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A phylogenetic analysis of the Neotropical riodinid butterfly genera *Juditha*, *Lemonias*, *Thisbe* and *Uraneis*, with a revision of *Juditha* (Lepidoptera: Riodinidae: Nymphidiini)

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Abstract. A cladistic analysis is presented for all twenty-four species in the Neotropical riodinid butterfly genera *Juditha* Hemming, *Lemonias* Hübner, *Thisbe* Hübner and *Uraneis* Bates based on sixty-nine characters of male and female morphology and external facies, and utilizing *Audre domina* Bates as the outgroup. All characters are illustrated. The analysis confirms the monophyly of *Juditha* and *Uraneis*, but indicates that *Lemonias* is polyphyletic and *Thisbe* is paraphyletic with respect to *Uraneis*, leading us to synonymize *Uraneis* with *Thisbe* (syn.n.). *Juditha* is found to be the sister clade to true *Lemonias* +(*Thisbe* + *Uraneis*). A revision of *Juditha* is presented which includes discussions on the taxonomy, biology and distribution of its species, and illustrations of the adults and male and female genitalia of all taxa and the early stages of an exemplar, *J. caucana*. Eight species are recognized in *Juditha*, including two, *J. naza* and *J. inambari*, which are described as new. The following new generic combinations are made: *rubigo* Bates is transferred from *Juditha* to *Pachythone* Bates; *agave* Godman & Salvin and *leucogonia* Stichel are transferred from *Lemonias* to *Pseudonymphidia* Callaghan; *ochracea* Mengel, *theodora* Godman and *albofasciata* Godman are transferred from *Audre* Hemming to *Lemonias*; *fenestrella* Lathy is transferred from *Thisbe* to *Synargis* Hübner; *hyalina* Butler, *ucubis* Hewitson and *incubus* Hall, Lamas & Willmott are transferred from *Uraneis* to *Thisbe*; and *odites* Cramer (= *phylleus* Auctt.) is transferred from *Synargis* to *Juditha* (comb.n.).

Introduction

Members of the predominantly Neotropical butterfly family Riodinidae exhibit a fascinating array of adult (Callaghan, 1983; Hall, 1999a) and early stage biological traits, particularly those relating to myrmecophily (Ross, 1966; Harvey, 1987; DeVries, 1988, 1990, 1991, 1997; Fiedler, 1991), and are conspicuous for their morphological (Stichel, 1911) and phenotypic (d'Abrera, 1994) diversity. However, the group has historically remained understudied, and the first detailed phylogenetic studies have only recently been completed (Hall, 1999b; Penz & DeVries, 1999). The purpose of this paper is three-fold: (1) to present a revision of *Juditha* Hemming, a widespread Neotropical genus in subtribe Lemoniadina of the large myrmecophilous tribe Nymphidiini (*sensu* Hall, 1999a), whose species diversity has been underestimated and whose members are typically misidentified in the literature; (2) to preliminarily place *Juditha* within a phylogenetic context in the subtribe by conducting a comprehensive species-level phylogeny for *Juditha* and the three putatively most closely related genera, *Lemonias* Hübner, *Thisbe* Hübner and *Uraneis* Bates (Penz & DeVries, 1999), critically assessing the monophyly of each; and (3) to illustrate and describe in detail the ultrastructure of the myrmecophilous early stages of an exemplar *Juditha* species to highlight the potential of such characters for future phylogenetic studies.

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Materials and methods

Morphology

Dissections were made using standard techniques, after abdomens were soaked in hot 10% potassium hydroxide solution for approximately 5 min, and subsequently stored in glycerol. A total of 133 dissections were examined, including eighty-five males and forty-eight females (see Table 1 for a list of all non-*Juditha* dissections examined; those for *Juditha* are given in individual species accounts). Morphological terms for genitalia follow Klots (1956) and Eliot (1973), and the terminology for wing venation follows Comstock & Needham (1918). The ultrastructure of the egg, mature larva and pupa of *J. caucana* and the male genitalia of *J. azan* are described for the first time. Material for scanning electron microscopy was prepared by air drying and coating with gold palladium in a Hummer V sputter coater. Micrographs of early stages were taken with an ISI Super IIIA and those of genitalia with a Leica Stereoscan 440. Light microscopic images were taken using a Nikon HC-300Zi attached to a Wild M400 microscope.

Museum acronyms

Juditha specimens were examined, and their label data recorded, in the following collections, whose acronyms are used throughout the text: AME, Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, Florida, U.S.A.; BMNH, The Natural History Museum, London, England; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; FSCA, Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, Florida, U.S.A.; GWB, Collection of George W. Busby, Boston, Massachusetts, U.S.A.; JHKW, Collection of Jason P. W. Hall & K. R. Willmott, Washington, District of Columbia, U.S.A.; MNHN, Museé national d'Histoire naturelle, Paris, France; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; RNH, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands; USNM, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, U.S.A.; and ZMHU, Zoologisches Museum für Naturkunde, Humboldt Universität, Berlin, Germany.

Taxa studied

All species seemingly related to the type species of *Juditha*, *Lemonias*, *Thisbe* and *Uraneis* were included in the phylogenetic analysis. Of these twenty-four included species, only sixteen were listed by Callaghan & Lamas (2001) as belonging in these four genera, but after dissecting the male and female genitalia of most species (> 95%) in subtribe Lemoniadina (*c.*

Table 1. Dissections examined for non-*Juditha* taxa included in the phylogenetic analysis. *Juditha* dissections are indicated with unique numbers among locality data listed for each species.

Taxon	Dissections examined
domina Bates, 1864	1♂, 'Panama' (FSCA); 1♂, 1♀, Panama, Canal Zone, La Pita (USNM)
albinus C. & R. Felder, 1861	1♂, 'Panama' (USNM); 1♀, Panama, Panamá, Cerro Campana (USNM)
glaphyra Westwood, [1851]	1♂, Brazil, Mato Grosso, Diamantino, Alto Rio Arinos (USNM); 1♂, 1♀, Paraguay, Paraguarí, Sapucay (USNM)
caliginea Butler, 1867	1♂, 2♀, Mexico, Veracruz (USNM)
zygia Hübner, [1807]	1♂, Peru, Madre de Dios, 10 km N Puerto Maldonado (USNM); 1♂, 1♀, French Guiana, Saint Laurent du Maroni, St Elie (USNM)
egaensis Butler, 1867	1♂, Ecuador, Pastaza, Puyo (USNM); 1♂, Ecuador, Napo, Pimpilala (JHKW); 1♂, Brazil, Rondônia, vicinity of Cacaulândia (USNM); 1♂, 1♀, Peru, Loreto, Río Sucusari, Explornapo-ACEER (USNM); 1♂, 1♀, Brazil, Amazonas, Tefé (AME)
ochracea Mengel, 1902	1♂, 2♀, Paraguay, Paraguarí, Sapucay (USNM)
theodora Godman, 1903	1♂, 1♀, Brazil, Mato Grosso, Cuiabá (BMNH)
albofasciata Godman, 1903	1♂, 'Arouary' (BMNH); 1♀, no locality data (BMNH)
stalachtioides Butler, 1867	1♂, Brazil, Paraná, Castro (USNM); 1♀, Brazil, Mato Grosso, Diamantino, Alto Rio Arinos (USNM)
sontella Schaus, 1902	1♂, 1♀, Brazil, Paraná, Castro (USNM)
molela Hewitson, 1865	1♂, Brazil, Rondônia, vicinity of Cacaulândia (USNM); 1♂, 1♀, French Guiana, Saint Laurent du Maroni, Saint Laurent du Maroni (USNM)
irenea Stoll, 1780	1♂, Panama, Canal Zone, Gamboa (USNM); 1♂, Ecuador, Napo, Pimpilala (JHKW); 1♂, 1♀, Panama, Canal Zone, Cocoli (USNM); 1♀, Ecuador, Manabí, Ayampe (JHKW)
lycorias Hewitson, [1853]	1♂, 'Panama' (FSCA); 1♂, 1♀, Panama, Chiriquí, Bugaba (USNM); 1♂, 1♀, Panama, Panamá, Cerro Campana (USNM)
hyalina Butler, 1867	1♂, French Guiana, Cayenne, Galion (USNM); 1♂, 1♀, Colombia, Meta, Río Negro (USNM)
ucubis Hewitson, 1870	1♂, 'Panama' (FSCA); 1♂, 1♀, Panama, Panamá, Cerro Campana (USNM)
incubus Hall, Lamas & Willmott, 2001	1♂, Peru, Amazonas, PV3, Alfonso Ugarte (MUSM); 1♂, Peru, San Martín, km 18 Tarapoto-Yurimaguas Rd. (USNM); 1♀, Ecuador, Pastaza, Mera (CMNH)

70 species), it became apparent that several additional taxa belonged in them. On the basis of all species sharing a unique character of the male genitalia (ch. 48), *pulcherrima* was placed in *Juditha* by Hall & Harvey (2001) and *odites* (= *phylleus* Auctt., see that species account) is placed there in this study. Two new species of *Juditha*, *J. inambari* and *J. naza*, are also included. The taxa *albinus*, *ochracea* (which clearly includes *phyciodes* Hayward, treated by Callaghan & Lamas, 2001, as a distinct species), *theodora* and *albofasciata*, currently treated in *Audre* Hemming, appeared to share several characters of wing pattern and genital morphology with members of *Lemonias*, and for this reason they were included in the ingroup for this study.

Conversely, it is clear that several other taxa listed by Callaghan & Lamas (2001) as belonging in these four genera, in fact, do not. By possessing forewing vein R3+4 touching vein M1 distal to the end of the discal cell, and several shared characters of the male and female genitalia, the sister taxa *agave* Godman & Salvin and *leucogonia* Stichel, currently placed in *Lemonias*, and *rubigo* Bates, currently placed in *Juditha* (see also *History of classification* below), can be placed in a group containing *Lamphiotes* Callaghan, *Machaya* Hall & Willmott, *Pachythone* Bates, *Pixus* Callaghan, *Pseudonymphidia* Callaghan and *Roeberella* Strand (Hall, unpublished data). Based on similarities in genital morphology, antennal length and wing pattern, we tentatively place *agave* and *leucogonia* in *Pseudonymphidia*, and *rubigo* in *Pachythone* until the phylogenetic relationships among all relevant taxa can be critically assessed. The fact that all the species of these genera lack a spot above vein Sc + R1 at the base of the ventral hindwing, a character that is present in all members of Lemoniadina when this region of the wing is not obscured by other pattern elements, indicates that they belong outside Lemoniadina.

The wing pattern and male and female genitalia of *fenestrella* Lathy, currently treated in *Thisbe*, are so similar to those of species in the '*phliasus* Cramer group' of *Synargis* Hübner that it clearly belongs in that genus as currently conceived. It should be noted that for the first time Callaghan & Lamas (2001) regard *Lemonias epone* Godart, from south-eastern Brazil, as a species distinct from *zygia*. Although the arrangement of the vesical cornuti in the male genitalia do appear to differ very slightly in these taxa, we do not believe it is clear that this taxon deserves specific status and it is not included in the analysis (it would be scored with all the same character states as *zygia*). Note that *zamuro* Thieme has previously been regarded as a valid species in *Uraneis*, but Hall & Lamas (2001) placed it in synonymy with *U. hyalina*. *Audre domina* was used as the outgroup because it is the type species of the genus believed to be most closely related to the ingroup genera (Penz & DeVries, 1999).

Cladistic analysis

The phylogenetic analysis is based on morphological characters derived from the wings, appendages and male and female genitalia of twenty-four species of *Juditha*, *Lemonias*, *Thisbe* and *Uraneis* (Figs 1–3). Autapomorphies were excluded, although these are given in the relevant species accounts below. The analysis, based on maximum parsimony, was performed using a heuristic search with 500 random addition sequence TBR replicates in PAUP version 4.0b4a (Swofford, 2000). All characters were equally weighted and unordered, therefore making no a priori assumptions about the relative importance of characters or the evolutionary history of their component states. A posteriori reweighting, in the form of successive approximations character weighting (Farris, 1969), was implemented using the rescaled consistency index of each character. The strength of branch support was estimated by means of 1000 bootstrap replicates in PAUP (Felsenstein, 1985), and by calculating decay indices (Bremer, 1988, 1994) (using the pre-successive weighted cladogram length to generate integers) using the program AUTODECAY 4.0 (Eriksson, 1998) in combination with PAUP. Character distribution was studied using MacClade version 3.05 (Maddison & Maddison, 1995).

Results and discussion

Sixty-nine characters were identified (Appendix 1) from the venation, wing shape and pattern (twenty-four), head (two), thorax (one), legs (one), abdomen (ten), male genitalia (fifteen) and female genitalia (sixteen) (see Appendix 2 for character matrix). Two of these were first noted by Stichel (1911) and three by Harvey (1987), and two additional characters were identical to those independently found by Penz & DeVries (1999), whereas another six were similar to such characters found by them. The initial heuristic search generated four most parsimonious cladograms (MPCs) with length 135 steps, CI 0.77 and RI 0.90. These differed in the placement of *J. naza*, one placing it basal to *J. dorilis*, the other placing it between *J. dorilis* and *J. azan*, *J. molpe* and *J. caucana*, and in the placement of *glaphyra* + *albinus* as sister to the remainder of the ingroup or as sister to *Lemonias* + (*Thisbe* + *Uraneis*). After one iteration of successive weighting, a single MPC was generated (Fig. 4), with length 97.76, CI 0.89 and RI 0.96. Universal synapomorphies for each genus are given in Appendix 3.

The analysis confirms the monophyly of *Juditha* (as preconceived with the inclusion of *odites*) and *Uraneis*, but indicates that *Thisbe* is paraphyletic with respect to *Uraneis*, necessitating the synonymy of *Uraneis* with *Thisbe*. Penz & DeVries (1999), in a broader consideration of phylogenetic relationships among species in Lemoniadina, recovered two monophyletic groups for these two latter taxa from their analysis, one with *irenea* + *molela* and the other with *lycorias* + *hyalina* + *incubis*. However, their analysis included only nine species from *Juditha*, *Lemonias*, *Thisbe* and *Uraneis,* did not include any (phylogenetically highly informative) wing pattern characters, and provided only weak bootstrap support and no convincing character support for the grouping *irenea* + *molela*. There is strong bootstrap and decay support for most nodes within *Thisbe* as recognized here, and four extra steps would be required to bring out *irenea* + *molela* as a monophyletic group.

Fig. 1. Adult males of non-*Juditha* taxa (dorsal surface at left, ventral surface at right). A, *Audre domina*, Gatun, Panama (USNM); B, '*Lemonias' glaphyra*, Sapucay, Paraguay (USNM); C, '*Audre' albinus*, Cocoli, Panama (USNM); D, *Lemonias caliginea*, 'Veracruz', Mexico (USNM); E, *Lemonias zygia*, Cacao, French Guiana (USNM); F, *Lemonias ochracea*, Sapucay, Paraguay (USNM); G, *Lemonias theodora*, Cuiabá, MG, Brazil (BMNH); H, *Lemonias stalachtioides*, Chapada, MG, Brazil (USNM); I, *Thisbe molela*, Cacao, French Guiana (USNM); J, *Thisbe irenea*, Cocoli, Panama (USNM); K, *Thisbe lycorias*, Cerro Campana, Panama (USNM); L, *Thisbe ucubis*, Altos de Pacora, Panama (USNM).

