) and immature stage morphology (Appendix 2). Uninformative characters which showed variation amongst the studied taxa were included because they might prove to be informative in analyses at other taxonomic levels, or

when more information (e.g. of immature stages) becomes available, and because character distance between taxa is relevant to many studies. Immature stage information was obtained from personal observations, Brown & Freitas (1994), Haber (2005) and Janzen & Hallwachs (2005). All characters were equally weighted and all multistate characters were treated as unordered.

The character matrix (Appendix 3) was analysed using PAUP\* 4.0b10 (Swofford, 1998), using 1000 random addition sequence heuristic searches with tree bisection and reconnection (TBR) branch swapping and maximum parsimony as the optimality criterion. Bootstrap values were calculated based on searches of 1000 resampled data matrices, with each search including ten random addition sequence replicates. Decay indices (Bremer, 1994) were calculated in PAUP from constraint trees generated by AUTODECAY 4.0 (Eriksson, 1998).

## Systematics

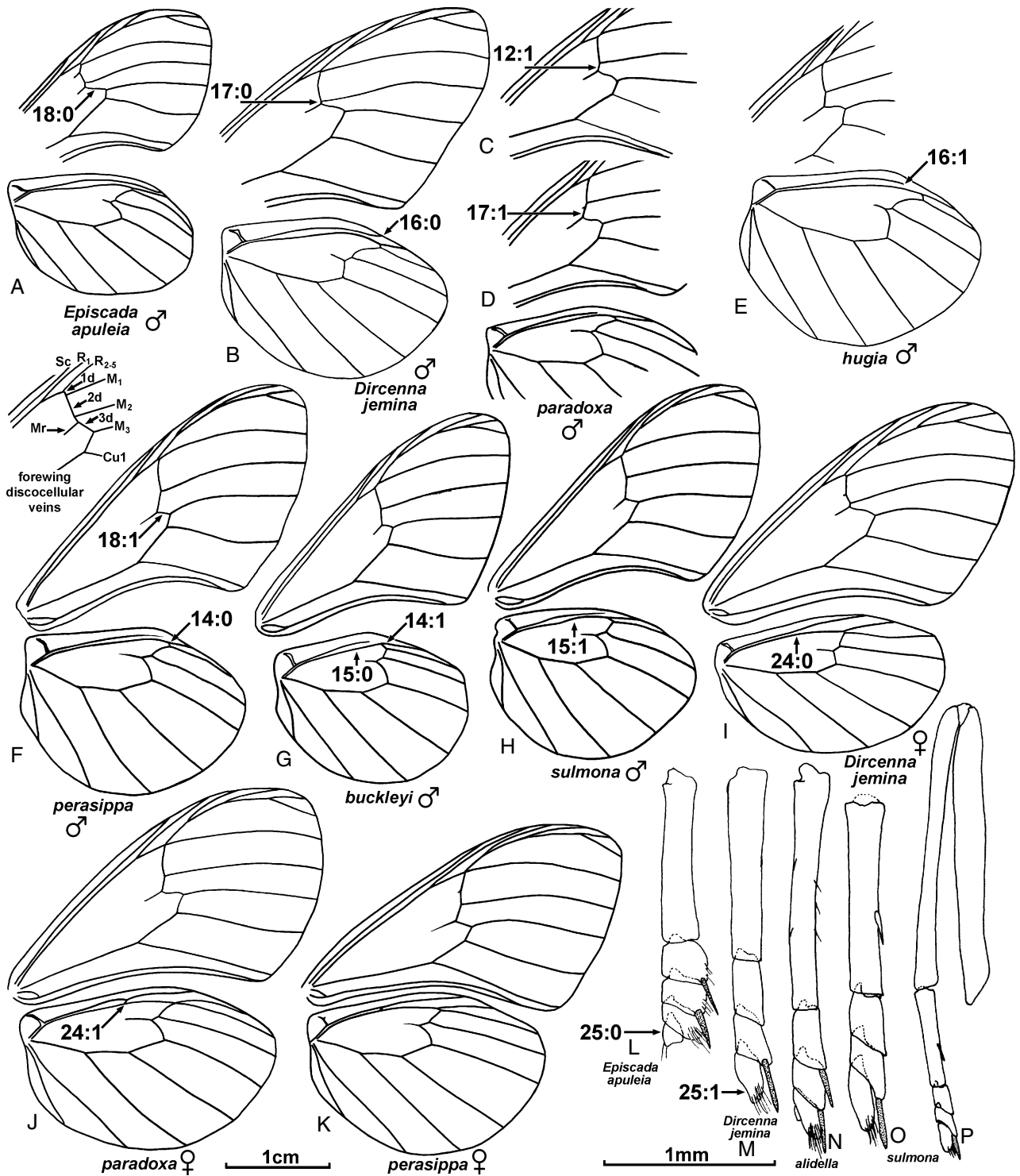
### Generic relationships

*Hyalenna* females have the mid-dorsal edge of the fused eighth sternites curved inwards, a synapomorphy for Dircennini + Godyradini (K. R. Willmott & A. V. L. Freitas, unpublished data), and, like other members of Dircennini (D'Almeida, 1941; Brown & D'Almeida, 1970), males have a strongly sclerotized gnathos. *Hyalenna* and *Dircenna* apparently form a sister clade to other dircennines, with the position of *Callithomia* unresolved (K. R. Willmott & A. V. L. Freitas, unpublished data).

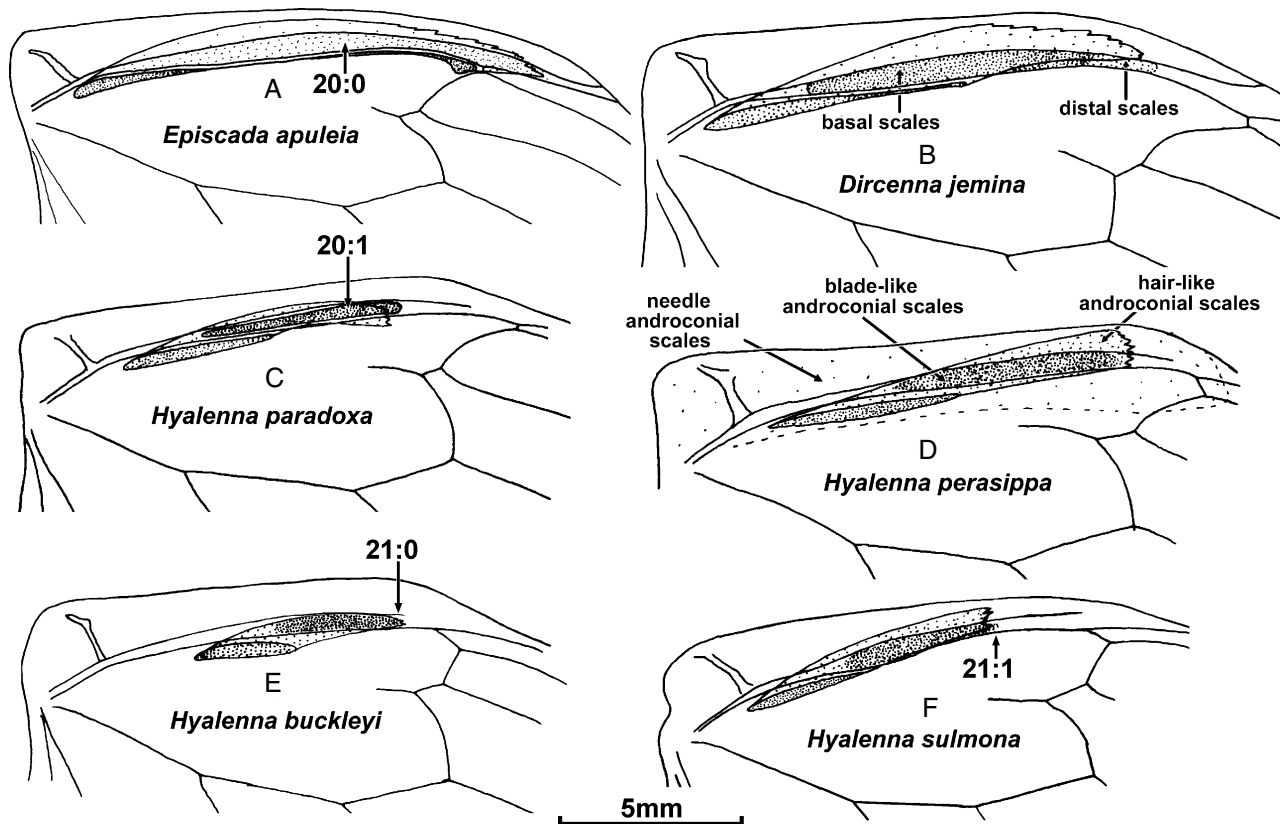
In *Dircenna* and *Hyalenna*, the female foreleg has only four tarsal segments, a unique synapomorphy within the Dircennini + Godyradini (char. 25:1; Fig. 1M–P). Although Forbes (1942) claimed that *Hyalenna* have a five-segmented female foreleg tarsus, and figured it as such (his fig. 5 – '*H. teresita*'), the figured specimen probably is *Pteronymia teresita* (Hewitson, 1863). Because of the rarity of female *Hyalenna* in collections, it seems that Forbes did not examine any other material. The shape of the sockets of the androconial scales underlying the DHW hair pencil in the male is a further synapomorphy for *Hyalenna* + *Dircenna* (char. 23:1; Fig. 3D–G). Additional probable synapomorphies for the two genera include the larvae being covered in short hairs (char. 1:1; Figs 3K; 4; 5; Brown & Freitas, 1994), the pupal cremaster bearing protuberances at the base (char. 8:1; Figs 3M; 4H; 5G; also found within Dircennini in *Callithomia*) and the mottled green and pale grey dorsal pattern of later instars (char. 2:1; Figs 3K; 4D; hardly visible in some *Hyalenna* as a result of the adoption of a uniform greyish green colour).

### Cladistic analysis and generic diagnosis

Morphological study of *Hyalenna* and *Dircenna* resulted in the coding of forty-five characters (thirty-five



**Fig. 1.** Wing venation and female foreleg morphology. Male wing venation: A, *Episcada apuleia apuleia*; B, *Dircenna jemina jemina*; C, *Hyaletta paradoxa praestigiosa*, Ecuador, Morona-Santiago (forewing discal area only); D, *H. paradoxa praestigiosa*, Ecuador, Sucumbios; E, *H. hugia* (lectotype); F, *H. perasippa perasippa*; G, *H. buckleyi buckleyi* (holotype); H, *H. sulmona lobusa*. Female wing venation: I, *D. j. jemina*; J, *H. paradoxa paradoxa*, Colombia, Antioquia; K, *H. perasippa valencia* (holotype). Female foreleg tarsus (except P, tarsus, tibia and femur): L, *E. apuleia*; M, *D. j. jemina*; N, *H. alidella alidella*; O, P, *H. sulmona lobusa*.



**Fig. 2.** Male hindwing discal cell and androconial scales (extent of needle androconial scales similar for all species, shown on *Hyalenna perasippa* only): A, *Episcada apuleia apuleia*; B, *Dircenna jemina jemina*; C, *H. paradoxa praestigiosa*; D, *H. perasippa perasippa*; E, *H. buckleyi buckleyi* (holotype); F, *H. sulmona lobusa*.

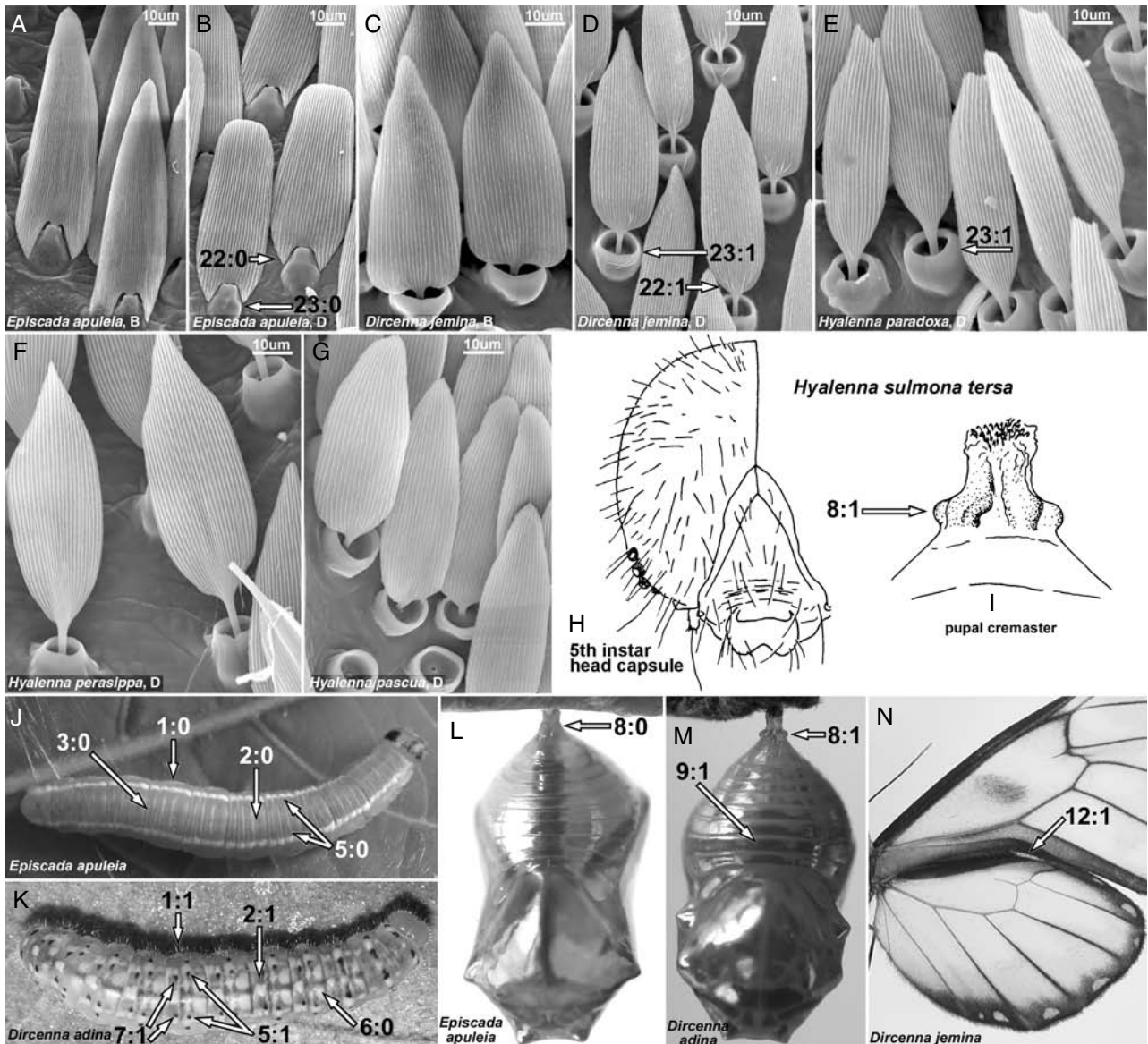
informative) (Appendix 2), illustrated in Figs 1–18. The cladistic analysis found twelve most parsimonious trees with a length of 74 steps (CI = 0.71, excluding uninformative characters, RI = 0.86), summarized as a strict consensus in Fig. 19. We illustrate character changes in Fig. 19, predominantly under ACCTRAN optimization and favouring character reversals or losses over multiple origins.

Two principal clades were found, one containing the type species of *Dircenna* (*D. jemina*) and the other containing the type species of *Hyalenna* (*H. perasippa*). The latter clade also contained two species placed formerly in *Dircenna*: *Ithomia paradoxa* Staudinger and *Dircenna hugia* Schaus, which form a sister clade to *H. perasippa*. The former placement of these taxa in *Dircenna* has been based on the presence of a cross-vein (R1) linking Rs and Sc + R<sub>1</sub> on the female hindwing (Fig. 1J; Lamas, 1994, 2004). However, this vein is present prominently in *H. perasippa* (Fig. 1K), some *Ceratinia* Hübner, 1816 and present but inconspicuous in other *Hyalenna*. In his original description of *Hyalenna*, Forbes noted that the type species, *H. perasippa*, and other species he included in the genus, shared the unique derived character of forewing vein Mr being placed nearer the base of vein M<sub>3</sub> than M<sub>2</sub>. Our analysis indicates that this character is homoplasious and that *Hyalenna*

species as conceived by Forbes share at least six other synapomorphies with *I. paradoxa* and *D. hugia* (see Table 1). Therefore, we transfer *I. paradoxa*, *D. hugia* and their currently recognized subspecies, *Pteronymia catenata* Kaye and *Episcada praestigiosa* Haensch, to *Hyalenna* (comb.n.). With their removal, both *Dircenna* and *Hyalenna* become monophyletic genera that are diagnosed readily by several morphological autapomorphies (Table 1).

#### Phylogeny of *Hyalenna*

Two main clades were found within *Hyalenna*. *H. perasippa* is sister to *hugia* + *paradoxa*, but the character support for this clade of three species is weak (Fig. 19). Larval character 6 is unknown in *H. hugia* and *H. perasippa* and has likely been lost in other *Hyalenna*; the absence of marginal spots in the female (char. 13:0; Figs 6, 7) is a synapomorphy only if it applies to the unknown female of *H. hugia*, which we regard as highly unlikely; and the 'hood'-like ductus ejaculatorius in the male genitalia (char. 40:1; Fig. 12D, I) is common in other dircennines (e.g. *Episcada*, *Pteronymia*). More characters are needed to clarify this part of the tree and it remains possible that



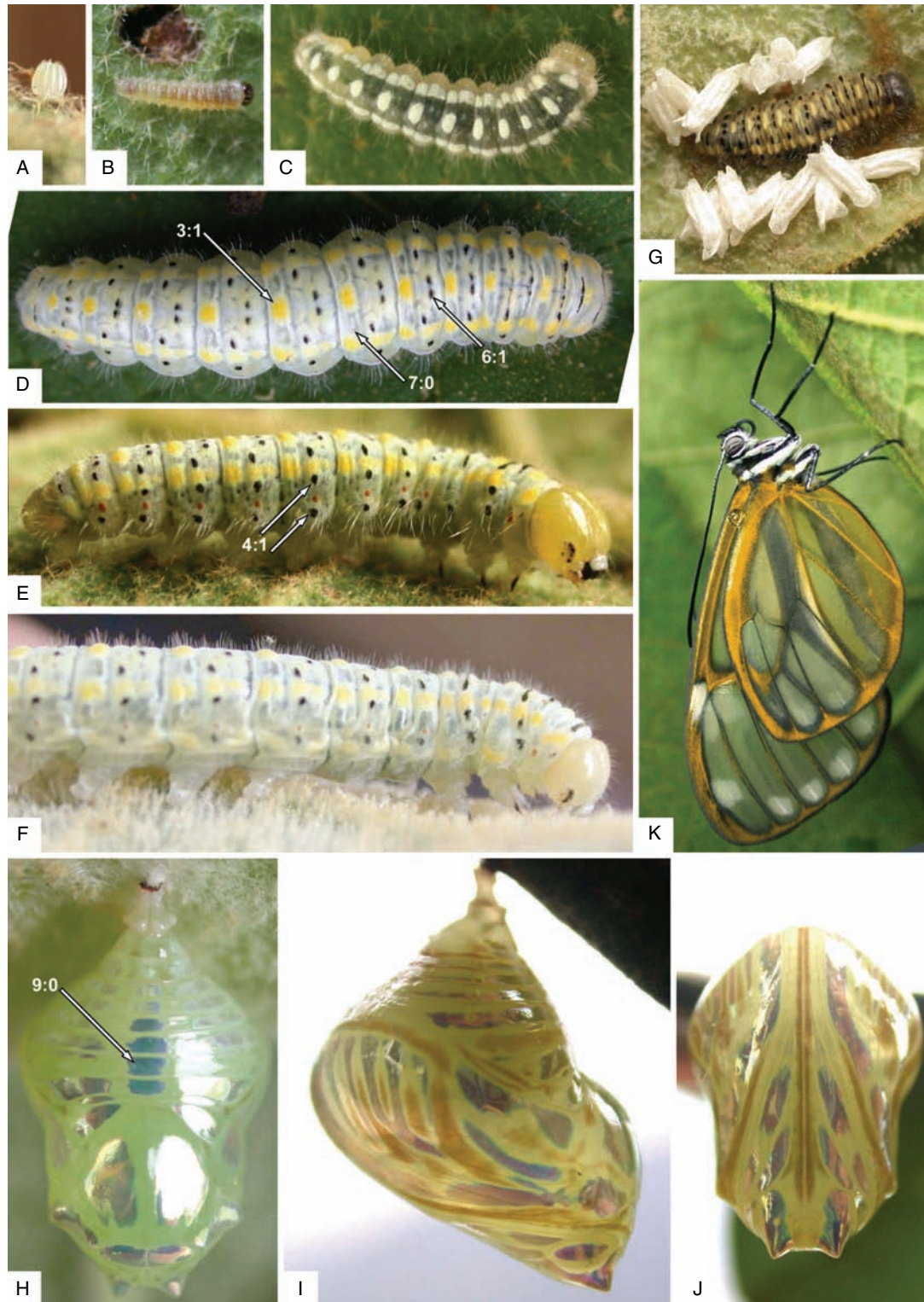
**Fig. 3.** Morphology of *Episcada*, *Dircenna* and *Hyalenna*. Male dorsal hindwing androconial scales between veins Rs and Sc + R<sub>1</sub> (see Fig. 2B for location of basal (B) and distal (D) scales): A, *Episcada apuleia apuleia*, basal scales; B, *E. a. apuleia*, distal scales; C, *Dircenna jemina jemina*, basal scales; D, *D. j. jemina*, distal scales; E, *Hyalenna paradoxa praestigiosa*, distal scales; F, *H. perasippa ortygiosa*, distal scales; G, *H. pascua*, distal scales. Immature stages: H, *Hyalenna sulmona tersa*, Ecuador, Sucumbíos, fifth instar larva head capsule; I, same as H except pupal cremaster, dorsal view; J, *E. a. apuleia* (KRW-265), Ecuador, Zamora-Chinchipe, fifth instar larva dorsal view; K, *D. adina lorica* Weymer, 1875 (KRW-9), Ecuador, Sucumbíos, fifth instar larva dorsal view; L, *E. a. apuleia* (KRW-215), Ecuador, Zamora-Chinchipe, pupa dorsal view; M, *D. adina lorica* (KRW-26), Ecuador, Sucumbíos, pupa dorsal view. Male ventral wing: N, *D. jemina visina* Haensch, 1903, Ecuador, Carchi.

*paradoxa* + *hugia* will prove to be a clade sister to the remaining *Hyalenna*. Notwithstanding this possibility, the strong character support for *Hyalenna*, as now conceived, argues for the inclusion of these two species in the genus.

The remaining four *Hyalenna* species form a strongly supported clade, with the following unambiguous synapomorphies: white ventral abdomen (char. 11:1; Figs 8–10), shortened hindwing discal cell (char. 14:1; Fig. 1G, H), straight (char. 26:0) and short (char. 32:1) aedeagus

(Figs 13, 14), ‘teeth’ on inner valva face (char. 35:1; Figs 13I; 14C, H, M) and antrum a broad sclerotized tube (char. 43:1; Figs 17J; 18E, J, O). Within this clade, *H. buckleyi* is sister to an unresolved clade containing *H. alidella*, *H. sulmona* and *H. pascua*. These last three species show no evident consistent differences in structural morphology, and share, amongst other characters: HW veins Sc + R<sub>1</sub> and Rs curving around the androconial scale patch (char. 15:1; Fig. 1H), a more basally positioned



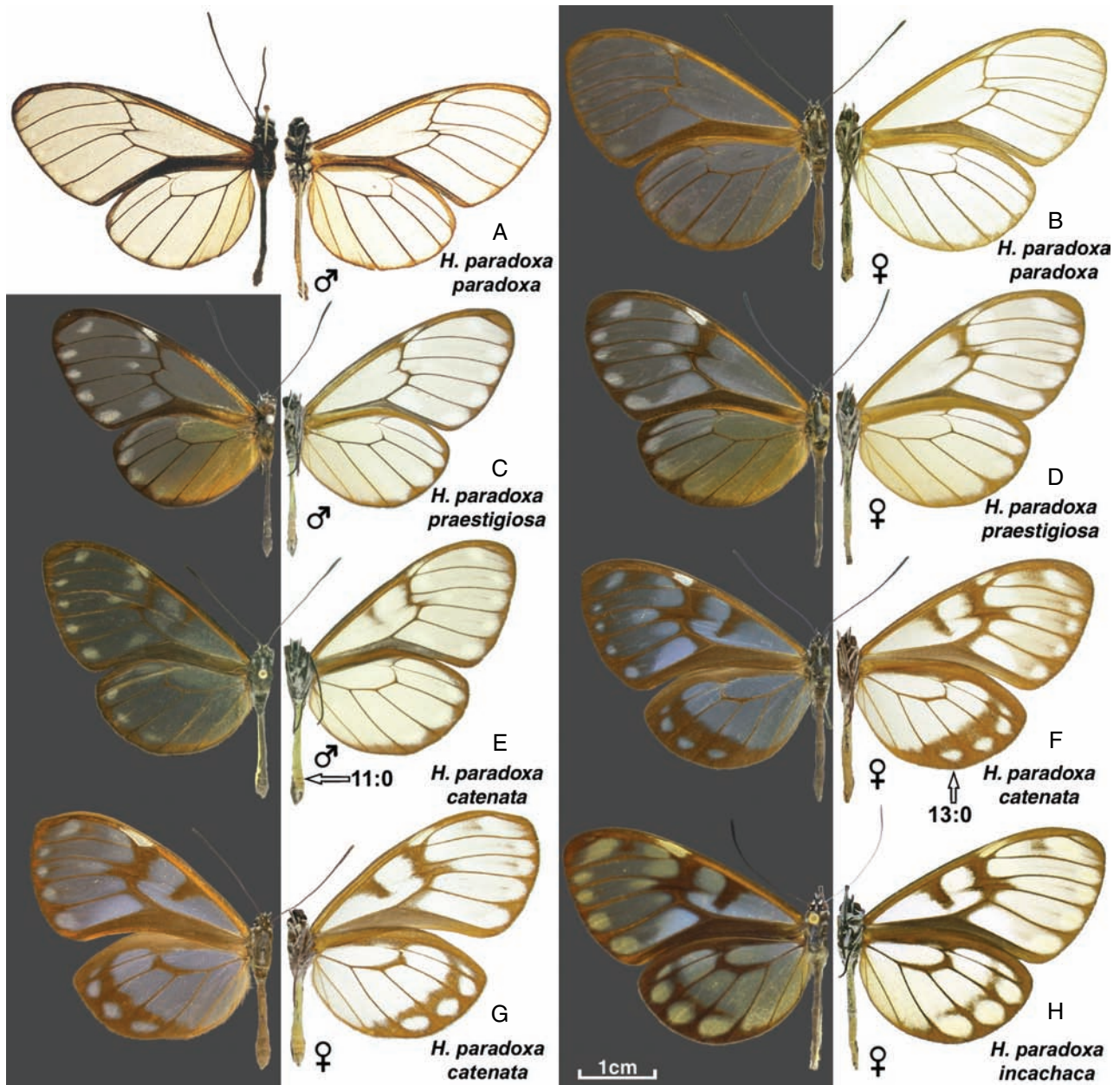


**Fig. 4.** *Hyalenna paradoxa praestigiosa* on various Solanaceae (see Appendices 4 and 5), Ecuador. A, egg, lateral view (KRW-263); B, first instar, dorsal view (KRW-084); C, third instar, dorsal view (KRW-014–2); D, fifth instar, dorsal view (KRW-018); E, fifth instar, lateral view (KRW-262); F, fifth instar, lateral view (KRW-020); G, fifth instar, dorsal view, parasitized by Microgastrinae, *Glyptapanteles?* (Hymenoptera: Braconidae) (KRW-019); H, pupa, dorsal view (KRW-018); I, pupa, lateral view (KRW-262); J, pupa, ventral view (KRW-262); K, adult female just after eclosion (KRW-110).



**Fig. 5.** *Hyalenna sulmona tersa* (KRW-174, all except F) and *Hyalenna* sp. (KRW-042, F, probably *H. sulmona tersa*) on *Solanum lepidotum*, Ecuador. A, first instar larva; B, fourth instar larva, dorsal view; C, D, fifth instar larva, dorsal view; E, F, fifth instar larva, lateral view; G, pupa, dorsal view; H, pupa, lateral view; I, pupa, ventral view; J, adult male just after eclosion.





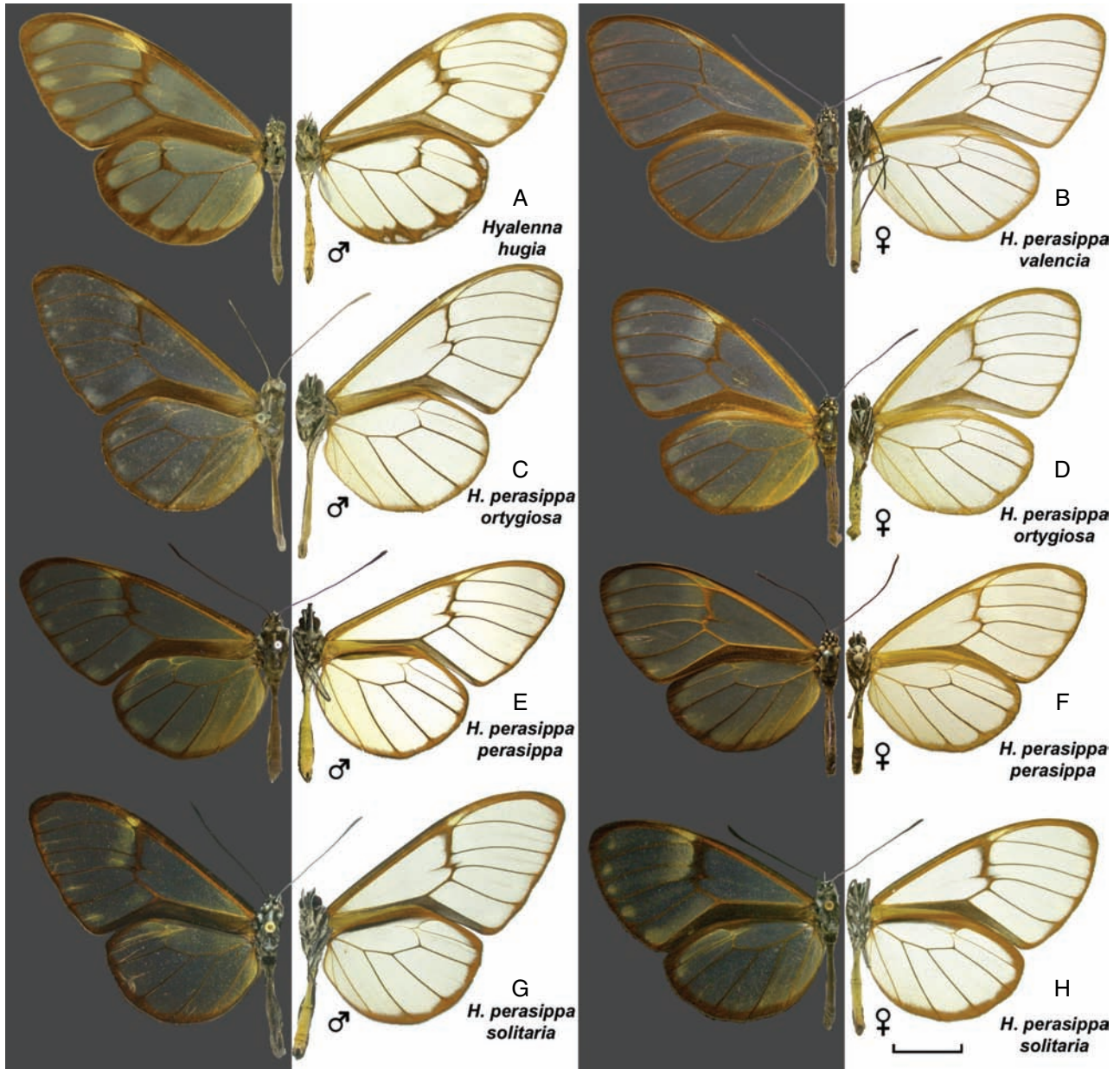
**Fig. 6.** *Hyalenna paradoxa*: A, *H. p. paradoxa*, ♂, Colombia, ICNB; B, *H. p. paradoxa*, ♀, Colombia, BMNH; C, *H. p. praestigiosa*, ♂, Ecuador, KWJH; D, *H. p. praestigiosa*, ♀, Ecuador, KWJH; E, *H. p. catenata*, ♂, Peru, MUSM; F, *H. p. catenata*, ♀, Peru, BMNH; G, *H. p. catenata*, ♀, Peru, BMNH; H, *H. p. incachaca*, ♀, holotype, Bolivia, BMNH.

DHW androconial scale patch (char. 21:1; Fig. 2F), the valva narrowing and curving dorsally at its tip (char. 33:1; Fig. 14A, F, K) and the inner arms from the valval costa crossing beneath the gnathos (char. 38:1; Fig. 14C, H, M).

#### Generic characteristics

**Adult.** Like many Ithomiinae, all *Hyalenna* have largely transparent wings (Figs 6–10) through reduction of the wing

scales to ‘needle’-like and ‘pitchfork’-like scales. The costal, distal and anal margins, and often a forewing discocellular bar, are opaque dark blackish brown. The wings usually bear either yellow or white translucent markings, in the discal cell and posterior of vein  $Cu_1$ , as a submarginal series of spots, and as a postdiscal band on the forewing only. The opaque wing borders and forewing discocellular bar of the ventral surface are usually orange–brown, with a variable series of white, semicircular marginal spots on the hindwing and apical spots on the forewing. The hindwing



**Fig. 7.** *Hyalenna hugia* and *H. perasippa*: A, *H. hugia*, ♂, lectotype, Bolivia, USNM. *H. perasippa*: B, *H. p. valencia*, ♀, holotype, Colombia, BMNH; C, *H. p. ortygiosa*, ♂, Colombia, MUSM; D, *H. p. ortygiosa*, ♀, holotype, Ecuador, BMNH; E, *H. p. perasippa*, ♂, Ecuador, BMNH; F, *H. p. perasippa*, ♀, Ecuador, BMB; G, *H. p. solitaria*, ♂, holotype, Peru, MUSM; H, *H. p. solitaria*, ♀, paratype, Peru, MUSM.

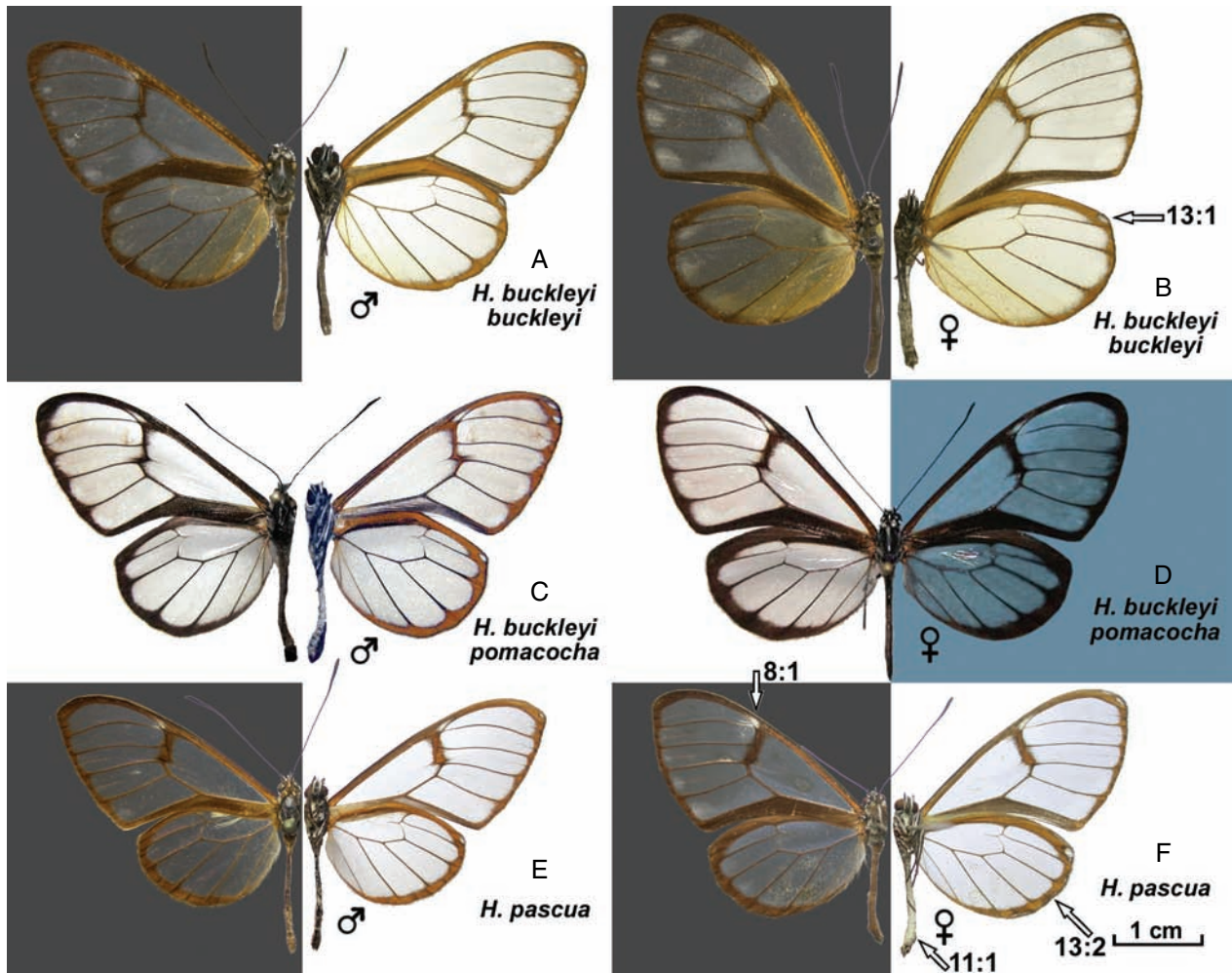
costa often has a more or less distinct yellow stripe at its base.

The male hindwing has 1d present, as in *Dircenna* and most other dircennine genera, and Mr is on 3d, which is sharply kinked, as in all Dircennini (Figs 1, 2). Mr is relatively long in females and in *H. perasippa*, *H. paradoxa* and *H. hugia*. In males, vein Sc + R<sub>1</sub> terminates near the base of vein Rs, not reaching the distal margin (char. 16:1; Fig. 1C–H). The forewing of both sexes has Mr on 3d, with the anterior portion of 3d long, approximately equal

in length to 2d, with which it is aligned, except in some individuals of *H. paradoxa*, in which 2d is much longer (Fig. 1C). This character varies continuously in *H. paradoxa* without correlation with genital or other morphological differences (Fig. 1C, D).

As in all Ithomiinae, the male DHW has a single patch of elongate androconial scales, the 'hair pencil', at the anterior edge of the discal cell, extending from near the humeral vein about one-third the distance to the discal cell end (Fig. 2). This patch of hairs is comparatively small and





**Fig. 8.** *Hyalenna buckleyi* and *H. pascua*. *H. buckleyi*: A, *H. b. buckleyi*, ♂, paratype, Ecuador, KWHJ; B, *H. b. buckleyi*, ♀, paratype, Ecuador, GTB; C, *H. b. pomacocha*, ♂, holotype, Peru, MUSM; D, *H. b. pomacocha*, ♀, paratype, Peru, PB. *H. pascua*: E, ♂, Brazil, MNRJ; F, ♀, Brazil, MNRJ.

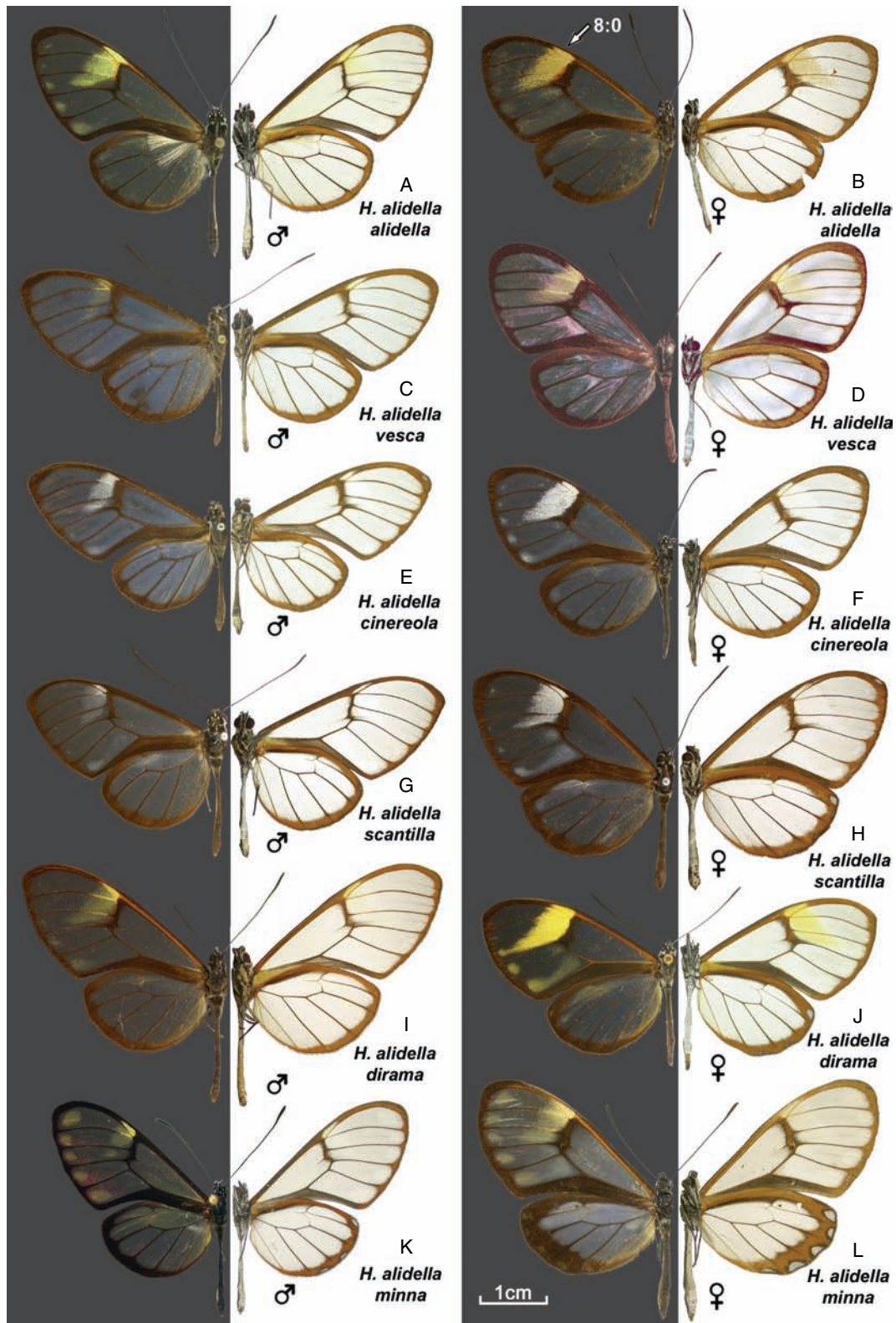
short, and the hairs are pale. Underlying the hair patch in cell  $Rs-Sc + R_1$  is a patch of modified androconial scales that are white, shaped like rounded diamonds and sparsely overlapping (Fig. 3E–G). These scales are erect and held in sockets that are broad, upright and cup-shaped (char. 23:1; Fig. 3E–G). The extent of the scale patch and hair pencil varies between species and clades.

The palpi and walking legs differ little in morphology from other dircennines. The female fore-tarsus has the segments elongate, with the fifth (terminal) segment being fused to the fourth (*H. sulmona*) or just visible as a small bump (*H. alidella*) (char. 25:1; Fig. 1N–P). Spurs are present on both third and fourth segments (*H. alidella*; Fig. 1N) or just the fourth segment (*H. sulmona*; Fig. 1O).

The male has a genital capsule similar in overall form to other Dircennini, especially *Dircenna*, *Callithomia*, *Ceratinia* and *Episcada*, with a bulging, rounded tegumen in dorsal view tapering to a short, broad, blunt uncus, which has dense lateral hairs (Figs 12–14). The gnathos is

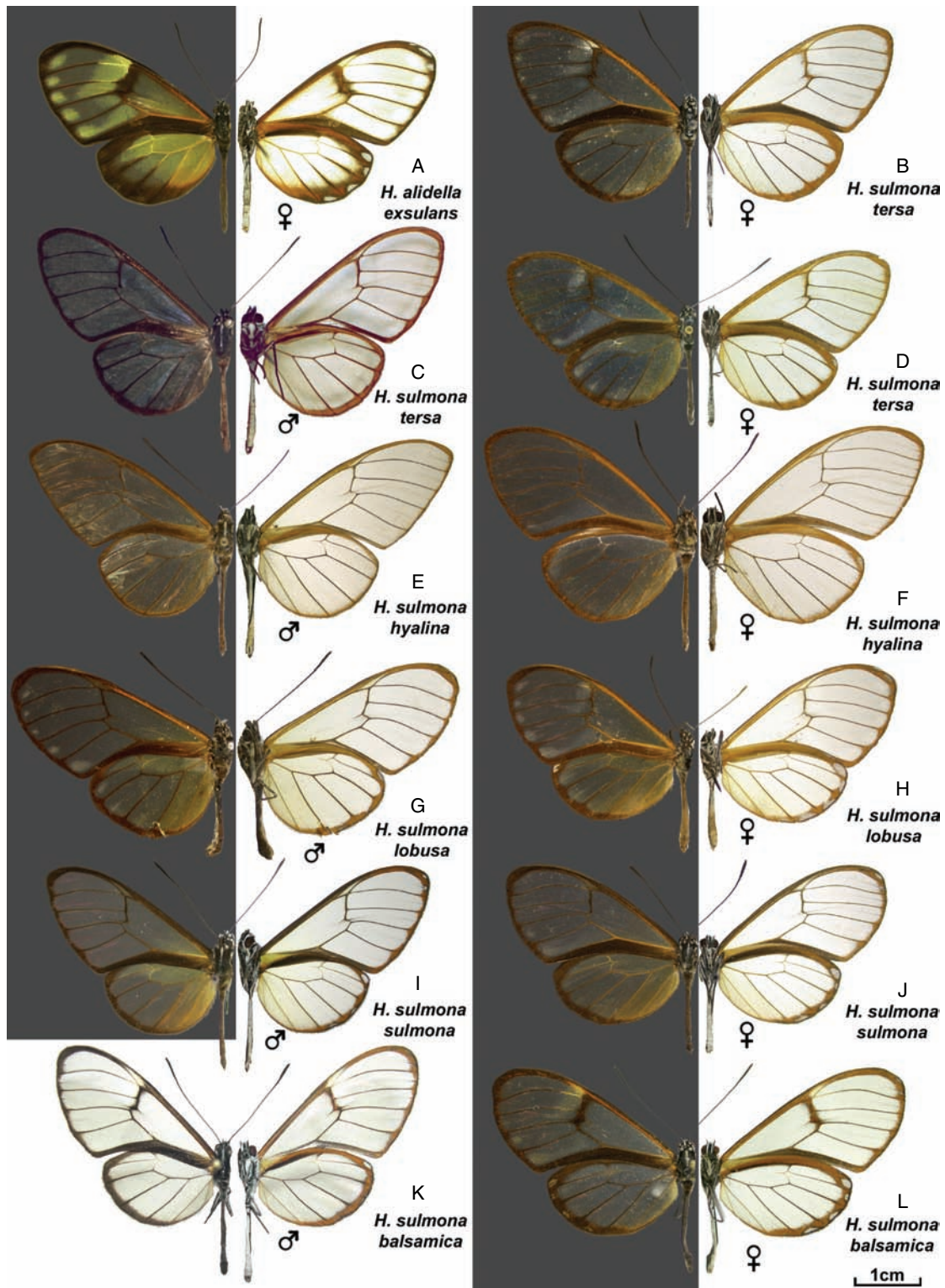
strongly and evenly sclerotized, forming a continuous band which is elongated centrally into a blunt, posteriorly pointing projection common to the previously mentioned four genera. The valvae are simple in lateral outline, approximately trapezoidal, and vary between some species. The inner costal projections of the valva are strongly sclerotized, as in *Haenschia* and *Pteronymia*, but less asymmetrical and not twisted. The vesica, as in almost all other Dircennini and Godyridini, has no obvious cornuti, only an indistinct, encircling band of tiny nodules. The saccus is short, similar in length to the tegumen + uncus.

The female abdomen has the eighth sternite preserved as two sclerotized lateral plates fused to a sclerotized antrum, which is asymmetrical, opening to the left. The ductus seminalis originates near the antrum and the ductus bursae is narrow. The corpus bursae is oval, with small, evenly scattered signa over the entire inner surface, and a smaller, rounded appendix bursae near the anterior tip.



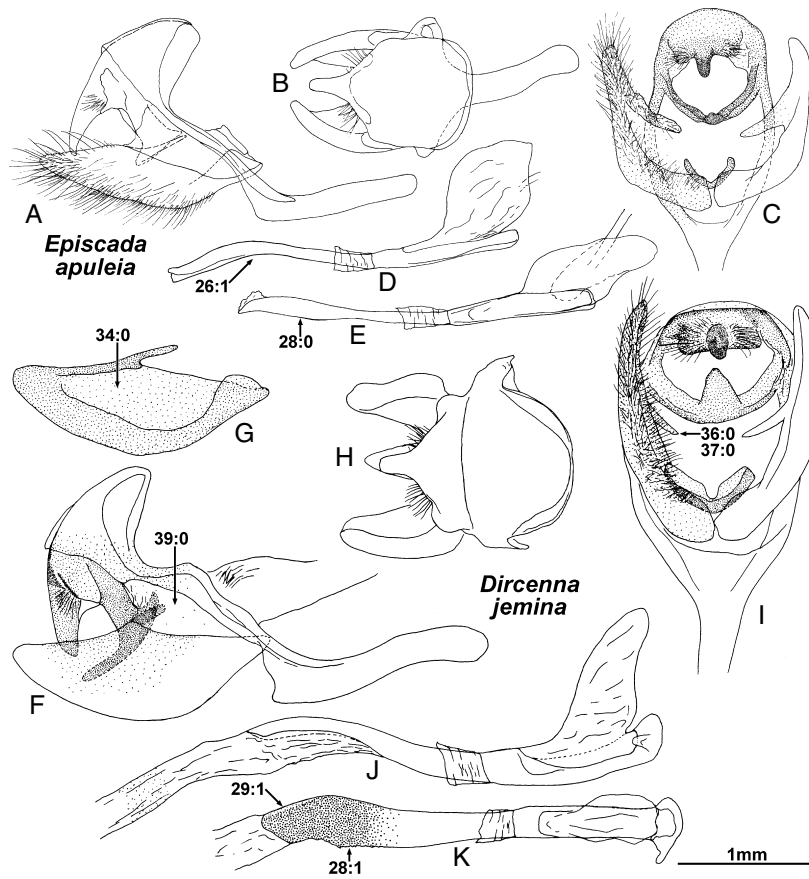
**Fig. 9.** *Hyalemma alidella*: A, *H. a. alidella*, ♂, Venezuela, AFEN; B, *H. a. alidella*, ♀, Colombia, BMNH; C, *H. a. vesca*, ♂, holotype, Colombia, MUSM; D, *H. a. vesca*, ♀, paratype, Colombia, LMC; E, *H. a. cinereola*, ♂, Colombia?, MUSM; F, *H. a. cinereola*, ♀, holotype, Colombia, BMNH; G, *H. a. scantilla*, ♂, Ecuador, BMNH; H, *H. a. scantilla*, ♀, Ecuador, BMNH; I, *H. a. dirama*, ♂, Peru, BMNH; J, *H. a. dirama*, ♀, Peru, MUSM; K, *H. a. minna*, ♂, Bolivia, GTB; L, *H. a. minna*, ♀, Bolivia, GTB.



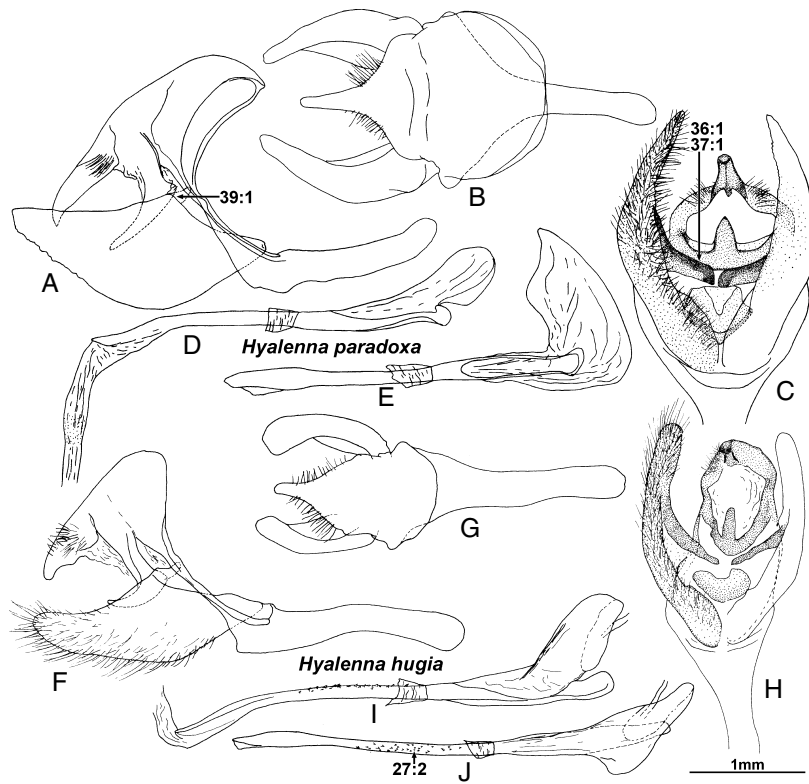


**Fig. 10.** *Hyalenna alidella exsulans* and *H. sulmona*. *H. alidella*: A, *H. a. exsulans*, ♀, holotype, Panama, USNM. *H. sulmona*: B, *H. s. tersa*, ♀, Ecuador (El Corazón), KWJH; C, *H. s. tersa*, ♂, paratype, Colombia, LMC; D, *H. s. tersa*, ♀, holotype, Colombia, MUSM; E, *H. s. hyalina*, ♂, paratype, Colombia, BMNH; F, *H. s. hyalina*, ♀, holotype, Colombia, BMNH; G, *H. s. lobusa*, ♂, Colombia, BMNH; H, *H. s. lobusa*, ♀, Colombia, BMNH; I, *H. s. sulmona*, ♂, Ecuador, KWJH; J, *H. s. sulmona*, ♀, Ecuador, KWJH; K, *H. s. balsamica*, ♂, paratype, Peru, OD; L, *H. s. balsamica*, ♀, paratype, Peru, GTB.

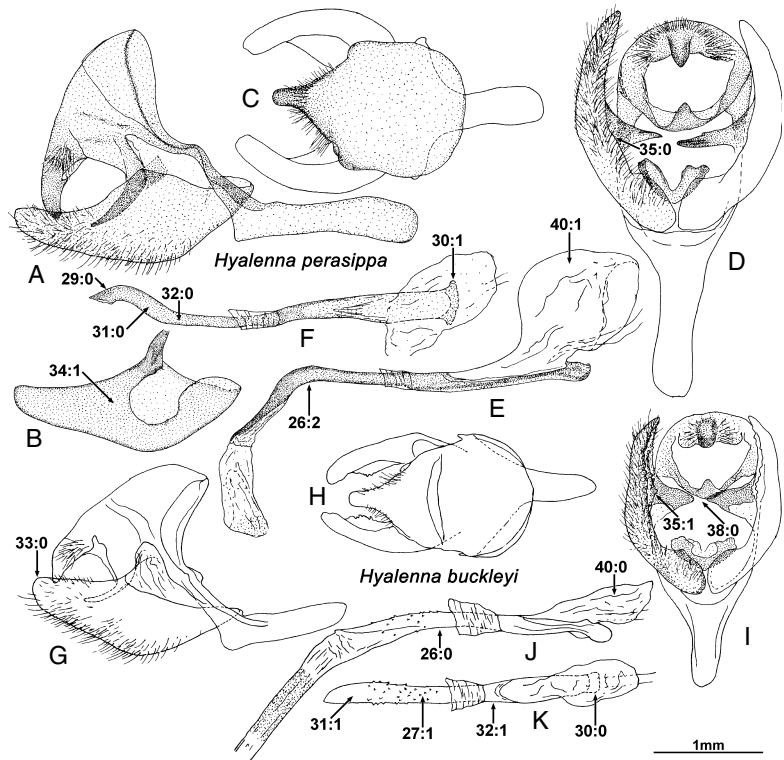




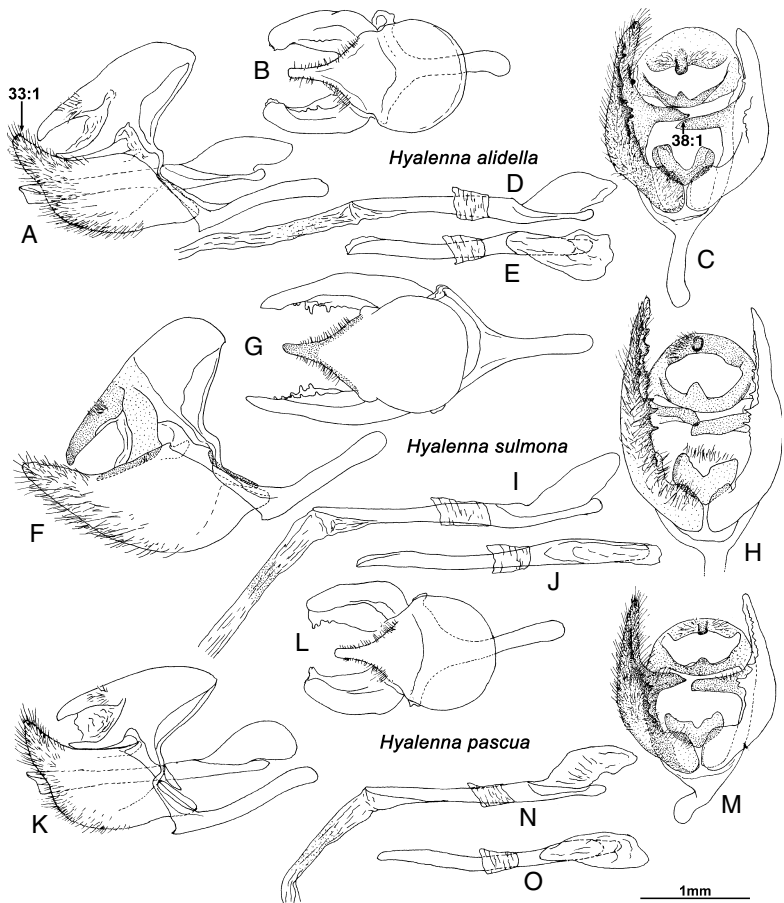
**Fig. 11.** Male genitalia. *Episcada apuleia apuleia* (A–E) and *Dircenna jemina jemina* (F–K): A, F, lateral view; B, H, dorsal view; C, I, ventral view; D, J, aedeagus, lateral view, vesica everted; E, K, aedeagus, dorsal view, vesica not everted; G, left valva, internal view.