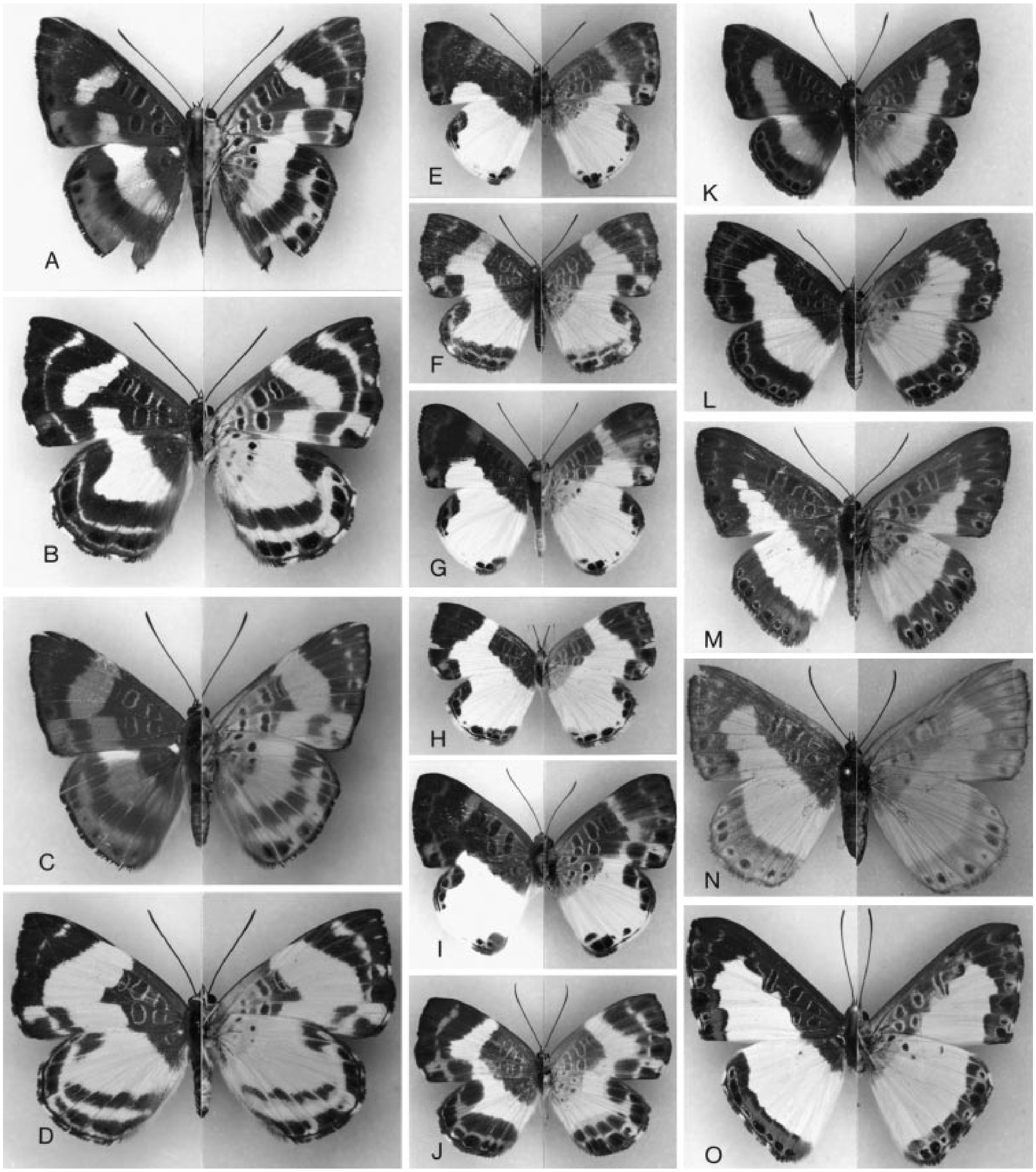


Fig. 2. Adults of *Juditha* (dorsal surface at left, ventral surface at right). A, *Juditha odites odites*, ♂, Galion, French Guiana (USNM); B, *J. odites odites*, ♀, Arcadia, Peru (USNM); C, *J. odites praeclarum*, ♂, Piña, Panama (USNM); D, *J. odites praeclarum*, ♀, Gatun, Panama (USNM); E, *J. pulcherrima pulcherrima*, ♂, Balsapuerto, Peru (MNHN); F, *J. pulcherrima pulcherrima*, ♀, km 18 Tarapoto-Yurimaguas Rd, Peru (USNM); G, *J. pulcherrima comparata*, ♂, Parque Nacional Manu, Pakitza, Peru (USNM); H, *J. pulcherrima comparata*, ♀, Parque Nacional Manu, Pakitza, Peru (USNM); I, *J. inambari*, holotype ♂, Manicoré, Rio Madeira, Am, Brazil (MNHN); J, *J. inambari*, allotype ♀, 'Amazon' (USNM); K, *J. dorilis*, ♂, N of El Llano, Panama (USNM); L, *J. dorilis*,♀, Gatun, Panama (USNM); M, *J. naza*, holotype ♂, Valdivia, Colombia (BMNH); N, *J. naza*, allotype ♀, Valdivia, Colombia (BMNH); O, *J. azan azan*, ♂, Tijuca, RJ, Brazil (USNM).

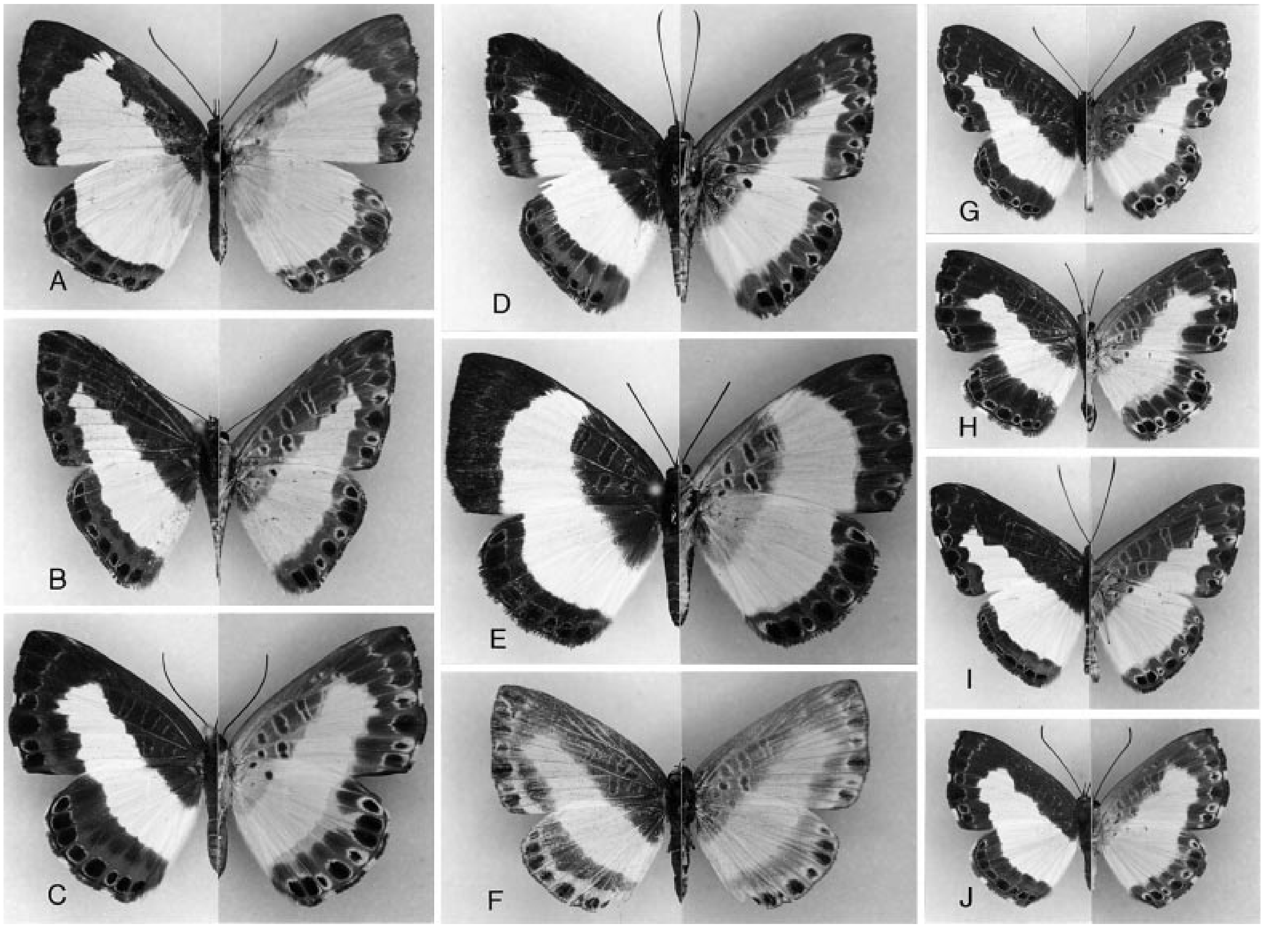


Fig. 3. Adults of *Juditha* (dorsal surface at left, ventral surface at right). A, *Juditha azan azan*, ♀, 'Santa Catarina', Brazil (USNM); B, *J. azan majorina*, ♂, Montsinéry, French Guiana (USNM); C, *J. azan majorina*, ♀, Route de L'est, French Guiana (USNM); D, *J. azan completa*, ♂, Apuya, Ecuador (JHKW); E, *J. azan completa*, ♀ morph one, Finca San Carlo, Ecuador (JHKW); F, *J. azan completa*, ♀ morph two, Finca San Carlo, Ecuador (JHKW); G, *J. molpe*, ♂, vicinity of Cacaulândia, Ro, Brazil (USNM); H, *J. molpe*, ♀, Diamantino, MG, Brazil (USNM); I, *J. caucana*, ♂, Cocoli, Panama (USNM); J, *J. caucana*, ♀, Gatun, Panama (USNM).

The taxa *ochracea*, *theodora* and *albofasciata*, currently treated in *Audre*, appear as a sister clade to *stalachtioides* + *sontella* in *Lemonias*, to which genus we transfer them. Even with the inclusion of these three species, *Lemonias* is found to be polyphyletic. Because *zygia* is the type species of *Lemonias*, we restrict that genus to include *zygia*, *egaensis*, *caliginea*, *ochracea*, *theodora*, *albofasciata*, *stalachtioides* and *sontella*, whereas *glaphyra* and *albinus*, currently treated in *Lemonias* and *Audre*, respectively, require a new genus. Penz & DeVries (1999) found *Lemonias* to be paraphyletic with respect to *Juditha* because they included *agave* in their analysis, which, as we have outlined in the previous section, is an unrelated member of *Pseudonymphidia*.

The analysis indicates *Juditha* to be the sister clade to true *Lemonias* plus the newly conceived *Thisbe*, with *albinus* + *glaphyra* ancestral to these three genera. The types of *Lemonias* and *Thisbe* were first recognized by Harvey (1987) as forming a monophyletic group in his '*Lemonias* section' of Lemoniadina. Penz & DeVries (1999) reported *Juditha* to be sister to true *Lemonias*, a clade that was in turn closely related to but not explicitly sister to our newly conceived *Thisbe*. Although there is no bootstrap support and only a decay index of 1 supporting *Lemonias* and *Thisbe* as sister genera, the great similarity in wing pattern and morphology (some of it uncodable) between certain *Lemonias* and *Thisbe* species leaves little doubt as to the veracity of this hypothesis. In further support of the hypothesis, after the current paper was completed, we received a manuscript from C. Callaghan containing the description of a new *Thisbe* species from southeastern Brazil which closely resembles *Thisbe molela* above, with greatly reduced hindwing blue, and most closely resembles *Lemonias caliginea* below. We did not include this species in the presented analysis because it currently remains undescribed and many characters in Appendix 1 could not be coded for it. However, an analysis that did include it, using those characters we could score from external facies and male genitalia, indicated it to be the sister species of *T. molela*.

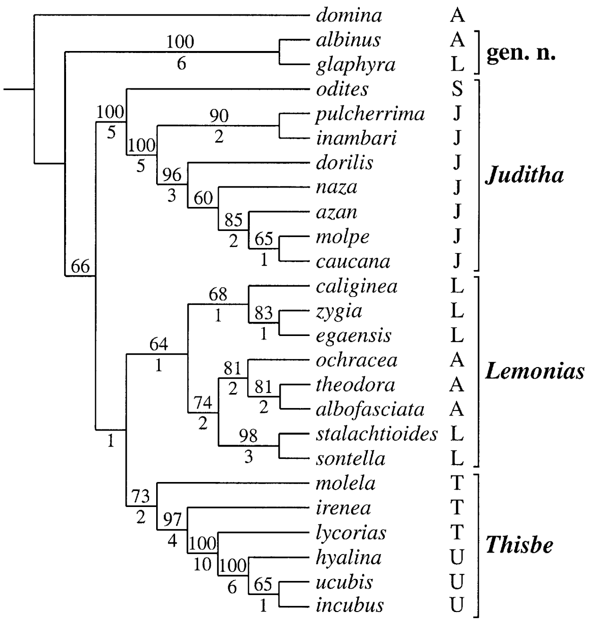


Fig. 4. The single most parsimonious cladogram resulting from one round of successive weighting after the heuristic analysis of sixty-nine characters for twenty-five taxa. Estimates of branch support are given in the form of bootstrap values above branches and decay indices below branches. Letter codes to the right of the cladogram indicate which genus each species was classified in prior to this study. A = *Audre*, J = *Juditha*, L = *Lemonias*, S = *Synargis*, T = *Thisbe*, U = *Uraneis*.

In addition to the above, it is notable that the larvae of members within two of the monophyla of *Lemonias* and within one of the more basal members of *Thisbe*, but not *Juditha*, are known to feed on *Croton* (Euphorbiaceae) (*zygia*, Monte, 1934; *egaensis* (as *zygia*), DeVries *et al.*, 1994; *caliginea*, Ross, 1964a; *stalachtioides*, Zikán, 1953; *irenea*, Robbins & Aiello, 1982). The only other hostplant records for members of the study group outside of *Juditha* are *Cassia alata* (Leguminosae) for *T. lycorias* and *Phoradendron* sp. (Loranthaceae) for *T. hyalina* (DeVries *et al.*, 1994; DeVries, 1997). The shift for the most derived *Thisbe* species away from *Croton* and *Cassia* to toxic mistletoes mirrors that to a highly modified and presumably mimetic wing pattern.

The *glaphyra* group shares many characters with the outgroup, most notably the possession of an eighth abdominal sternite produced into two narrow elongate toothless projections (ch. 33) and asymmetrically positioned signa of the female genitalia (ch. 58). Although these characters appear as symplesiomorphies in this analysis, both are derived for the Riodinidae, suggesting that the *glaphyra* group may form a monophyletic group with *Audre*. Although there are a few wing pattern and genitalic characters the *glaphyra* group share with the *Lemonias* + *Thisbe* clade (e.g. chs 25, 28, 30, 45, 65), suggesting a reasonably close relationship, there are no universal synapomorphies uniting it with *Juditha* + (*Lemonias* + *Thisbe*). Our analysis found no convincing adult morphological character support for the sister relationship of *Juditha* to *Lemonias* + *Thisbe*. However, from an extensive examination of genitalia and wing pattern characters in the remainder of Lemoniadina, no clear sister-group relationship is apparent between *Juditha* and any other genus either. In conclusion, the true sister group to *Juditha* remains uncertain. Comprehensive species-level phylogenies are needed to assess the monophyly of the remaining genera in Lemoniadina, and, perhaps by isolating the basal member of each, further progress can be made in elucidating the intergeneric relationships of Lemoniadina and how the members of this group relate to those of the remaining two subtribes of the Nymphidiini (Hall & Harvey, unpublished data).

Revision of *Juditha*

History of classification

Stichel (1911) was the first author to recognize many of the species revised below as a discrete group, although he erroneously applied the generic name *Peplia* Hübner, [1819] to them, which is a junior objective synonym of *Nymphidium* Fabricius, 1807 (Hemming, 1967). They were previously typically treated in *Nymphidium*. Stichel (1911) initially included *grande*, *dorilis*, *ipsea*, *azan*, *molpe* and *caucana* (the last three under *lamis*), recognizing four species, but subsequently added *rubigo* (Stichel, 1930–31), and it is for these species that Hemming (1967) provided the generic name *Juditha*, with *azan* (as *lamis*) as the type species. Due to an editorial error (the volume was edited for publication after his death), Hemming (1967) inadvertently described the synonym *Pseudopeplia* in the same work. d'Abrera (1994) and Bridges (1994) subsequently treated *Juditha* as containing these same five species. The rearing of the taxon *grande*, described from a female, established that it was conspecific with *palaeste* Hewitson, 1870, described from a male, which belonged in *Synargis* (Harvey, 1987; DeVries, 1997). Callaghan & Lamas (2001) thus excluded *grande* from *Juditha*, and split *molpe* off from *azan*, thus again recognizing five species. As mentioned earlier, Hall & Harvey (2001) transferred *pulcherrima* (and the names *comparata* and *felicis*) from *Calociasma* Stichel to *Juditha*. We here move *odites* (= *phylleus* Auctt.) from *Synargis* to *Juditha*, and, based on dissection of the unique holotype, transfer *rubigo* from *Juditha* to *Pachythone*. Also as a result of this study, *molpe* and *caucana* were found to be genitally distinct, necessitating their recognition as species, *ipsea* to be synonymous with *dorilis*, and two phenotypes found to require description as new species, one previously confused with *azan* and the other with *pulcherrima*.