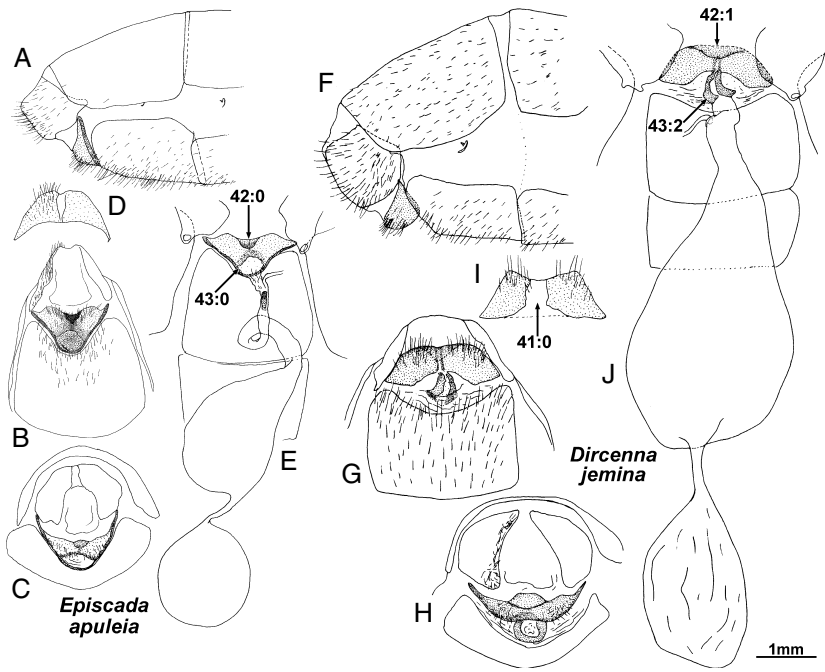
**Fig. 12.** Male genitalia. *Hyalenna paradoxa praestigiosa* (A–E) and *H. hugia* (F–J): A, F, lateral view; B, G, dorsal view; C, H, ventral view; D, I, aedeagus, lateral view, vesica everted; E, J, aedeagus, dorsal view, vesica not everted.



**Fig. 13.** Male genitalia. *Hyalenna perasippa ortygiosa* (A–F) and *H. buckleyi buckleyi* (G–K): A, G, lateral view; B, left valva, internal view; C, H, dorsal view; D, I, ventral view; E, J, aedeagus, lateral view, vesica everted; F, K, aedeagus, dorsal view, vesica not everted.



**Fig. 14.** Male genitalia. *Hyalenna alidella alidella* (A–E), *H. sulmona lobusa* (F–J) and *H. pascua* (K–O): A, F, K, lateral view; B, G, L, dorsal view; C, H, M, ventral view; D, I, N, aedeagus, lateral view, vesica everted; E, J, O, aedeagus, dorsal view, vesica not everted.

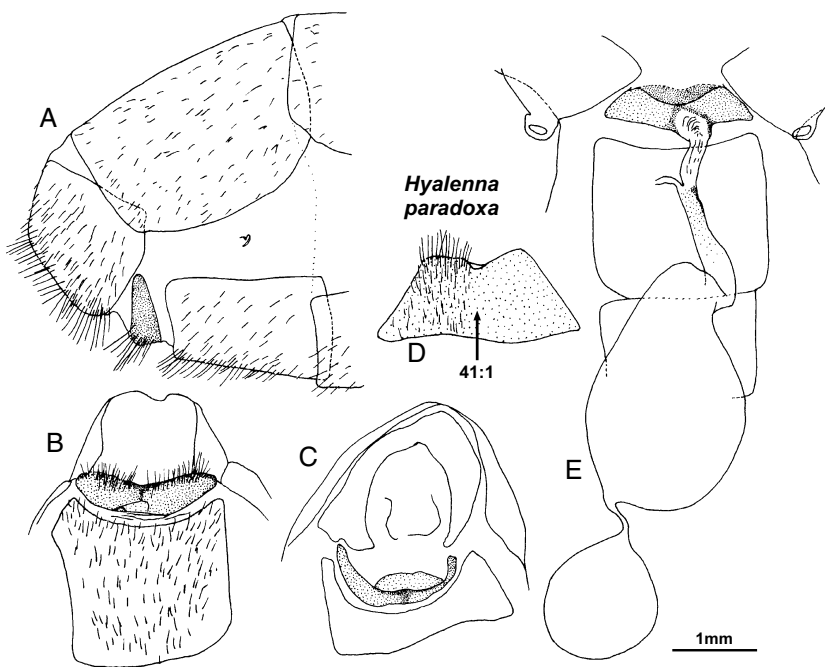


**Fig. 15.** Female abdomen and genitalia. *Episcada apuleia apuleia* (A–E) and *Dircenna jemina jemina* (F–J): A, F, posterior tip abdomen, lateral view; B, G, posterior tip abdomen, ventral view; C, H, posterior tip abdomen, posterior view; D, I, terminal tergite, dorsal view; E, J, genitalia, dorsal view.

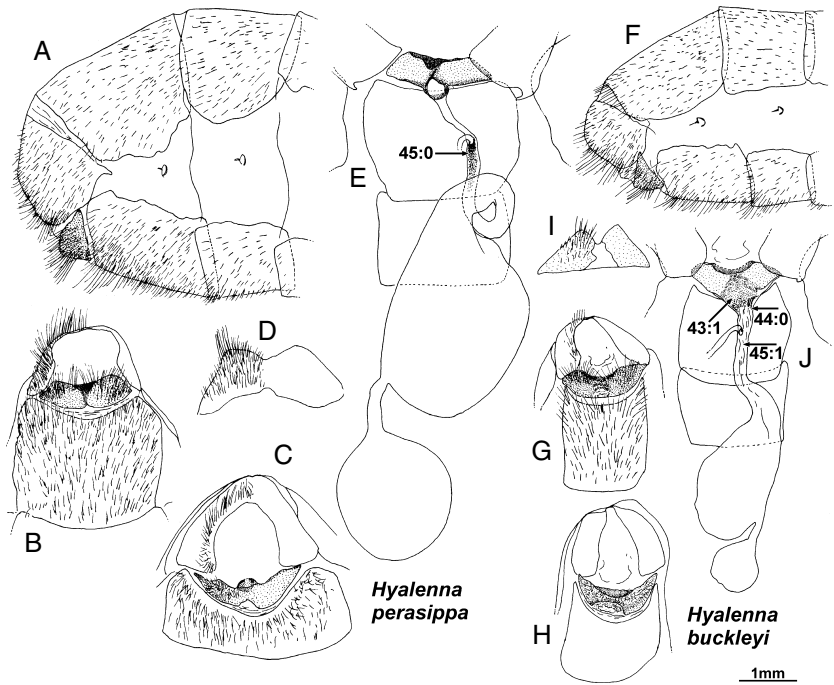
**Immature stages.** The following summary is based on Brown & Freitas (1994) for *H. pascua*, and on recent fieldwork in Ecuador by KRW for *H. paradoxa praestigiosa* and *H. sulmona tersa* (see Appendices 4 and 5). More detailed descriptions are given in the species accounts.

The egg is a truncate dome with sculpturing similar to *Dircenna*: there are approximately fifteen vertical ribs lined with apparently stellate spines, with more finely spaced horizontal ribs (Fig. 4A). As in all Ithomiinae, the larval

head capsule is rounded and smooth and bears sparse setae (Fig. 3H). The first instar head capsule may be pale (*H. pascua*) or, unusually within the Dircennini, black (*H. paradoxa*) (Fig. 4B). Head capsules of remaining instars are pale yellowish green, except for the stemmata, labrum and mandibles, which are pale to black. As is typical of the subfamily, all instars lack any kind of spines, scoli or chalazae, but are covered with fine setae similar only to *Dircenna* (char. 1:1). The fleshy dorsal thoracic filaments that are present in some basal Ithomiinae are



**Fig. 16.** Female abdomen and genitalia. *Hyalenna paradoxa praestigiosa*: A, posterior tip abdomen, lateral view; B, posterior tip abdomen, ventral view; C, posterior tip abdomen, posterior view; D, terminal tergite, dorsal view; E, genitalia, dorsal view.

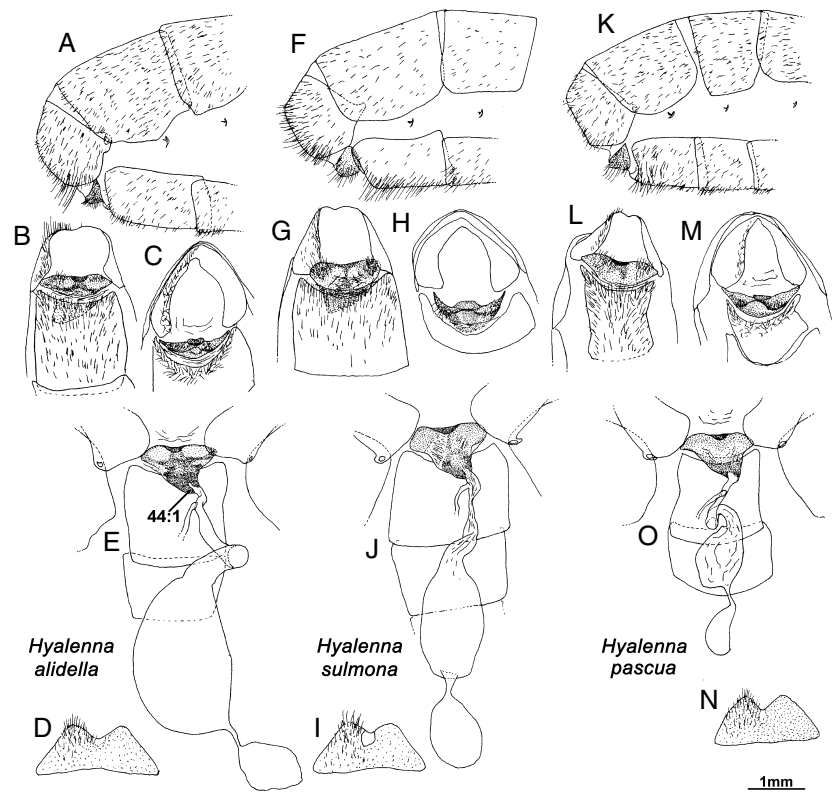


**Fig. 17.** Female abdomen and genitalia. *Hyalenna perasippa solitaria* (A–E) and *H. buckleyi pomacocha* (F–J): A, F, posterior tip abdomen, lateral view; B, G, posterior tip abdomen, ventral view; C, H, posterior tip abdomen, posterior view; D, I, terminal tergite, dorsal view; E, J, genitalia, dorsal view.

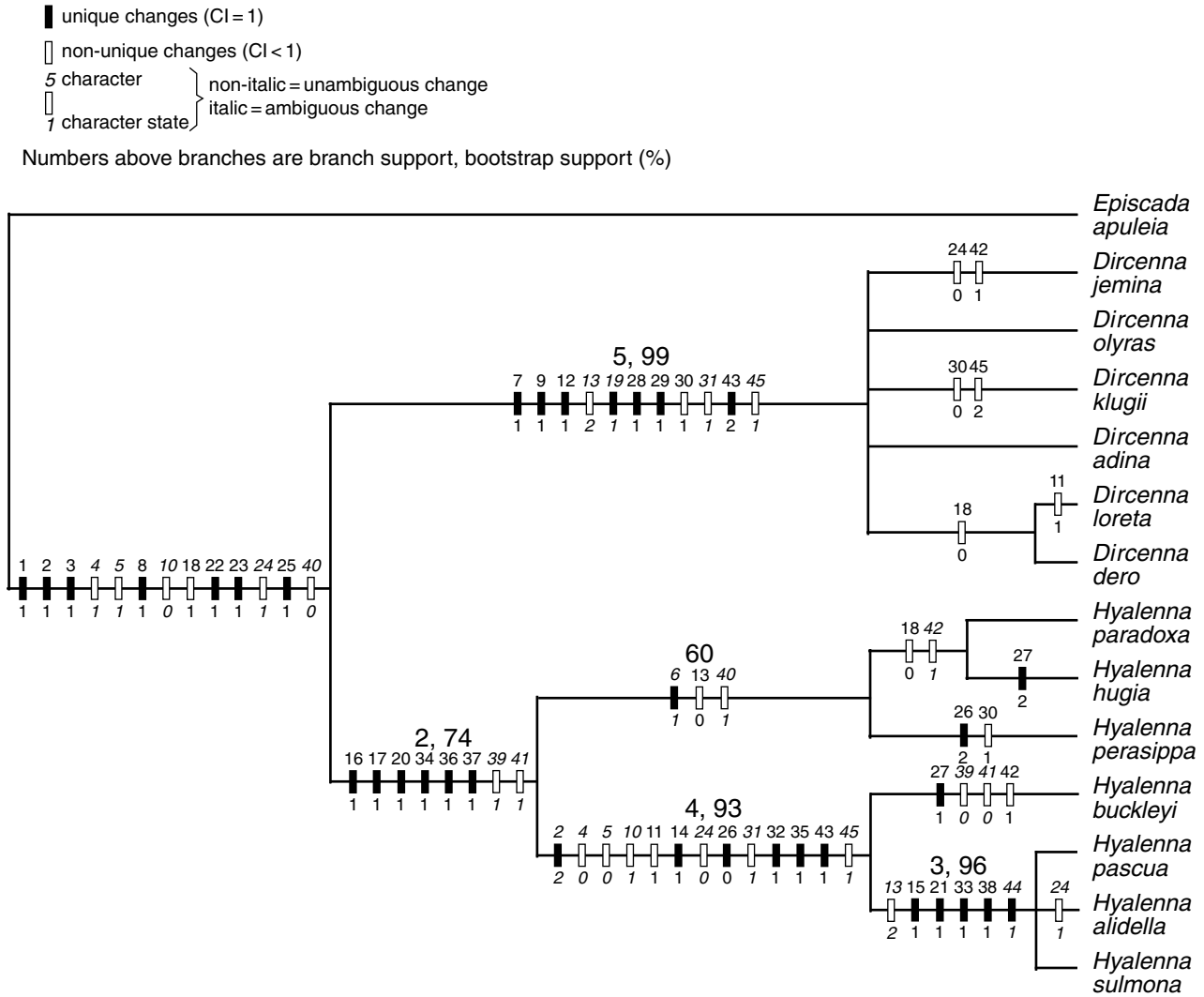
absent. Early instars are pale greenish, with pale legs (Figs 4A; 5A). Later instars may be mottled green dorsally, bear yellow dorsal and subdorsal markings and black lateral and dorsal spots, similar to *Dircenna* (*H. paradoxa*), or

be almost entirely pale opaque green, with a trace of yellow dorsal and subdorsal markings (*H. sulmona*, *H. pascua*).

The pupa is smooth and unadorned, resembling *Dircenna* (and other Dircennini) in being sharply angled at the



**Fig. 18.** Female abdomen and genitalia. *Hyalenna alidella alidella* (A–E), *H. sulmona lobusa* (F–J) and *H. pascua* (K–O): A, F, K, posterior tip abdomen, lateral view; B, G, L, posterior tip abdomen, ventral view; C, H, M, posterior tip abdomen, posterior view; D, I, N, terminal tergite, dorsal view; E, J, O, genitalia, dorsal view.



**Fig. 19.** Strict consensus of twelve most parsimonious trees illustrating phylogenetic relationships amongst *Hyalenna* and *Dircenna*. CI = 0.71 (excluding uninformative characters), RI = 0.86; character transformations indicated from ACCTRAN optimization.

middle (Figs 4I; 5H). In dorsal view, protuberances are visible at the base of the cremaster stalk, as in *Dircenna* (char. 8:1; Figs 3I; 4H; 5G). The pupa may be pale yellowish to greyish green, with areas of reflective silver markings, especially on the wing case, thorax and in three dorsal bands on the abdomen. Either one (*H. paradoxa*) or two (*H. pascua*, *H. sulmona*) pairs of lateral, conical protuberances near the wing bases are visible in dorsal view.

*Taxonomy*

Seven species of *Hyalenna* are recognized, including two monotypic species and five polytypic species with a total of twenty-four taxa. One new species and eleven new sub-species are described here.

*Hyalenna* Forbes, 1942: 37, figs 1–5. Type species: *Ithomia perasippa* Hewitson, 1877, by original designation

- paradoxa* (Staudinger, [1884]) **comb.n.**
- p. praestigiosa* (Haensch, 1903) **comb.n.**
- p. catenata* (Kaye, 1918) **comb.n.**
- syn. *grandipennis* (Kaye, 1918) **comb.n.**
- p. incachaca* Lamas & Willmott, **ssp.n.**
- hugia* (Schaus, 1902) **comb.n., stat.rev.**
- perasippa* (Hewitson, 1877)
- p. valencia* Willmott & Lamas, **ssp.n.**
- p. ortygiosa* Willmott & Lamas, **ssp.n.**
- p. solitaria* Lamas & Willmott, **ssp.n.**
- buckleyi* Willmott & Lamas, **sp.n.**
- b. pomacocha* Lamas & Willmott, **ssp.n.**
- pascua* (Schaus, 1902)
- alidella* (Hewitson, 1869)



- a. minna* (Schaus, 1902)  
*a. dirama* (Haensch, 1905)  
*a. scantilla* (Hewitson, 1877)  
*a. vesca* Lamas & Willmott, **ssp.n.**  
*a. cinereola* Lamas & Willmott, **ssp.n.**  
*a. exsulans* Lamas & Willmott, **ssp.n.**  
*sulmona* (Hewitson, 1877)  
*s. lobusa* (Haensch, 1909)  
*s. tersa* Willmott & Lamas, **ssp.n.**  
*s. hyalina* Lamas & Willmott, **ssp.n.**  
*s. balsamica* Lamas & Willmott, **ssp.n.**

Names erroneously included in *Hyalenna*:

- '*Hyalenna*' *maculata* Röber, 1930 (*Episcada perasippa maculata*) [= *Godyris panthyle panthyle* (C. Felder & R. Felder, 1862)] (Forbes, 1942; misidentification of *Hyalenna sulmona lobusa* or *tersa*);  
 '*Hyalenna*' *teresita* Hewitson, 1863 (*Ithomia teresita*) [= *Pteronymia teresita teresita* (Hewitson, 1863)] (Forbes, 1942; misidentification of *Hyalenna sulmona sulmona*).

#### Key to *Hyalenna* taxa

A combination of forewing venation, hindwing shape, the translucent wing markings and the ventral marginal spots permits identification of species without dissection, and genitalia of both sexes (not included here but discussed in species accounts) provide diagnostic characters for *H. paradoxa*, *H. hugia*, *H. perasippa* and *H. buckleyi*.

1. FW medial recurrent vein (Mr) nearer to vein M<sub>3</sub> than vein M<sub>2</sub> (e.g. Fig. 1F) . . . . . 2  
 FW medial recurrent vein (Mr) nearer to vein M<sub>2</sub> than vein M<sub>3</sub> (e.g. Fig. 1C; *paradoxa*, *hugia*). . . . . 20
2. FW length ≤ 30 mm; with or without marginal spots on HW below; abdomen below white to dirty white or yellowish white . . . . . 3  
 FW length > 32 mm; no marginal spots on HW below; abdomen below bright yellow (Fig. 7B–H; *perasippa*). . . . . 17
3. FW with a yellow translucent or opaque postdiscal band . . . . . 4  
 FW with a white translucent or opaque postdiscal band, or such a band absent . . . . . 9
4. HW with heavy translucent yellow throughout, becoming orange at anal margin; E Panama (Fig. 10A) . . . . . *alidella exsulans*  
 HW with faint translucent white tinge or largely colourless except slight yellow tinge along anal margin and anterior half discal cell; Andes . . . . . 5
5. FW with translucent yellow submarginal spots in tornus, becoming smaller and vanishing towards apex; Venezuela–S Peru . . . . . 6  
 FW with large, even translucent yellow submarginal spots throughout wing, from tornus to apex; Bolivia (Fig. 9K, L) . . . . . *alidella minna*
6. VHW in male with no white marginal spots or trace in apex, in female with white apical spot and marginal spots tiny or absent (Fig. 9; *alidella*) . . . . . 7

- VHW in male with white apical spot and trace of marginal spots, in female with white apical spot and large marginal spots (Fig. 10K, L) *sulmona balsamica*
7. FW with broad opaque to semiopaque yellow postdiscal band and yellow translucent spots in tornus and adjacent submargin . . . . . 8  
 FW with narrow translucent yellow postdiscal band and no yellow translucent submarginal spots (Fig. 9C, D) . . . . . *alidella vesca*
  8. Range Venezuela–Colombia (Cordillera Oriental) (Fig. 9A, B) . . . . . *alidella alidella*  
 Range Peru (Fig. 9I, J) . . . . . *alidella dirama*
  9. FW discocellular veins covered by a black bar, hindwing colourless or with some white translucence . . . . . 10  
 FW discocellular veins not covered by a black bar, or if with some black scaling then hindwing has translucent yellow in posterior half (anal margin) . . . . . 12
  10. FW with broad white translucent or opaque postdiscal band, extending across cell M<sub>3</sub>–M<sub>2</sub>; Andes . . . . . 11  
 FW with trace of a white translucent postdiscal spot visible at most in cell M<sub>2</sub>–M<sub>1</sub>; SE Brazil (Fig. 8E, F) . . . . . *pascua*
  11. FW white postdiscal band in male opaque, in female with straight distal edge; no yellow at base VHW costa (Fig. 9E, F) . . . . . *alidella cinereola*  
 FW white postdiscal band in male translucent, in female with uneven distal edge; yellow stripe at base VHW costa (Fig. 9G, H) . . . . . *alidella scantilla*
  12. FW discocellular veins covered by a thin black bar . . . . . 13  
 FW discocellular veins clear, not covered by a black bar (Fig. 10E–J; *sulmona*) . . . . . 15
  13. VHW apical angle at vein M<sub>1</sub> approximately 120°; VFW with white apical spots (Fig. 8A–D; *buckleyi*) 14  
 VHW apical angle at vein M<sub>1</sub> more acute, approximately 100°; VFW without white apical spots (Fig. 10B–D) . . . . . *sulmona tersa*
  14. HW with yellowish translucence in discal cell and between vein Cu<sub>2</sub> and anal margin; dark distal marginal borders narrower than costal borders (Fig. 8A, B) . . . . . *buckleyi buckleyi*  
 HW with yellowish translucence absent or only right at anal margin; dark distal marginal borders broader, similar width to costal borders (Fig. 8C, D) . . . . . *buckleyi pomacocha*
  15. Distal marginal borders very narrow; ventral white marginal spots absent or in HW apex only; wings entirely colourless except slight translucent yellow at HW anal margin (Fig. 10E, F) . . . . . *sulmona hyalina*  
 Distal marginal borders broader, slightly narrower than costal border; ventral white marginal spots present on HW in apex and distal margin; wings with translucent yellow in HW discal cell and posterior wing area, FW with translucent marginal spots . . . . . 16
  16. FW translucent white submarginal spots extending to apex; VHW orange–brown immediately posterior of yellow stripe at base costa (Fig. 10G, H) . . . . . *sulmona lobusa*

**Table 1.** Principal synapomorphies for species in *Hyalenna* and *Dircenna*.

Character	Distribution
<i>Hyalenna</i>	
Male HW with vein Sc + R <sub>1</sub> terminating before wing margin (char. 16:1, Fig. 1E)	Universal; also in <i>Haenschia</i> and many Godyridini
Male FW with upper part of 3d similar in length to two-thirds length 2d (char. 17:1, Fig. 1C)	Except in some <i>H. paradoxa</i> , where apparently a reversal; unique in Dircennini
Male HW androconial scale patch in cell Rs–Sc + R <sub>1</sub> short, not extending basally beyond origin vein Cu <sub>2</sub> or distally beyond origin vein M <sub>2</sub> (char. 20:1, Fig. 2C)	Universal; also in <i>Haenschia</i> , among Dircennini
Valva inner face between sacculus and costa sclerotized (char. 34:1, Fig. 13B)	Universal; difficult to evaluate in more distant genera
Valva basal inner projection from costa strongly sclerotized, more so than rest of valva (char. 36:1, Fig. 12C)	Universal; also in <i>Pteronymia</i> and a few other genera
Valva basal inner projection from costa bent inwards, almost meeting or crossing beneath gnathos (char. 37:1, Fig. 12C)	Universal; also in <i>Pteronymia</i> and a few other genera
Valva anterior dorsal edge close to vinculum (ratio valva edge–vinculum/maximum height valva, <i>v</i> , < 0.3) (char. 39:1, Fig. 12A)	Except in <i>H. buckleyi</i> , where an apparent reversal; also in <i>Pteronymia</i> , among Dircennini
<i>Dircenna</i>	
Male with elongate white spot at VHW costa in cell Rs–Sc + R <sub>1</sub> near discocellulars present (char. 12:1, Fig. 3N)	Universal; almost unique among Dircennini
Male DHW androconial scales beneath hair pencil strongly differentiated, with a basal patch of dense, broad scales and distal patch of sparse, blade-like scales (char. 19:1, Fig. 3C, D)	Universal; unique (other ithomiines have differentiated scales, but of different morphology)
Aedeagus with a line of ‘teeth’ at right posterior tip: absent (0); present (char. 28:1, Fig. 11K)	Universal; unique – <i>H. buckleyi</i> and <i>H. hugia</i> have ‘teeth’ scattered over much of aedeagus
Aedeagus with a clear, weakly sclerotized line at left distal edge present (char. 29:1, Fig. 11K)	Universal; difficult to evaluate in more distant genera

DHW, dorsal hindwing; FW, forewing; HW, hindwing; VHW, ventral hindwing.

- FW translucent white submarginal spots absent or in tornus only; VHW black immediately posterior of yellow stripe at base costa (Fig. 10I, J) . . . . . *sulmona sulmona*
17. Wings with translucent yellow or white postdiscal, discal and submarginal markings . . . . . 18  
Wings almost colourless (Fig. 7B). . . . . *perasippa valencia*
18. FW with yellow translucent postdiscal band and submarginal spots . . . . . 19  
FW with white translucent postdiscal band and submarginal spots (Fig. 7C, D). . . . . *perasippa ortygiosa*
19. Female with discocellular veins and bases of veins Cu<sub>2</sub>–M<sub>1</sub> scaled orange; range SE Ecuador–NE Peru (Fig. 7E, F). . . . . *perasippa perasippa*  
Female with discocellular veins and bases of veins Cu<sub>2</sub>–M<sub>1</sub> scaled black; range C Peru (Junín) (Fig. 7G, H) . . . . . *perasippa solitaria*
20. VHW with white marginal spots absent. . . . . 21  
VHW with white marginal spots present (Fig. 7A). . . . . *hugia*
21. VHW lacking submarginal line or band basal of translucent marginal spots . . . . . 22  
VHW with black submarginal line or band basal of translucent marginal spots . . . . . 23

22. Wings almost colourless, dark distal margins on both wings almost absent (Fig. 6A, B) . . . . . *paradoxa paradoxa*  
Wings with yellow in posterior half HW, white postdiscal and submarginal translucent spots on FW (Fig. 6C, D) . . . . . *paradoxa praestigiosa*
23. Translucent submarginal and postdiscal wing areas white, hindwing black submarginal line broad (Fig. 6E–G). . . . . *paradoxa catenata*  
Translucent submarginal and postdiscal wing areas yellow, hindwing black submarginal line narrow (Fig. 6H). . . . . *paradoxa incachaca*

### Distribution and natural history

*Hyalenna* is confined largely to the tropical Andes, from Venezuela to Bolivia, with a single species extending into the Darién region of extreme eastern Panamá, and one species endemic to south-eastern Brazil (Figs 20, 21). The highest diversity of species occurs in the Andes of Colombia to north-eastern Peru, where five of the six Andean species can be found. All species are confined to relatively undisturbed montane forest, and collectively range from 900 to 2850 m.

The eggs of all known species are laid singly on the larval food plant, often near holes or veins (Brown & Freitas, 1994; Appendix 4). All food plants are in the Solanaceae, as for all other known Dircennini and Godyradini. Larvae feed from the edge of the leaf and, in *H. pascua* and *H. paradoxa*, roll the edges of leaves and fasten them with silk to make shelters, like *Dircenna* (Brown & Freitas, 1994; Willmott, pers. obs.). The larvae and pupae are well camouflaged against the undersides of their food plant leaves, and differing leaf colour and morphology may be responsible for the colour pattern differences observed between *H. paradoxa*, and *H. pascua* and *H. sulmona* (see individual species accounts). The immature stages may be much more abundant than the adults, with several individuals on a single plant. The development time from egg to pupa is approximately 32 days, while the pupa ecloses after an additional 13–20 days (Appendix 5). Recorded parasitoids include Braconidae (Hymenoptera), possibly of the genus *Glyptapanteles* Ashmead, 1905 (Microgastrinae) (J. Whitfield, University of Illinois, Urbana, pers. comm.), which parasitized two third or earlier instars of *H. paradoxa* and emerged to pupate in the fifth instar.

Adult *Hyalenna* generally are rare, particularly in the Andes, with only 320 (132 males, 188 females) specimens examined (see Appendix 6). Andean species are encountered as single individuals, amongst large mixed-species groups of male ithomiines, feeding in the early to mid-morning, or in the late afternoon, on Asteraceae flowers at forest edges and wide trails. Males and females have been observed flying from 1 to 4 m above the ground across trails and open areas on forested ridgetops, and females have been found settling on leaves at 2–3 m above the ground inside the forest. Known host plants are most abundant in rocky soils along the edges of primary forest, either along wide trails or open streams, and females seen flying in such habitats are presumably searching for oviposition sites. Males of *H. buckleyi* perch in small groups high (10–15 m) above streams, where they engage in vigorous spiralling flights with other conspecific males. This high flight probably accounts in part for the scarcity of members of most species (particularly males) of the genus in collections. *H. pascua*, the only species occurring exclusively outside the Andes, may be common locally in south-eastern Brazil (Ebert, 1969; Brown, 1992), but is still relatively rare in collections.

*Hyalenna* species are involved extensively in Müllerian mimicry, with each other as well as with numerous other ithomiines, especially those in the genera *Pteronymia*, *Episcada* and *Greta* Hemming, 1934. All *Hyalenna* species are presumed to be unpalatable to predators because of their possession of pyrrolizidine alkaloids (Brown, 1984, 1985), the chemical precursors of which are obtained by males feeding on Asteraceae flowers or other alkaloid sources (Brown, 1985) (see under *H. alidella alidella*).

## Species accounts

### *Hyalenna paradoxa* (Staudinger, [1884]) comb.n. (Figs 1C, D, J; 2C; 3E; 4; 6; 12A–E; 16; 20A)

*Identification, taxonomy and variation.* *H. paradoxa* and *H. hugia* are unique within the genus in having the FW medial recurrent vein (Mr) closer to the base of vein M<sub>2</sub> than M<sub>3</sub> (Fig. 1C–E, J); in all other *Hyalenna*, it is closer to the base of M<sub>3</sub> (Fig. 1F–H, K). This character can be difficult to assess when the discocellular veins are obscured by black scaling, and confusion is most likely with *H. perasippa*, which shares with these two species a yellow ventral abdomen (in all other species it is white).

Although there are no synapomorphies that group *H. paradoxa* subspecies, all included taxa may be distinguished from the closest and most similar relatives, *H. hugia* and *H. perasippa*, by several additional morphological characters. The aedeagus (not examined in *H. p. incachaca* as the male is unknown) is smooth (spinose in *H. hugia*), not strongly bent ventrally at the posterior tip (strongly bent in *H. perasippa*), and the VHW lacks white marginal spots (spots are present in the male, and probably female, of *H. hugia*). Four taxa are included here under *H. paradoxa* based on their lack of morphological differences, allopatry and similar elevations at which they occur. We consider *H. paradoxa* and *H. hugia* as distinct species for reasons discussed under the latter species.

*Range.* Colombia (Cordillera Central and Oriental) to Bolivia, along the eastern slope of the Andes. Rare, in cloud forest from 1400 to 2850 m.

*Specimens examined.* 26♂, 45♀ (Appendix 6).

### *Hyalenna paradoxa paradoxa* (Staudinger, [1884]) comb.n. (Figs 1J; 6A, B; 16; 20A)

*Ithomia paradoxa* Staudinger, [1884]: pl. 30, fig. [2]. Type locality: [Colombia, Caldas, Manizales]. Holotype ♀, ZMHU.

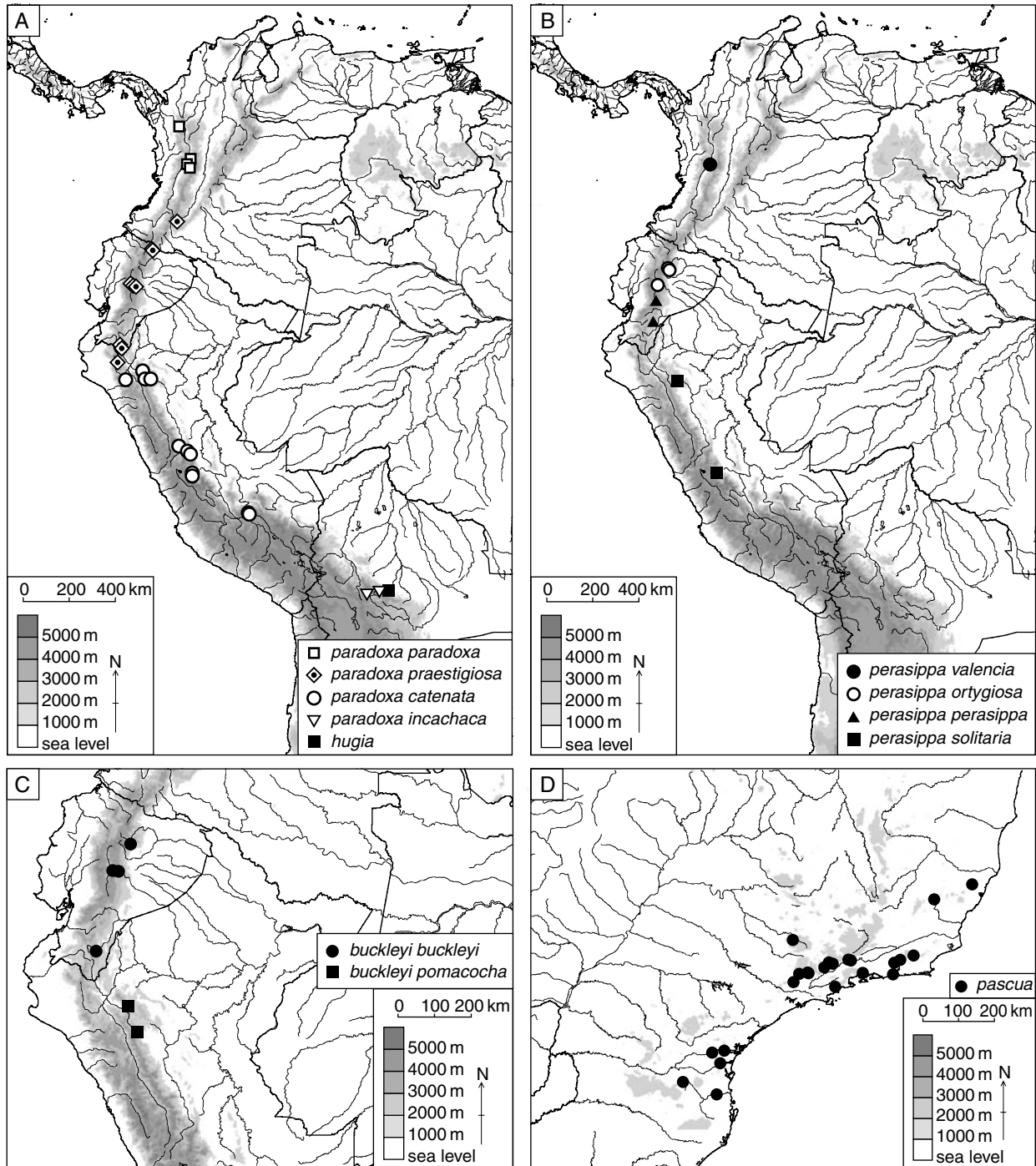
*Ithomia paradoxa*: Staudinger, 1885: 63, 69; Haase, 1893: 53.

*Episcada paradoxa*: Haensch, 1909: 152; Bryk, 1937: 592; D'Almeida, 1978: 306.

*Dircenna paradoxa paradoxa*: Lamas, 2004: 186.

*Identification, taxonomy and variation.* The nominate subspecies is distinguished by the translucent postdiscal markings on both wings being much reduced, with less intense yellow colouring on the HW, and by the reduced distal marginal borders, especially on the HW.

Staudinger (1884) introduced the name for this species by illustrating a female (from Colombia, Manizales, as indicated by examination of its original label), and later



**Fig. 20.** Recorded localities for *Hyalenna* species. A, *H. paradoxa*, *H. hugia*; B, *H. perasippa*; C, *H. buckleyi*; D, *H. pascua*.

(Staudinger, 1885) stated that it came from the 'Cauca valley' in Colombia. There is no doubt about the identity of the taxon from the original illustration, and the holotype is in the ZMHU. Lamas (2004) placed it in the genus *Dircenna*, and we now transfer it to *Hyalenna* for reasons given in the generic discussion.

*Range, habitat and adult ecology.* Colombia, northern Cordillera Central in Antioquia, Caldas and Risaralda (Fig. 20A). Presumably, this taxon flies with and mimics *H. perasippa valencia* and *H. sulmona hyalina*, amongst many other almost entirely transparent ithomiine taxa.

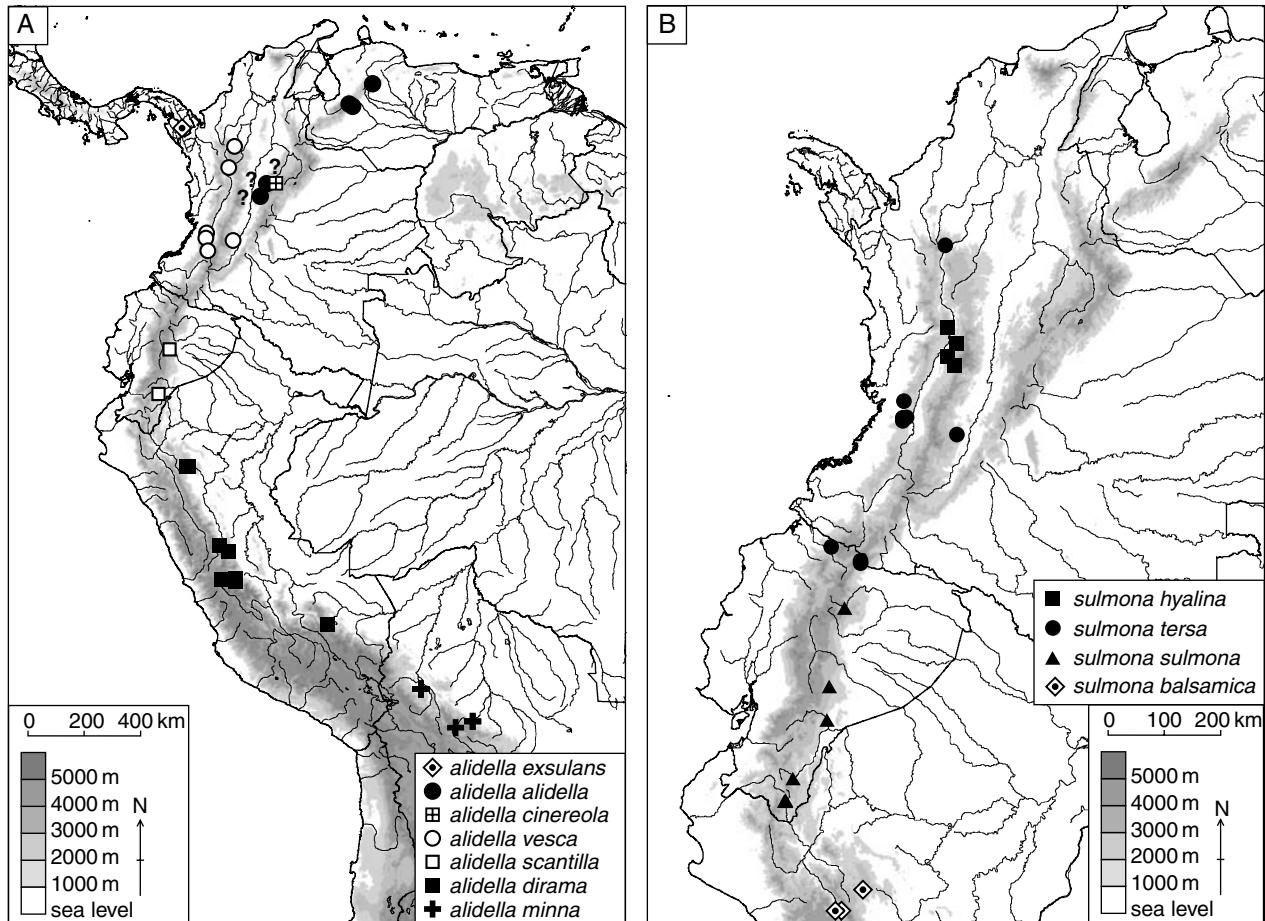


Fig. 21. Recorded localities for *Hyalenna* species. A, *H. alidella*; B, *H. sulmona*.

*Specimens examined.* 1♂, 9♀ (Appendix 6).

***Hyalenna paradoxa praestigiosa* (Haensch, 1903) comb.n.**  
(Figs 1C, D; 2C; 3E; 4; 6C, D; 12A–E; 16; 20A)

*Episcada praestigiosa* Haensch, 1903: 196. Type locality: Ecuador, [Tungurahua], [Volcán] Tungurahua. Lectotype ♂, ZMHU.

= *Pteronymia grandipennis* Kaye, 1918: 84, 85. Type locality: '? Peru, [Pasco], Pozuzo'. Holotype ♀, BMNH. **comb.n.**

*Episcada praestigiosa*: Haensch, 1909: 152; Bryk, 1937: 592; D'Almeida, 1978: 308; D'Abbrera, 1984: 248.

*Dircenna paradoxa* ?ssp.: D'Abbrera, 1984: 276, fig.

*Dircenna paradoxa praestigiosa*: Lamas, 1994: 290; Racheli & Racheli, 2001: 358; Racheli & Racheli, 2003: 215; Lamas, 2004: 186.

*Identification, taxonomy and variation.* This subspecies is characterized by the combination of conspicuous white translucent postdiscal and submarginal markings on the

FW and apical area of the HW, and by an intense yellow–orange translucent coloration in the HW discal cell and wing between vein  $Cu_2$  and the anal margin. Additional differences are discussed under the other subspecies. There is some variation in the yellow colouring of the HW, which may be almost absent in specimens from the extreme south of the range.

Haensch (1903) described the taxon *Episcada praestigiosa* from a single male and female collected in March on Volcán Tungurahua, and Lamas (1994) designated the male specimen in the ZMHU as the lectotype. Without mentioning *H. paradoxa praestigiosa*, Kaye (1918) described rather briefly a single female as *Pteronymia grandipennis*, without providing a figure, but fortunately the holotype is in the BMNH. Kaye (1918: 85) stated that the type locality was unknown, but, as the holotype was 'amongst some *Velamysta torquatilla* from Pozuzo, Peru', he guessed that this was where it had been collected. The specimen does not differ from typical *praestigiosa* except in the yellow colouring on the HW being much reduced, and it represents either an aberrant specimen or perhaps one from southern Ecuador that is slightly intermediate to



*H. p. catenata* (see below). Lamas (1994) regarded *praestigiosa* as a subspecies of '*Dircenna*' *paradoxa*, and later (Lamas, 2004) placed *grandipennis* as its synonym, and here we transfer both names to *Hyalenna* (**comb.n.**) for reasons given in the generic discussion.

A single specimen of *H. p. praestigiosa*, in the FV, is labelled 'Pomacochas' (Amazonas), a locality in which *H. p. catenata* apparently is common but *H. p. praestigiosa* otherwise is unknown (P. Boyer, Le Puy St. Reparade, France, pers. comm.; T. Racheli, University of Rome, pers. comm.). In Ecuador, *H. p. praestigiosa* is a close mimic of *Greta ortygia ortygia* (Weymer, 1890), amongst numerous other species with this type of colour pattern. In Amazonas, this mimicry ring is replaced by one in which the HW is transparent colourless, rather than yellow (as in *Greta ortygia pyrezi* Vitale & Bollino, 2001). Given the absence of additional specimens of *H. p. praestigiosa* in collections from Amazonas and its anomalous colour pattern were it really to occur there, we believe the specimen in the FV is mislabelled. Two females of *H. p. praestigiosa* collected near Valladolid in southern Ecuador (AS, KWJH) are slightly intermediate in wing pattern between this subspecies and *H. p. catenata*, having a faint trace of a dark postdiscal band on the HW and reduced yellow on the HW. We believe that these specimens may be transitional to *H. p. catenata*.

*Range, habitat and adult ecology.* Colombia, southern Cordillera Oriental (Huila), to extreme north-eastern Peru (Cajamarca) (Fig. 20A), from 1800 to 2600 m in primary cloud forest. Like other subspecies, females of this rare taxon generally are more common in collections and in the field. Indeed, we have never observed adult males in the field. Solitary females may be seen searching for oviposition sites 1–3 m above the ground, along wide trails or streams at the forest edge, where the larval food plants tend to occur.

*Immature stages.* The immature stages of this species (Fig. 4), in surprising contrast to the adults, are relatively easy to locate, with 128 individuals being recorded in 10 weeks in Ecuador. In Ecuador, ninety-three eggs were found, all laid singly 0.2–3 m above the ground on the undersides of leaves (Appendix 4) of four or five Solanaceae food plants: two or three species of *Solanum* section *torvum* Sw., 1788, *Solanum hispidum* Pers., 1805 and *Dunalia solanacea* Kunth, 1818. In the La Bonita area (Sucumbios), where the majority of individuals were found, the most commonly used food plants were two species of *Solanum* section *torvum*, although this may just reflect the relative natural abundances of these plants. Known food plants grow as bushes to small trees (10 m) in rocky soil beside or near forest edges, either along rivers, roads or in large clearings.

An additional thirty-five larvae were also found in Ecuador (first instar, 6; second instar, 18; third instar, 8; fourth instar, 3), always on the undersides of leaves in a similar height range to eggs. The undersides of the food plant leaves bear dense, stellate spicules, and the setose

bodies and mottled pattern of all instars provide an effective camouflage.

Of the 128 individuals found, forty-three died or failed to hatch as eggs, eighteen died as first instar, seventeen as second instar, nine as third instar, five as fourth instar, eight as fifth instar and six as pupae (Appendix 5). Fourteen individuals were reared through to adult from the following stages: egg, 5; first instar, 1; second instar, 4; third instar, 3; fourth instar, 2. Only two individuals, both found as third instars on *Dunalia solanacea*, were parasitized (Fig. 4G). Larvae of the parasitoid emerged from the fifth instar, killing the host, and pupated (fourteen pupa were found in one larva). The parasitoid cocoons are similar to those of several species of *Glyptapanteles* (Hymenoptera: Braconidae: Microgastrinae) (J. Whitfield, University of Illinois, Urbana, pers. comm.). The remaining individuals apparently succumbed to pathogens or to poor food quality. The development time from egg to pupa was approximately 32 days, the pupal stage lasting 19–20 days. Cast final instar head capsules, pupal cases and larvae preserved in alcohol are in the BMNH.

In eastern Ecuador, *H. paradoxa* may be sympatric at lower elevations with *D. adina*, and larvae of the two may be distinguished by the yellowish subdorsal bands being present only at the posterior margin of each segment in *D. adina* (compare Figs 3K; 4D), and by the presence of black spots in the anterior half of each segment in *H. paradoxa*. These characters, other distinctive markings of this species in comparison with other Ithomiinae and elevational range were used to identify immature stages not reared through to adult (Appendices 4 and 5).

*Egg.* Truncate, bearing *c.* fifteen vertical ribs lined with stellate hairs (Fig. 4A).

*Larvae.* All instars bear short setae over entire body, becoming longer laterally (Fig. 4B–F). First instar translucent pale cream, with barely visible cream bars at posterior edge of each segment, head capsule black (Fig. 4B). Second to fourth instars variable, ranging from almost uniformly dark green dorsally, with a cream to yellow subdorsal longitudinal band and dorsal row of cream to yellow bars at posterior edge of each sternite (Fig. 4C), to mottled dorsally, like later instars, with more prominent black dots and dashes. Head capsule very pale green to yellow.

Fifth instar variable, with mottled dorsal pattern of translucent grey–green ground colour and opaque patches of greyish green to yellowish green (Fig. 4D). Dorsal mottled area bounded by pair of subdorsal bands of yellow to cream spots, more or less fused. Each segment dorsally bears four additional markings: a single, dorsal yellow to cream bar or spot at posterior edge, two black subdorsal spots at middle, immediately dorsal of pale subdorsal line, and a dorsal pair of black spots near anterior edge, which may be fused into a single line. Laterally, each segment bears two black spots in middle, one dorsal and one ventral of spiracle (Fig. 4E, F), and a yellow stripe, or pair of

spots, sublaterally on each segment immediately below lower black spot. Spiracles brown. Head capsule pale yellow to cream, except for stemmata, mandibles and labrum, which are black (Fig. 4E).

*Pupa.* Varying from green, yellowish green to pale green, with extensive areas of reflective silver markings, especially lining veins of wing case, on thorax and in three dorsal bands on abdomen (Fig. 4H–J). Some individuals with brownish shading between reflective areas (Fig. 4I, J). A single pair of lateral, conical protrusions at junction of wing cases and thorax, visible in dorsal view (Fig. 4H), with posterior pair apparently absent, unlike other known *Dircenna* and *Hyalenna*. Angle between dorsal edge of thorax and abdomen relatively shallow, also in contrast to other *Hyalenna* and *Dircenna*.

*Specimens examined.* 10♂, 19♀ (Appendix 6).

***Hyalenna paradoxa catenata* (Kaye, 1918) comb.n.**  
(Figs 6E, F, G; 20A)

*Pteronymia catenata* Kaye, 1918: 84. Type locality: Peru, [Pasco], Pozuzo, 5000–6000 ft. Holotype ♀, BMNH.

*Pteronymia catenata*: D'Almeida, 1950: 394; D'Almeida, 1978: 319.

*Dircenna catenata*: D'Abbrera, 1984: 276, fig.

*Dircenna paradoxa catenata*: Lamas, 2003: 83, 184, 210, 220, pl. 30, fig. 343a–b; 2004: 186.

*Identification, taxonomy and variation.* This subspecies is distinguished from *H. p. praestigiosa* by having a dark cell bar in the FW discal cell in both sexes, dark scaling on the HW discocellular vein between the bases of veins  $Cu_1$  and  $M_3$ , and by a number of other characters. The male of *H. p. catenata* has pale yellowish buff translucent markings, rather than white or yellow, the FW discal cell is largely translucent yellowish buff, and the HW lacks the strong yellow coloration in the posterior part of the wing, with this area instead being largely colourless. The female of *H. p. catenata* has heavier dark scaling around the FW discal cell, a prominent opaque, dark submarginal band on the HW, and the HW transparent areas entirely translucent white. There is slight variation in the extent of the dark markings, especially on the HW discocellular veins, and in the orange scaling along the FW costa and margin (see Fig. 6F, G).

Kaye (1918) described this taxon clearly, in the genus *Pteronymia*, based on a single female from Pozuzo, now in the BMNH. Lamas (2004) placed it as a subspecies of '*Dircenna paradoxa*', and here we transfer it to *Hyalenna* (**comb.n.**) for reasons given in the generic discussion.

*Range, habitat and adult ecology.* This subspecies occurs throughout Peru (Amazonas to Cuzco) (Fig. 20A), from 1700 to 2850 m inside cloud forest. Like *H. p. praestigiosa*, females are more common in collections than males. The remarkable sexual dimorphism suggests that

males and females typically fly at different heights and/or in different microhabitats within the forest.

*Specimens examined.* 15♂, 15♀ (Appendix 6).

***Hyalenna paradoxa incachaca* Lamas & Willmott, ssp.n.**  
(Figs 6H; 20A)

*Description and diagnosis* (Fig. 6H). *Holotype* ♀: FW length 33.5 mm. Females distinguished from those of neighbouring and most similar subspecies *H. p. catenata* by yellow (not white) translucent coloured wing markings, except in base of FW cell  $Cu_2$ – $Cu_1$  and posterior part of discal cell. In comparison with *H. p. catenata*, translucent submarginal spots larger, black HW submarginal band reduced and black scaling over HW discocellular veins more extensive. Male unknown.

*Type material.* *Holotype*, ♀, BOLIVIA: Cochabamba: Incachaca, [c. 17°14'S, 66°29'W], 24.iv.1985 (*M. J. Adams & G. I. Bernard*) (BMNH). *Paratype*, BOLIVIA: Cochabamba: 1♀, Cochabamba-Villa Tunari, km 77, [c. 17°07.6'S, 65°47.5'W], 2600 m, 18.xi.2001 (*P. Boyer*) (PB).

*Etymology.* Named after the type locality, treated as a noun in apposition.

*Taxonomy and variation.* There is little variation between the two examined specimens. This subspecies differs from other *H. paradoxa* subspecies in the colour and size of the translucent wing areas and extent of dark markings, which are characters that differ between other *H. paradoxa* taxa. Reasons for not considering the known specimens to represent the female of *H. hugia* are discussed under that species.

*Range.* Known only from the department of Cochabamba in Bolivia (Fig. 20A), but presumably also occurring north into La Paz, based on ranges of putative comimics. Very rare, known from 2400 to 2600 m. It is particularly similar to and presumably mimics *Greta enigma* (Haensch, 1905), *Greta theudelinda* cyrcilla (Hewitson, 1874) and sympatric *Greta ortygia* (Weymer, 1890).

***Hyalenna hugia* (Schaus, 1902) comb.n., stat.rev.**  
(Figs 1E; 7A; 12F–J; 20A)

*Dircenna hugia* Schaus, 1902: 383. Type locality: Bolivia. Lectotype ♂ (here designated), USNM.

*Dircenna hugia*: Haensch, 1903: 139; Haensch, 1909: 139; Bryk, 1937: 545; D'Almeida, 1960: 8, pl. 5, figs 1–2; Mielke & Brown, 1979: 154, 196; D'Abbrera, 1984: 278.

*Dircenna paradoxa hugia*: Lamas, 2004: 186.

*Identification, taxonomy and variation.* The cladistic analysis places *H. hugia* as sister to *H. paradoxa*, which

shares similar FW venation and genitalia, notably the shape of the aedeagus, and the two species may be sympatric in Bolivia. Males are most similar to those of *H. p. catenata* (see also discussion below), but have conspicuous white VHW marginal spots and lack a black discal cell bar on the FW. These two species may be distinguished from all other congeners by the position of the FW medial recurrent vein Mr, which is nearer the base of vein M<sub>2</sub> rather than M<sub>3</sub>. *Hyalenna hugia* is also similar to some species of *Dircenna*, but these have a white costal streak on the VHW between the discal cell and vein Sc + R<sub>1</sub>, as well as differences in the FW discocellular venation (see generic introduction). Uniquely within the genus, *H. hugia* has scattered, anteriorly pointing spines on the dorsal surface of the aedeagus in the basal two-thirds of the posterior section; although *H. buckleyi* also has spines on the posterior section of the aedeagus, they are randomly orientated and placed in the posterior half, so we regard them as unlikely to be homologous. The male genitalia of *H. hugia* further differ from *H. paradoxa* in having a much shorter uncus and tegumen, a less projecting gnathos, less pointed and upswept valvae, and thinner, less heavily sclerotized inner dorsal projections from the valval costa. The male HW venation of *H. hugia* differs from that of *H. paradoxa* in the distal tip of the discal cell (vein 1d) being closer to the wing apex. The ratio of the distance from the base of the wing to vein 1d to the distance between the base of the wing and the wing margin at vein M1 was as follows: *H. p. paradoxa*, 0.65; *H. p. praestigiosa*, 0.63; *H. p. catenata*, 0.61 (n = 1 in each case); *H. hugia*, 0.75, 0.73 (n = 2).

Schaus (1902) described this species from Bolivia in the genus *Dircenna*, presumably based on a unique male, now in the USNM. Although the original description cites a type number, which appears on the single USNM specimen, Schaus apparently assigned the number to the taxon or the type series, and in some cases several type specimens are known which bear the same number (J. Hall, National Museum of Natural History, Washington, D.C., pers. comm.). The USNM specimen is therefore designated as the lectotype. Lamas (2004) placed this taxon as a subspecies of '*Dircenna*' *paradoxa*, and for the reasons discussed in the generic introduction we transfer it to *Hyalenna* (**comb.n.**). *Hyalenna hugia* is known to us from only two males, while *H. paradoxa* is known from Bolivia from only two females. Initially, we considered the two taxa conspecific, but there are a number of genital differences between the only male of *H. hugia* dissected and *H. paradoxa*, and wing venation differences, discussed above. Furthermore, there are no other known cases of Ithomiinae in which males have white marginal spots on the VHW but females do not, although the reverse is often true. Although there are pattern similarities between males of *H. hugia* and females of *H. paradoxa incachaca*, such as the extensive dark scaling on the HW discocellular veins, these pattern elements are also common in other Bolivian comimetic Ithomiinae. Therefore, we regard the two as distinct species (**stat.rev.**).

*Range.* Known only from the Bolivian Andes in the department of Cochabamba (Fig. 20A), at around 1000 m, where it is extremely rare.

*Specimens examined.* 2♂ (Appendix 6).

***Hyalenna perasippa* (Hewitson, 1877)**

(Figs 1F, K; 2D; 3F; 7B–H; 13A–F; 17A–E; 20B)

*Identification, taxonomy and variation.* This is one of the largest *Hyalenna* species. The aedeagus is sharply bent downwards towards the tip (Fig. 13E), a unique apomorphy within *Hyalenna*. The female has the antrum as a narrow sclerotized ring, rather than a broad, tapering tube (Fig. 17E), and a prominent cross-vein joining veins Sc + R<sub>1</sub> and Rs on the HW (Fig. 1K), as in *H. paradoxa* (and probably *H. hugia*). Both sexes have FW vein Mr positioned nearer the base of vein M<sub>3</sub> than M<sub>2</sub> (Fig. 1F), differentiating the species from *H. paradoxa* and *H. hugia*. Males of other *Hyalenna* species that share this FW venation have a shorter HW discal cell (Fig. 1). In wing pattern, *H. perasippa* may be similar to *H. paradoxa*, *H. buckleyi* and some subspecies of *H. sulmona*, but both sexes may be distinguished from the last two of these species by the bright yellow, instead of white to dirty yellowish white, ventral abdomen. *H. perasippa* is further distinguished from *H. buckleyi* by the absence of white apical spots on the ventral surface. The heavy scaling on the FW discocellulars of most subspecies further distinguishes them from similar subspecies of *H. sulmona* (except *H. s. tersa*). There is variation in the translucent colouring of both wings and width of marginal borders, and four subspecies are recognized.

*Range.* Colombia (Cordillera Central [and Oriental?]) to central Peru, along the eastern slope of the Andes. Very rare, in cloud forest from 1400 to 2200 m.

*Specimens examined.* 16♂, 8♀ (Appendix 6).

***Hyalenna perasippa perasippa* (Hewitson, 1877)**

(Figs 1F; 2D; 3F; 7E, F; 20B)

*Ithomia perasippa* Hewitson, 1877: 85. Type locality: Ecuador, [Azuay], Jima [= Gima]. Lectotype ♂ (here designated), BMNH.

*Ithomia perasippa*: Kirby, 1877: 841; Kirby, 1879: 43; Hemming, 1967: 223.

*Episcada perasippa*: Haensch, 1909: 151, pl. 39e, fig. [6]; Röber, 1930: 21.

*Ithomia perasippe* [sic]: Riley & Gabriel, 1925: 38.

*Episcada perasippe* [sic]: Bryk, 1937: 592.

*Hyalenna perasippe* [sic]: Forbes, 1942: 39, fig. 3; Brown & D'Almeida, 1970: 15; Smart, 1975: 269.

*Hyalenna perasippa*: Lewis, 1973: 229, pl. 46, fig. 4; Moreno *et al.*, 1997: 152; Racheli & Racheli, 2001: 358; Racheli & Racheli, 2003: 216; Lamas, 2004: 186.