Based on the examination of 1322 specimens (775 males, 547 females) and seventy-nine dissections (fifty-three males, twenty-six females), we recognize eight species and four subspecies of *Juditha*. In the synonymic checklist below, Callaghan & Lamas (2001) is used as the taxonomic reference upon which the nomenclatural changes are based. A single dash, '–', denotes a subspecies, and a double dash, '– –', a synonym.

Juditha Hemming, 1964

azan (Westwood, [1851])
– – *australis* (C. Felder, 1862)
– *completa* (Lathy, 1904)
– *majorina* Brévignon & Gallard, 1998
– – *lamis* (Stoll, 1780) preocc. (Cramer, 1779)
caucana (Stichel, 1911), stat.n.
dorilis (Bates, 1866)
– – *ipsea* (Godman & Salvin, 1886), syn.n.
– – *licinias* (Staudinger, [1887]), syn.n.
inambari Hall & Harvey, sp.n.
molpe (Hübner, [1808])
– – *bahiana* (Stichel, 1929), syn.n.
naza Hall & Harvey, sp.n.
odites (Cramer, 1775), comb.n.
– – *apame* (Hewitson, 1865), syn.n.
– – *laodamia* (Stichel, 1923), syn.n.
– – *magnifica* (Stichel, 1911), syn.n.
– – *oditis* (Hübner, [1819])
– – *orontes* (Stichel, 1923), syn.n.
– – *phylacis* (Godart, [1824])
– – *phyllea* (Hübner, [1819])
– – *phylleus* (Cramer, 1775), syn.n.
– *praeclarum* (Bates, 1866), comb.n.
pulcherrima (Butler, 1867)
– – *felicis* (Rebillard, 1958), syn.n.
– *comparata* (Stichel, 1911)

Key to the males of Juditha

1. Postdiscal band on dorsal hindwing orange 2
– Postdiscal band on dorsal hindwing white............ 3
2(1). Postdiscal forewing band laterally discontinuous medially.. *odites*
– Postdiscal forewing band laterally continuous .... *dorilis*
3(1). Postdiscal forewing band with white and orange elements.. 4
– Postdiscal forewing band entirely white 5
4(3). White portion of postdiscal forewing band with broad block extending to at least vein Cu2; projections of eighth abdominal sternite with teeth along distal half of inner edge................................ *pulcherrima*
– White portion of postdiscal forewing band restricted to small triangle below middle of cell Cu2; projections of eighth abdominal sternite with teeth restricted to tip .... *inambari*
5(3). Forewing length > 20 mm 6
– Forewing length < 18 mm 7
6(5). Lower processes of genitalic valvae symmetrical .... *naza*
– Lower processes of genitalic valvae asymmetrical .. .. *azan*
7(5). Lower processes of genitalic valvae strongly asymmetrical, with left lower process shorter than upper processes.. *molpe*
– Lower processes of genitalic valvae only very slightly asymmetrical, with both longer than upper processes... *caucana*

Key to the females of Juditha

1. Postdiscal band on dorsal hindwing abruptly broadens medially... 2
– Postdiscal band on dorsal hindwing approximately even in width 4
2(1). Forewing length > 22 mm; submarginal coloration cream or yellow .... *odites*
– Forewing length < 18 mm; submarginal coloration pale orange 3
3(2). Sclerotized region between ostium bursae and papillae anales of genitalia divided by very broad membranous area and positioned laterally .... *pulcherrima*
– Sclerotized region between ostium bursae and papillae anales of genitalia divided by very narrow membranous area and positioned centrally .... *inambari*
4(1). Postdiscal bands and submarginal rings cream or yellow .... *dorilis*
– Postdiscal bands white, submarginal rings bluish-white... 5
5(4). Forewing length > 21 mm 6
– Forewing length < 19 mm 7
6(5). Ostium bursae of female genitalia with straight ventral lip, concealed within shallow pouch; sclerotization in posterior portion of ductus bursae reduced to narrow ring .... *naza*
– Ostium bursae of female genitalia with sharply indented ventral lip medially, projects prominently; posterior portion of ductus bursae sclerotized for considerable distance .... *azan*
7(5). Sclerotized portion of ductus bursae of uniform width with 2 small raised medial bumps anteriorly.......... .... *caucana*
– Sclerotized portion of ductus bursae broadens sharply and briefly anteriorly with raised medial bumps...... .... *molpe*

Characteristics of Juditha

Members of *Juditha* are medium to large-sized riodinids with orange, yellow (in females) or white postdiscal bands over orange-brown or brown ground colours with orange or white ringed ocelli at the base of the forewing and at the submargins of both wings. The forewing has four radial veins. Three universal wing pattern synapomorphies are listed in Appendix 3 for *Juditha* that are unique within those taxa included in the phylogenetic analysis (chs 12, 24, 31), but not one is unique for Lemoniadina or distinguishes *Juditha* from the phenotypically most similar genus *Synargis*. The eyes of all *Juditha* species are bare, the frons is brown or orange-brown, and the second and third palpal segments are elongate. The

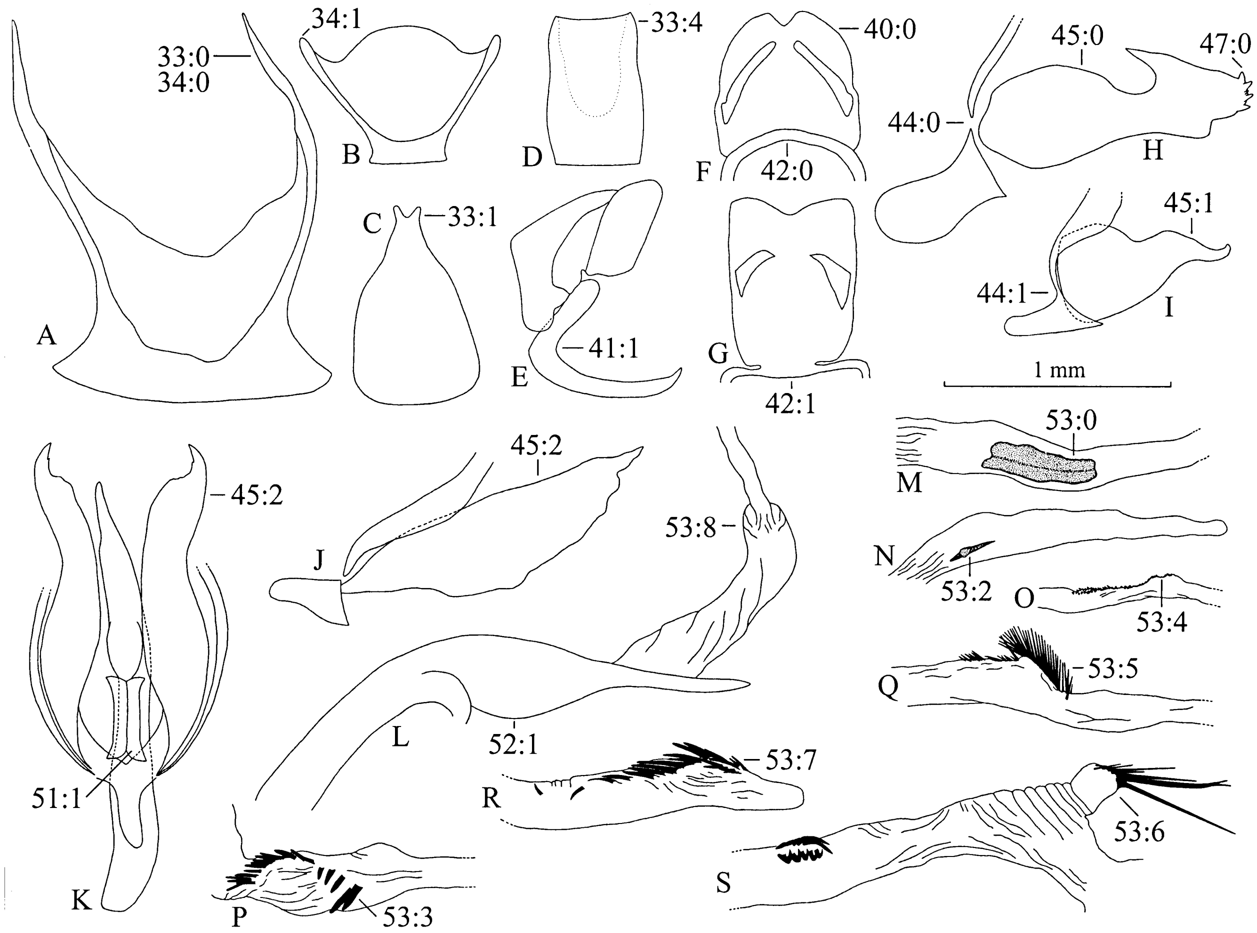


Fig. 5. Male terminalia for non-*Juditha* taxa. A–D = eighth abdominal sternite in ventral view; E = lateral view of tegumen, uncus and falces; F,G = uncus in dorsal view; H–J = valve and vinculum in lateral view; K= valvae, vinculum and aedeagus in ventral view; L = aedeagus and everted vesica; M–S = everted aedeagal vesica. A, *Audre domina*; B, '*Audre*' *albinus*; C, *Lemonias zygia*; D, *Lemonias ochracea*; E, '*Lemonias*' *glaphyra*; F, *Lemonias zygia*; G, *Lemonias ochracea*; H, *Audre domina*; I, *Lemonias zygia*; J–L, *Thisbe incubus*; M, *Audre domina*; N, *Lemonias ochracea*; O, *Lemonias stalachtioides*; P, *Lemonias egaensis*; Q, *Lemonias caliginea*; R, *Thisbe molela*; S, *Thisbe irenea*.

antennae, which are about three-quarters the length of the forewing, are black with white scaling at the base of each segment and variably sized areas devoid of scales ventrolaterally on each segment, and the elongate, tubular, orange-tipped clubs are completely devoid of scales ventrolaterally. As is typical of fast flying, territorial butterflies (see *Biology* below), the thorax is robust and the abdomen is of approximately the same width; both the thorax and abdomen are paler ventrally. The sexes are typically monomorphic, but if dimorphic only weakly so; the second and third palpal segments are notably more elongate, and the ventrolateral margin of the antennae completely denuded of scales in females. The legs are unremarkable, the foreleg of the male having a unimerous tibia, and the mid- and hindlegs having a single tibial spur and clusters of spines on the tibial segments.

The last abdominal male sternite of all *Juditha* species, except *odites*, is highly modified and formed into two long projections with spines along their inner distal tips (chs 33, 35–38; Fig. 9). Such projections were used by Harvey (1987) (his bifurcate rami) to define his Lemoniini (= Lemoniadina, see Hall & Heppner, 1999; Hall, 1999a), and although not universal in that group (e.g. they are not present in *Lemonias* and *Thisbe*), they are prevalent in the large genera *Synargis* and *Audre*. However, no other genera have such sternal spines (these are limited to the tip in *Synargis*) or lack a membranous region connecting the two projections. Having established in the cladistic analysis that *odites*, which possesses a plain rectangular last sternite, is the most basal species in *Juditha*, it is reasonable to assume that the bifurcate state in the other *Juditha* species is an independently derived condition.

The male genitalia of all *Juditha* species (Figs 7, 8, 10A,B) are rather uniform in all respects except the valvae, which clearly delineate the three species groups ('*odites*', '*pulcherrima*' and '*azan*' groups) (ch. 45). *Juditha odites* has a unique strongly sclerotized 'V'-shaped tip to the valvae, '*pulcherrima*

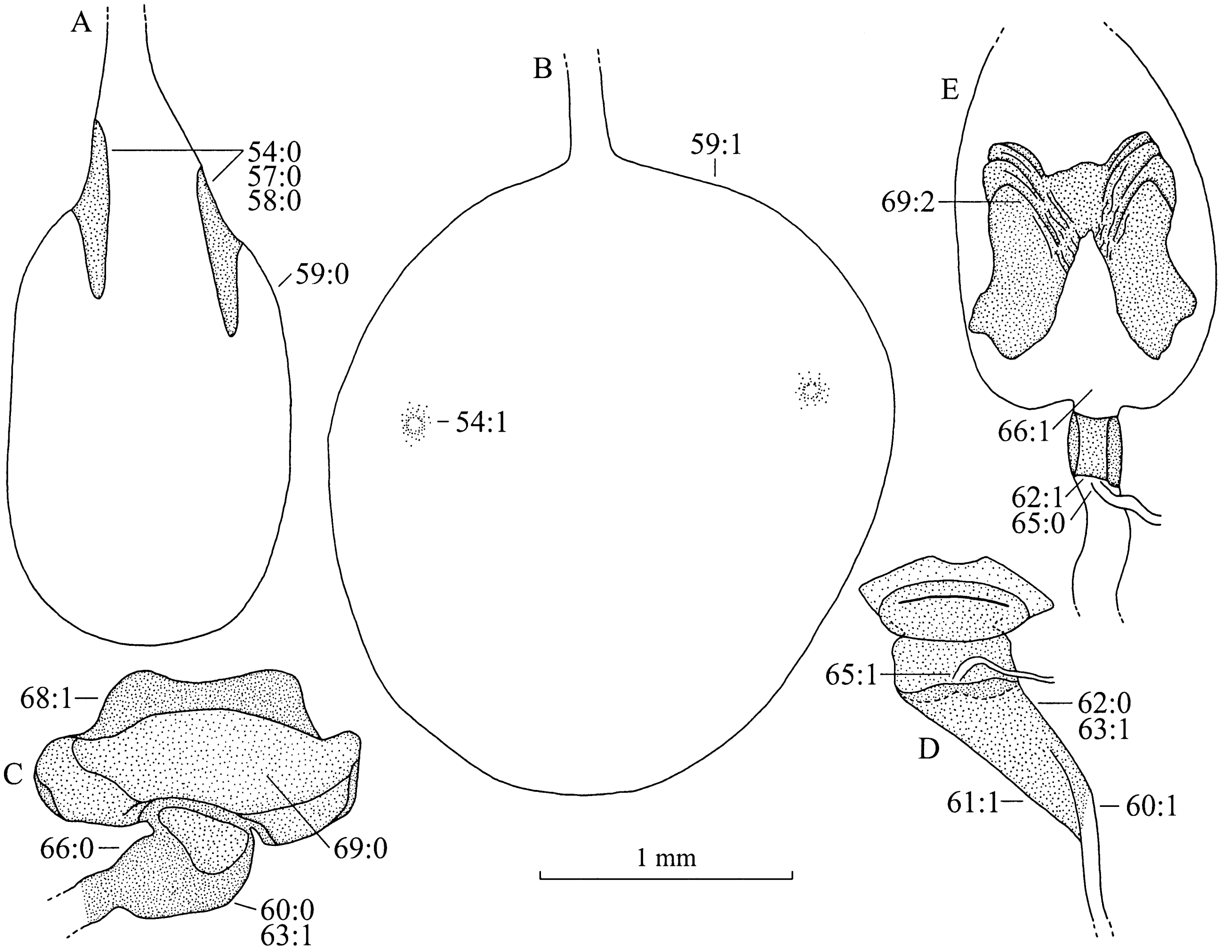


Fig. 6. Female genitalia for non-*Juditha* taxa. Stippled regions represent sclerotization (the eighth sternite in E is weakly sclerotized but not indicated as such for clarity). A,B = corpus bursae in lateral view; C–E = posterior portion of ductus bursae, ostium bursae and region between ostium and papillae anales (C,E only) in ventral (C) or dorsal view (D,E). A, '*Lemonias*' *glaphyra*; B, *Thisbe hyalina*; C, '*Audre*' *albinus*; D, *Lemonias zygia*; E, *Thisbe hyalina*.

group' species have broadly triangular valvae, whereas '*azan* group' species have bifurcate valvae, with lower processes that are asymmetric in the most derived species (ch. 46). None of these valve types are seen elsewhere in Lemoniadina. The uncus is angular in lateral view and all species except *J. odites* have a prominent square notch at the dorsal medial margin (ch. 39). The vinculum is dorsally almost complete, with only a very lightly sclerotized gap medially, associated with a small desclerotized region of the tegumen (ch. 42), variably enlarged in its upper portion, and often desclerotized ventrally (a character that is widespread in Lemoniadina), before the dorso-ventrally flattened saccus (ch. 44). Unique within the Riodinidae to the '*azan* group' of *Juditha* is the presence of a variably elongate semisclerotized projection of the annelar region between the upper portions of the vinculum (ch. 43). The relatively short aedeagus is approximately even in width throughout, before tapering to a pointed tip, and is strongly dorsally bowed medially. The everted vesica of all species contains a small, roughened, yellowish, semisclerotized patch towards its dorsal right base (ch. 53), which appears to be unique within Lemoniadina. Under a scanning electron microscope, this roughened area can be seen to consist of unevenly distributed clusters of very small spines (Fig. 10E).