*Hyalenna perasippe perasippe* [sic]: D'Almeida, 1978: 302; D'Abrera, 1984: 271, fig.  
*Hyalenna perasippa perasippa*: Mielke & Brown, 1979: 165.

**Identification, taxonomy and variation.** The nominate subspecies differs from *H. p. ortygiosa* in having yellow postdiscal and submarginal markings on the FW, amongst other differences; identification with respect to *H. p. solitaria* is discussed under that taxon. Hewitson (1877) described this species from one or more males in his own collection collected by Buckley in Ecuador at 'Jima' (= Gima). The true collection locality was probably in the vicinity of Chigüinda, at around 1800 m, on the trail to the lowlands from Gima. The description mentions the diagnostic straight, steep FW discocellulars, and a single male in the BMNH, matching Hewitson's original description, is designated here as the lectotype.

The FW coloured translucent markings vary somewhat in size and may be more or less intense yellow. The only known female, at the BMB, is labelled simply 'Ecuador', but was probably also collected by Buckley in the same region as the type series.

**Range.** South-eastern Ecuador (Morona-Santiago), probably extending into Zamora-Chinchiipe and extreme northern Peru (Cajamarca, Amazonas) (Fig. 20B); known only from around 1600 m.

**Specimens examined.** 6♂, 1♀ (Appendix 6).

***Hyalenna perasippa valencia* Willmott & Lamas, ssp.n.**  
(Figs 1K; 7B; 20B)

[*Dircenna paradoxa paradoxa*: D'Abrera, 1984: 276, fig. – misidentification]

**Description and diagnosis** (Fig. 7B). **Holotype** ♀: FW length 35 mm. Distinguished from all other *H. perasippa* taxa by absence of coloured translucent markings on both wings, except a slight yellow tint along HW anal margin. Dark markings also reduced on both wings, leaving narrow distal marginal borders that are not scalloped at basal edge.

**Type material.** **Holotype**, ♀, COLOMBIA: *Risaralda*: Distrito de Pereira, [c. 4°49'N, 75°43'W], 1886 (*R. M. Valencia*) (BMNH).

**Etymology.** Named after Román M. Valencia, collector of the holotype and many other comimetic ithomiine taxa from this region of Colombia. The name is used as a noun in apposition.

**Taxonomy and variation.** The holotype specimen was figured by D'Abrera (1984: 276) under the name '*Dircenna paradoxa paradoxa*', a remarkably similar taxon from the same region of Colombia (Fig. 6A, B). *H. p. valencia* is distinguished from *H. p. paradoxa* by the posterior

position of the medial recurrent vein on the FW. It is associated with other *H. perasippa* taxa because of the yellow ventral abdomen and large size, both distinctive characters of this species.

**Range, habitat and adult ecology.** Northern region of the Cordillera Central in Colombia, currently known only from Risaralda province but presumably occurring also in Antioquia and Caldas, from where other comimics are known (Fig. 20B). It presumably flies with and mimics a number of other ithomiines, including *H. s. hyalina* (Fig. 10E, F), *H. p. paradoxa* (Fig. 6A, B), *Godyrus panthyle quinta* (Staudinger, 1885), *Ithomia avella miraculosa* Lamas, 2003 and *Pagyris ulla dimidiata* (Staudinger, 1885), amongst others.

***Hyalenna perasippa ortygiosa* Willmott & Lamas, ssp.n.**  
(Figs 7C, D; 13A–F; 20B)

[*Hyalenna perasippe* [sic]: Vélez & Salazar, 1991: 139, fig. – misidentification].

**Description and diagnosis** (Fig. 7C, D). **Holotype** ♀: FW length 33 mm. Both sexes distinguished from most similar taxa (*H. p. perasippa* and *H. p. solitaria*) by white (not yellow) FW translucent markings. Female further distinguished from neighbouring nominate subspecies by having black FW veins (not orange–brown in centre of wing). Males (based on Colombian specimens) further distinguished by having reduced, or no, dark scaling around FW discocellular veins and FW translucent markings reduced.

**Type material.** **Holotype**, ♀, ECUADOR: *Tungurahua*: Baños, [1°24'S, 78°25'W], 1800 m, iv–v.1912 (*M. G. Palmer*) (BMNH). **Paratypes**, ECUADOR: *Napo*: 1♀, Guacamayos, [0°37'S, 77°49'W], 1400 m, 7.x.1984 (*C. Velástegui*) (GTB); 1♀, Yanayacu, [near Cosanga, 0°34.2'S, 77°52.2'W, 2000 m] (*H. Greeney*) (FV).

**Etymology.** From the specific name of the similar, comimetic ithomiine taxon *Greta ortygia ortygia*.

**Taxonomy and variation.** This taxon is treated as a subspecies of *H. perasippa* for the same reasons as discussed under *H. p. valencia*. Specimens from Colombia appear to be referable to this subspecies, but, given the paucity of material examined and poor locality data, we exclude such specimens from the type series.

**Range, habitat and adult ecology.** This is a very rare taxon occurring from central eastern Ecuador (Pastaza) to Colombia (Fig. 20B), from around 1400 to 2000 m in cloud forest habitats. All data of examined Colombian specimens are vague, but labels stating 'Bogotá' suggest the Cordillera Oriental, whereas the presence of *H. perasippa valencia* in Risaralda implies this subspecies possibly also occurs in the

southern Cordillera Central. Apparently, it occurs with and mimics *H. buckleyi buckleyi* (Fig. 8A, B), *H. paradoxa praestigiosa* (Fig. 6C, D), *Godyris panthyle panthyle* and *Greta ortygia ortygia*, amongst others.

*Specimens examined.* 7♂, 4♀ (Appendix 6).

***Hyalenna perasippa solitaria* Lamas & Willmott, ssp.n.**  
(Figs 7G, H; 17A–E; 20B)

*Description and diagnosis* (Fig. 7G, H). *Holotype* ♂: FW length 32.5 mm. Both sexes distinguished from neighbouring and most similar subspecies, *H. p. perasippa*, as follows. Translucent yellow submarginal markings on both wings reduced, especially in cells Cu<sub>1</sub>–M<sub>3</sub> and M<sub>3</sub>–M<sub>2</sub>, FW postdiscal band slightly more intense yellow, noticeably more distinct in female. Dark HW distal marginal border and FW discocellular bar broader. Female also has black veins on FW, instead of orange–brown in middle of wing.

*Type material.* *Holotype*, ♂, PERU: Junín: 1 km S Mina Pichita, 11°05'S, 75°25'W, 2100 m, 12.xi.2003 (G. Lamas) (MUSM). *Paratypes*, 1♂, 2♀, same locality data as holotype, 27.ix.1985, 14.v.2002, 21.viii.2003 (K. S. Brown, Jr., G. Lamas) (MUSM).

*Etymology.* Derives from the Latin adjective 'solitarius', referring to the rarity of this taxon.

*Taxonomy and variation.* The taxon is associated with *H. perasippa* on the same grounds as *H. p. valencia*. Little variation has been observed within the small type series from Junín. A single male specimen from Amazonas in northern Peru is treated for the present as this taxon, although only a photograph has been examined. Given the mimicry associations of *H. perasippa* elsewhere, and ithomiine fauna known from Amazonas, it seems likely that this specimen will prove to belong to a distinct, undescribed subspecies.

*Range, habitat and adult ecology.* East Andean slopes in central Peru (Junín), possibly extending north to Amazonas (Fig. 20B) (see discussion above). The majority of known specimens have been collected at the same dense cloud forest site in Chanchamayo (Junín) at around 2000 m. A male was collected whilst traversing a path inside the forest, flying at approximately 3.5 m, the second male was resting on a leaf by the side of another trail at c. 4 m. A female was encountered resting on a leaf inside the forest at c. 2.5 m.

*Specimens examined.* 3♂, 2♀ (Appendix 6).

***Hyalenna buckleyi* Willmott & Lamas, sp.n.**  
(Figs 1G; 2E; 8A–D; 13G–K; 17F–J; 20C)

*Identification, taxonomy and variation.* *Hyalenna buckleyi* sp.n. is most easily distinguished from all other

*Hyalenna* by several characters in the genitalia: in the male, the small spines on the aedeagus and short, blunt uncus are unique, and the serrate inner edge of the valvae, less tapering valvae and straight aedeagus further distinguish it from *H. perasippa*. The remaining three species, *H. alidella*, *H. sulmona* and *H. pascua*, further differ in having a broad valva which tapers and sweeps upwards abruptly at the tip. The antrum differs from that of female *H. perasippa* in being a broad, sclerotized tapering tube (like other *Hyalenna*) instead of a narrow sclerotized ring. The antrum is similar to that of female *H. sulmona*, *H. alidella* and *H. pascua*, but slightly less sclerotized and more symmetrical at the anterior tip, and the inverted 'lip' at the postero-dorsal edge of the fused eighth sternite plates is broad, about half the width of these plates, instead of a quarter (see Fig. 17J). The terminal tergite (Fig. 17I) is unique in *Hyalenna* (in the one specimen dissected) in being mesially divided by unsclerotized tissue, like *Dircenna*. In outward appearance, *H. buckleyi* most resembles *H. sulmona*, especially *H. sulmona tersa*, but (at least in the male) has a rounder HW (less acutely angled at the apex) and more triangular FW, on the FW there is heavier dark scaling on the discocellulars and whitish translucent postdiscal spots, and on the VHW there are no submarginal spots except at the apex. The position of the DHW androconial hair pencil is unique, being located near the middle of the discal cell (Fig. 2E); in all other species, the basal part of the hair pencil is approximately opposite the humeral vein (Fig. 2C, D, F). The HW venation (Fig. 2E) is also unique in having 1d only slightly shorter, rather than much shorter, than 2d.

This species has the diagnostic characters of the genus and is sister to *H. alidella* + *H. sulmona* + *H. pascua* (Fig. 19). There is some variation in the colour of the translucent wing markings, and two subspecies are recognized.

*Range.* Central eastern Ecuador to north-eastern Peru. Very rare in cloud forest from 1250 to 2500 m.

*Specimens examined.* 7♂, 4♀ (Appendix 6).

***Hyalenna buckleyi buckleyi* Willmott & Lamas (sp.n.)**  
(Figs 1G; 2E; 8A, B; 13G–K; 20C)

*Hyalenna* sp.n.: Lamas, 2004: 186.

*Diagnosis.* The nominate subspecies is distinguished from *H. b. pomacocha* under the description of that taxon. Identification and apomorphies of the species are discussed above.

*Description.* Male (Fig. 8A). *Holotype*: FW length 31 mm. *Dorsal surface*: both wings largely colourless transparent except for fine black hair-like scales; costal, distal and anal margins of both wings, and narrow FW discocellular bar, blackish brown, except for FW costal

vein basal of discocellulars, which is orange; inner edge of distal margins of both wings slightly scalloped at veins. Forewing with translucent whitish colouring forming five submarginal spots decreasing in size from tornus to apex, a discal spot in cells  $R_5$ – $M_2$ , and a large spot filling base of cell  $Cu_1$ – $Cu_2$ . Hindwing with whitish translucent colouring filling discal cell and extending just beyond discocellulars and into base cell  $M_3$ – $Cu_1$ , also forming submarginal dots in cells  $M_3$ – $Cu_1$  and  $M_2$ – $M_3$ ; yellowish translucent colouring between anal margin and vein  $Cu_2$ . *Ventral surface*: similar to dorsal surface except margins coloured uniform yellowish brown, three silvery-white apical spots on FW in cells  $R_3$ – $M_1$  and a similar apical spot on HW in cell  $M_1$ – $M_2$ . *Androconia*: DHW with a single patch of pale, elongate androconial hair-like scales at inside anterior edge of the discal cell; underlying hair patch in cell  $Rs$ – $Sc + R_1$  is a patch of modified androconial scales that are white, shaped like rounded diamonds and sparsely overlapping. Veins  $Sc + R_1$  and  $Rs$  approximately parallel, diverging slightly distally. *Venation*: HW with 1d present, Mr on 3d, which is sharply kinked; HW discal cell relatively short, with 1d similar distance from wing base as 3d; vein  $Sc + R_1$  terminating near base of vein  $Rs$ , not reaching distal margin; FW with Mr on 3d, anterior portion of 3d long, approximately equal in length to and aligned with 2d; Mr near posterior side of discal cell. *Body*: eyes dark brown and bare; labial palpi white with a black ventro-lateral stripe; antennae black; frons black with lateral white vertical bands; patagia white except for a narrow black medial line; tegula black with a white horizontal band; thorax dorsally black with scattered white lateral scales and medial white band, ventrally white with black bands where legs rest against body, from eucoxae to episterna; legs black with scattered white scales, lacking tibial spurs; abdomen dorsally blackish brown, ventrally black with scattered, dirty white scales. *Genitalia* (Fig. 13G–K): uncus and tegumen broad in lateral view, uncus short, thick and blunt; gnathos uniformly strongly sclerotized terminating posteriorly in a point; valva roughly trapezoidal, blunt, similar to *H. perasippa*, with two serrate, sclerotized ridges on inner edge; valva inner dorsal arms strongly sclerotized, approximately equal in size; saccus short; aedeagus straight in dorsal view, slightly curved ventrally in lateral view, in distal third bearing sparse, small, dorsal and lateral spines; vesica with trace of cornuti apparently forming a band encircling vesica.

*Female* (Fig. 8B). *Paratype*: FW length 30 mm. Similar to male, except as follows. *Dorsal surface*: all translucent coloured markings slightly expanded, HW yellow paler. *Ventral surface*: FW apex lacking any white spots. *Androconia*: DHW lacking any modified androconial scales. *Venation*: similar to congeners, HW with veins  $M_1$  and  $Rs$  nearly touching at base;  $Sc + R_1$  running close to  $Rs$  near base and extending to wing margin; according to F. Vitale, (Lecce, Italy, pers. comm., only photograph available for examination),  $Sc + R_1$  and  $Rs$  are not joined by a cross-vein and the humeral vein has a single main

projection (i.e. not strongly bifid). *Abdomen and genitalia*: not available for examination.

*Type material*. *Holotype*, ♂, ECUADOR: *Tungurahua*: ‘env[irons] d’Ambato’ (*I. Blanc*) (BMNH). *Paratypes*, ECUADOR: 1♀, *Tungurahua*: Chinchin, [1°26’S, 78°16’W], 1800 m, 18.viii.1988 (*C. Velástegui*) (GTB); 4♂, *Zamora-Chinchipe*: Quebrada Chorrillos, km 7 Zamora-Loja old rd., 1250 m, 4°02.10’S, 78°59.30’W, 3.iv.1995 (*K. Willmott & J. Hall*) (KWJH, 2♂ MECN, 2♂).

*Etymology*. Named after Clarence Buckley, the pioneering collector who captured the first known specimens of two other *Hyalenna* species.

*Discussion*. Little variation is apparent in the nominate subspecies among the seven specimens examined and two males dissected. One examined female (excluded from the type series) was collected by H. Greeney and donated to F. Vitale without locality data, but almost certainly collected at Yanayacu (Ecuador, Napo).

*Range, habitat and adult ecology*. The species is known currently from Ecuador (Napo) to northern Peru (San Martín), with the nominate subspecies occurring only as far south as southern Ecuador (Zamora-Chinchipe) (Fig. 20C), from 1250 to 2000 m. The type locality is probably imprecise, and the holotype was most likely collected lower down on the Río Pastaza. We have observed the nominate subspecies on two occasions, in April and May, towards the end of the wet season, at Quebrada Chorrillos, in south-eastern Ecuador. On both occasions, males perched at the top of the same bush approximately 15 m above a steep ravine, with one bank a small, recent pasture and the other primary forest. Several males were observed chasing one another, as well as other ithomiines and butterflies that flew in the vicinity. Visits to the same locality at other times of the year produced no sightings. Both sexes are accurate mimics of several other sympatric ithomiines, particularly *H. paradoxa praestigiosa* (Fig. 6C, D), *Greta enigma* (Haensch, 1905), *Greta ortygia ortygia* and *Godyris panthyle panthyle*.

*Specimens examined*. 5♂, 2♀ (Appendix 6).

***Hyalenna buckleyi pomacocha* Lamas & Willmott, ssp.n.** (Figs 8C, D; 17F–J; 20C)

*Description and diagnosis* (Fig. 8C, D). *Holotype* ♂: FW length 30 mm. Both sexes differ from nominate subspecies as follows: *Dorsal surface*: FW with costa mostly black, orange only near base; HW translucent yellow coloration much reduced, so wings appear largely colourless except for white postdiscal and submarginal spots on FW, white submarginal spots and white coloration in discal cell on HW; all distal black margins broader, especially in female, where nearly twice width of



nominate subspecies. *Ventral surface*: marginal orange-brown colour perhaps slightly darker (not clear from digital photographs). *Body*: ventral surface of abdomen white, not blackish with sparse white scales.

*Female. Abdomen and genitalia* (Fig. 17F–J): terminal tergite mesially divided with soft tissue, not closely appressed to seventh tergite; eighth sternite plates mesially fused and fused to antrum, triangular in lateral view extending ventrally from mid-point of ventral edge of terminal tergite; dorso-posterior edge of fused eighth sternites inverted forming a broad ‘shelf’ half width of sternites; antrum not closely appressed to posterior edge of seventh sternite; anterior portion of antrum moderately (not strongly) sclerotized, opening to ductus bursae slightly asymmetrical to left side; appendix bursae present.

*Type material. Holotype*, ♂, PERU: Amazonas: Pomacochas, 5°49’S, 77°58’W, 2500 m (MUSM, ex coll. FV). *Paratypes*, PERU: San Martín: 1♂, Afluente, nr. Jorge Chávez, 800–1500 m (OD); 1♀, same data as preceding except ii.2003 (*P. Meléndez*) (PB); 1♀, Jorge Chávez, 6°41’S, 77°40’W, 1400 m, ii.2003 (*J. A. Tafur*) (PB).

*Etymology*. From the type locality.

*Taxonomy and variation*. There is little variation amongst the few specimens known. The male genitalia are similar to those of the nominate subspecies, in particular in having numerous spines on the aedeagus (F. Vitale, Lecce, Italy, pers. comm., specimen not available for examination), an apomorphy for this species.

*Range, habitat and adult ecology*. This subspecies is known only from a small region in north-eastern Peru, in the departments of Amazonas and San Martín (Fig. 20C), from about 1400 to 2500 m. It presumably mimics sympatric *Greta enigma* and *Greta ortygia pyrezi*.

***Hyalenna pascua* (Schaus, 1902)**  
(Figs 3G; 8E, F; 14K–O; 18K–O; 20D)

*Episcada pascua* Schaus, 1902: 384. Type locality: Brazil, [Rio de Janeiro], Petrópolis. Lectotype ♂ (here designated), USNM.

*Episcada carcinia pasena* [sic]: Haensch, 1909: 151.

*Episcada carcinia pascua*: Zikán, 1928: 7; Bryk, 1937: 589.

*Episcada pascua*: Zikán, 1935: 75, figs 3–4; Zikán, 1941: 108, 111; Zikán, 1942: 270, fig. 20, 273, fig. 14; D’Almeida, 1960: 16, pl. 3, figs 3–4; D’Almeida & Mielke, 1967: 72, fig. 9; Zikán & Zikán, 1968: 48; Silva *et al.*, 1968: 331; Ebert, 1969: 40; D’Almeida, 1978: 307; D’Abrera, 1984: 248.

*Episcada pasana* [sic]: Dufrane, 1948: 194.

[*Episcada carcinia* f. *pascua*: Hayward, 1951: 247 misidentification]

*Hyalenna pascua*: Brown & D’Almeida, 1970: 15; Brown & Domingues, 1970: 213; Mielke & Brown, 1979: 165;

Brown, 1985: 449; Brown & Freitas, 1994: 10, figs 2, 7F; Lamas, 2004: 186.

*Identification, taxonomy and variation*. Distinguished from all other *Hyalenna* by the almost colourless wings except for whitish scaling at the DFW costa distal of a black discocellular bar.

Schaus (1902) described this species from an unstated number of specimens from Brazil, Petrópolis, and the single male in the USNM, matching the original description, is designated here as the lectotype (see discussion under *H. hugia* for status of Schaus type specimens). This taxon forms a clade with *H. sulmona* and *H. alidella* and it may prove to be conspecific with one of these species, but, given the current geographical separation, smaller size of *H. pascua* and lack of information as to the relationships between the three species, we keep them distinct.

*Range, habitat and adult ecology*. Eastern Brazil, from Minas Gerais and Rio de Janeiro south to Paraná (Fig. 20D). Hayward (1951) cited it (as a form of *Episcada ‘carcinia’*) from Misiones, Argentina, but this was a misidentification. This is the most common species in the genus, ranging from at least 800 to 1700 m in montane forests. It was reported to be common locally in the Serra do Japi, São Paulo (Brown, 1992), and not uncommon at Poços de Caldas (Ebert, 1969) in February and May in low primary and secondary (‘capoeira’) forest. Brown (1985) reported that adult dry body weight may consist of up to 3.4% pyrrolizidine alkaloids, the defensive chemicals that render adults unpalatable, a fraction typical of members of the tribe.

*Immature stages*. The only recorded host plant is *Solanum* nr. *schwackeanum* L. B. Sm. & Downs, 1964 (Brown & Freitas, 1994). Zikán & Zikán (1968) stated that the larva was found ‘on an Euphorbiaceae’, which undoubtedly is wrong. This was repeated by Silva *et al.* (1968). The eggs are all laid singly on the larval food plant, often near holes or veins (Brown & Freitas, 1994). All instars and pupa closely resemble those of *H. sulmona tersa* (see Brown & Freitas, 1994), described under that taxon.

*Specimens examined*. 39♂, 46♀ (Appendix 6).

***Hyalenna alidella* (Hewitson, 1869)**  
(Figs 1N; 9; 10A; 14A–E; 18A–E; 21A)

*Identification, taxonomy and variation*. This species is distinguished from all other *Hyalenna* (except *H. sulmona balsamica*) by the combination of a usually broad, opaque or translucent, white or yellow FW postdiscal band (narrower or absent in other species) and largely colourless FW discal cell and HW (except in *H. a. exsulans* and females of *H. a. minna*; the HW is partially translucent yellow in *H. hugia*, *H. perasippa*, *H. buckleyi*

*buckleyi* and similar *H. sulmona*). Morphological characters also permit certain identification of *H. alidella* from all species except *H. sulmona* and *H. pascua*, particularly the short, straight, smooth aedeagus and distinctive upwardly curving valva in the male genitalia (Fig. 14).

One possible synapomorphy for *H. alidella* taxa is the presence of a cross-vein joining veins Rs and Sc + R<sub>1</sub> of the female HW; this has been observed in all *H. alidella* taxa except *H. a. minna* and *H. a. vesca*, for which we have been unable to examine specimens, and is absent in all *H. sulmona* taxa, *H. pascua* (although sometimes faintly visible in cleared wings) and *H. buckleyi* (F. Vitale, pers. comm.). Given the variation in this character, taxa are grouped principally on the basis of similarity of wing patterns in neighbouring taxa and elevational and geographical range information. All known taxa have been regarded until recently as distinct species, but, given the lack of morphological differences, close allopatry and similar habitats, we regard them as conspecific. There is variation in the width, opacity and colour of the FW postdiscal band, the size of the translucent FW submarginal spots, the HW colour and width of the marginal border, and VHW white marginal spots, and seven subspecies are recognized.

**Range.** Eastern Panama to north-western Venezuela, south to central Bolivia, along the Andes. Rare, in cloud forest from 1000 to 2100 m.

**Specimens examined.** 39♂, 65♀ (Appendix 6).

***Hyalenna alidella alidella* (Hewitson, 1869)**  
(Figs 1N; 9A, B; 14A–E; 18A–E; 21A)

*Ithomia alidella* Hewitson, 1869: [24], pl. [13], fig. 174. Type locality: 'New Granada' [= Colombia]. Lectotype ♀ (designated by Lamas, 1994: 279), BMNH.

*Ithomia alidella*: Kirby, 1871: 30; Kirby, 1879: 46; Weymer, 1899: 308; Riley & Gabriel, 1925: 7.

*Pteronymia alidella*: Haensch, 1903: 197.

*Episcada dirama* f. *alidella*: Haensch, 1909: 151.

*Episcada alidella*: Bryk, 1937: 588.

*Hyalenna alidella alidella*: Forbes, 1942: 38; D'Almeida, 1978: 301; Mielke & Brown, 1979: 165; D'Abbrera, 1984: 271, fig.; Lamas, 2004: 186.

*Hyalenna alidella*: Brown & D'Almeida, 1970: 15; Lamas, 1994: 279.

**Identification, taxonomy and variation.** The nominate subspecies is similar to the Colombian *H. a. vesca*, and especially to south Andean *H. a. dirama*, and distinguished under the accounts for those taxa. It is separated geographically from the latter by the white-banded subspecies *H. a. scantilla*. Hewitson (1869) described and clearly figured this taxon from one or more females in his collection. A female in the BMNH was designated as lectotype by Lamas (1994).

**Range, habitat and adult ecology.** North-western Venezuela to Colombia, presumably the eastern slope of the Cordillera Oriental (Fig. 21A), from about 1400 to 1800 m in premontane cloud forest. We have seen no specimens with reliable, precise data from Colombia, but the range can be inferred from ranges of other probably comimetic and sympatric ithomiines. According to A. Neild (London, UK, pers. comm.), Paquito Romero has encountered this taxon most frequently in September and October in Barinas state, Venezuela. Males are attracted to pyrrolizidine alkaloid sources including *Eupatorium* (Eupatoriae) flowers and, in drier months, to bait of dried *Heliotropium* (Boraginaceae).

**Specimens examined.** 5♂, 16♀ (Appendix 6).

***Hyalenna alidella exsulans* Lamas & Willmott, ssp.n.**  
(Figs 10A; 21A)

**Description and diagnosis** (Fig. 10A). Differs from nominate subspecies as follows. **Dorsal surface:** FW with yellow postdiscal band less opaque, and continuing through base of cell M<sub>3</sub>–Cu<sub>1</sub> to almost fill cell Cu<sub>1</sub>–Cu<sub>2</sub>; five large translucent yellow submarginal spots present; some yellowish translucence present in discal cell. Hindwing with dark marginal border twice as broad as nominate with more indistinct and undulate basal edge; discal cell and postdiscal area translucent yellow, becoming slightly orange towards marginal border at tornus. **Ventral surface:** similar to dorsal surface, except borders and FW discocellular bar orange–brown, three white apical spots on FW and four white apical spots on HW, each surrounded by black.

**Type material.** *Holotype*, ♀, PANAMA: Darién: Cerro Pirre, 8°00'N, 77°40'W, 1000 m, vi.1979 (G. B. Small, Jr.) (USNM).

**Etymology.** From the Latin adjective 'exsulans' (= wandering, exiled), with reference to this taxon's extra-Andean distribution.

**Taxonomy and variation.** This taxon is associated with *H. alidella* on the basis of the wing shape, broad FW postdiscal band and capture elevation, which is most similar to *H. alidella*.

**Range.** Only known from the type locality, but presumably occurring in adjacent mountains in north-western Colombia (Fig. 21A).

***Hyalenna alidella cinereola* Lamas & Willmott, ssp.n.**  
(Figs 9E, F; 21A)

*Hyalenna alidella* n. ssp: Lamas, 2004: 186.

*Description and diagnosis* (Fig. 9E, F). Differs from otherwise similar Ecuadorian *H. a. scantilla* in having a more opaque white FW band, reduced white in HW discal cell and lack of a yellow stripe at base of VHW costa. Female further differs in distal edge of white FW postdiscal band being straight and well defined and in white marginal spots on VHW being confined to apex.

*Type material.* *Holotype*, ♀, COLOMBIA: Cundinamarca: 'Bogotá', 1898 (BMNH). *Paratypes*, COLOMBIA: Boyacá: 1♂, 'S. Salvador' [5°36'N, 73°43'W] (MUSM); *No specific locality*: 1♀, 'Colombia' (MUSM); 1♀, 'Colombia' (G. Kalbreyer) (MUSM).

*Etymology.* A feminine adjective, from the Latin 'cinereus' (= ash-coloured, grey), referring to the largely colourless, translucent greyish wings of this subspecies.

*Taxonomy and variation.* We deliberated about the description of this taxon because of the poor locality data available. However, the specimens examined are consistent in all diagnostic features, sharply differentiated from other Colombian *H. alidella*, and the likely range of the taxon can be inferred with reasonable confidence based on ranges of other comimetic ithomiines (see below).

*Range.* There are no reliable, precise distribution data for this taxon. However, the wing pattern, with the broad, opaque white FW band, is similar to a mimetic complex of ithomiine species that apparently occur on the western slopes of the Cordillera Oriental north-west of Bogotá, including: *Episcada salvinia apia* (C. Felder & R. Felder, 1865) and undescribed subspecies of *Oleria santinezia* and *Pteronymia artema*. The paratype male in the MUSM, labelled 'S. Salvador', most plausibly was collected in the vicinity of San Salvador in Boyacá, a town situated along a relatively well-travelled route between Tunja and Chiquinquirá. Other Colombian localities with the same name (in Valle del Cauca, Atlántico, Cesar and Arauca) are much less likely, being remote from known Lepidoptera collecting localities and/or extra-Andean. The specimen collected by G. Kalbreyer and labelled 'Colombia' could have been collected in the vicinity of Ocaña (Norte de Santander), where he was from 1877 to 1878 and in 1880. An additional female specimen in the ZMHU from 'Colombia' is excluded from the type series because of the imprecise label data.

***Hyalenna alidella vesca* Lamas & Willmott, ssp.n.**  
(Figs 9C, D; 21A)

*Hyalenna alidella* n. ssp.: Lamas, 2004: 186.

*Description and diagnosis* (Fig. 9C, D). Differs from *H. alidella alidella* in FW postdiscal band (in males) being about half width and more translucent, and in lacking

translucent yellow markings in FW submargin and HW discal cell.