Perhaps the strongest, or most convincing, synapomorphy uniting all species of *Juditha* is the possession of long 'sponge'-like setae (Fig. 10D) on an unsclerotized region between the pedicel and the base of the valvae (ch. 48), which becomes a better defined (ch. 49) and broader pad with more setal sockets (ch. 50) in the more derived species. The pad is sparsely covered with uneven clusters of very small spines (Fig. 10C). This unique structure within Riodinidae, which is presumed to function as an androconial organ, was first illustrated by Stichel (1911) and used by Penz & DeVries (1999) to unite *J. azan* and *J. caucana* (as *J. molpe*). It should

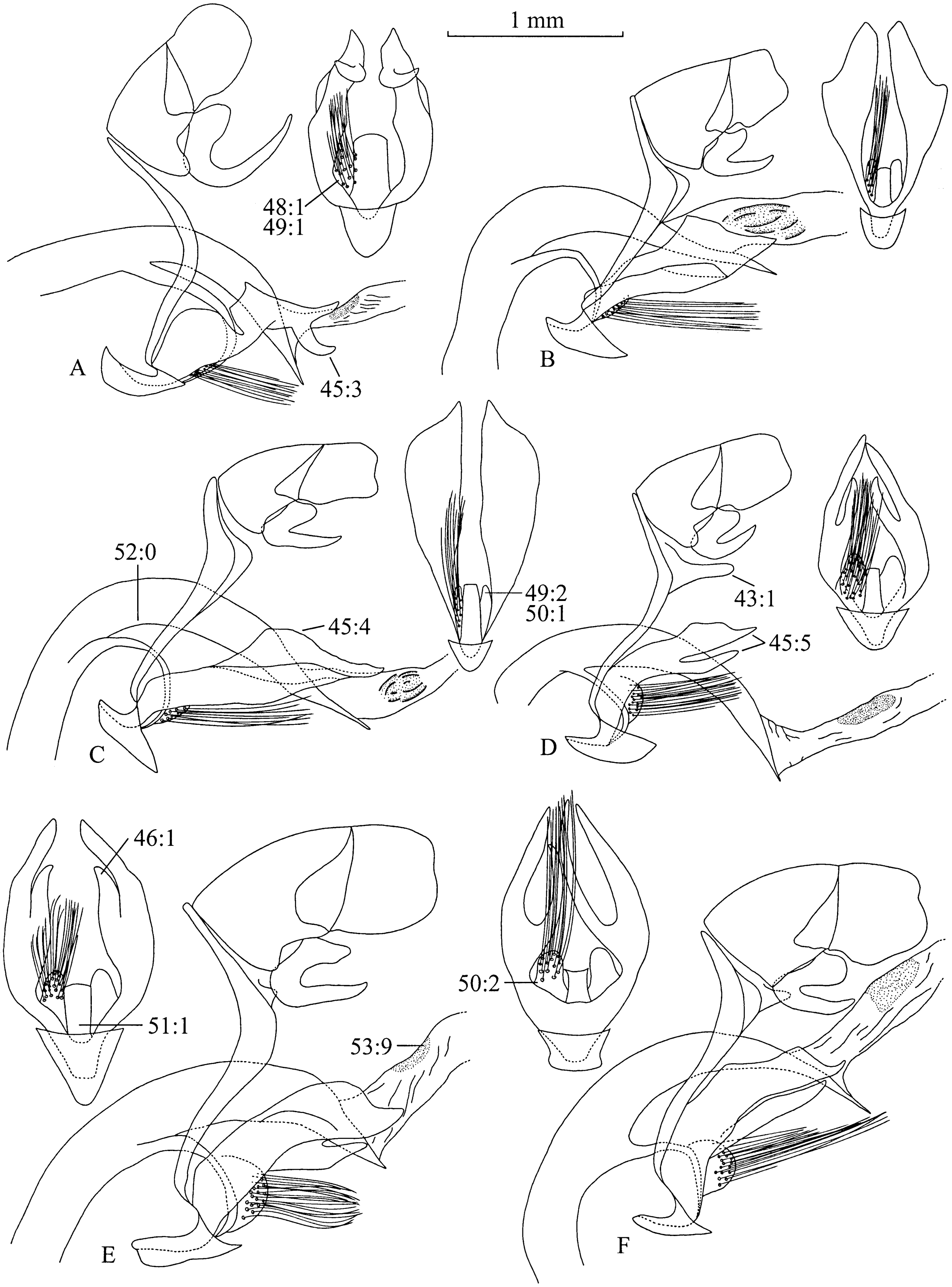


Fig. 7. Lateral view of male genitalia and ventral view of valvae for *Juditha* taxa. A, *Juditha odites*, 'Guyana' (USNM); B, *J. pulcherrima*, Parque Nacional Manu, Pakitza, Peru (USNM); C, *J. inambari*, Manicoré, Rio Madeira, Am, Brazil (MNHN); D, *J. dorilis*, El Llano, Panama (USNM); E, *J. naza*, Río Cachaví, western Ecuador (JHKW); F, *J. azan*, Cacao, French Guiana (USNM).

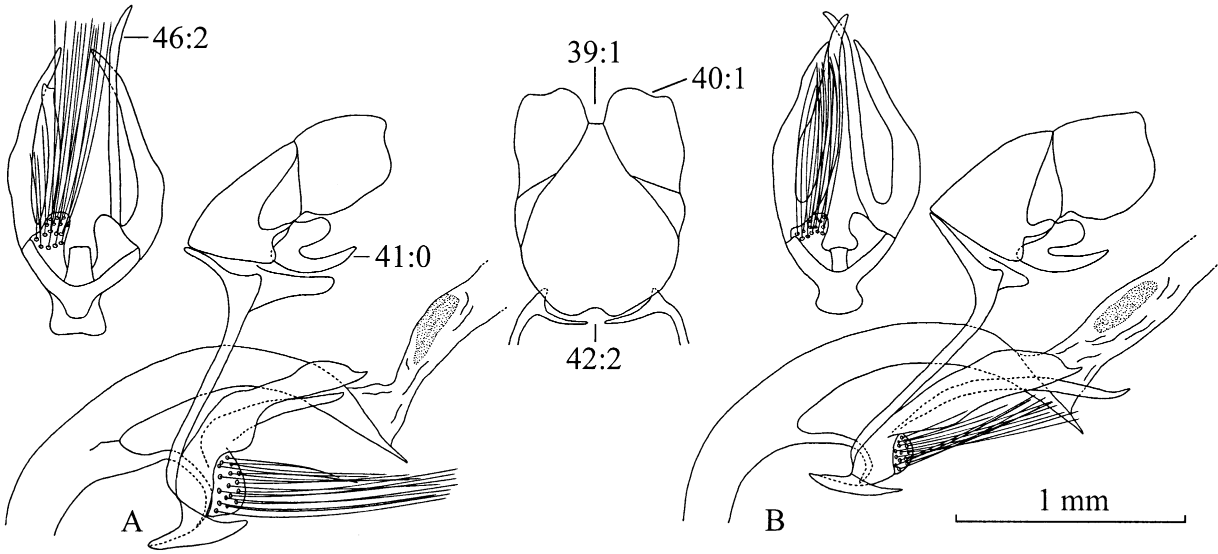


Fig. 8. Lateral view of male genitalia, ventral view of valvae and dorsal view of uncus (A only). A, *Juditha molpe*, Cacao, French Guiana (USNM); B, *J. caucana*, Madden Forest, Panama (USNM).

be noted that Penz & DeVries (1999) report and claim to figure (in their Figs 13B and 15A) such setae in *Theope publius* C. & R. Felder and *Thysanota galena* (Bates), but in the former case these setae actually originate on the valvae (see illustrations in Hall, 1999a, for *Theope*). The error in the former case results from mistaken homologies, regarding the 'horn'-shaped last male abdominal sternite in *T. publius* as the valvae (in their character 87) and consequently the species as having only seven sternal segments (in their character 39). In *T. galena*, a few setae are positioned along the weakly sclerotized ventral margin of the valvae and on the region between the valvae and pedicel, a condition that is found to varying degrees in several related species of *Synargis*, but these are short and sparse.

The corpus bursae of the female genitalia of *Juditha* (Fig. 11) is elongate and all species have 'horn'-shaped invaginated signa positioned at least the distance of the signal wall away from the ductus bursae (ch. 57). In all other taxa studied here, the signa touch the entrance of the ductus bursae (Fig. 6A). All members of *Juditha* except *odites* have serrate inner edges to the signa (ch. 56) to a degree not seen elsewhere in Nymphidiini (Hall, unpublished data). The posterior membranous portion of the ductus bursae is typically loosely coiled and joins to a variably short sclerotized portion, with the ductus seminalis attaching at the junction of these two regions (ch. 65) instead of within the sclerotized portion as in members of the clade *Lemonias* + *Thisbe*. The ostium bursae consists of an often protruding, sclerotized ring, and a sclerotized region of vaiable size is present between the ostium and the papillae anales, which is crossed with transverse ribs.

Biogeography

Juditha are widely distributed in the Neotropics from central Mexico, through Central America to western Ecuador, throughout the Guianas and Amazon to southeastern Brazil, Paraguay and northeastern Argentina (Figs 13–16). Colombia and Ecuador have the highest recorded number of *Juditha* species (seven out of eight) (Table 2), a pattern of species diversity that is typical for the family (Hall, 1999a). The genus is evenly distributed between the east and west Andean regions, which both contain five species, although *J. molpe* is largely restricted to the eastern Andes. The highest diversity occurs in the western Amazon, where four species occur sympatrically, again a pattern typical for Riodinidae (Hall, 1999a), as well as other groups of organisms such as birds, mammals and angiosperms (e.g. McNeely *et al.*, 1990). Most *Juditha* species are widespread and none is restricted to the Guianan shield or Atlantic coastal regions of endemism. However, *J. naza* is apparently restricted to the most notable area of endemism for Riodinidae, the Chocó of western Colombia and western Ecuador (Callaghan, 1985; Hall, 1999a), and *J. inambari*, is apparently restricted to the Inambari region of endemism (e.g. see Cracraft, 1985) in the Rio Purus-Rio Madeira drainage of the southern Amazon basin. The most noteworthy biogeographical feature of *Juditha* is that all the closely related sister species pairs exhibit parapatric distributions.

Biology

Habitats and ecology of adults. Juditha species occur in a wide variety of habitats, from dry semi-deciduous woods to wet pluvial forest, in primary habitats or secondary forest and even overgrown pastures, but like all myrmecophilous genera they are restricted to the lowlands. No species occurs above 1200 m. Whereas *J. dorilis* and *J. naza* are rather rare, most species are relatively common, with *J. caucana* and *J. molpe* sometimes being the most common riodinid species in a given

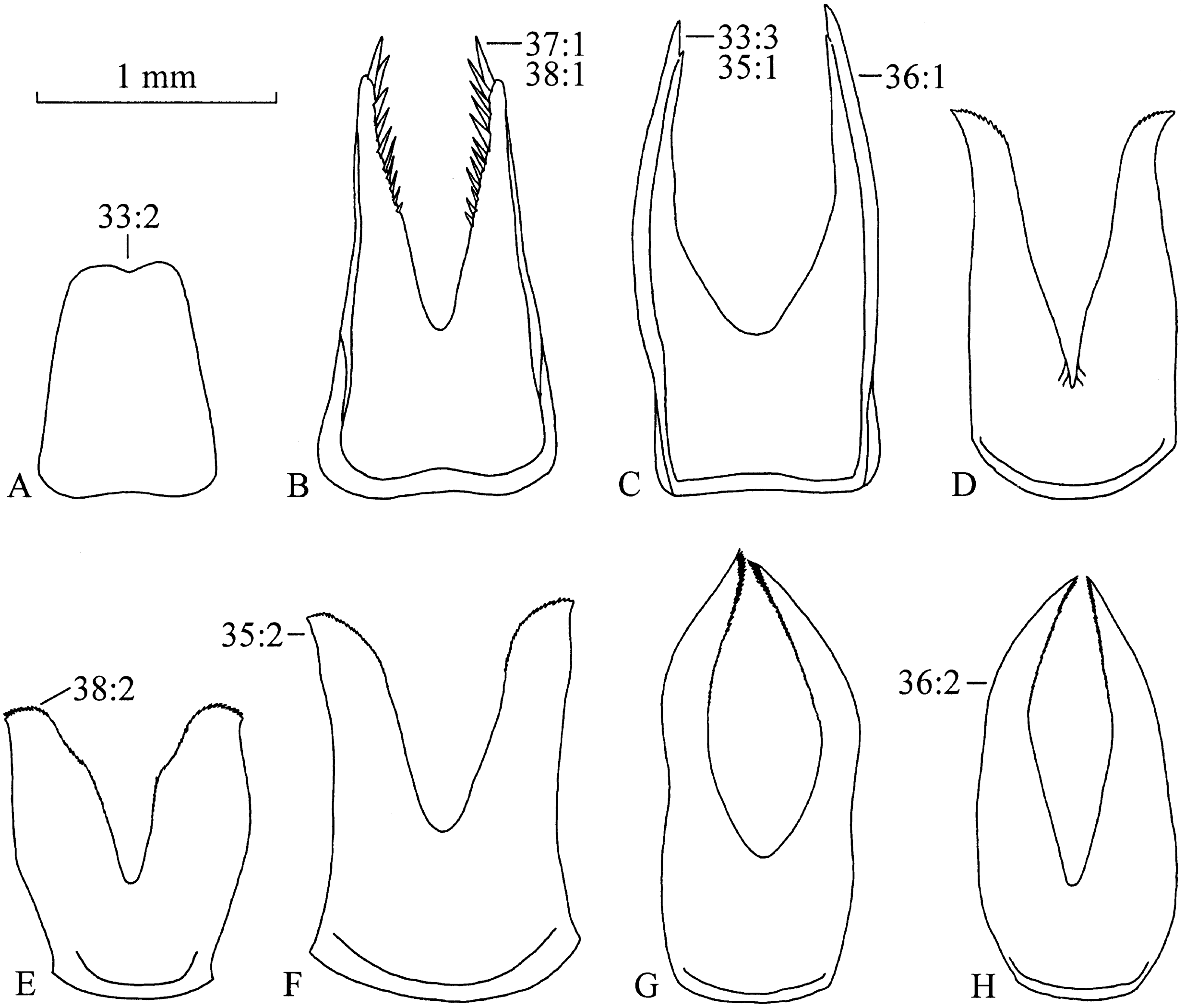


Fig. 9. Eighth abdominal sternite of *Juditha* taxa in ventral view. A, *Juditha odites*; B, *J. pulcherrima*; C, *J. inambari*; D, *J. dorilis*; E, *J. naza*; F, *J. azan*; G, *J. molpe*; H, *J. caucana*.

locality. *Juditha* males are typically encountered perching alone or in small groups along forest edges and streamsides, and on hilltops, from late morning until late afternoon (approximately 17.30 hours). They perch on the tips of leaves with their wings half or fully open and make rapid sorties to investigate passing butterflies of the same colour. Both sexes are known to visit a variety of flowers, such as those of *Lantana* and *Croton*, and males are known to drink at extrafloral nectaries (DeVries, 1997).