*Type material.* *Holotype*, ♂, COLOMBIA: Valle del Cauca: Saladito, 3°29.0'N, 76°37.0'W, 1650 m, 10.viii.1976 (G. B. Small, Jr.) (MUSM). *Paratypes*, 1♂, Cauca: Pescador, 2°47'N, 76°33'W, 1450 m, 20.i.1974 (S. R. & L. Steinhauser) (MGCL); 1♀, Valle del Cauca: Cali, km 14 via al Mar, 3°28.2'N, 76°37.2'W, 1600 m, 30.vi.1983 (L. M. Constantino) (LMC); 1♀, Cali, km 18 via al Mar, 3°29'N, 76°38'W, 1800 m, i.1981 (L. M. Constantino) (LMC); 1♂, El Topacio, Rio Pance, c. 3°19'N, 76°38'W, 1600 m, 2.ix.1985 (L. M. Constantino) (LMC); 2♂, same data as holotype (MUSM); 1♂, Saladito, 3°29'N, 76°37'W, 2000 m, 28.ii.1981 (C. Callaghan) (MUSM); 1♀, San Antonio, above Cali, km 14, 3°29'N, 76°38'W, 1800 m, 10.i.1982 (L. M. Constantino) (LMC).

*Etymology.* From the Latin adjective 'vescus' (= weak, poor, thin), referring to the reduced FW postdiscal band in comparison with the nominate subspecies.

*Taxonomy and variation.* Little variation has been observed in the few specimens examined.

*Range, habitat and adult ecology.* This taxon occurs in Colombia, on the eastern slope of the Cordillera Occidental, the western slope of the Cordillera Central (Antioquia, Cauca) and also possibly the eastern slope (Fig. 21A); one specimen from Huila (photograph examined) is tentatively treated as this taxon. The three female specimens from Antioquia and Huila are excluded from the type series. The taxon seems to be uncommon and has been recorded from 1450 to 2000 m.

***Hyalenna alidella scantilla* (Hewitson, 1877)**  
(Figs 9G, H; 21A)

*Ithomia scantilla* Hewitson, 1877: 86. Type locality: Ecuador, [Azuay], Jima [= Gima]. Lectotype ♂ (here designated), BMNH.

*Ithomia scantilla*: Kirby, 1877: 841; Kirby, 1879: 43; Riley & Gabriel, 1925: 44.

*Pteronymia scantilla*: Haensch, 1903: 200.

*Episcada scantilla*: Haensch, 1909: 151; Bryk, 1937: 593.

[*Hyalenna teresita*: Forbes, 1942: 39, fig. 1].

*Hyalenna scantilla*: D'Abrera, 1984: 271, fig.; Racheli & Racheli, 2001: 358; Racheli & Racheli, 2003: 217.

*Hyalenna alidella scantilla*: Lamas, 2004: 186.

*Identification, taxonomy and variation.* Differs from the nominate subspecies in the white, rather than yellow, colour of the translucent markings, and the constricted FW postdiscal marking at vein M<sub>2</sub>. Distinguished from *H. alidella cinereola* under the account for that taxon.

Hewitson (1877) described this taxon from both sexes in his collection, from specimens collected by Clarence Buckley in Ecuador. The type locality, 'Jima' [= Gima], is in the dry highlands of Azuay province, and the specimens probably originated somewhere along the old trail to the lowlands from Gima through the village of Chigüinda. The original description of the male mentions the oblique FW discocellulars, whereas that of the female notes a black FW discocellular bar and white submarginal spots. We have selected the single male in Hewitson's collection (BMNH) as the lectotype of *scantilla*; two further females in the same collection are regarded as paralectotypes. Although this taxon has previously been treated as a full species, there are few pattern and no morphological differences compared with *H. alidella alidella*, which is otherwise allopatric. Furthermore, there are other species which show similar polymorphism in the colour of the FW postdiscal band from yellow to white (e.g. sexual dimorphism in *Episcada mira* (Hewitson, 1877)), and so we regard *scantilla* as a subspecies of *H. alidella* (Lamas, 2004).

*Range, habitat and adult ecology.* Eastern Ecuador, from Tungurahua south to Morona-Santiago, but presumably more widespread both north and south (Fig. 21A); appears to range from approximately 1300 to 1600 m.

*Specimens examined.* 3♂, 10♀ (Appendix 6).

***Hyalenna alidella dirama* (Haensch, 1905)**

(Figs 9I, J; 21A)

*Episcada dirama* Haensch, 1905: 172, pl. 5, fig. 19. Type locality: Bolivia, [La Paz], Yungas [error?]. Holotype ♂, ZMHU.

*Episcada dirama*: Haensch, 1909: 151, pl. 39f, fig. [1]; Zikán, 1935: 75; Zikán, 1941: 111; Ureta, 1941: 34.

*Episcada alidella dirama*: Bryk, 1937: 589.

*Hyalenna alidella dirama*: Forbes, 1942: 38; D'Almeida, 1978: 302; D'Abbrera, 1984: 271; Lamas, 2003: 210; Lamas, 2004: 186.

*Hyalenna* [sic] *dirama*: Lewis, 1973: 229.

*Identification, taxonomy and variation.* This subspecies is almost identical to the nominate subspecies, except for a possibly more translucent yellow FW band, but it is geographically separated from it by *H. a. scantilla*. As *H. a. scantilla* is most plausibly sister to either *H. a. alidella* or *H. a. dirama*, recognition of the last two as disjunct populations of the same subspecies would make that subspecies paraphyletic.

Haensch (1905) described this taxon as a species of *Episcada*, based on a single male in his collection captured by Gustav Garlepp in the Yungas [of La Paz], Bolivia. The original figure and the holotype in the ZMHU show it to be a member of the genus *Hyalenna*, where it was placed by Forbes (1942). The translucent markings are very similar in

pattern to those of *H. a. scantilla*, and, given the lack of other genital or structural differences, we treat this taxon as a subspecies of *H. alidella*.

*Range, habitat and adult ecology.* This subspecies is known from northern to southern Peru (Amazonas to Cuzco) (Fig. 21A). The holotype supposedly was collected in Bolivia (La Paz), but we have also examined specimens of *H. a. minna* collected recently in the same area by Tello, and so regard the holotype probably as mislabelled. However, it is also possible that it is the La Paz specimens of *H. a. minna* that are mislabelled and that these were collected further south in Cochabamba/Santa Cruz, so that *H. a. dirama* may occur as far south as La Paz. Both males and females have been captured feeding at white flowers of Eupatoriae (Asteraceae), in upper montane and cloud forest habitats in Peru, from 1200 to 2100 m.

*Specimens examined.* 12♂, 17♀ (Appendix 6).

***Hyalenna alidella minna* (Schaus, 1902)**

(Figs 9K, L; 21A)

*Pteronymia minna* Schaus, 1902: 384. Type locality: Bolivia.

Lectotype ♂ (here designated), USNM.

*Pteronymia minna*: Haensch, 1909: 155; Bryk, 1937: 603;

D'Almeida, 1960: 14, pl. 2, figs 4–5; D'Almeida, 1978: 328.

*Hyalenna minna minna*: Mielke & Brown, 1979: 165.

*Hyalenna minna*: D'Abbrera, 1984: 271, fig.

*Hyalenna alidella minna*: Lamas, 2004: 186.

*Identification, taxonomy and variation.* Males of this subspecies differ from those of *H. a. dirama* in having a series of yellow translucent submarginal spots extending to the apex, a reduced and more translucent yellow FW postdiscal band, more pronounced yellow translucence in the HW discal cell and white apical and marginal spots on the VHW. Females differ from those of *H. a. dirama* on the FW in a similar manner to males, while the HW has a much broader dark brown opaque marginal border, which has much more prominent white ventral spots, and the transparent area is coloured translucent white.

The name *minna* was based by Schaus (1902) on an unstated number of specimens from Bolivia, and the single male in the type collection at the USNM, matching the original description, is designated here as the lectotype (see discussion under *H. hugia* for status of Schaus's type specimens). Two other specimens in the USNM were also in Schaus's collection: a male labelled 'Bolivia' and a female mislabelled 'Peru' (misidentified by Schaus as '*alidella*'). The former is presumably also part of the original type series. The taxon was described as a species in the genus *Pteronymia* but transferred to *Hyalenna* by Mielke & Brown (1979). As this taxon shares typical *H. alidella* pattern elements, such as the broad translucent FW band and largely colourless HW (except for the discal cell), and shows no structural differences, we treat it as a subspecies of *H. alidella* (Lamas, 2004).

*Range.* Bolivia, departments of La Paz and Cochabamba (Fig. 21A).

*Specimens examined.* 12♂, 11♀ (Appendix 6).

***Hyalenna sulmona* (Hewitson, 1877)**

(Figs 1H, O, P; 2F; 3H, I; 5; 10B–L; 14F–J; 18F–J; 21B)

*Identification, taxonomy and variation.* The various taxa that comprise *H. sulmona* share no synapomorphies, but are grouped on the basis of close allopatry and wing pattern similarity. Morphologically, the species is indistinguishable from *H. alidella* and *H. pascua*, except perhaps by the presence in *H. alidella* of a cross-vein joining veins Sc + R<sub>1</sub> and Rs on the female HW. This vein is absent or indistinct in *H. pascua* and in all known *H. sulmona* taxa, and present in all examined *H. alidella* taxa (see under that species). In wing pattern, however, *H. sulmona* is most likely to be confused with *H. perasippa* and *H. buckleyi*, which may also have yellow translucence in the discal cell and posterior third of the HW. Most subspecies of *H. sulmona* (except *H. s. balsamica* and some individuals of *H. s. tersa*) are distinguished from these two species by the lack of dark scaling surrounding the FW discocellular veins, as well as genital differences (see under those species accounts).

There is variation in the presence or absence of translucent markings in the FW, the FW discocellular bar and white submarginal spots on the ventral surface, and five subspecies are recognized.

*Range.* Western Colombia to northern Peru, along the Andes. Rare in cloud forest from 1600 to 2400 m.

*Specimens examined.* 12♂, 24♀ (Appendix 6).

***Hyalenna sulmona hyalina* Lamas & Willmott, ssp.n.**

(Figs 10E, F; 21B)

*Hyalenna sulmona* n. ssp.: Lamas, 2004: 186.

*Description and diagnosis* (Fig. 10E, F). Differs from other subspecies of *H. sulmona* in near absence of translucent coloured markings on both wings, as well as in reduction in width of dark margins (Fig. 10E, F). Differs further from *H. s. sulmona* and *H. s. lobusa* in lack of white submarginal spots on ventral surface, except for at HW apex. Females have slightly more translucent whitish colouring in HW discal cell.

*Type material.* *Holotype*, ♀, COLOMBIA: Caldas: Manizales, 5°05'N, 75°32'W (*A. M. Patiño*) (BMNH). *Paratypes*, COLOMBIA: *Risaralda*: 1♂, Municipio Pereira, Parque Ucumari, W hacia Salento, c. 4°38'N, 75°35'W, 2200 m, 15.vi.1989 (*G. Andrade*) (ICNB); 1♂, Distrito de Pereira, 4°49'N, 75°43'W, 1886 (*R. M.*

*Valencia*) (BMNH). Not located: 1♀, 'Cauca valley' (BMNH).

*Etymology.* From the Latin adjective 'hyalinus' (= glassy).

*Taxonomy and variation.* There is slight variation in the width of the dark margins, and some specimens have translucent markings similar to *H. s. lobusa* and *H. s. tersa*, but much fainter. This taxon is treated as a subspecies of *H. sulmona* because of similarities in morphology, including absence of a cross-vein joining veins Sc + R<sub>1</sub> and Rs on the female HW, faint yellow translucence in the posterior portion of the HW and lack of FW discocellular bar.

*Range, habitat and adult ecology.* Colombia, in the central part of the Cordillera Central (Manizales area) (Fig. 21B). An additional male in the IAVH is assumed to be mislabelled from 'Pital, Lago Calima' (where *H. s. tersa* occurs) and is excluded from the type series. Nothing has been reported on this evidently rare taxon, which presumably flies with and mimics *H. paradoxa paradoxa* (Fig. 6A, B) and *H. perasippa valencia* (Fig. 7B), amongst other ithomiines.

***Hyalenna sulmona tersa* Willmott & Lamas, ssp.n.**

(Figs 3H, I; 5; 10B–D; 21B)

*Hyalenna sulmona* n. ssp.: Lamas, 2004: 186.

*Description and diagnosis* (Fig. 10B–D). Differs from other *H. sulmona* taxa, except *H. s. hyalina*, in lacking white marginal spots at VFW apex and on VHW (except at apex). Differs from *H. s. hyalina* in having translucent yellow in posterior half and discal cell of HW, a white translucent postdiscal band and submarginal spots on FW, and broader opaque margins on both wings.

*Type material.* *Holotype*, ♀, COLOMBIA: Valle del Cauca: Cerro San Antonio, 3°29'N, 76°38'W, 2200 m, 1.vii.2001 (*G. Lamas*) (MUSM). *Paratypes*, COLOMBIA: Valle del Cauca: 1♂, Peñas Blancas, Alto Río Cali, c. 3°31'N, 76°38.6'W, 2000 m, 22.vii.1982 (*L. M. Constantino*) (LMC); 1♂, same data as preceding except 7.viii.1985 (LMC); 1♀, Río Bravo, Calima, 3°53.59'N, 76°37.3'W (FV).

*Etymology.* From the Latin adjective 'tersus' (= clean, unmarked), referring to the distinct reduction or absence of white distal marginal spots on the VHW.

*Taxonomy and variation.* This subspecies is variable and may need to be subdivided when better data are available. At present, specimens from geographical areas that typically contain distinct subspecies, such as north-eastern Ecuador, north-western Ecuador (Fig. 10B) and the Colombian Cordillera Occidental (Fig. 10D), are

treated as this taxon. These specimens all share the unmarked VFW apex and almost unmarked VHW margin, which typically has a white apical spot, although this is absent in the single specimen known from north-western Ecuador (Fig. 10B). The FW discocellular veins may or may not have dark scaling forming a thin discocellular bar. Specimens from north-eastern Ecuador have more pronounced translucent submarginal spots on the FW, at least in males (Fig. 5J), and may be transitional to *H. s. lobusa* in the Colombian Cordillera Oriental. As a result of this variation, the type series is restricted to specimens from the Colombian Cordillera Occidental where the taxon is most common, and an additional 2♂, 4♀ from elsewhere are excluded.

*Range, habitat and adult ecology.* Colombia (Cordillera Occidental and southern Cordillera Central) to northern Ecuador on both Andean slopes (Fig. 21B; but see also discussion above). A single female in the GR (examined as a photograph) from Antioquia, in northern Colombia, apparently represents this taxon, differing only in having slightly heavier scaling around the FW discocellular veins. This taxon is a rare inhabitant of cloud forest from 1600 to 2400 m. In Ecuador, occasionally we have encountered males flying along forest edges. A female was captured in north-western Ecuador flying approximately 4 m above the ground at 11:00 h at the edge of forest and pasture on a ridgetop.

*Immature stages.* Two early (probable first) instars of *H. s. tersa* were found in Ecuador, both on bushes of *Solanum lepidotum* Dunal, 1816 (Solanaceae), at the edge of fields and forest (Appendices 4 and 5). One individual was 1.5 m above the ground on the underside of a leaf of a 7 m high bush. The uniformly pale coloured *H. sulmona* larvae and pupa are well camouflaged against the smooth, whitish grey undersides of the food plant leaves, which also bear indistinct yellow spots, like the larvae (Fig. 5F).

The first larva was found (KRW-042) on 16.xii.2001 and pupated on 10.i.2002, but fell during pupation, resulting in a deformed pupa that failed to eclose. The pupa was subsequently preserved in alcohol. The second larva (KRW-174) was found on 6.i.2002, pupated on 10.ii.2002 and eclosed on 22.ii.2002 (see Appendices 4 and 5). The fifth instar head capsule, pupal skin and adult voucher specimen are to be deposited in the BMNH.

The immature stages of this species apparently are almost indistinguishable from those of the closely related *H. pascua* (Brown & Freitas, 1994). Although the eggs of *H. sulmona* have not been observed, presumably they are laid singly, as early instars are solitary.

*Larvae.* First instar pale, mottled green with dense, short, dark hairs, head capsule pale (Fig. 5A). Second to fourth instars similar to final instar, which bears short hairs and is almost entirely uniform, pale opaque greyish green dorsally, becoming translucent pale green laterally and ventrally. In some individuals and instars, yellow spots

visible at posterior margin of each segment, forming one dorsal and two subdorsal lines (Fig. 5C, D). Spiracles very pale brown. Head capsule pale greyish cream, stemmata and mandibles darker (Fig. 5E).

*Pupa.* Very pale green, similar in colour to later larval instars. Abdomen flared, wider than thorax, decorated dorsally with three bands of greenish silver lines (Fig. 5G), similar to *H. paradoxa*. Similar greenish silver lines circle anterior edge of prothoracic segment and continue around costal margin of wings. Two pairs of lateral conical protrusions at junction of wing cases and thorax, similar to *Dircenna adina* (Fig. 5G). Dorsal edge of pupa strongly angled at junction between thorax and abdomen (Fig. 5H).

#### *Hyalenna sulmona lobusa* (Haensch, 1909)

(Figs 1H, O, P; 2F; 5; 10G, H; 14F–J; 18F–J; 21B)

*Episcada lobusa* Haensch, 1909: 152. Type locality: Colombia. Lectotype ♀ (designated by Lamas, 1994: 284), ZMHU.

*Episcada lobusa*: Bryk, 1937: 591; D'Almeida, 1978: 306; D'Abbrera, 1984: 248.

[*Hyalenna maculata*: Forbes, 1942: 39, fig. 2 – misidentification]

*Hyalenna lobusa*: Lewis, 1973: 229.

*Hyalenna minna lobusa*: Mielke & Brown, 1979: 165.

*Hyalenna sulmona lobusa*: Lamas, 1994: 284; Lamas, 2004: 186.

*Identification, taxonomy and variation.* This taxon differs from the nominate subspecies in having a trace of translucent white postdiscal band and submarginal spots on the FW, as well as a yellowish brown margin (not black) on the VHW posterior to the yellow basal costal stripe. The female also has more extensive and enlarged white VFW and VHW marginal spots, in comparison with *H. s. sulmona* and *H. s. tersa*. *Hyalenna s. hyalina* is distinguished under that account.

Haensch (1909) described this taxon from an unspecified number of specimens in the genus *Episcada*, noting that it differed from *H. paradoxa praestigiosa* in having large white spots in the VHW margin. This character also distinguishes the taxon from the otherwise similar *H. sulmona sulmona* and *H. s. tersa*, where the marginal spots are smaller or absent. A female in the ZMHU was designated as lectotype by Lamas (1994) and shows *lobusa* to be a member of *Hyalenna*, where it was placed by Lewis (1973). The taxon is morphologically similar to *H. s. sulmona*, and replaces it in eastern Colombia, and so we treat it as a subspecies of *H. sulmona* (Lamas, 1994).

*Range.* This taxon is known only from Colombia, with the only more precise label data being the certainly erroneous 'Bogotá'. Nevertheless, specimens are likely to have been collected in the neighbouring Cordillera Oriental, possibly on both slopes.

*Specimens examined.* 2♂, 5♀ (Appendix 6).

***Hyalenna sulmona sulmona* (Hewitson, 1877)**

(Figs 10I, J; 21B)

*Ithomia sulmona* Hewitson, 1877: 86. Type locality: Ecuador, [Azuay], Jima [= Gima]. Lectotype ♀ (here designated), BMNH.

*Ithomia sulmona*: Kirby, 1877: 841; Kirby, 1879: 43; Riley & Gabriel, 1925: 46.

*Pteronymia sulmona*: Haensch, 1909: 154; Bryk, 1937: 605; D'Almeida, 1978: 333.

[*Hyalenna teresita*: Forbes, 1942: 39, fig. 1 – misidentification].

*Hyalenna sulmona*: D'Abrera, 1984: 270–271, fig.; Moreno *et al.*, 1997: 152; Racheli & Racheli, 2001: 358; Racheli & Racheli, 2003: 216.

*Hyalenna sulmona sulmona*: Lamas, 2004: 186.

**Identification, taxonomy and variation.** The nominate subspecies is distinguished from remaining *H. sulmona* taxa by the combination of the translucent yellow HW colouring, almost colourless FW and black VHW margin posterior of the yellow basal costal stripe.

Hewitson (1877) described this species immediately after *H. perasippa* and *H. a. scantilla*, based on a specimen or specimens of what he regarded as males, collected by Buckley in Ecuador, in the same area as these two species. The description notes the oblique FW discocellulars, colourless FW and yellow-tinted HW which are characteristic of the subspecies. The single specimen from Hewitson's collection in the BMNH, matching the original description, is in fact a female, as noted by Riley & Gabriel (1925), and is here designated the lectotype. Forbes (1942) mistakenly referred to the species as '*H. teresita*', the name of a *Pteronymia* species, and figured the male genitalia under that name, and D'Abrera (1984) finally correctly placed the species in *Hyalenna*.

**Range, habitat and adult ecology.** Eastern Ecuador (Pastaza to Zamora-Chinchipec), probably extending into extreme northern Peru (Cajamarca) (Fig. 21B). A rare inhabitant of cloud forest from 1600 to 2200 m. We have encountered females flying across open areas on ridges in primary forest and males along forest edges, from 2 to 3 m above the ground. Both sexes are close mimics of *Pteronymia t적이다 t적이다* (Hewitson, 1869), among other ithomiines.

**Specimens examined.** 2♂, 8♀ (Appendix 6).

***Hyalenna sulmona balsamica* Lamas & Willmott, ssp.n.**

(Figs 10K, L; 21B)

*Hyalenna sulmona* n. ssp.: Lamas, 2004: 186.

**Description and diagnosis** (Fig. 10K, L). Distinguished from all other *H. sulmona* by unique combination of characters. Forewing with strong dark discocellular bar (approached only in some *H. s. tersa*), broad, yellowish, strongly translucent postdiscal band (some *H. s. tersa*

have similar, although narrower, whitish band), HW almost colourless (as in *H. s. hyalina*), prominent white ventral marginal spots (similar to *H. s. sulmona* and *H. s. lobusa*).

**Type material.** *Holotype*, ♀, PERU: Amazonas: km 363 Balsas-Chachapoyas, 2000 m, [06°51'S, 77°57'W], 7.iii.1985 (G. Lamas) (MUSM). *Paratypes*, PERU: Amazonas: 1♂, 1♀, environs Mendoza (= 'Rodríguez de Mendoza'), 6°24'S, 77°29'W, 1500 m, iv.2002 (*local collector*) (OD); 1♀, Cajamarca: Quebrada Limón, 6°51'S, 78°04'W, 1800 m, ii.2000 (GTB).

**Etymology.** An arbitrary name containing part of the type locality.

**Taxonomy and variation.** This taxon differs from all other *H. sulmona* in having a broad translucent FW postdiscal band, dark FW discocellular bar and almost colourless HW, although the first two character states are approached in some specimens of *H. s. tersa* and the last in *H. s. hyalina*. In these respects, it is similar to *H. alidella*, but *H. s. balsamica* is sympatric with *H. a. dirama* in northern Peru. It differs notably from *H. a. dirama* in having more pronounced white ventral marginal spots, which are present (and reduced) only in the female of that taxon. Females also lack a cross-vein joining veins Sc + R<sub>1</sub> and Rs on the ventral HW, as in all *H. sulmona* but no examined *H. alidella*. For these last two reasons, and because the taxon is morphologically indistinguishable from and apparently replaces other *H. sulmona*, we treat it as a subspecies of *H. sulmona*.

**Range, habitat and adult ecology.** Northern Peru (Amazonas, Cajamarca) (Fig. 21B), from 1500 to 2000 m, in cloud forest.

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**Appendix 1.** Genital dissections examined of *Hyalenna*, *Dircenna* and outgroup.

Taxon	Sex	Locality	Collection	Dissection
<i>Episcada a. apuleia</i>	♂	Ecuador: Loja, environs de Loja	BMNH <sup>a</sup>	6287
<i>Episcada a. apuleia</i>	♀	Ecuador: Loja, environs de Loja	BMNH <sup>a</sup>	6705
<b><i>Dircenna</i></b>				
<i>D. dero</i> (Hübner, 1823) ssp.	♂	Brazil: Santa Catarina	BMNH	6772
<i>D. dero</i> ssp.	♀	Brazil: Santa Catarina	BMNH	6695
<i>D. dero</i> ssp.	♂	Ecuador: Napo, Chichicorrumi	KWJH	
<i>D. jemina jemina</i>	♂	Venezuela: Carabobo, San Esteban	BMNH <sup>a</sup>	6771
<i>D. jemina jemina</i>	♀	Venezuela: Distrito Federal, Caracas	BMNH <sup>a</sup>	6694
<i>D. adina adina</i> (Hewitson, [1855])	♂	Venezuela: Mérida, Laguneta de la Montaña	BMNH	7187
<i>D. adina steinheili</i> (Staudinger, [1884])	♂	Ecuador: Pichincha, San Pablo	MGCL	
<i>D. adina steinheili</i>	♀	Ecuador: 'Loja, Río Uchima' (mislabelled)	MGCL	
<i>D. klugii klugii</i> (Geyer, 1837)	♂	Mexico: Veracruz, Omealco	BMNH	7189
<i>D. klugii klugii</i>	♂	Mexico: Oaxaca	MGCL	
<i>D. klugii klugii</i>	♀	Mexico: Chiapas, Sierra del Soconusco	MGCL	
<i>D. loreta loreta</i> Haensch, 1903	♂	Colombia: Meta, Villavicencio-Monte Redondo	BMNH	7190
<i>D. loreta loreta</i>	♂	Ecuador: Napo, Río Coca	MGCL	
<i>D. loreta loreta</i>	♀	Ecuador: 'El Oro, Bellavista' (mislabelled)	MGCL	
<i>D. olyras olyras</i> (C. & R. Felder, 1865)	♂	Colombia: 'Bogotá'	BMNH	7188
<i>D. olyras olyras</i>	♂	Colombia: Boyacá, Muzo	MGCL	
<i>D. olyras olyras</i>	♀	Colombia: Valle del Cauca, Calima	MGCL	
<i>D. olyras bairdii</i> Reakirt, 1868	♂	Colombia: Boyacá, Muzo	MGCL	
<i>D. olyras bairdii</i>	♀	Colombia: Boyacá, Muzo	MGCL	
<b><i>Hyalenna</i></b>				
<i>H. paradoxa praestigiosa</i>	♂	Ecuador: Morona-Santiago, Chigüinda	BMNH <sup>a</sup>	6326
<i>H. paradoxa praestigiosa</i>	♀	Ecuador: Tungurahua, Baños	BMNH <sup>a</sup>	6696
<i>H. paradoxa praestigiosa</i>	♂	Ecuador: Sucumbíos, old rd to La Alegría	BMNH	7182
<i>H. paradoxa praestigiosa</i>	♀	Ecuador: Sucumbíos, old rd to La Alegría	BMNH	7183
<i>H. paradoxa praestigiosa</i>	♀	Ecuador: Sucumbíos, old rd to La Alegría	BMNH	7184
<i>H. paradoxa praestigiosa</i>	♂	Peru: Tabaconas	BMNH	7185
<i>H. paradoxa catenata</i>	♂	Peru: Pasco, Cushi	MUSM	
<i>H. paradoxa catenata</i>	♀	Peru: Pasco, Cushi	BMNH	7191
<i>H. hugia</i>	♂	Bolivia	USNM <sup>a</sup>	Lectotype
<i>H. perasippa ortygiosa</i>	♂	Colombia: 'Bogotá'	BMNH <sup>a</sup>	6775
<i>H. perasippa ortygiosa</i>	♀	Ecuador: Tungurahua, Baños	BMNH	7186
<i>H. perasippa perasippa</i>	♂	Ecuador: Morona-Santiago, Chigüinda	BMNH	7086
<i>H. perasippa solitaria</i>	♀	Peru: Junín, 0–1 km E Mina Pichita	MUSM <sup>a</sup>	
<i>H. buckleyi buckleyi</i>	♂	Ecuador: Tungurahua, environs d'Ambato (HT)	BMNH <sup>a</sup>	7056
<i>H. buckleyi buckleyi</i>	♂	Ecuador: Zamora-Chinchi, Qbda. Chorrillos (PT)	KWJH	
<i>H. buckleyi pomacocha</i>	♀	Peru: Amazonas, Afluente	PB <sup>a</sup>	BM-7154
<i>H. alidella alidella</i>	♂	Colombia: 'Bogotá'	BMNH <sup>a</sup>	7057
<i>H. alidella alidella</i>	♀	Colombia: 'Bogotá'	BMNH <sup>a</sup>	7061
<i>H. alidella dirama</i>	♂	Peru: Pasco, Cushi	BMNH	7060
<i>H. alidella minna</i>	♂	Bolivia	BMNH	7059
<i>H. alidella scantilla</i>	♂	Ecuador: Morona-Santiago, Chigüinda	BMNH	7062
<i>H. sulmona hyalina</i>	♂	Colombia: Risaralda, Distrito de Pereira (PT)	BMNH	7058
<i>H. sulmona lobusa</i>	♀	Colombia: 'Bogotá'	BMNH <sup>a</sup>	6699
<i>H. sulmona lobusa</i>	♂	Colombia	BMNH <sup>a</sup>	6774
<i>H. pascua</i>	♂	Brazil: Nat. Park (Itatiaia?)	BMNH <sup>a</sup>	7055
<i>H. pascua</i>	♀	Brazil: Rio de Janeiro, Teresópolis	MUSM <sup>a</sup>	

<sup>a</sup>Indicates a figured specimen.

## Appendix 2

Characters used in cladistic analysis (CI = maximum consistency index)

### Immature stages

1. *All instars with covering of short hair*: (0) absent (Fig. 3J); (1) present (Fig. 3K) [uninformative; CI = 1].
2. *Fifth instar larva dorsal coloration*: (0) uniform pale green (Fig. 3J); (1) broken green and pale grey markings (Fig. 3K); (2) uniform pale grey (Fig. 5C) [CI = 1].
3. *Fifth instar larva segments with yellow mid-dorsal marking at posterior edge*: (0) absent (Fig. 3J); (1) present (Figs 4D; 5D) [uninformative; CI = 1].
4. *Fifth instar larva segments with pair of lateral black spots, one dorsal, one ventral of spiracle*: (0) absent (Fig. 5E); (1) present (Fig. 4E) [CI = 0.5].
5. *Fifth instar larva segments with pair of dorsal black spots in middle of segment, adjacent to dorsal edge of pale subdorsal line*: (0) absent (Fig. 3J); (1) present (Fig. 3K) [CI = 0.5].
6. *Fifth instar larva segments with pair of dorsal black spots, or line, in anterior half of segment*: (0) absent (Fig. 3K); (1) present (Fig. 4D) [uninformative; CI = 1].
7. *Fifth instar larva segments with pair of dorsal black spots, one either side of yellow mid-dorsal marking*: (0) absent (Fig. 4D); (1) present (Fig. 3K) [CI = 1].
8. *Protuberances at base of pupa cremaster stalk in dorsal view*: (0) absent or vestigial (Fig. 3L); (1) conspicuous (Fig. 3I, M) [uninformative; CI = 1].
9. *Metallic markings on pupa dorsal thorax*: (0) divided by nonreflective bands of green (Fig. 4H); (1) almost entirely covering thorax (Fig. 3M) [CI = 1].

### Adults

#### External

10. *Forewing length*: (0) > 32 mm (Fig. 7); (1) < 32 mm (Fig. 8) [CI = 0.3].
11. *Ventral abdomen pale scales*: (0) bright yellow (Fig. 6E); (1) white or yellowish white (Fig. 8F) [CI = 0.5].
12. *Male with elongate white spot at VHW costa in cell  $R_s$ - $Sc + R_1$  near discocellulars*: (0) absent (Fig. 6); (1) present (Fig. 3N) [CI = 1].
13. *Female VHW submarginal spots*: (0) absent (Fig. 6F); (1) present in apex only (Fig. 8B); (2) present in apex and margin (Fig. 8F) [CI = 0.3].
14. *Male HW discal cell with anterior portion*: (0) longer than posterior portion (Fig. 1F); (1) equal length to posterior portion (Fig. 1G) [CI = 1].
15. *Male HW with  $Sc + R_1$  and  $R_s$  while adjacent to androconial scale patch*: (0) parallel or diverging distally,  $R_s$

straight (Fig. 1G); (1) converging distally,  $R_s$  curving (Fig. 1H) [CI = 1].

16. *Male HW with vein  $Sc + R_1$  terminating*: (0) at wing margin (Fig. 1B); (1) before wing margin (Fig. 1E) [CI = 1].
17. *Male FW with upper part of 3d*: (0) much shorter (< half length) than 2d (Fig. 1B); (1) similar in length to two-thirds length 2d (Fig. 1C) [CI = 0.5].
18. *Male FW with lower part of 3d*: (0) longer than discocellular connecting base of veins  $Cu_1$  and  $M_3$  (Fig. 1A); (1) equal to or shorter than discocellular connecting base of veins  $Cu_1$  and  $M_3$  (Fig. 1F) [CI = 0.3].
19. *Male HW androconial scales between  $R_s$  and  $Sc + R_1$* : (0) uniformly dense or slightly less dense distally (Fig. 3A, B); (1) much less dense distally (Fig. 3C, D) [uninformative; CI = 1]. [*Hyalenna* are coded unknown as the androconial scale patch is much reduced in extent, with probable absence of the basal scales.]
20. *Male HW androconial scale patch between  $R_s$  and  $Sc + R_1$* : (0) long, extending basally beyond origin vein  $Cu_2$  and distally past origin vein  $M_2$  (Fig. 2A); (1) short, not extending basally beyond origin vein  $Cu_2$  or distally beyond origin vein  $M_2$  (Fig. 2C) [CI = 1].
21. *If male HW androconial scale patch between  $R_s$  and  $Sc + R_1$  short (char 20:1), then patch terminating*: (0) distally of basal tip vein  $Mr$  (Fig. 2E); (1) basally of basal tip vein  $Mr$  (Fig. 2F) [CI = 1].
22. *Male HW distal androconial scales between  $R_s$  and  $Sc + R_1$  with scale base*: (0) auriculate (Fig. 3B); (1) smoothly tapering (Fig. 3D) [uninformative; CI = 1].
23. *Male HW distal androconial scales between  $R_s$  and  $Sc + R_1$  with sockets*: (0) narrow (Fig. 3B); (1) broad (Fig. 3D, E) [uninformative; CI = 1].
24. *Female HW with cross-vein between  $R_s$  and  $Sc + R_1$* : (0) absent (Fig. 1I); (1) present (Fig. 1J) [CI = 0.3].
25. *Female foretarsus with*: (0) five tarsal segments (Fig. 1L); (1) four tarsal segments (Fig. 1M) [uninformative; CI = 1].

#### Male genitalia

26. *Aedeagus with posterior portion*: (0) straight (Fig. 13J); (1) bent slightly downwards near tip (Fig. 11D); (2) bent strongly downwards near tip (Fig. 13E) [CI = 1].
27. *Aedeagus posterior section*: (0) smooth (Fig. 13F); (1) with numerous tiny spines in middle (Fig. 13K); (2) with numerous tiny, recurved spines in basal two-thirds (Fig. 12J) [uninformative; CI = 1].
28. *Aedeagus with a line of teeth at right posterior tip*: (0) absent (Fig. 11E); (1) present (Fig. 11K) [CI = 1].
29. *Aedeagus with a clear, weakly sclerotized line at left distal edge*: (0) absent (Fig. 13F); (1) present (Fig. 11K) [CI = 1].
30. *Aedeagus with lateral projections at anterior tip*: (0) absent (Fig. 13K); (1) present (Fig. 13F) [CI = 0.5].
31. *Aedeagus*: (0) broadening at posterior tip (Fig. 13F); (1) even in width (Fig. 13K) [CI = 0.5].

32. *Aedeagus*: (0) long, > 1.4× length valva (Fig. 13F); (1) short, < 1.3× length valva (Fig. 13K) [CI = 1].
33. *Valvae*: (0) roughly triangular (Fig. 13G); (1) narrow and curving dorsally at tip (Fig. 14A) [CI = 1].
34. *Valva inner face between sacculus and costa*: (0) unsclerotized soft tissue (Fig. 11G); (1) sclerotized (Fig. 13B) [CI = 1].
35. *Valva sacculus with several 'teeth' directed inwards*: (0) absent (Fig. 13D); (1) present (Fig. 13I) [CI = 1].
36. *Valva basal inner projection from costa*: (0) sclerotized similar to rest of valva (Fig. 11I); (1) strongly sclerotized, more so than rest of valva (Fig. 12C) [CI = 1].
37. *Valva basal inner projection from costa*: (0) in line with costal inner edge (Fig. 11I); (1) bent inwards, almost meeting or crossing beneath gnathos (Fig. 12C) [CI = 1].
38. *If valva basal inner projection from costa bent inwards (37:1)*: (0) not meeting beneath gnathos (Fig. 13I); (1) crossing beneath gnathos (Fig. 14C) [CI = 1].
39. *Valva anterior dorsal edge*: (0) far from vinculum (ratio valva edge–vinculum/maximum height valva,  $v$ , > 0.5) (Fig. 11F); (1) close to vinculum ( $v$  < 0.3) (Fig. 12A) [CI = 0.5].
40. *Ductus ejaculatorius*: (0) a small 'hood', not constricted at base (Fig. 13J); (1) an expanded 'hood', constricted at base (Fig. 13E) [CI = 0.5].

*Female abdomen and genitalia*

41. *Female eighth tergite*: (0) mesially divided with soft tissue (Fig. 15I); (1) evenly sclerotized (Fig. 16D) [CI = 0.5].
42. *'Shelf' at dorsal edge of fused female eighth sternites*: (0) narrow (less than half width of sternites) (Fig. 15E); (1) broad (more than half width of sternites) (Fig. 15J) [CI = 0.3].
43. *Antrum*: (0) a narrow, sclerotized ring (Fig. 15E); (1) a broad sclerotized tube (Fig. 17J); (2) two dorsal sclerotized bands (Fig. 15J) [CI = 1].
44. *If antrum a broad sclerotized tube (43:1), then tube is*: (0) moderately sclerotized anteriorly, merging into ductus bursae (Fig. 17J); (1) strongly sclerotized anteriorly, sharply meeting ductus bursae (Fig. 18E) [uninformative; CI = 1].
45. *Ductus bursae immediately anterior of ductus seminalis*: (0) with anteriorly fading internal sclerotization (Fig. 17E); (1) unsclerotized (Fig. 17J) [CI = 0.7].

**Appendix 3.** Character state distribution

Species	Character								
	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45
<i>Episcada apuleia</i>	00000	00001	00100	00000	?0000	10000	00000	00?01	000?0
<i>Dircenna jemina</i>	11111	01110	01200	00110	?1101	10111	10000	00?00	012?1
<i>Dircenna dero</i>	11111	01110	01200	00010	?1111	10111	10000	00?00	002?1
<i>Dircenna loreta</i>	?????	?????	11200	00010	?1111	10111	10000	00?00	002?1
<i>Dircenna adina</i>	11111	0111[01]	01200	00110	?1111	10111	10000	00?00	002?1
<i>Dircenna klugii</i>	11111	01110	01200	00110	?1111	10110	10000	00?00	002?2
<i>Dircenna olyras</i>	?????	?????	01200	00110	?1111	10111	10000	00?00	002?1
<i>Hyalenna paradoxa</i>	11111	10100	00000	1[01]0?1	01111	10000	00010	11011	110?0
<i>Hyalenna hugia</i>	?????	?????	00?00	110?1	011??	12000	00010	11011	?????
<i>Hyalenna perasippa</i>	?????	?????	00000	111?1	01111	20001	00010	11011	100?0
<i>Hyalenna buckleyi</i>	?????	?????	10110	111?1	01101	01000	11011	11000	01101
<i>Hyalenna pascua</i>	12100	00101	10211	111?1	11101	00000	11111	11110	10111
<i>Hyalenna alidella</i>	?????	?????	10[12]11	111?1	11111	00000	11111	11110	10111
<i>Hyalenna sulmona</i>	12100	00101	10[012]11	111?1	11101	00000	11111	11110	10111

**Appendix 4.** Collection data for immature stages of *Hyalemma paradoxa praestigiosa* and *H. stalmona tersa* from eastern Ecuador, December 2001 to February 2002

Species	Rearing code	Locality (Su:Sucumbios, Lo: Loja)	Elevation (m)	Date found	Plant genus	Plant species	Plant location	Height on plant	Location on plant
<i>paradoxa</i>	KRW-013	Su: old rd. to La Alegria	2400	12-Dec-01	<i>Solanum</i>	sect. <i>torvum1</i>	Edge field and secondary growth, ridgetop	1	Underside leaf, nr. vein junctions or leaf damage hole
<i>paradoxa</i>	KRW-014/1	Su: old rd. to La Alegria	2400	12-Dec-01	<i>Solanum</i>	sect. <i>torvum2</i>	Edge primary forest and track, steep slope	0.5	Underside leaf, usu. nr. vein junctions
<i>paradoxa</i>	KRW-014/2	Su: old rd. to La Alegria	2400	12-Dec-01	<i>Solanum</i>	sect. <i>torvum2</i>	Edge primary forest and track, steep slope	0.5	Underside leaf, usu. nr. vein junctions
<i>paradoxa</i>	KRW-015	Su: old rd. to La Alegria	2400	12-Dec-01	<i>Solanum</i>	sect. <i>torvum1</i>	Edge primary forest and track, steep slope	0.2	Underside leaf, nr. vein junctions or leaf damage hole
<i>paradoxa</i>	KRW-016	Su: old rd. to La Alegria	2400	12-Dec-01	<i>Solanum</i>	sect. <i>torvum1</i>	Edge primary forest and track, steep slope	0.2	Underside leaf, nr. vein junctions or leaf damage hole
<i>paradoxa</i>	KRW-017	Su: old rd. to La Alegria	2400	12-Dec-01	<i>Solanum</i>	sect. <i>torvum1</i>	Edge primary forest and track, steep slope	0.2	Underside leaf, nr. vein junctions or leaf damage hole
<i>paradoxa</i>	KRW-018	Su: old rd. to La Alegria	2400	12-Dec-01	<i>Dunalia</i>	<i>solanacea</i>	Edge primary forest and track, steep slope	3	Underside leaf
<i>paradoxa</i>	KRW-019	Su: old rd. to La Alegria	2400	12-Dec-01	<i>Dunalia</i>	<i>solanacea</i>	Edge primary forest and track, steep slope	3	Underside leaf
<i>paradoxa</i>	KRW-020	Su: old rd. to La Alegria	2400	12-Dec-01	<i>Dunalia</i>	<i>solanacea</i>	Edge primary forest and track, steep slope	3	Underside leaf
<i>paradoxa</i>	KRW-021	Su: old rd. to La Alegria	2400	12-Dec-01	<i>Solanum</i>	sect. <i>torvum2</i>	Edge primary forest and track, steep slope	1	Underside leaf
<i>paradoxa</i>	KRW-022	Su: old rd. to La Alegria	2400	12-Dec-01	<i>Solanum</i>	sect. <i>torvum1</i>	Edge primary forest and track, steep slope	1	Underside leaf
<i>paradoxa</i>	KRW-025	Su: old rd. to La Alegria	2400	13-Dec-01	<i>Solanum</i>	sect. <i>torvum1</i>	Secondary growth on wide track on hillside in primary forest	1	Underside leaves, often nr. veins
<i>paradoxa</i>	KRW-026	Su: old rd. to La Alegria	2400	13-Dec-01	<i>Solanum</i>	sect. <i>torvum1</i>	Secondary growth on wide track on hillside in primary forest	1	Underside leaves, often nr. veins
<i>paradoxa</i>	KRW-027	Su: old rd. to La Alegria	2400	13-Dec-01	<i>Solanum</i>	sect. <i>torvum2</i>	Secondary growth on wide track on hillside in primary forest	1	Underside leaves, often nr. veins
<i>paradoxa</i>	KRW-066	Su: old rd. to La Alegria	2400	19-Dec-01	<i>Solanum</i>	sect. <i>torvum1</i>	Secondary growth, ridgetop near forest	1-2	Under leaf, not nr. veins
<i>paradoxa</i>	KRW-067	Su: old rd. to La Alegria	2400	19-Dec-01	<i>Solanum</i>	sect. <i>torvum1</i>	Secondary growth, ridgetop near forest	1-2	Under leaf, not nr. veins

<i>paradoxa</i>	KRW-068/1	Su: old rd. to La Alegria	2400	19-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 1	Secondary growth, ridgetop near forest	1-2	Under leaf
<i>paradoxa</i>	KRW-068/2	Su: old rd. to La Alegria	2400	19-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 1	Secondary growth, ridgetop near forest	1-2	Under leaf
<i>paradoxa</i>	KRW-069	Su: old rd. to La Alegria	2400	19-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 1	Secondary growth on wide trail, primary forest hillside	1-2	Under leaf
<i>paradoxa</i>	KRW-069/1	Su: old rd. to La Alegria	2400	19-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 1	Secondary growth on wide trail, primary forest hillside	1-2	Under leaf
<i>paradoxa</i>	KRW-069/2	Su: old rd. to La Alegria	2400	19-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 1	Secondary growth on wide trail, primary forest hillside	1-2	Under leaf
<i>paradoxa</i>	KRW-071	Su: old rd. to La Alegria	2400	19-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 1	Secondary growth on wide trail, primary forest hillside	1-2	Under leaf, nr. vein or not nr. vein
<i>paradoxa</i>	KRW-072	Su: old rd. to La Alegria	2400	19-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 2	Secondary growth on wide trail, primary forest hillside	1-2	Under leaf
<i>paradoxa</i>	KRW-074	Su: old rd. to La Alegria	2400	19-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 2	Edge of primary forest edge wide trail, hillside	1-2	Under leaf
<i>paradoxa</i>	KRW-077	Su: old rd. to La Alegria	2400	19-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 2	Edge of primary forest edge wide trail, hillside	1	Under leaf
<i>paradoxa</i>	KRW-084	Su: old rd. to La Alegria	2400	22-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 1	Secondary growth on wide trail, primary forest hillside	0.5-1	Under leaf, some nr. vein or hole, some not
<i>paradoxa</i>	KRW-085	Su: old rd. to La Alegria	2400	22-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 1	Secondary growth on wide trail, primary forest hillside	1	Under leaf
<i>paradoxa</i>	KRW-087	Su: old rd. to La Alegria	2400	22-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 2	Secondary growth on wide trail, primary forest hillside	1	Under leaf, nr. or touching midrib
<i>paradoxa</i>	KRW-088	Su: old rd. to La Alegria	2400	22-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 2	Secondary growth on wide trail, primary forest hillside	1	Under leaf
<i>paradoxa</i>	KRW-089	Su: old rd. to La Alegria	2400	22-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 2	Secondary growth on wide trail, primary forest hillside	1	Under leaf



## Appendix 4. Continued.

Species	Rearing code	Locality (Su:Sucumbios, Lo: Loja)	Elevation (m)	Date found	Plant genus	Plant species	Plant location	Height on plant	Location on plant
<i>paradoxa</i>	KRW-110	Su: old rd. to La Alegria	2400	28-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 2			
<i>paradoxa</i>	KRW-111	Su: old rd. to La Alegria	2400	28-Dec-01	<i>Dunalia</i>	<i>solanacea</i>			
<i>paradoxa</i>	KRW-124	Su: Quebrada Garrapatal	2200	31-Dec-01	<i>Solanum</i>	sect. <i>torvum</i> 3	Logged forest understory 20 m from field	1	Under leaf by midrib
<i>paradoxa</i>	KRW-129	Su: old rd. to La Alegria	2400	01-Jan-02	<i>Solanum</i>	sect. <i>torvum</i> 2	Secondary growth on open ridgetop, forested sides	1	Underside leaf
<i>paradoxa</i>	KRW-262	Lo: Cerro Toledo rd.	2600	24-Jan-02	<i>Solanum</i>	<i>hispidum</i>	Edge of cloud forest beside road	1	Under leaf
<i>paradoxa</i>	KRW-263	Lo: Cerro Toledo rd.	2600	24-Jan-02	<i>Solanum</i>	<i>hispidum</i>	Edge of cloud forest beside road	2	Under leaf, single or two per leaf, nr. veins
<i>sulmona</i>	KRW-042	Su: La Bonita, trail to Quebrada Garrapatal	2000	16-Dec-01	<i>Solanum</i>	<i>lepidotum</i>	Edge field and secondary forest	1.5	Under leaf
<i>sulmona</i>	KRW-174	Su: La Bonita, trail to Río Chingual	1800	06-Jan-02	<i>Solanum</i>	<i>lepidotum</i>			

Appendix 5. Rearing data for immature stages of *Hyalella paradoxa praestigiosa* and *H. sulmona tersa* from Ecuador, December 2001 to February 2002

Species	Species ID status	Rearing code	Stage found	No.	Date egg	Date 1st instar	Date 2nd instar	Date 3rd instar	Date 4th instar	Date 5th instar	End date pupa	Last stage	Sex	Fate	Comments
<i>paradoxa</i>	Likely	KRW-013	Egg	14	23/12/2001							Egg		Failed to hatch	
<i>paradoxa</i>	Voucher	KRW-014/1	Egg	2	19/12/2001	23/12/2001		05/01/2002		20/01/2002	09/02/2002	Adult	M	Adult	
<i>paradoxa</i>	Likely	KRW-014/1	Egg	1	19/12/2001	23/12/2001		05/01/2002				3		Died	
<i>paradoxa</i>	Likely	KRW-014/1	Egg	3	19/12/2001	23/12/2001						1		Died	
<i>paradoxa</i>	Voucher	KRW-014/1	Egg	1	19/12/2001	23/12/2001		05/01/2002		21/01/2002	10/02/2002	Adult	M	Adult	
<i>paradoxa</i>	Voucher	KRW-014/2	Egg	1	19/12/2001	23/12/2001	23/12/2001	05/01/2002		20/01/2002	08/02/2002	Adult	F	Adult	
<i>paradoxa</i>	Likely	KRW-014/2	Egg	3	23/12/2001							1		Died	
<i>paradoxa</i>	Likely	KRW-014/2	Egg	3	19/12/2001		23/12/2001					2		Died	
<i>paradoxa</i>	Likely	KRW-014/2	Egg	1	19/12/2001		23/12/2001	05/01/2002				3		Died	
<i>paradoxa</i>	Likely	KRW-014/2	Egg	1	19/12/2001		23/12/2001	02/01/2002				3		Died	
<i>paradoxa</i>	Likely	KRW-015	Egg	4	23/12/2001							Egg		Failed to hatch	
<i>paradoxa</i>	Likely	KRW-016	2	1				29/12/2001				3		Died	
<i>paradoxa</i>	Likely	KRW-016	Egg	1				29/12/2001				3		Died	
<i>paradoxa</i>	Likely	KRW-017	2	1						08/01/2002		5		Died	
<i>paradoxa</i>	Likely	KRW-017	Egg	1								1		Died	
<i>paradoxa</i>	Likely	KRW-018	2	1	12/12/2001							1		Died	
<i>paradoxa</i>	Likely	KRW-018	Egg	1			24/12/2001					2		Died	
<i>paradoxa</i>	Voucher	KRW-018	4	1								?		?	
<i>paradoxa</i>	Likely	KRW-018	2	1				24/12/2001		18/12/2001	08/01/2002	Adult	M	Adult	
<i>paradoxa</i>	Likely	KRW-018	2	1						03/01/2002		5		Died	
<i>paradoxa</i>	Voucher	KRW-018	2	1						05/01/2001	10/01/2002	Pupa		Killed	
<i>paradoxa</i>	Likely	KRW-019	3	1								Adult		Adult	
<i>paradoxa</i>	Likely	KRW-019	3	1						23/12/2001	29/12/2001	5		Parasitized	By ? <i>Ghyptapaniteles</i>
<i>paradoxa</i>	Likely	KRW-020	2	1						23/12/2001	29/12/2001	5		Parasitized	By ? <i>Ghyptapaniteles</i>
<i>paradoxa</i>	Likely	KRW-021	4	1						10/01/2001		4		Died	
<i>paradoxa</i>	Likely	KRW-022	Egg	1	19/12/2001	19/12/2001						1		Died	
<i>paradoxa</i>	Likely	KRW-022	2	1								2		Died	
<i>paradoxa</i>	Likely	KRW-022	2	1						19/12/2001	10/01/2002	Pupa		Killed	
<i>paradoxa</i>	Likely	KRW-022	Egg	2	19/12/2001	27/12/2001						2		Died	
<i>paradoxa</i>	Likely	KRW-022	Egg	1	19/12/2001	19/12/2001						1		Died	
<i>paradoxa</i>	Likely	KRW-025	Egg	1	19/12/2001	21/12/2001						1		Died	
<i>paradoxa</i>	Likely	KRW-025	1	1			27/12/2001					1		Died	
<i>paradoxa</i>	Likely	KRW-025	Egg	2	16/12/2001	19/12/2001						1		Died	
<i>paradoxa</i>	Likely	KRW-026	Egg	4	23/12/2001							Egg		Failed to hatch	
<i>paradoxa</i>	Voucher	KRW-026-2	2	1				23/12/2001		01/01/2002	15/01/2002	Adult	?	Adult	
<i>paradoxa</i>	Likely	KRW-027	Egg	1	18/12/2001			08/01/2002				3		Died	
<i>paradoxa</i>	Likely	KRW-027	Egg	1	18/12/2001	23/12/2001						1		Died	
<i>paradoxa</i>	Likely	KRW-066	Egg	2	27/12/2001	31/12/2001						1		Died	
<i>paradoxa</i>	Likely	KRW-066	Egg	6	27/12/2001							Egg		Failed to hatch	
<i>paradoxa</i>	Likely	KRW-066	Egg	1	27/12/2001	31/12/2001						1		Died	
<i>paradoxa</i>	Likely	KRW-067	Egg	7	26/12/2001							Egg		Failed to hatch	
<i>paradoxa</i>	Likely	KRW-067	Egg	1	21/12/2001							2		Died	
<i>paradoxa</i>	Likely	KRW-067	Egg	2	22/12/2001							2		Died	

## Appendix 5. Continued.

Species	Species ID status	Rearing code	Stage found	No.	Date egg	Date 1st instar	Date 2nd instar	Date 3rd instar	Date 4th instar	Date 5th instar	End date pupa	Last stage	Sex	Fate	Comments
<i>paradoxa</i>	Voucher	KRW-068/1	3	1						07/01/2002	25/01/2002	Adult		Adult	
<i>paradoxa</i>	Likely	KRW-068/2	3	1						10/01/2002	31/01/2002	Pupa		Died	
<i>paradoxa</i>	Likely	KRW-069	3	1				31/12/2001				3		Died	
<i>paradoxa</i>	Likely	KRW-069/1	2	1						08/01/2002	10/01/2002	Pupa		Killed	
<i>paradoxa</i>	Voucher	KRW-069/2	3	1						13/01/2002	03/02/2002	Adult		Adult	
<i>paradoxa</i>	Likely	KRW-071	Egg	2	26/12/2001							Egg		Failed to hatch	
<i>paradoxa</i>	Likely	KRW-071	Egg	1	26/12/2001	29/12/2001						1		Died	
<i>paradoxa</i>	Likely	KRW-072	2	1					08/01/2001			4		Died	
<i>paradoxa</i>	Likely	KRW-072	2	1				30/12/2001				3		Died	
<i>paradoxa</i>	Likely	KRW-074	2	1					02/01/2002	07/01/2002		5		Died	
<i>paradoxa</i>	Voucher	KRW-074	2	1					02/01/2002	08/01/2002		Adult	F	Adult	
<i>paradoxa</i>	Likely	KRW-074	2	1					02/01/2002	08/01/2002		Pupa		?	Pupa deformed
<i>paradoxa</i>	Voucher	KRW-077	3	1					02/01/2002	01/01/2002	14/01/2002	Adult	F	Adult	
<i>paradoxa</i>	Likely	KRW-084	Egg	3								Egg		Failed to hatch	
<i>paradoxa</i>	Likely	KRW-084	Egg	3	31/12/2001		08/01/2002					?		Died	
<i>paradoxa</i>	Likely	KRW-084	Egg	1	31/12/2001		05/01/2002					2		Died	
<i>paradoxa</i>	Likely	KRW-084	Egg	2	23/12/2001		30/12/2001					2		Died	
<i>paradoxa</i>	Likely	KRW-085	3	1						05/01/2002		5		Died	
<i>paradoxa</i>	Likely	KRW-087	Egg	2	31/12/2001							Egg		Failed to hatch	
<i>paradoxa</i>	Likely	KRW-087	Egg	1	31/12/2001					07/02/2002	15/02/2002	Pupa		Died	
<i>paradoxa</i>	Likely	KRW-087	Egg	1	31/12/2001							?		Died	
<i>paradoxa</i>	Likely	KRW-088	1	2				05/01/2002	08/01/2001			4		Died	
<i>paradoxa</i>	Likely	KRW-088	1	1					07/01/2002			4		Died	
<i>paradoxa</i>	Likely	KRW-088	1	1								?		Died	
<i>paradoxa</i>	Likely	KRW-089	2	1				01/01/2002				3		Died	
<i>paradoxa</i>	Voucher	KRW-110	4	1						08/01/2002	23/01/2002	Adult		Adult	
<i>paradoxa</i>	Likely	KRW-111	1	1			07/01/2002					2		Died	
<i>paradoxa</i>	Likely	KRW-124	Egg	1	08/01/2002		19/01/2002		31/01/2002	15/02/2002		5		Killed	Preserved in alcohol
<i>paradoxa</i>	Voucher	KRW-129	Egg	1	05/01/2002				31/01/2002	11/02/2002	28/02/2002	Adult	M	Adult	
<i>paradoxa</i>	Likely	KRW-129	Egg	1	05/01/2002							Egg		Failed to hatch	
<i>paradoxa</i>	Voucher	KRW-262	2	1					14/02/2002	04/03/2002		Adult	M	Adult	
<i>paradoxa</i>	Probable	KRW-263	Egg	3	03/02/2002				17/02/2002			3/4		Died	
<i>paradoxa</i>	Likely	KRW-263	Egg	1	03/02/2002							1		Killed	
<i>paradoxa</i>	Likely	KRW-263	Egg	1	03/02/2002			13/02/2002				2/3		Died	
<i>submona</i>	Probable		29/12/2001	09/01/2002											
KRW-042			200228/01/2002	pupa def											
11			ormed	from cremaster,											
<i>submona</i>	Voucher	KRW-174	1	1			14/01/2002		29/01/2002	09/02/2002	22/02/2002	Adult	M	Adult	

## Appendix 6.

Specimen locality data for *Hyalenna**Hyalenna paradoxa paradoxa* (1♂, 9♀)

COLOMBIA: *Antioquia*: Frontino, 6°46'N, 76°08'W (*Salmon*), 1♀ (BMNH); *Caldas*: Bocatoma, Manizales, c. 5°04.12'N, 75°31.14'W, 2300–2400 m (*Vélez, Schmidt-Mumm*), 12.x.1985, 10.i.1986, 3♀ (MUSM); Manizales, 5°05'N, 75°32'W (*Steinheil*), 1♀ [HT *paradoxa*] (ZMHU); Río Cajones, Manizales, c. 5°04.12'N, 75°31.14'W [specimen data not recorded] (MHNUC); *Risaralda*: Distrito de Pereira, 4°49'N, 75°43'W (*Valencia*), 1886, 1♀ (BMNH), 1♀ (MUSM); W. hacia La Pastora, Parque de Ucumari, Municipio Pereira, c. 4°38'N, 75°35'W, 2200 m (*Andrade*), 16.vi.1989, 1♂ (ICNB); *No specific locality*: 'Colombia', 1♀ (MUSM), 1♀ (USNM).

Note added in proof: Recent additional specimens of *H. perasippa* from Amazonas clearly belong to a subspecies distinct from *H.p. solitaria*, to be described elsewhere.