Morphology and ecology of immature stages. The first description of *Juditha* immature stages was given by Guppy (1904) for *J. molpe* in Trinidad, and since then information of variable detail has been reported on the immature stages of three other species, *J. odites*, *J. dorilis* and *J. caucana* (Callaghan, 1982; Harvey, 1987; DeVries *et al.*, 1994; DeVries, 1997). *Juditha* larvae, and *J. caucana* in particular, utilize a wide range of unrelated hostplants from twelve families (summarized in Appendix 4 with attending ant symbionts), a phenomenon probably explained by their obligate association with *Dolichoderus* ants (Dolichoderinae). The symbiotic relationship is so strong that adult females probably use the presence of these ants instead of any plant chemical cues as an oviposition stimulus (Pierce, 1983; Fiedler, 1991; DeVries, 1997), a phenomenon also seen in the riodinid genera *Theope* Doubleday and *Synargis* (Harvey, 1987; DeVries, 1997; Hall, 1999a). *Juditha* larvae are recorded as feeding on leaves and mature flower buds, but the fact that *J. odites* and *J. dorilis* females oviposit on or near membracid homopteran nymphs, and the adults of at least *J. odites* exhibit greasiness of the wings (Hall & Willmott, 1995; DeVries, 1997; Hall, 1999a), suggests that their larvae may be carnivorous (DeVries *et al.*, 1994). This is a behavioural trait that is undoubtedly common throughout Nymphidiini

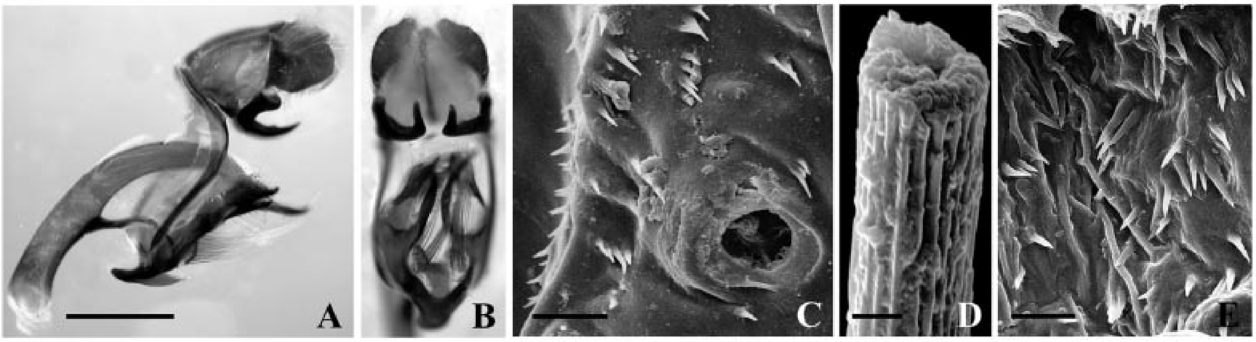


Fig. 10. Scanning electron micrographs of the male genitalia of *Juditha azan*. A, Lateral view of genitalia; B, ventral view of genitalia; C, magnified portion of androconial setal pad between base of valvae and pedicel; D, cross-section of seta from setal pad; E, magnified portion of dorsal 'roughened' area on everted vesica. Scales = A,B, 1 mm; C,E, 10 µm; D, 2 µm.

(*sensu* Hall, 1999a), but is thus far only established for *Setabis lagus* (Cramer) (Urich in Kaye, 1921; DeVries *et al*., 1994).

Life history details are given in each species account below where relevant, and what follows is an account of the biology and morphology of the immature stages of a single exemplar species, *J. caucana*. The following natural history observations are summarized from Callaghan (1982) and Harvey (unpublished data). Eggs are laid individually on the plant wherever *Dolichoderus* ants are present (Callaghan also reports, perhaps erroneously, *Camponotus* as attending *J. caucana*), but upon hatching, the larvae move to nearby mature flower buds or new leaf growth where they remain to feed for at least the first two instars. The larvae of all instars also drink extrafloral nectar and the honeydew secretion produced by Homoptera (DeVries, 1997; see also Boulard, 1981; for a discussion and illustration of this behaviour in a possible *J. molpe* larva). The ants begin attending third-instar individuals and 'drum' their legs on the larva to elicit the production of honeydew from the tentacle nectary organs. The prepupal stage, in which the larva remains motionless on the stem of the plant, lasts for two or three days before final pupation occurs.

The larval and pupal ultrastructure of taxa in Lemoniadina clearly exhibits significant differences at the generic level (Downey & Allyn, 1973; Schremmer, 1978; Harvey, unpublished data), and such characters should prove phylogenetically informative once more species have been reared. Below we describe the ultrastructure of the egg, mature larva and pupa of *J. caucana*.

Egg (Fig. 12A–C). The egg was superficially described by Callaghan (1982) and DeVries (1997). It is round in dorsal view, dorsally flattened, wider than high, and has a width of 0.52 mm (Fig. 12A). The micropylar region is slightly depressed, the micropyle possessing four pores at the centre of four indented, petal-shaped cells (Fig. 12B). Two additional ranks of cells occur before the annulus, which is marked with a series of indentations. The remaining dorsal surface of the egg is flat, with three rows of cells, the inner two small, the outer row of twenty-one elongated, with irregular surfaces and low rides between adjacent cells. The lateral surface of the egg has four rows of polygonal cells (usually hexagonal but sometimes pentagonal) bounded by ribs. Projections at vertices of ribs bear single aeropyles (Fig. 12C).

Mature larva (Fig. 12D–J). The larva (Fig. 12D) was illustrated by Donahue (1979), Callaghan (1982), DeVries (1997) and Janzen & Hallwachs (2000), and superficially described by the second and third of these authors. The head capsule is roughly circular in outline (Fig. 12E) and the dorsal surface of the epicranium has roughened areas below the vibratory papillae (see below) (Fig. 12F). 'Stellate' setae (see below) are present on the frontal and lateral portions of the headcapsule, interspersed with perforated cupola organs (PCOs) (*sensu* Malicky, 1969, 1970; Cottrell, 1984). The prothorax has a chitinized shield that bears two pairs of anteriorly projecting 'horns', long dorsal ones and shorter lateral ones, which bear two long setae at their apices. A filiform seta (Fig. 12H), arising directly below these two setae, is thinner than other setae, slightly branched, and its recessed socket is surrounded by cuticular elaborations. Similarly modified setae occur in the same position on other members of Lycaenidae and Riodinidae (Ballmer & Pratt, 1989; Harvey, unpublished data). The surface of the shield is sculptured with hemispherical projections, and bears stellate setae, each set within a depression in the cuticle, along with scattered PCOs. The two elongate, club-shaped, vibratory papillae (*sensu* Ross, 1964a), which surfaces are annulated along their distal portion, are located on the anterior margin of the prothoracic shield (Fig. 12G).

The dorsal surface of T2-A10 lacks the long tactile setae that form a lateral fringe around the larva. A single type of stellate seta is distributed evenly over the entire dorsal surface of these segments, these being white or brown, short, radially branched and set within slight depressions on the cuticle. PCOs also occur on the dorsal surface of the larva (Fig. 12I), slightly elevated above the surrounding cuticle, their sieve plates bearing distinct pores on the surface. Although some are scattered on all segments, most are located in clusters found in specific locations on the

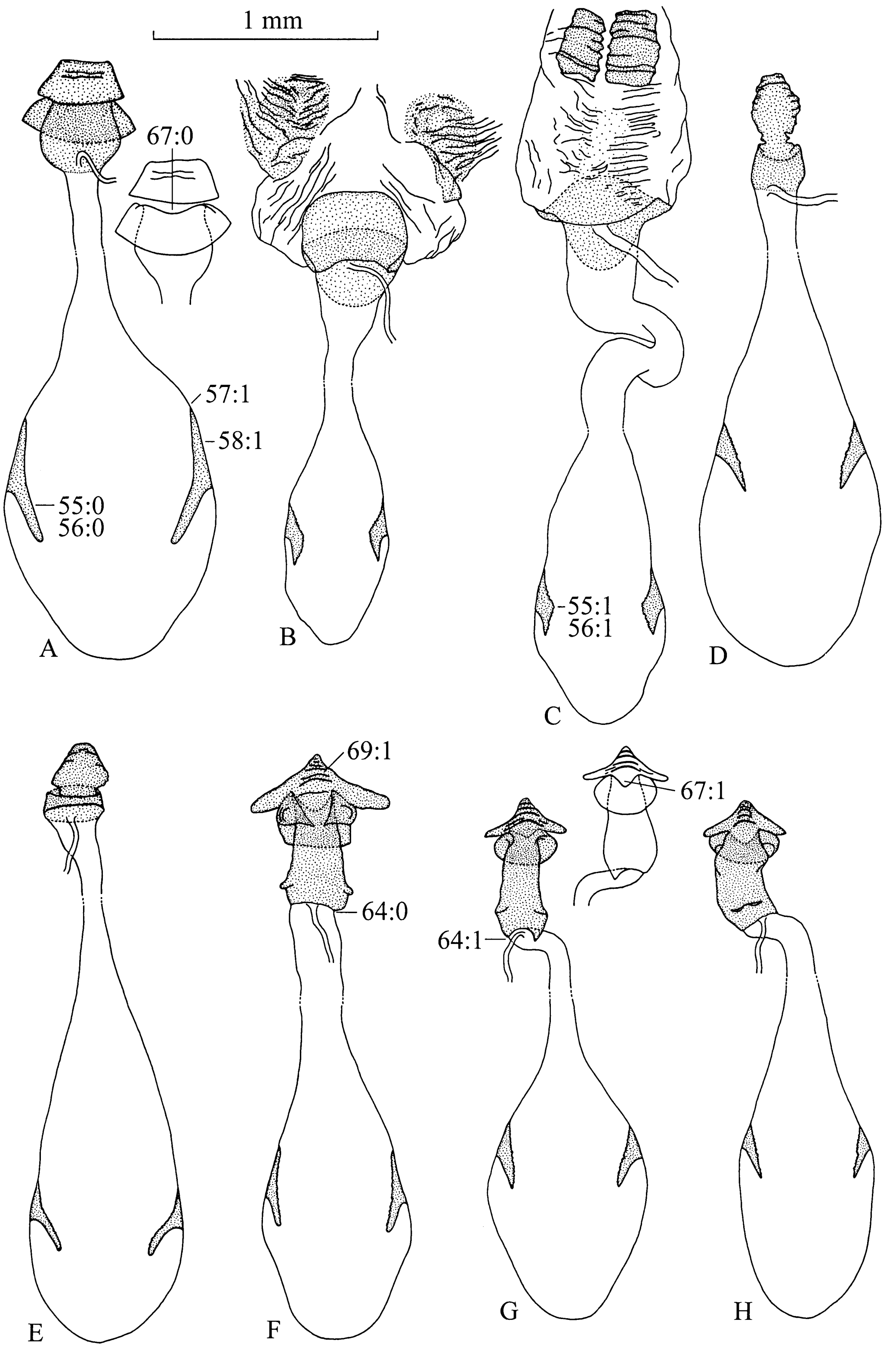
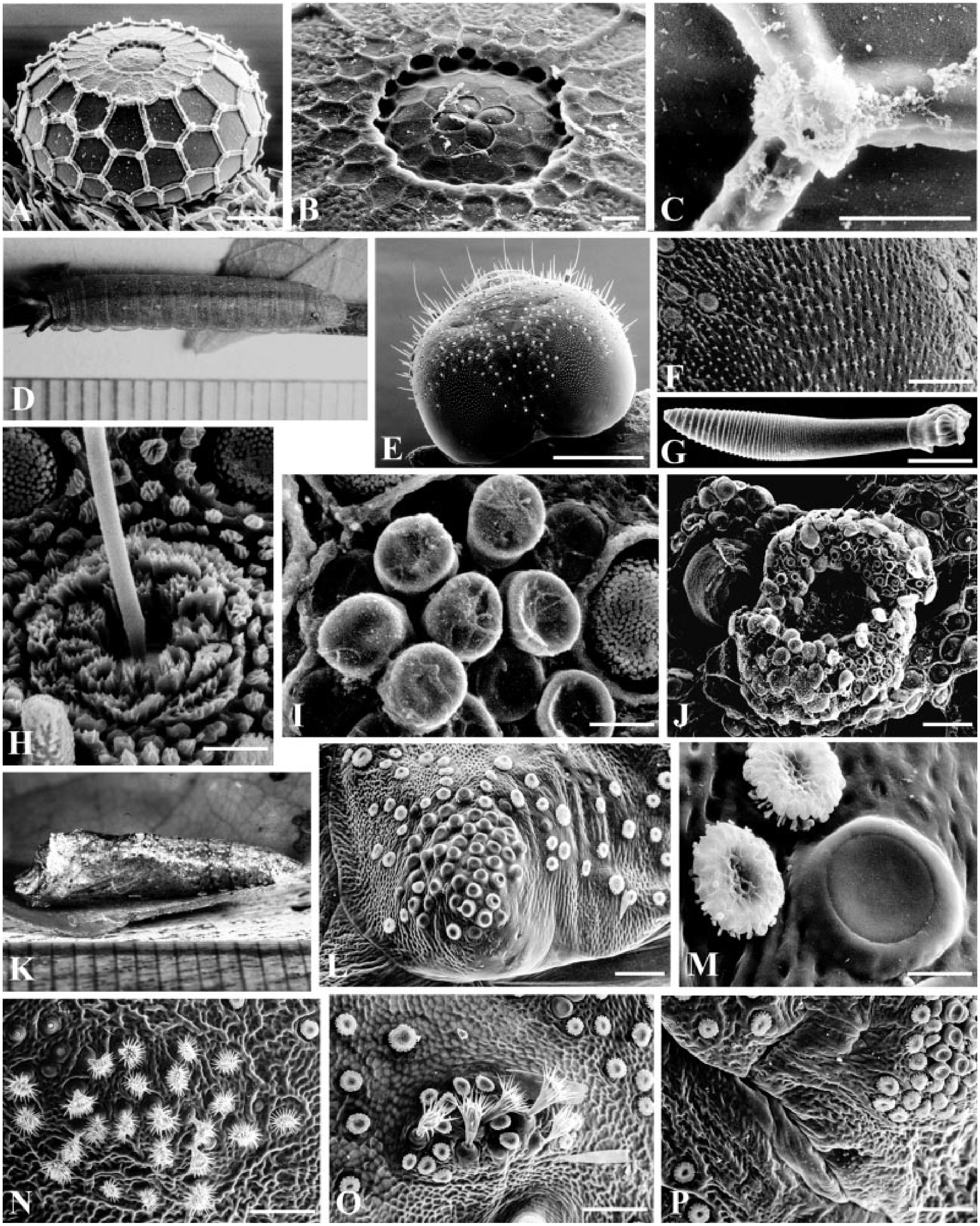


Fig. 11. Female genitalia in dorsal view (unless otherwise noted) for *Juditha* taxa. A, *Juditha odites*, Chapada Guimarães, MG, Brazil (USNM), also ostium bursae in ventral view; B, *J. pulcherrima*, Parque Nacional Manu, Pakitza, Peru (USNM); C, *J. inambari*, 'Amazon' (USNM); D, *J. dorilis*, Colón, Panama (USNM); E, *J. naza*, Valdivia, Colombia (BMNH); F, *J. azan*, Montagnes des Singes, French Guiana (USNM); G, *J. molpe*, Pointe de Kaw, French Guiana (USNM), also ostium bursae in ventral view; H, *J. caucana*, Madden Forest, Panama (USNM).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larva, arranged as follows (segment no.: no. on right, left): a subdorsal row on T2: 18, 17; A2: 13, 15; A3: 16, 16; A4: 13, 19; A5: 19, 18; A6: 14, 14; a subdorsal cluster, anterior and more mesal than the previous, on T2: 5, 6; a lateral series, at the level of spiracles on more posterior segments, on A1: 25, 26; and just dorsal to the spiracle on A5: 19, 18; A6: 15, 21; A7: 12, 20. The arrangement of clusters on a second larva examined was the same, but numbers of PCOs were almost 50% fewer.

The surface of the larva has scattered depressions dorsally and laterally on each segment, corresponding to the 'pores' of Kitching & Luke (1985). A depression in the cuticle on the dorsolateral portion of the metathorax occurs in the position of the anterior tentacle organ (ATO) described by Ross (1964a) (see also Cottrell, 1984). The cuticle surrounding this depression bears no unusual setae or pore cupolas, and there was no evidence of a functional ATO. A tentacle nectary organ (TNO) (*sensu* Cottrell, 1984) is located dorsal and posterior to each of the spiracles on A8 (Fig. 12J). The slitlike orifice of the TNO is flanked by two, convex, chitinized plates, and dissection of the larvae revealed that it is located between A8 and A9. The plates are connected mesially and laterally by thin regions of flexible cuticle, and their surfaces bear stellate setae along with a few PCOs. The setae closest to the orifice have a greater height. A cluster of PCOs is visible near the base of the inverted organ. The spiracle on A1 is in a completely ventral position, whereas those on A2–A8 are in the normal dorsal position, an arrangement that is characteristic of all other genera in Lemoniadina that have been reared (Harvey, 1987).

Pupa (Fig. 12K–P). The pupa (Fig. 12K) was illustrated by DeVries (1997). The dorsal surface of the pupa has scattered stellate setae very similar to those described for the larva (Fig. 12L,M). A second type of seta, with a longer shaft and sparser branching occurs in clusters on the prothorax and on the verrucae located near the spiracles on A5–A8 (Fig. 12N,O). PCOs occur in two clusters on the pupa, one on the prothorax, and the other on the lateral portion of the metathoracic segment (the metathoracic pupal gland of Ross, 1964a) (Fig. 12L,M). A 'scar' of the larval TNO is visible dorsal and posterior to the spiracle on A8, between segments A8 and A9 (Fig. 12P), but shows no evidence of being a functional secretory organ.

Juditha Hemming, 1964

Juditha Hemming, 1964: 147. Type species by original designation: *Papilio lamis* Stoll, 1780.

= *Pseudopeplia* Hemming, 1967: 351. Type species by default: *Papilio lamis* Stoll, 1780.

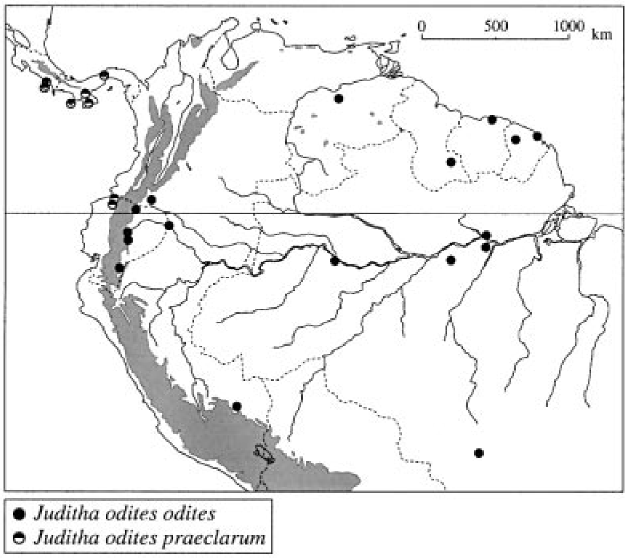

Fig. 13. The geographical distribution of *Juditha odites*.

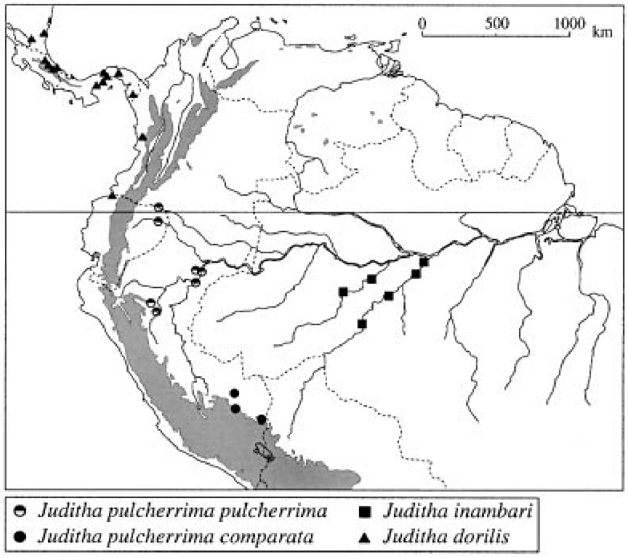

Fig. 14. The geographical distribution of *Juditha pulcherrima*, *J. inambari* and *J. dorilis*.

Fig. 12. Immature stages of *Juditha caucana* (D,K, photographs, others SEMs). A, Whole egg, dorsolateral view; B, dorsal surface of egg; C, aeropyle; D, mature larva, dorsal view; E, head capsule, dorsal view; F, sculpturing and setae on epicranium; G, vibratory papilla on T1; H, base of filiform seta on T1; I, cluster of perforated cupola organs (PCOs) on lateral A6; J, orifice of tentacle nectary organ (TNO) and A8 spiracle; K, pupa, lateral view; L, PCOs and 'stellate' setae on lateral tubercle of A1; M, 'stellate' setae and PCO on A3; N, 'brush' setae on subspiracluar verruca of A5; O, 'brush' and 'stellate' setae on supraspiracular verruca of A4; P, TNO 'scar' at junction of A7/8.

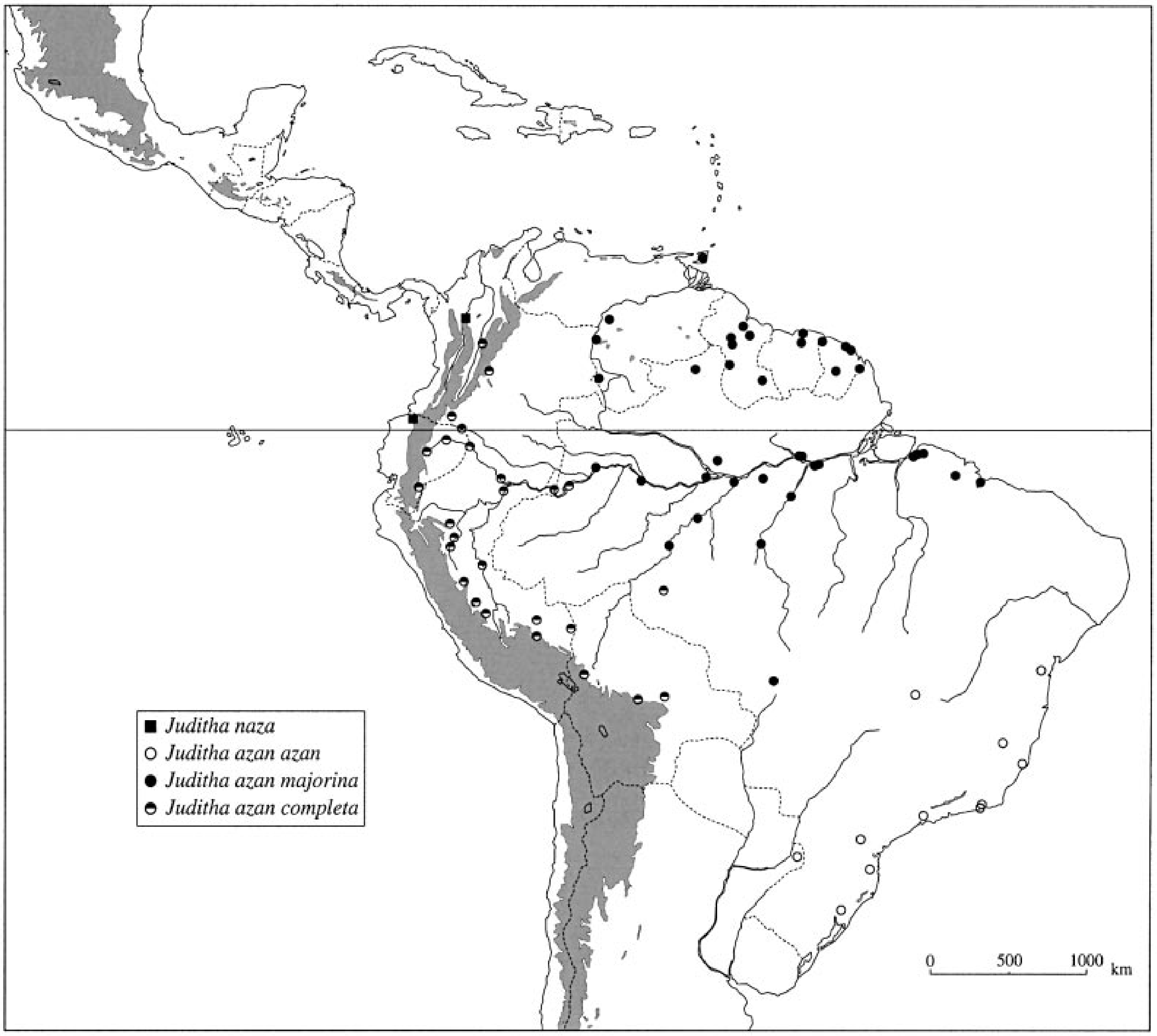

Fig. 15. The geographical distribution of *Juditha naza* and *J. azan*.

Juditha odites odites **(Cramer, 1775), comb.n.**

(Figs 2A,B; 7A; 9A; 11A; 13)

Papilio odites Cramer, 1775: 16, Pl. 11, Figs E,F. Type locality: Surinam. Syntype ♀ RNH; type photograph (examined, courtesy of G. Lamas).

= *Papilio phylleus* Cramer, 1775: 98, Pl. 63, Figs D,E. Type locality: Surinam. Syntype ♂(s) unknown. Syn.n.

= *Synargis oditis* Hübner, [1819]: 19. Unnecessary emendation of *odites* Cramer, 1775.

= *Synargis phyllea* Hübner, [1819]: 18. Unnecessary emendation of *phylleus* Cramer, 1775.

= *Nymphalis phylacis* Godart, [1824]. *In* Latreille, P. & J. Godart: 426. Unnecessary replacement name for *phylleus* Cramer, 1775.

= *Nymphidium apame* Hewitson, 1865: Pl. 55, Figs 13–15. Type locality: Amazon. Syntype ♂ BMNH (examined). Syn.n.

= *Nymula praeclara magnifica* Stichel, 1911: 371, Pl. 27, Fig. 100. Type locality: Arouany, French Guiana. Holotype ♀ (# 3832) ZMHU (examined). Syn.n.

= *Nymula phylleus laodamia* Stichel, 1923: 311. Type locality: Mato Grosso, S.W. Brazil. Syntype ♂ ZMHU (examined). Syn.n.

= *Nymula phylleus orontes* Stichel, 1923: 311. Type locality: Madre de Dios, S. Peru. Syntype ♂ ZMHU (examined). Syn.n.

Diagnosis. Typical forewing length: male 23 mm, female 26 mm. *Juditha odites* is the most basal species of the

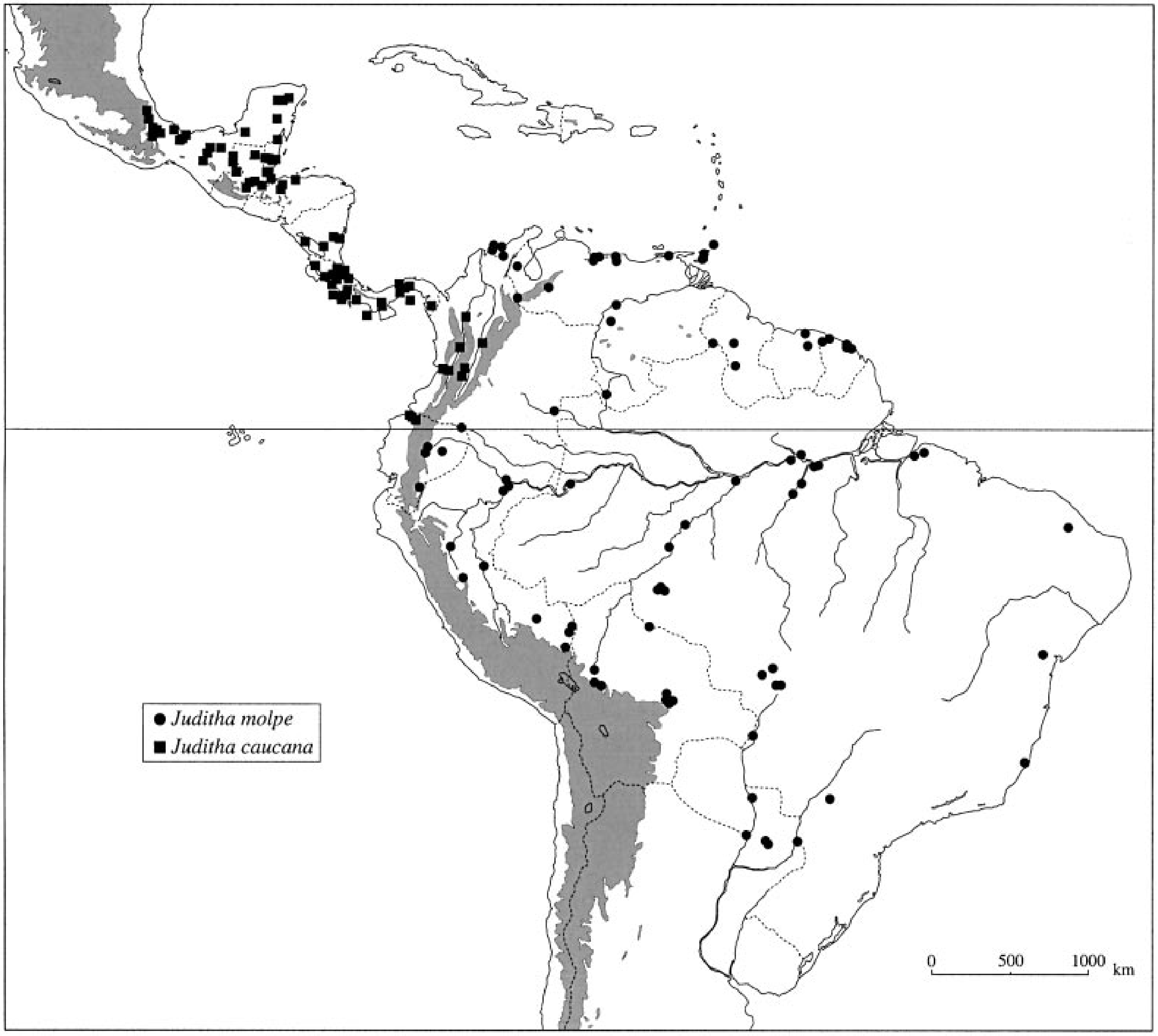

Fig. 16. The geographical distribution of *Juditha molpe* and *J. caucana*.

genus, and males superficially resembles only those of *J. dorilis*. However, they are larger (FW length 23 mm instead of 20 mm), have a more pointed wing shape, more extensive marginal orange and an orange forewing band that is distally displaced at vein Cu1. The valvae of the male genitalia (Fig. 7A) have a strongly sclerotized 'V'-shaped tip and are quite unlike those of any other species in the genus, as is the last abdominal sternite, which is a simple rectangle with only a variable small medial indentation posteriorly (Fig. 9A). The patch of long setae between the base of the valvae and the pedicel is also located in an ill-defined region instead of being positioned on a discrete raised pad. Female *J. odites* superficially resembles female *J. dorilis*, *J. pulcherrima* and *J. inambari*, but is significantly larger than all three (FW length 26 mm instead of 16.5–20 mm), has a more prominently discontinuous postdiscal forewing band, a postdiscal hindwing band that is broader medially than in *J. dorilis*, but less so than in *J. pulcherrima* and *J. inambari*, and lacks any submarginal orange. The female genitalia of *J. odites* (Fig. 11A) differ from those of all other *Juditha* by having a smooth instead of serrate inner edge to the signa.

Taxonomy. Cramer (1775) described the conspecific taxa *odites*, based on a female, and *phylleus*, based on a male, on Figs 11 and 63, respectively, of the same work, and, as determined under the plenary powers of the International Commission of Zoological Nomenclature (ICZN, 1958), during the same year. As the name *odites* clearly has page priority, a criterion which usage is recommended in the fourth edition of the ICZN (1999) in determining the nomenclatural priority of names published in the same work during the same year, we give *odites* priority over *phylleus*. It is not clear why

Table 2. The distribution of all *Juditha* species by country. Solid circles represent known records and question marks represent expected records.

Taxon	Mexico	Belize	Guatemala	El Salvador	Honduras	Nicaragua	Costa Rica	Panama	Venezuela	Colombia	Ecuador	Peru	Bolivia	Argentina	Brazil	Paraguay	Guyana	Surinam	French Guiana	Trinidad
odites						?	●	●	●	●	●	●	?		●		●	●	●	?
pulcherrima										●	●	●	?		?					
inambari															●					
dorilis						●	●	●		●	●									
naza								?		●	●									
azan									●	●	●	●	●	●	●	?	●	●	●	●
molpe									●	●	●	●	●	?	●	●	●	●	●	●
caucana	●	●	●	?	●	●	●	●		●	●									
Total recorded	1	1	1	0	1	2	3	3	3	7	7	4	2	1	4	1	3	3	3	2
Total expected	1	1	1	1	1	3	3	4	3	7	7	4	4	2	5	2	3	3	3	3

previous authors did not recognize the two taxa as conspecific given the accurate illustrations in Cramer (1775), particularly Stichel (1911, 1930–31), who even listed *odites* as 'spec. non agnosc.'.

Although *J. odites* (as *phylleus*) was historically often treated in *Nymphidium (*e.g. Westwood, 1850–52; Bates, 1868; Staudinger, 1884–88; Seitz, 1916–20) and *Nymula* (e.g. Stichel, 1911, 1930–31; Lewis, 1973), it has universally been treated in *Synargis* in recent years (e.g. Bridges, 1994; d'Abrera, 1994; DeVries, 1997). However, the genital morphology of *J. odites* is quite unlike that of members of that genus, and the presence of long setae between the base of the valvae and the pedicel in the male genitalia place it and all its affiliated taxa in *Juditha*.