*Hyalenna paradoxa praestigiosa* (10♂, 19♀)

COLOMBIA: *Huila*: above San José de Isnos, 1°57'N, 76°13'W, 2050 m (*Adams, Hardy*), 4.viii.1979, 1♀ (BMNH); Finca Meremburg, Belén-Leticia, 1♀ (MHNUC); *Nariño*: La Planada, 1°35'N, 77°31'W – (dubious), 1700 m, 1♂ (IAVH); *no specific locality*, 1♀ (IAVH). ECUADOR: *Azuay*: 'Gualaceo' – (error) (*Lafebre*), Mar 1970, 1♀ [probably Gualaceo–Limón road, Morona-Santiago] (MGCL); *Loja*: Cerro Toledo rd., E. of Yangana, 4°23'S, 79°09.3'W, 2600 m (*Willmott*), 24.i.2002, 1♂ [KRW-262] (KWJH); *Napo*: 'Sarzacu' – (error) (*Lafebre*), i.1969, 1♂ (MUSM); San José, 1800 m (*Velástegui*), 30.iv.1972, 1♂ (MUSM); *Sucumbios*: El Higuerón, 0°30.9'N, 77°32.2'W, 2200–2600 m (*Willmott*), 10.xi.1997, 2♀ (KWJH); old rd. to La Alegría, km 19 La Bonita–Tulcán rd., 0°33.7'N, 77°31.7'W, 2400 m (*Willmott*), 12.xii.2001, 1♂ (KWJH), 12.xii.2001, 1♂, 1♀ [KRW-14-1, KRW-18] (BMNH), 19 Dec 2001, 1♂ [KRW-68-1] (BMNH), 19 Dec 2001, 2♀ (KWJH), 22.xii.2001, 1♀ (BMNH); *Tungurahua*: env[irons] d'Ambato, c. 1°15'S, 78°37'W (*Blanc*), 1♀ (MUSM), 2♀ (BMNH); Río Blanco, 1°23'S, 78°20'W, 1650–2000 m (*Lafebre*), iv.1968, 1♂ [2800 m] (MGCL); Río Blanco, 1°23'S, 78°20'W, 1800 m (*Velástegui*), 20.v.1979, 1♀ (MUSM); Volcán Tungurahua, c. 1°24'S, 78°25'W, Mar, 1♀ [PLT *praestigiosa*] (ZMHU), Mar, 1♂ [LT *praestigiosa*] (ZMHU); *Zamora-Chinchi*: Quebrada Tapichalaca, nr. Valladolid, 4°30.75'S, 79°07.75'W, 1950 m, 4.xi.1997, 1♀ (KWJH); Valladolid, 4°32.6'S, 79°07.6'W, 2000 m (*Sourakov*), 17–21.v.1993, 1♀ (AS). PERU: *Amazonas*: 'Pomacochas, 2000 m' – (error) (*Calderón*), xi.1999, 1♀ (FV); *Cajamarca*: Río Tabaconas, 5°19'S, 79°17'W, 1800 m (*A.E., F. Pratt*), 1912, 1♂ (BMNH). NO LOCALITY DATA: no data, 1♀ [HT *grandipennis*; '? Peru'] (BMNH).

*Other records*: ECUADOR: *Sucumbios*: old rd. to La Alegría, km 19 La Bonita–Tulcán rd., 0°33.7'N, 77°31.7'W, 2400 m (*Willmott*), 13.xii.2001, 1.i.2002 (*Willmott & Hall*, sight records).

*Hyalenna paradoxa catenata* (15♂, 15♀)

PERU: *Amazonas*: 2 km NW Ocol, 6°15'S, 77°35'W, 2550 m, 1♀ (MUSM); Chachapoyas, 6°14'S, 77°53'W, 2345 m (*de Mathan*), 1889, 1♀ (BMNH); Quebrada Chido, 5°50'S, 78°00'W, 2300–2500 m (*Calderón*), viii.2000, 1♂, 1♀ (MUSM); *Cajamarca*: Naranja, 6°16'S, 78°51'W, 2300 m (*Grados*), 18.x.1998, 1♂ (MUSM); *Cuzco*: entre Intipunco y Wiñaywayna, Santuario Histórico Machu Picchu, 13°10.5'S, 72°32'W, 2700 m (*Lamas*), 27.v.1997, 1♀ (MUSM); Mándor, Santuario Histórico Machu Picchu, 13°09'S, 72°33'W, 1800–1950 m (*Lamas*), 29.x.2001, 1♂ (MUSM); *Huánuco*: 'Tingo María' – (error) (*Fontaine*), 21.viii.1962, 1♀ (MUSM); *Carpish*, Acomayo, 9°43'S, 76°06'W, 2850 m (*Büche*), 22.iii.1989, 2♀ (MUSM); *Junín*: 1–2 km W, 1–3 km SW, 0–3 km S Mina Pichita, 11°05'S, 75°25'W, 2000–2200 m (*Brown, Lamas, Ramírez, Grados*), 27.ix.1985, 26.viii.1988, 16–17.x.1989, 12.ix.2001, 9.ix.2002, 21–22.xiii., 12.xi.2003, 10♂, 6♀ (MUSM); Quebrada Siete Jeringas, 11°12'S, 75°24'W, 1700 m (*Ramírez*), 29.viii.2003, 1♂ (MUSM); *Pasco*: Cushi, 9°58'S, 75°42'W, 1900 m (*Hoffmanns*), 1♀ (BMNH), 1♂ (MUSM); Pozuzo, 10°07'S, 75°32'W, 1500–1800 m (*native collector*), 1♀ [HT *catenata*] (BMNH).

*Hyalenna paradoxa incachaca* (2♀)

BOLIVIA: *Cochabamba*: Cochabamba-Villa Tunari, km 77, c. 17°07.6'S, 65°47.5'W, 2600 m (*Boyer*), 18.xi.2001, 1♀ [PT *incachaca*] (PB); Incachaca, 17°14'S, 66°29'W, 2400 m (*Adams, Bernard*), 24.iv.1985, 1♀ [HT *incachaca*] (BMNH).

*Hyalenna hugia* (2♂)

BOLIVIA: *Cochabamba*: Yungas del Palmar, Chapare, 17°08'S, 65°25'W, 1000 m (*Zischka*), 5.v.1952, 1♂ (ZSBS); *No specific locality*: 'Bolivia' (*Schaus*), 1♂ [LT *hugia*] (USNM).

*Hyalenna perasippa perasippa* (6♂, 1♀)

ECUADOR: *Morona-Santiago*: 'Logroño' – (error), 1♂ [probably Chigüinda area] (FV); Chigüinda, 3°17.6'S, 78°40.6'W, 1600 m (*Buckley*), 3♂ (BMNH); Nueve de Octubre, 2°12.2'S, 78°31.1'W, 1♂ (FV); *No specific locality*: 'Ecuador', 1♂ [LT *perasippa*] (BMNH), (*Buckley*), 1♀ (BMB).

*Hyalenna perasippa valencia* (1♀)

COLOMBIA: *Risaralda*: Distrito de Pereira, 4°49'N, 75°43'W (*Valencia*), 1886, 1♀ [HT *valencia*] (BMNH).

*Hyalenna perasippa ortygiosa* (7♂, 4♀)

COLOMBIA: *Cundinamarca*: 'Bogotá' – (error), 1♀ (MCZ), 1♂ (BMNH), 1♂ (MUSM); *No specific locality*: 'Colombia', 1♂ (SMTD), 1♂ (ZMHU), (*Ovalle*), 1♂ (AMNH); *Not located*: Milán-Manizales, 1♂ (IAVH).  
ECUADOR: *Napo*: Guacamayos, 0°37'S, 77°49'W, 1400 m (*Velástegui*), 7.x.1984, 1♀ [PT *ortygiosa*] (GTB); Yanayacu, nr. Cosanga, 0°34.2'S, 77°52.2'W, 2000 m (*Greeney*), 1♀ [PT *ortygiosa*] (FV); *Tungurahua*: Baños, 1°24'S, 78°25'W, 1800 m (*Palmer*), iv–v.1912, 1♀ [HT *ortygiosa*] (BMNH); *No specific locality*: 'Ecuador', 1♂ (MCZ).

*Hyalenna perasippa solitaria* (3♂, 2♀)

PERU: *Amazonas*: Quebrada Piruro, 3 km N Nueva Esperanza, 6°23'S, 77°26'W, 1700 m (*local collector*), iv.2002, 1♂ (OD) (photo from Fabio Vitale); *Junín*: 0–1 km E Mina Pichita, 11°05'S, 75°25'W, 2000 m (*Brown*), 27 Sep 1985, 1♀ [PT *solitaria*] (MUSM); 1 km S Mina Pichita, 11°05'S, 75°25'W, 2100 m (*Lamas*), 14.v.2002, 21.viii.2003, 12.xi.2003, 2♂, 1♀ [HT, PT *solitaria*] (MUSM). \*Note added in proof: Recent additional specimens of *H. perasippa* from Amazonas clearly belong to a subspecies distinct from *H. p. solitaria*, to be described elsewhere.

*Hyalenna buckleyi buckleyi* (5♂, 2♀)

ECUADOR: *Napo*: Yanayacu, nr. Cosanga, 0°34.2'S, 77°52.2'W, 2000 m (*Greeney*), 1♀ [locality data probable but uncertain] (FV); *Tungurahua*: Chinchin, 1°26'S, 78°16'W, 1800 m (*Velástegui*), 18.viii.1988, 1♀ [PT *buckleyi*] (GTB); env[irons] d'Ambato, c. 1°15'S, 78°37'W (*Blanc*), 1♂ [HT *buckleyi*] (BMNH); *Zamora-Chinchipe*: Quebrada Chorrillos, 4°02.1'S, 78°59.3'W, 1250 m (*Willmott, Hall*), 3.iv.1995, 2♂ [PT *buckleyi*] (KWJH), 2♂ [PT *buckleyi*] (MECN).

*Other records*: ECUADOR: *Zamora-Chinchipe*: Quebrada Chorrillos, 4°02.1'S, 78°59.3'W, 1250 m, May (*Willmott & Hall*, sight records).

*Hyalenna buckleyi pomacocha* (2♂, 2♀)

PERU: *Amazonas*: Pomacochas, 5°49'S, 77°58'W, 2500 m, ii.2003, 1♂ [HT *pomacocha*; ex. coll. FV] (MUSM); *San Martín*: Afluente, nr. Jorge Chávez, c. 6°41'S, 77°40'W, 800–1500 m, 1♂ [PT *pomacocha*] (OD), (*Meléndez*), ii.2003, 1♀ [PT *pomacocha*] (PB); Jorge Chávez, 6°41'S, 77°40'W, 1400 m (*Tafur*), ii.2003, 1♀ [PT *pomacocha*] (PB).

*Hyalenna pascua* (39♂, 46♀)

BRAZIL: *Minas Gerais*: Poços de Caldas, 21°47'S, 46°33'W, 1250 m, 23.ii.1963, 5♂, 2♀ (UFP); Vale Verde, Parque Nacional Caparaó, 20°25.7'S, 41°51.16'W (*Brown*), 16.ii.1968, 1♀ (KSB); *Paraná*: Morretes, Alto da Serra, 25°28'S, 48°49'W, 800 m (*Mielke*), 1.ii.1991, 1♂ (OHM); Pontal do Itararé, 25°52'S, 48°57'W (*Brown*), 8.ii.1968, 1♀ (KSB); Posto Alpino, Vale de Capiuari (*Mielke*), 6.ii.1966, 1♀ (MNRJ); São José dos Pinhais, 25°31'S, 49°13'W, 850 m (*Mielke*), 20.iii.1994, 1♀ (OHM); *Rio de Janeiro*: 'Nat. Pk.' [do Itatiaia?] (*Zikán*), 22.i.1936, 1♂ (BMNH); Alto da Serra, Petrópolis, 22°53'S, 44°14'W, iv., ix.1960, 1961, 2♀ (UFP) (*Mielke*), 15.viii.1960, 1♀ (MNRJ), 15.viii.1960, 1♂, 4♀ (OHM), 28.v.1961, 1♀ (MNRJ), 5.ii.1961, 1♂ (MNRJ); Itatiaia, 22°27'S, 44°37'W (*Pohl*), Jun, Oct 1928, 2♀ (MZSP); Itatiaia, 22°27'S, 44°37'W, 700 m (*Zikán*), 27.iv.1938, 1♀ (UFP); Itatiaia, 22°27'S, 44°37'W, 800 m, 13.i.1927, 1♂ (ZSBS) (*May*), 1♂ (MNRJ), 24.ii.1926, 1♂ (MNRJ) (*H. Ebert*), 12.iv.1965, 1♂ (UFP); Itatiaia, km 12, c. 22°25.7'S, 44°42'W, 1700 m (*Zikán*), 5.ii.1931, 1♂ (USNM); Maromba, Itatiaia, c. 22°27'S, 44°42'W, 1100 m (*Zikán*), 27.ix.1930, 1♂ (UFP); Nova Friburgo, 22°17'S, 42°33'W (*Ebert*), 1♀ (UFP); Parque Nacional Itatiaia, 22°27'S, 44°37'W, 800 m (*Mielke*), 12.vii.1961, 1♂, 1♀ (UFP), 5.vii.1961, 1♂, 1♀ (OHM); Parque Nacional Itatiaia, 22°27'S, 44°37'W, 900 m (*Mielke*), 12.vii.1961, 1♂, 12.vii.1963, 1♂, 16.vii.1963, 1♀, 18.vii.1963, 1♂, 3.vii.1963, 1♀ (MNRJ); Parque Nacional Serra das Orgãos, Teresópolis, 22°26'S, 42°59'W, 1100 m (*Mielke*), 1♀ (UFP); Petrópolis Independência, 22°32'S, 43°11'W, 900 m (*Callaghan*), 1971, 1♀ (MGCL), (*Mielke*), 29.v.1965, 1♀ (OHM); Petrópolis, 22°32'S, 43°11'W, 1000–1500 m, 1♂ [LT *pascua*] (USNM), (*Ebert*), 30.vii.1966, 1♀ (MUSM), (*D'Almeida, Nyalo, Cesar*), 16.viii.1958, 1♀ (UFP); Petrópolis, 22°32'S, 43°11'W, 1100–1200 m (*Ebert*), ii–iv.1966, 1968, 1971, 5♀ (UFP); Resende, Parque Nacional Itatiaia, c. 22°27'S, 44°37'W, 1000 m (*Mielke*), 2.v.1985, 2♂, 1♀ (UFP); Rio de Janeiro, 22°55'S, 43°14'W, 1♂ (BMNH); S side Itatiaia, c. 22°27'S, 44°37'W, 1000–1200 m (*Ebert*), ii., vii.1960, 1963, 2♀ (UFP); Teresópolis, 22°27'S, 43°01'W, 1100 m, 3.viii.1965, 1♀ (AMNH), Feb, 1♂ (USNM), (*Brown*), 17.vi.1965, 1♀ (MUSM); *Santa Catarina*: Blumenau, 26°55'S, 49°04'W, 1♀ (MNRJ); Monte Castelo, 26°30'S, 50°11'W, 900 m (*Mielke, Casagrande*), 24.i.1997, 1♂ (OHM); *São Paulo*: Jundiá, Serra do Japi, 23°10.7'S, 46°31.5'W, 1000 m (*Brown*), 27.iv.1985, 3♂, 2♀ (MUSM); Santos, 23°58'S, 46°20'W – (dubious), 1♀ (ZSBS); *No specific locality*: 'Brazil', 1♂ (BMNH). NO LOCALITY DATA: no data, 1♂ ['No. 14/878'] (MNRJ).

*Other records*. BRAZIL: *Espírito Santo*: Santa Teresa, Matadouro, 19°56.08'S, 40°36.01'W, 850 m (*Brown*), vi.1994, 1♂ (AVLF); *Minas Gerais*: Monte Verde, 22°51.35'S, 46°03.57'W, 1600 m (*Francini*), 6.iv.1989, 1♀ (AVLF); Serra de Extrema, 22°54.15'S, 46°20.36'W, 1600 m, xii.1989, 1♂ (AVLF); Trilha do Platô, Monte

Verde, 22°53.16'S, 46°01.55'W, 1600 m (*Freitas*), 21.xii.2002, 1♂, 1♀ (AVLF); Wenceslau Brás, 22°32.06'S, 45°21.47'W, 1400 m (*Francini*), 29.iv.1989, 1♂ (AVLF); *São Paulo*: Alto da Serra de Piquete, Piquete, 22°34.13'S, 45°13.29'W, 1500 m, 17.xii.1990, 1♀ (AVLF), (*Francini*), 30.iv.1989, 1♂, 1♀ (AVLF); Núcleo Santa Virginia, São Luis do Paraitinga, 23°20.1'S, 45°08.46'W, 1100 m (*Brown*), 15.iii.2001, 1♂ (AVLF); Parque Estadual Campos do Jordão, Campos do Jordão, 22°41.24'S, 45°29.22'W, 11.i.2001, 3♂ (AVLF) (A. Freitas, Universidade de Campinas, Campinas, Brazil, pers. comm.).

*Hyalenna alidella alidella* (5♂, 16♀)

COLOMBIA: *Boyacá*: Muzo, 5°32'N, 74°06'W – (dubious), 400–800 m, 1♀ (SMTD), 1♀ (ZMHU); *Cundinamarca*: ‘Bogotá’ – (error), 1♀ (MUSM), 1♂, 3♀ (BMNH); La Vega, 5°01'N, 74°21'W, 1900 m, 1♀ (ZSBS); *Guaviare*: ‘San José del Guaviare’ – (error), 2♀ (JFL); *No specific locality*: ‘Colombia’, 1♀ [‘Colombia W. Cordillera’] (SMF), 2♀ (SMTD), (*Ovalle*), 1♀ (AMNH); ‘New Granada’, 1♀ [LT *alidella*] (BMNH). VENEZUELA: *Barinas*: Barinas–Sto. Domingo, 8°49'N, 70°29'W, 1400 m (*Neild*), ix.1989, ix.1995, viii.–ix.1992, 3♂, 1♀ (AFEN); *Lara*: Arroyo Sanare, 9°45'N, 69°39'W, 20.ii.1955, 1♀ (MUSM); *Mérida*: track above La Mina, km 30 Barinitas–Sto. Domingo, c. 8°52.1'N, 70°35.8'W, 1450 m (*Neild*), 31.x.1999, 1♂ (AFEN).

*Hyalenna alidella exsulans* (1♀)

PANAMA: *Darién*: Cerro Pirre, 8°00'N, 77°40'W, 1000 m (*Small*), vi.1979, 1♀ [HT *exsulans*] (USNM).

*Hyalenna alidella cinereola*: (1♂, 4♀)

COLOMBIA: *Boyacá*: San Salvador, 5°36.51'N, 73°43.15'W, 1♂ [PT *cinereola*]; ‘S. Salvador’] (MUSM); *Cundinamarca*: ‘Bogotá’ – (error), 1898, 1♀ [HT *cinereola*] (BMNH); *No specific locality*: ‘Colombia’, 1♀ (ZMHU), 1♀ [PT *cinereola*] (MUSM), (*Kalbreyer*), 1♀ [PT *cinereola*] (MUSM).

*Hyalenna alidella vesca* (6♂, 6♀)

COLOMBIA: *Antioquia*: El Socorro-Amagá, 6°15.14'N, 75°41.31'W, 1650 m (*Muriel*), 6.v.2004, 1♀ (S. Muriel collection); *Valdivia*, 7°09'N, 75°27'W (*Pratt*), 1897, 1♀ (MGCL); *Cauca*: Pescador, 2°47'N, 76°33'W, 1450 m (*S.R., L. Steinhäuser*), 20.i.1974, 1♂ [PT *vesca*] (MGCL); *Huila*: Chapinero, 3°11.17'N, 75°30.39'W, 1500 m, 1♀ (GR); *Valle del Cauca*: Cali, km 14 via al Mar, 3°28.2'N, 76°37.2'W, 1600 m (*Constantino*), 30.vi.1983, 1♀ [PT *vesca*] (LMC); Cali, km 18 via al Mar, 3°29'N, 76°38'W, 1800 m (*Constantino*), i.1981, 1♀ [PT *vesca*] (LMC); El Topacio,

Río Pance, c. 3°19'N, 76°38'W, 1600 m (*Constantino*), 2.ix.1985, 1♂ [PT *vesca*] (LMC); Saladito, 3°29'N, 76°37'W, 1650 m (*Small*), 10.viii.1976, 3♂ [HT, PT *vesca*] (MUSM); Saladito, 3°29'N, 76°37'W, 2000 m (*Callaghan*), 28.ii.1981, 1♂ [PT *vesca*] (MUSM); San Antonio, above Cali, km 14, 3°29'N, 76°38'W, 1800 m (*Constantino*), 10.i.1982, 1♀ [PT *vesca*] (LMC).

*Hyalenna alidella scantilla* (3♂, 10♀)

ECUADOR: *Morona-Santiago*: Chigüinda, 3°17.6'S, 78°40.6'W, 1600 m (*Buckley*), 1♂, 1♀ (BMNH), (*Aldas*), xi.1999, 1♂, 1♀ (FV); *Tungurahua*: Santa Inés, 1°25'S, 78°12'W, 1♀ (ZMHU), (*Simson*), 1♀ (BMNH); *No specific locality*: ‘Ecuador’, 1♀ (MUSM), 1♂ [LT *scantilla*] (BMNH), 2♀ (BMNH), 2♀ [PLT *scantilla*] (BMNH). NO LOCALITY DATA: 1♀ (BMNH).

*Hyalenna alidella dirama* (12♂, 17♀)

BOLIVIA: *La Paz*: ‘Yungas’ – (error?) (*Garlepp*), 1♂ [HT *dirama*] (ZMHU). PERU: *Amazonas*: El Cedro (= ‘Cedro de Piruro’) [Quebrada Piruro], 6°23'S, 77°26'W, 2100–2200 m (*local collector*), iv.2002, 1♀ [‘2000 m’] (OD) (photo from Fabio Vitale); Mendoza (= ‘Rodríguez de Mendoza’), 6°24'S, 77°29'W, 1500 m, 10.v.1994, 1♂ (GTB), 7.vii.1998, 1♀ (GTB); Quebrada Yanahuayco, Mendoza, 6°24'S, 77°26'W, 1600–1800 m (*Calderón*), viii.1998, 1♀ (MUSM); *Cuzco*: ‘Wilcanota, 3000 m’ – (error) (*Garlepp*), 1♀ (MUSM); San Pedro, 13°03'S, 71°33'W, 1300–1600 m (*Mielke, Casagrande*), 5–10.xi.2001, 3♂ (OHM); San Pedro, 13°03'S, 71°33'W, 1400–1650 m (*Lamas*), 17.viii.2001, 7., 8.xi.2001, 2♂, 2♀ (MUSM); San Pedro, 13°03'S, 71°33'W, 1400 m (*Perlman, Weinstein*), 10–19.iv.1996, 1♂ (MUSM); Santa Isabel, Cosñipata, 13°03'S, 71°32'W, 1200–1500 m (*Lamas*), 5–11.ii.1975, 1♂, 1♀ (MUSM); *Huánuco*: Carpath, Acomayo, 9°43'S, 76°06'W, 1100–1400 m, v.1992, 1♀ (GTB); *Junín*: 0–1 km E Mina Pichita, 11°05'S, 75°25'W, 2000 m (*Lamas, Pérez*), 18.xi.1984, 1♂ (MUSM), (*Brown*), 27.ix.1985, 1♀ (MUSM); 1 km S Mina Pichita, 11°05'S, 75°25'W, 2100 m (*Lamas, Ramírez*), 21.viii.2003, 12.xi.2003, 2♀ (MUSM); 1–3 km SW Mina Pichita, 11°05'S, 75°25'W, 2100 m (*Lamas*), 24–25.viii.1988, 2♀ (MUSM); 2 km N Mina San Vicente, 11°13'S, 75°24'W, 1850 m (*Ramírez*), 30.vi.2004, 1♀ (MUSM); Junín, 11°10'S, 76°00'W, 1♀ [‘4100 m’] (PB); Quebrada Siete Jeringas, 11°12'S, 75°24'W, 1700 m (*Grados, Ramírez*), 28.vi.–2.vii.2004, 1♂, 2♀ (MUSM); *Pasco*: Cushi, 9°58'S, 75°42'W, 1900 m (*Hoffmanns*), 1♂ (BMNH).

*Hyalenna alidella minna* (12♂, 11♀)

BOLIVIA: *Cochabamba*: Cochabamba, 17°24'S, 66°09'W, 1♀ (FV); Yungas del Palmar, Chapare, 17°08'S, 65°25'W,



1000 m, 1.v.1948, 1♂ (ZSBS), (*Schönfelder*), x.1948, 1♂, 1♀ (ZSBS); Yungas del Palmar, Chapare, 17°08'S, 65°25'W, 2000 m (*Zischka*), 25.iii.1949, 1♀ (ZSBS); *La Paz*: Caranavi area, c. 15°46'S, 67°36'W, 1100–2100 m (*Tello*), ii., xi., xii.2002, 2003, 3♂, 4♀ (GTB); Caranavi area, c. 15°46'S, 67°36'W, 1500 m (*Tello*), xii.2000, 2♀ (GTB); Caranavi area, c. 15°46'S, 67°36'W, 800–1800 m (*Tello*), xii.2000, 2002, 4♂ (GTB), x.2002, 1♀ (GTB); *No specific locality*: 'Bolivia', 1♂ (BMNH), 2♂ [LT & PLT *minna*] (USNM). PERU: *No specific locality*: 'Peru' – (error), 1♀ (USNM).

*Hyalenna sulmona hyalina* (3♂, 2♀)

COLOMBIA: *Caldas*: Cerro Ingrumá, 5°25.17'N, 75°42.49'W, 2300 m [specimen data not recorded] (MHNUC); Manizales, 5°05'N, 75°32'W (*Patiño*), 1♀ [HT *hyalina*] (BMNH); *Risaralda*: Distrito de Pereira, 4°49'N, 75°43'W (*Valencia*), 1886, 1♂ [PT *hyalina*] (BMNH); *W* hacia Salento, Parque de Ucumarí, Municipio Pereira, c. 4°38'N, 75°35'W, 2200 m (*Andrade*), 15.vi.1989, 1♂ [PT *hyalina*] (ICNB); *Valle del Cauca*: 'Pital, Lago Calima' – (error), 1♂ (IAVH); *Not located*: 'Cauca valley', 1♀ [PT *hyalina*] (BMNH).

*Hyalenna sulmona tersa* (4♂, 6♀)

COLOMBIA: *Antioquia*: Ituango, 7°10.22'N, 75°45.12'W, 1♀ (GR); *Huila*: Chapinero, 3°11.17'N, 75°30.39'W, 1500 m, 1♀ (GR) (photo from Fabio Vitale); *Valle del Cauca*: Cali-Buenaventura, km 18, c. 3°33'N, 76°34'W, 1800 m, 1♀ (IAVH); Cerro San Antonio, 3°29'N, 76°38'W, 2200 m (*Lamas*), 1.vii.2001, 1♀ [HT *tersa*] (MUSM); Peñas Blancas, Alto Río Cali, c. 3°31'N, 76°38.6'W, 2000 m (*Constantino*), 22.vii.1982, 7.viii.1985, 2♂ [PT *tersa*] (LMC); Río Bravo, Calima, 3°53.59'N, 76°37.3'W, 1♀ [PT *tersa*] (FV). ECUADOR: *Carchi*: El Corazón, c. 0°49.1'N, 78°09.6'W, 2400 m (*Willmott*), 15.ix.1997, 1♀ (KWJH); *Sucumbíos*: El Higerón, 0°30.9'N, 77°32.2'W, 2300 m (*Willmott*), 21.xii.2001, 1♂

(KWJH); La Bonita, 0°28.7'N, 77°32.7'W, 1800 m (*Aldaz*), 6.i.2002, 1♂ [KRW-174] (BMNH).

*Hyalenna sulmona lobusa* (2♂, 5♀)

COLOMBIA: *Cundinamarca*: 'Bogotá' – (error), 1898, 1♀ (MUSM), 2♀ (BMNH); *No specific locality*: 'Colombia', 1♂ (BMNH), (*Kalbreyer*), 1♀ (MUSM), 1♀ [LT *lobusa*] (ZMHU); *Not located*: 'north-east Peru' (*Bassler*), 1♂ ['N.E. Peru' F6186] (AMNH).

*Hyalenna sulmona sulmona* (2♂, 8♀)

ECUADOR: *Morona-Santiago*: Limón–Gualaceo road, km 18, c. 2°50'S, 78°15'W, 2200 m (*Willmott*), 3.xi.1996, 1♀ (KWJH); Río Abanico, 2°08'S, 78°12'W, 1600 m (*Willmott*), Dec, 1♂ (KWJH); *Napo*: El Arrayán, c. 0°28.5'S, 77°52.5'W, 2200 m (*Willmott*), Oct, 2♀ (KWJH); *Zamora-Chinchipe*: above Valladolid, 4°31.3'S, 79°07.8'W, 2000 m (*Hall*), May, 1♀ (KWJH); Valladolid, 4°32.6'S, 79°07.6'W, 1700 m (*Aldas*), xii.2000, 1♀ (FV); Zamora, 4°04'S, 78°58'W – (dubious), 950–1265 m, 1♀ (FV); *No specific locality*: 'Ecuador', 1♀ [LT *sulmona*] (BMNH), 1♂, 1♀ (BMNH).

*Other records*. ECUADOR: *Zamora-Chinchipe*: Loma San Norberto, nr. Valladolid, 4°32.8'S, 79°08.8'W, 2000 m, Nov (*Willmott & Hall*, sight records).

*Hyalenna sulmona balsamica* (1♂, 3♀)

PERU: *Amazonas*: Balsas-Chachapoyas, km 363, 6°51'S, 77°57'W, 2000 m (*Lamas*), 7.iii.1985, 1♀ [HT *balsamica*] (MUSM); environs Mendoza (= 'Rodríguez de Mendoza'), 6°24'S, 77°29'W, 1500 m (*local collector*), iv.2002, 1♂, 1♀ [PT *balsamica*] (OD) (photo from Fabio Vitale); *Cajamarca*: Quebrada Limón, 6°51'S, 78°04'W, 1800 m, ii.2000, 1♀ [PT *balsamica*] (GTB).