The names *oditis*, *phyllea* and *phylacis* have long been recognized as unnecessary emendations or replacements for *oditis* and *phylleus*, respectively. The taxon *apame* was described as a full species and subsequently downgraded to the status of subspecies by Stichel (1911). The male syntype has a constricted postdiscal forewing band medially compared to typical Guianan specimens, but the width of this section of the band, although frequently narrow, is variable throughout the Amazon basin and we synonymize *apame* with *odites*. The male syntypes of the taxa *laodamia* and *orontes* have less prominently discontinuous postdiscal forewing bands (this is also narrower medially in *laodamia*) and variably heavy orange scaling between the postdiscal band and submarginal orange of the dorsal hindwing. Since both of these characters vary substantially geographically, and all degrees of intermediates exist, we synonymize both of these names with *odites*. The female holotype of *magnifica* has a completely discontinuous postdiscal forewing band compared with the syntype of *odites*, but this character is as variable in females as it is in males, and we also synonymize *magnifica* with *odites*. In short, although both sexes of *J. odites* exhibit significant geographical variation, no discrete subspecies are recognizable within Amazonia.

Biology. In Ecuador, males of this uncommon species were encountered perching alone or more often in groups of up to four individuals along forest edges and on ridgetops and hilltops from 13.00 to 15.00 hours, and between 4 and 8 m above the ground. They typically rested on the tops of leaves with their wings outspread. In French Guiana, Brévignon & Gallard (1998) reported finding males perching in open forest edge microhabitats and on hilltops at 10.00 hours and again between 14.00 and 16.00 hours from 3 to 4 m above the ground.

Distribution. *Juditha odites odites* is known from throughout the Guianas and Amazon basin, from Venezuela to Peru and Brazil, although it is also surely present in Bolivia (Fig. 13). Additional literature records inlude Putumayo, Colombia (Salazar, 1995; as *Synargis phylleus*); Mato Grosso, Brazil (Brown, 1987, as *Synargis phylleus laodamia*); and Cacao, Matoury and Galion (*Cayenne*), French Guiana (Brévignon & Gallard, 1998; as *Synargis phylleus*).

Specimens examined. 20♂, 14♀. VENEZUELA: *Bolívar*, Suapure, 1♀, CMNH. ECUADOR: *Sucumbíos*, Cerro Lumbaquí Norte, 3♂, JHKW (1♂ dissected); *Napo*, 4 km W Misahuallí, 1♂, GWB; *Pastaza*, km 30 Puyo-Canelos Rd, 1♂, JHKW; *Morona-Santiago*, Bomboiza, 1♀, JHKW. PERU: *Loreto*, Arcadia, 1♀, USNM (DH# 2000–162); Río Sucusari, Explornapo-ACEER, 1♀, AME; *Madre de Dios*, Reserva Tambopata, 30 km SW Puerto Maldonado, 1♂, USNM; no specific locality, 1♂, ZMHU. BRAZIL: *Amazonas*, Tefé, 1♂, AME; Maués, 1♂, AME; *Pará*, Rio Arapiuns, 2♀, AME; Óbidos, 2♂, 2♀, AME; *Mato Grosso*, Colegio Buriti, Chapada dos Guimarães, 2♀, USNM (JH# SI–145); no specific locality, 1♂, ZMHU. GUYANA: *East Berbice-Corentyne*, Camp Jaguar, New River Triangle, 1♀, AME; no locality data, 1♂, 1♀, USNM (M: DH# 2000–86). SURINAM: no locality data, 1♀, RNH. FRENCH GUIANA: *Saint Laurent du Maroni*, Arouany, 1♀, ZMHU; *Cayenne*, Galion, 6♂, USNM; Route de L'est, 1♂, USNM.

Juditha odites praeclarum **(Bates, 1866), comb.n.**

(Figs 2C,D; 113)

Nymula praeclarum Bates, 1866: 156. Type locality: Lion Hill, Panama. Syntype ♀ BMNH (examined).

Diagnosis. This taxon was described as a full species, but first correctly treated as a subspecies (of *phylleus*) by Seitz (1916–20). The male of *J. odites praeclarum* differs from the nominotypical subspecies only by having a slightly broader upper portion to the postdiscal orange forewing band. The female also has a broader postdiscal forewing band, with the elements in cells Cu2 and Cu1 overlapping to a greater extent than occurs in nominate females, a postdiscal hindwing band that coalesces over a broader region with the submarginal line in the apex, and a hindwing submarginal line that thickens towards the tornus. Females vary from yellow to pale cream. There are no male or female genitalia differences between the two subspecies. Although this taxon has frequently been referred to under the emended name *praeclara* (e.g. Stichel, 1911, 1930–31; d'Abrera, 1994; DeVries, 1997), we prefer to use the original spelling.

Biology. The behaviour and preferred microhabitats of this taxon are the same as those of the nominotypical subspecies. Small (*in* DeVries, 1997) reported males perching between 10.30 and 11.00 hours in Panama, whereas in Ecuador males were encountered perching from late morning until mid-afternoon. DeVries (1997) reported that both sexes visit the flowers of *Lantana* and *Croton*, and that males drink at the extrafloral nectaries of *Croton* and *Inga*.

In Panama, DeVries (1997) observed females ovipositing eggs singly or in pairs between 11.30 and 12.30 hours in bright sunshine on flower buds or young shoots of plants in families Bombacaceae, Moraceae and Olacaceae that were infested with membracid homopteran nymphs tended by *Dolichoderus bispinosus* ants (Dolichoderinae) (see Appendix 4), suggesting that the larvae may be carnivorous. DeVries (1997) illustrated SEMs of the egg and first-instar larva of *J. odites praeclarum* (as *Synargis phylleus praeclara*) and provided the following descriptions: '*Egg* – white, round, broadest at base, slightly depressed on dorsum, and entirely covered with a fine net of knobbed sculpturing; micropyle deeply recessed and surrounded by a distinct, erect nipple-like ring.', '*First instar* – whitish green, the prothoracic shield is well developed and bears six long setae that project over the head; anal plate well developed with long prominent setae projecting along perimeter of anal plate; the subdorsal and lateral setae are prominent and highly unusual by being short, flattened triangles – a condition thus far unknown in other riodinid caterpillars.

Distribution. Juditha odites praeclarum is known from Costa Rica to northwestern Ecuador (Fig. 13). Additional literature records include Llorona, Sirena and Rincon (*Puntarenas*), Costa Rica (DeVries, 1997; as *Synargis phylleus praeclara*).

Specimens examined. 10♂, 34♀. COSTA RICA: *Puntarenas*, Parque Nacional Corcovado, 1♂, USNM (DH# 2000–294), 1♀, FSCA. PANAMA: *Veraguas*, Camp El María, Isla Coiba, 1♀, USNM; Santiago, 1♂, CMNH; *Los Santos*, Río Pedregal, 1♂, USNM; *Colón*, Nuevo Tonosi, 1♀, USNM (JH# SI–144); *Canal Zone*, Lion Hill, 1♀, BMNH; Piña, 2♂, USNM, 12♀, AME, 2♀, FSCA; Gatun, 6♀, USNM, 1♀, AME; Cocoli, 1♀, USNM; Summit, 1♀, USNM; Gamboa, 1♀, USNM, 2♀, AME; *Panamá*, Río Tortí, 1♀, USNM. COLOMBIA: unknown locality data, 2♂, 2♀, MNHN. ECUADOR: *Esmeraldas*, La Punta, km 44 Lita-San Lorenzo Rd, 2♂, JHKW (1♂ dissected); El Durango, km 40 Lita-San Lorenzo Rd, 1♂, JHKW; San Miguel, Río San Miguel, 1♀, JHKW.

Juditha pulcherrima pulcherrima **(Butler, 1867)**

(Figs 2E,F; 14)

Anatole pulcherrima Butler, 1867: 226, Pl. 6, Fig. 27. Type locality: Nauta, Peru. Syntype ♂ BMNH (examined).

= *Echenais pulcherrima felicis* Rebillard, 1958: 197, 199, Pl. 1, Fig. 5. Type locality: upper Putumayo, southern Colombia. Holotype ♀ MNHN (examined). Syn.n.

Diagnosis. Typical forewing length: male 16 mm, female 16.5 mm. The postdiscal white of the dorsal forewing always consists of a broad block in male *J. pulcherrima* that extends to at least vein Cu2, whereas in *J. inambari* it is reduced to a very small triangle that does not extend beyond the middle of cell Cu2. In lateral view, the genitalic valvae of *J. pulcherrima* are slightly shorter and more bluntly tapered distally than in *J. inambari*, and in ventral view they are broadest at their middle and have a broadly triangular tip (Fig. 7B). The projections of the last abdominal sternite are slightly narrower in *J. pulcherrima* than in *J. inambari*, and the teeth are not confined to their tip but extend along half of the inner margin (Fig. 9B). Nominotypical females of *J. pulcherrima* differ from those of *J. inambari* in having slightly broader postdiscal white on both wings, slightly reduced submarginal orange, and orange scaling in the upper half of the dorsal postdiscal forewing band. The genitalia of *J. pulcherrima* (Fig. 11B) differ from those of *J. inambari* in having distinct dorsal and ventral sclerotized portions to the ostium bursae, and two round, laterally positioned, ribbed, sclerotized pads between the ostium bursae and the papillae anales.

Taxonomy. The taxa *pulcherrima*, *comparata* and *felicis* were classified until recently in genus *Calociasma* (Bridges, 1994; Callaghan & Lamas, 2001), but Hall & Harvey (2001) transferred them to *Juditha* because they possessed long setae between the base of the valvae and the pedicel in the male genitalia. The taxon *felicis* was described and illustrated by Rebillard (1958) as a subspecies of *J. pulcherrima*, but this name represents the typical female phenotype for nominotypical *pulcherrima*, and is thus synonymized with it.

Biology. Unknown.

Distribution. *Juditha pulcherrima pulcherrima* is known from southern Colombia to northern Peru (Fig. 14).

Specimens examined. 9♂, 4♀. COLOMBIA: *Putumayo*, Jumbato, 1♂, MNHN; upper Putumayo, 1♀, MNHN. ECUADOR: no locality data, 1♀, ZMHU. PERU: *Loreto*, Balsapuerto, 4♂, MNHN (JH# MN–5); Río Cachiyacu, Iquitos, 1♂, BMNH (JH# BM–26); Iquitos, 1♂, MNHN; Río Nanay, 1♀, MNHN; Nauta, 1♂, BMNH (BMNH# 29843); *San Martín*, km 18 Tarapoto-Yurimaguas Rd (1250 m), 1♀, USNM (dissected); no locality data, 1♂, BMNH.

Juditha pulcherrima comparata (Stichel, 1911)

(Figs 2G,H; 7B; 9B; 11B; 14)

Calociasma pulcherrima comparata Stichel, 1911: 377. Type locality: Madre de Dios, southern Peru. Syntype ♂ (# 4030) and ♀ (# 4031) ZMHU (examined).

Diagnosis. Males of *J. pulcherrima comparata* differ from those of the nominotypical subspecies in having postdiscal white on the dorsal forewing that typically extends to vein Cu1 and occasionally even into cell M3 instead of being confined to below vein Cu2, and reduced black in the apex and tornus of the dorsal hindwing. Females differ in having significantly broader postdiscal white bands on both wings, and an entirely white dorsal forewing band without any orange scaling in the upper half.

Biology. Unknown.

Distribution. *Juditha pulcherrima comparata* is currently known only from southern Peru, but it should also occur in northern Bolivia (Fig. 14).

Specimens examined. 32♂, 8♀. PERU: *Madre de Dios*, Parque Nacional Manu, Pakitza, 31♂, 5♀, USNM (♂: JH# SI–10, 11; DH# 1999–14; ♀: JH# SI–143); no specific locality, 1♂, 1♀, ZMHU; *Cuzco*, Qbda. Quitacalzon, 1♀, USNM (DH# 1999–16); *Puno*, Yahuarmayo, 1♀, BMNH.

Juditha inambari Hall & Harvey, sp.n.

(Figs 2I,J; 7C; 9C; 11C; 14)

Male. Forewing length 16 mm. Forewing costa straight, convex towards apex, distal margin slightly convex. Hindwing rounded. Ground colour of dorsal forewing dark orange-brown; 3 pale orange-brown rings in discal cell, large ones at base and middle of cell, a narrow one toward end of cell, 2 pale orange-brown rings towards base of cell Cu2; postdiscal band consists of a small triangle of white that extends from anal margin to middle of cell Cu2, and a narrow pale orange-brown band that extends from costa to approximately vein M3; pale orange-brown submarginal line faintly encompasses dark orange-brown submarginal spots, most prominent in cell Cu2; fringe brown with faint white scaling in middle of cells Cu2 and M3. Ground colour of dorsal hindwing dark orange-brown; a single pale orange-brown ring at base of discal cell; distal two-thirds of wing white except for small areas in tornus and apex where a pale orange-brown submarginal line visible with small areas of dark orange-brown distally (forming 3 spots in apex, 2 in tornus) and proximally; fringe white except at apex and tornus. Ventral forewing differs from dorsal surface in following ways: ground colour pale brown, basal rings whitish-brown, postdiscal band continuous with anal portion white and costal portion faintly pale orange-white; submarginal pale orange-brown line less prominent with white scaling visible in cells Cu2 and M3. Hindwing differs from dorsal surface in following ways: ground colour pale brown, 7 darker brown spots encircled with dirty white at wing base, one in crotch of humeral vein at costa, 2 in cell Sc + R1, 2 in discal cell, and 2 in cell Cu2; submarginal pale orange-brown line less prominent with white scaling visible, an additional black submarginal spot in cell Cu1. *Head*: Dorsal surface of labial palpi dark brown, ventral surface pale brown; second and third segments long. Eyes bare and brown. Frons dark brown dorsally, pale brown ventrally. Antennal segments black with small patch of white scaling at base, increasingly broad area towards tip devoid of scales along inner ventral margin; tubular clubs black, tips orange. *Body*: Dorsal surface of thorax dark orange-brown, ventral surface whitish-brown; dorsal surface of abdomen dark orange-brown with dirty white scaling on posterior segments, ventral surface dirty white. All legs dirty white. *Genitalia* (Fig. 7C): Uncus rectangular in lateral view, shallowly notched at middle of distal dorsal margin; falces of normal size and shape; vinculum swollen dorsally, saccus short and triangular in ventral view; valvae approximately triangular in lateral view, produced into small medial lobes in ventral view with angular tips; narrow unsclerotized pad sparsely covered with very small spines between base of valvae and pedicel supports a tuft of elongate setae (nearly as long as valvae); aedeagus relatively short and bowed, tapering gradually to pointed tip, opens dorsally and slightly to right, everted vesica contains a roughened pad towards base, consisting of numerous small spines under high magnification; pedicel straplike and angular. Eighth sternite divided into 2 elongate triangular projections with sclerotized edges folded over dorsally and prominent teeth along distal half of inner margin (Fig. 9C).

Female. Differs externally from male in following ways: forewing length 16.5 mm. Both wings slightly more rounded. Dorsal ground colour of both wings pale brown, orange-brown scaling sparse at base of both wings, postdiscal forewing band continuous, entirely white, and broader, particularly in cells Cu1 and M3, postdiscal hindwing band approximately half width of male and particularly broad distal to discal cell; submarginal orange paler and more prominent on both wings, extending to join postdiscal white band towards apex of hindwing; thin line of white scaling defines distal margin of submarginal ocelli, additional white fringe elements in cells M1 and R4+5. Ventral surface differs from dorsal surface in same ways as male except: submarginal white present in cells Cu2 and M3 of both wings, tornal veins distal to postdiscal hindwing band outlined in white. *Head*: Second and third segments of labial palpi longer. *Genitalia* (Fig. 11C): Corpus bursae somewhat elongate, signa rectangular sclerotized invaginations with fine serrations along inner margin; ductus bursae coiled posteriorly and unsclerotized, ostium bursae positioned in an invaginated pouch with a broad sclerotized plate ventrally and only hardened tissue dorsally; 2 discrete regions between ostium bursae and papillae anales, first a centrally positioned, hardened and prominently ribbed pad, then 2 heavily sclerotized and prominently ribbed pads divided medially by unsclerotized tissue.

Type material. *Holotype*, ♂, BRAZIL: *Amazonas*, Manicoré, Rio Madeira, viii.1921 (*Fassl*) (MNHN). *Allotype*, ♀, BRAZIL: 'Amazon' (*ex* Coll. *Neumögen*, Brooklyn Museum) (USNM). *Paratypes*, BRAZIL: *Amazonas*, 1♂, 1♀, Nova Olinda, Rio Purus (*Klages*) (CMNH); 1♂, 'Amazon' (*ex* Coll. *Neumögen*, Brooklyn Museum) (USNM); 1♂, 1♀, Humaitá, Rio Madeira (BMNH); 16♂, 4♀, Manicoré, Rio Madeira, x.1923 (AME).

Etymology. The specific epithet refers to the Inambari region of endemism (e.g. Cracraft, 1985) to which the species appears to be restricted.

Diagnosis. Male *J. inambari* is clearly the sister species to *J. pulcherrima*. They differ relatively little in wing pattern, but *J. inambari* typically has only a small triangle of white at the anal margin of the dorsal forewing instead of a broad block that extends at least to vein Cu2, slightly more elongate postdiscal orange on the dorsal forewing, and enlarged areas of brown at the tornus and apex of the dorsal hindwing and the tornus of the ventral forewing. The projections of the last abdominal male sternite are slightly broader and more inwardly curved than those of *J. pulcherrima* and possess only two teeth at their tip instead of teeth along the distal half of the inner edge (Fig. 9C). In lateral view, the genitalic valvae of *J. inambari* are slightly longer and more gradually tapering distally, and in ventral view they are broadest at a point two-thirds the distance from base to tip and are finely pointed at the tip (Fig. 7C). Females of *J. inambari* most closely resembles those of *J. p. pulcherrima*, but have an entirely white postdiscal forewing band that lacks orange in its upper half. The female genitalia of *J. inambari* differ from those of *J. pulcherrima* in having only a ventral sclerotized portion to the ostium bursae, and two centrally positioned, heavily ribbed, variably sclerotized pads between the ostium bursae and papillae anales, the posteriormost one being divided by a narrow membranous area (Fig. 11C).

Biology. Unknown.

Distribution. Juditha inambari is currently known only from the Purus and Madeira Rivers of southern Amazonian Brazil (Fig. 14).

Specimens examined. 80♂, 21♀. BRAZIL: *Amazonas*, Nova Olinda, Rio Purus, 1♂, 1♀, CMNH; Tabocal, Río Purus, 1♂, BMNH; Humaitá, Rio Madeira, 30♂, 9♀, BMNH; Manicoré, Rio Madeira, 2♂, 2♀, BMNH, 1♂, MNHN (JH# MN-6), 17♂, 4♀, AME (♂: DH# 2000–275; ♀: DH# 4530 and 2000–276); Borba, Rio Madeira, 1♂, MNHN; Ipiranga, 1♂, AME (DH# 2000–279); Lower Rio Madeira, 2♂, BMNH; upper Amazon, 1♂, MNHN; Amazon, 3♂, BMNH, 2♂, MNHN, 1♂, 1♀, USNM (JH# SI–9, 142), 1♂, 1♀, CMNH. No locality data, 10♂, 2♀, BMNH, 2♂, 1♀, MNHN, 1♂, USNM, 1♀, CMNH. Mislabelled: Southern Brazil, 1♂, BMNH.

Juditha dorilis **(Bates, 1866)**

(Figs 2K,L; 7D; 9D; 11D; 14)

Nymphidium dorilis Bates, 1866: 156. Type locality: Lion Hill, Panama. Syntype ♂ BMNH (examined).

= *Nymphidium ipsea* Godman & Salvin, 1886: 476; 3: Pl. 45, Figs 17, 18. Type locality: Chontales, Nicaragua. Holotype ♀ BMNH (examined). Syn.n.

= *Nymphidium licinias* Staudinger, [1887]: 261; 2: Pl. 92. Type locality: Río San Juan, western Colombia. Syntype ♂ (2) and ♀ ZMHU (examined). Syn.n.

Diagnosis. Typical forewing length: male 20 mm, female 20 mm. Male *J. dorilis* somewhat resembles *J. odites* superficially, but is typically much smaller, has a continuous orange forewing postdiscal band, and quite different genitalia. Several morphological characters (see cladistic analysis) indicate that *J. dorilis* is the most basal member of a group that includes *J. naza*, *J. azan*, *J molpe* and *J. caucana*, but it is readily distinguished from all four by having orange instead of white postdiscal bands. The male genitalia of *J. dorilis* (Fig. 7D) are most similar to those of *J. naza* and these are the only two species of the five most derived *Juditha* to have symmetrical lower processes to the valvae. Females of *J. dorilis* closely resemble only those of *J. molpe* and *J. caucana*, but have yellow instead of white postdiscal bands, a shorter sclerotized portion to the ductus bursae of the genitalia, a straight instead of indented ventral lip to the ostium bursae and only a weakly ribbed sclerotized region between the ostium bursae and the papillae anales (Fig. 11D).

Taxonomy. The taxon *ipsea* was described from a female as a full species and has always been subsequently regarded as such, except by Seitz (1916–20), who treated it as a subspecies of *azan*, perhaps because of the paucity of material available. However, series of sympatrically collected specimens by G. Small in Panama show that *ipsea* is the female of *J. dorilis*, and we synonymize the former with the latter. In specimens of *J. dorilis* from the Darién of eastern Panama and the Chocó of western Colombia and western Ecuador, the postdiscal forewing orange extends around the discal cell end to actually or nearly reach the costa. This phenotype was described and illustrated as the subspecies *licinias* by Staudinger (1884–88), but as intermediate specimens exist from central-eastern Panama we also synonymize *licinias* with *dorilis*.

Biology. Juditha dorilis is uncommon in wet lowland rainforest habitats from sea-level to 1000 m. In Costa Rica, DeVries (1997) encountered males perching along forest edges and streams from 07.30 to 09.00 hours, whereas in Panama, Small (*in* DeVries, 1997) found males perching between 15.30 and 16.15 hours DeVries (1997) reported observing one female flying low to the ground along the forest edge at 08.15 hours and another repeatedly oviposit on the stipules of a mature *Ochroma lagapus* tree (Bombacaceae) that was infested with membracid homopterans being tended by

Dolichoderus validus ants (Dolichoderinae) between 10.15 and 10.30 hours (see also Appendix 4). Apparently the ants did not molest the female, but antennated her body before moving away. Although this oviposition report is similar to that for *J. odites*, the adults of *J. dorilis* do not exhibit greasiness of the wings, suggesting that the larvae may not be carnivorous. DeVries (1997) provided a scanning electron micrograph of the egg of *J. dorilis* and the following description: '*Egg* – a slightly compressed pale yellow sphere with a netlike sculpturing consisting of elongate rectangles that cover the egg except on the flattened dorsum; except for the dorsum, the entire egg is honeycombed with tiny pores; the micropyle consists of punctures that compose a circle whose diameter is about one-quarter the width of the egg. The egg is unusual for a riodinid in that it has clearly demarcated plastrons [*sic*]'.

Distribution. *Juditha dorilis* is known from Nicaragua to western Ecuador (Fig. 14). Additional literature records include Chilamate (*Heredia*), Guapiles (*Limón*), Turrialba, Tuis (*Cartago*) and La Vacita (*Puntarenas*), Costa Rica (DeVries, 1997).

Specimens examined. 15♂, 15♀. NICARAGUA: *Chontales*, no specific locality, 1♀, BMNH; *Zelaya*, Bluefields, 1♂, AME. COSTA RICA: *Heredia*, 3 km. SW of Puerto Viejo, 1♀, USNM; *Limón*, Limón, 1♀, USNM. PANAMA: *Canal Zone*, Colón, 3♀, USNM (DH# 1999–17); Piña, 1♂, 1♀, AME, 1♂, FSCA; Gamboa, 1♂, AME; Lion Hill, 1♂, BMNH; Gatun, 1♂, 1♀, USNM; *Panamá*, Cordillera de San Blas, N of El Llano, 3♂, 1♀, USNM (♂: DH# 1999–12); Coclé, nr El Copé, 1♂, USNM; Cerro Campana, 1♂, USNM; *Darién*, Caña, 1♂, 2♀, USNM (♂: DH# 1999–11; ♀: 2000–158); Cerro Pirre, 1♀, USNM; no locality data, 1♀, FSCA. COLOMBIA: *Chocó*, Río San Juan, 1♂, BMNH, 2♂, 1♀, ZMHU. ECUADOR: *Esmeraldas*, Estación Experimental La Chiquita, 1♀, JHKW.

Juditha naza **Hall & Harvey, sp.n.**

(Figs 2M,N; 7E; 9E; 11E; 15)

Male. Forewing length HT 21 mm; PTs 27 mm. Forewing costa straight, convex towards apex, distal margin approximately straight. Hindwing slightly pointed at apex and tornus with approximately straight distal margin. Ground colour of dorsal forewing brown; 3 blue-white rings in discal cell, one at middle, one toward end and one over end, 2 blue-white rings toward base of cell Cu2; a gradually narrowing white postdiscal band extends from costa into lower half of cell M2 (extends throughout cell M2 in PTs), distal margin of white in cell Cu2 concave; a single marginal blue-white ocellus present in cells Cu1 to R4+5, those toward apex larger, 2 in cell Cu2 with dark orange-brown scaling proximally extending to anal margin; fringe brown with faint white scaling in middle of cells Cu2 and M3. Ground colour of dorsal hindwing brown; a single dark brown spot at base of discal cell; a broad white postdiscal band of approximately even width and with an uneven distal margin extends diagonally from costa to anal margin; marginal blue-white ocelli present in cells 2A, 2 in cell Cu2, one in remainder, those in cells M2 and M1 partially coalesced to R4+5, those in cells M3 and R4+5 and upper ocellus in cell Cu2 slightly smaller than remainder, proximal orange-brown scaling extends from tornus to vein Cu1; fringe brown with faint white scaling in middle of cell M3 and as a continuous patch in cells M1 and R4+5. Ventral forewing differs from dorsal surface in following ways: ground colour pale brown, basal rings whitish-brown encircling dark brown, postdiscal band continues as a thin whitish-brown line into cell R4+5 then kinks inwards into cell R2, marginal ocelli dirty white with pointed proximal margins encircling dark brown. Hindwing differs from dorsal surface in following ways: ground colour pale brown, dark brown spot at base of discal cell encircled with whitish brown, an additional large dark brown spot encircled with whitish brown visible in cell Rs at proximal margin of white band and another smaller one above and towards base of vein Rs, marginal ocelli dirty white with pointed proximal margins encircling dark brown, orange-brown in tornus absent (present in same position as on dorsal surface in PTs). *Head*: Dorsal surface of labial palpi brown, ventral surface dirty white; second and third segments long. Eyes bare and brown. Frons brown. Antennal segments black with small patch of white scaling at base, broad continuous area of devoid of scales along inner ventral margin; tubular clubs black, tips orange. *Body*: Dorsal surface of thorax brown, ventral surface whitish brown; dorsal surface of abdomen brown with thin line of dirty white scaling along posterior margin of each segment, ventral surface dirty white. All legs pale brown. *Genitalia* (Fig. 7E): Uncus rectangular in lateral view, deeply notched at middle of distal dorsal margin; falces of normal size and shape; vinculum a narrow ribbon, posteriorly bowed medially, saccus short and triangular in ventral view; valvae consist of a narrow, elongate and bluntly pointed upper portion joined dorsally by unsclerotized tissue, and a shorter, blunt lower portion extending from middle of ventral margin of former, broad unsclerotized pad sparsely covered with very small spines between base of valvae and pedicel supports a clump of elongate setae (as long as upper valve process); aedeagus relatively short and evenly somewhat broad, tapering distally to pointed tip, opens dorsally and slightly to right, everted vesica contains a roughened pad towards base, consisting of numerous small spines under high magnification; pedicel straplike. Eighth sternite divided into 2 relatively broad, bluntly pointed projections with very fine teeth along distal third of inner margin (Fig. 9E).

Female. Differs externally from male in following ways: forewing length AT 23 mm. Both wings more elongate with distal margins convex, hindwing rounded. Dorsal ground colour of both wings paler brown creating darker brown marginal spots, postdiscal white band slightly broader on both wings, that on forewing extending into cell M1 and turning inwards, that on hindwing with convex distal margin, tornal orange-brown on both wings only faintly present. Ventral surface of both wings paler and 'washed-out', with basal and marginal markings fainter. *Head*: Second and third segments of labial palpi longer. *Genitalia* (Fig. 11E): Corpus bursae somewhat elongate, signa narrow and pointed, slightly downwardly curved sclerotized invaginations with faint serrations along inner margin, ovoid at base; ductus bursae sclerotized only at extreme posterior end; ostium bursae a sclerotized ring sunken into an unsclerotized invaginated pouch; a small triangular, ribbed, sclerotized region between ostium bursae and papillae anales.

Type material. Holotype, ♂, COLOMBIA: *Antioquia*, Valdivia, 1897 (*Pratt*) (BMNH). *Allotype*, ♀, COLOMBIA: same data as holotype. *Paratypes*, COLOMBIA: 1♀, *Boyacá*, Muzo, 400–800 m (*Fassl*) (MNHN). ECUADOR: 2♂, *Esmeraldas*, Río Cachaví, 1 km W of Alto Tambo, Lita-San Lorenzo Rd, 700 m, 5. ix.1999 (*Willmott*) (JHKW).

Etymology. The species epithet is a euphonious reversal of the name of its close relative, *azan*.

Diagnosis. The cladistic analysis indicates that *J. naza* is phylogenetically intermediate between *J. dorilis* and *J. azan*, although it is externally most similar to the latter species. Males of *J. naza* can externally be distinguished from those of *J. azan* only by the slightly more proximal position of the postdiscal white band on both wings. However, in the male genitalia (Fig. 7E) the vinculum is completely sclerotized dorsally where it is contiguous with the tegumen, the saccus is dorsoventrally broader, the upper portions of the valvae are broader with a convex ventral margin and a blunter tip, and the lower portions of the valvae are broader, also with a blunter tip, and, most diagnostically, short and symmetrical. The bifurcate last abdominal sternite is slightly shorter and both projections are slightly broader (Fig. 9E). The male genitalia are most similar to those of *J. dorilis*.

Females of *J. naza* are difficult to distinguish externally from those of *J. azan majorina*, the most similar of the three subspecies of *J. azan*, but the combination of a narrower postdiscal white forewing band that is angled somewhat inwards at its apex characterizes the few females of *J. naza* examined. The female genitalia of *J. naza* differ from those of *J. azan* in having a corpus bursae with slightly narrower and downwardly curved signa, only a very short section of sclerotization at the posterior end of the ductus bursae, and an ostium bursae that has an approximately straight instead of sharply medially indented ventral lip, and is positioned within an unsclerotized invagination instead of being prominently protruding (Fig. 11E).

Biology. *Juditha naza* is the most poorly represented *Juditha* species in collections, probably because of its restricted west Andean range, where it is known from 400 and 700 m. The two Ecuadorian males were encountered perching in an open streamside area along the forest edge around 13.15 hours, where they perched on top of leaves about 8 m above the ground (15 m above the stream) with their wings spread open.

Distribution. *Juditha naza* is currently known only from the Chocó region of northwestern Ecuador and northern and central Colombia (Fig. 15), but it should also occur in the intervening Chocó of western Colombia, and possibly the Darién of eastern Panama. Those historical Colombian specimens labelled ‘Bogotá’ and ‘Muzo’ (common labelling centres) were probably actually collected west of the central cordillera because a *J. azan* specimen with modern label data was collected in the Muzo area, and given the parapatric distribution of other sister species pairs in the genus, it seems unlikely that *J. naza* and *J. azan* are sympatric. More field work in central Colombia is clearly needed.

Specimens examined. 4♂, 5♀. COLOMBIA: *Antioquia*, Valdivia, 1♂, 1♀, BMNH (JH# BM–A,B); *Boyacá*, Muzo, 1♀, MNHN; *Cundinamarca*, Bogotá, 1♂, 1♀, BMNH, 1♀, MNHN; no locality data, 1♀, MNHN. ECUADOR: *Esmeraldas*, Río Cachaví, 1 km W of Alto Tambo, 2♂, JHKW (1♂ dissected).

Juditha azan azan **(Westwood, [1850])**

(Figs 2O, 3A, 15)

Nymphidium azan Westwood, [1851]. *In* Doubleday, E: 448, Pl. 73, Fig. 5. Type locality: Pará, E. Brazil [*sic*]. Syntype ♀ BMNH (examined).

= *Desmozona azan* var. *australis* C. Felder, 1862: 474. Type locality: Rio de Janeiro, southeastern Brazil. Syntype ♀ BMNH (examined).

Diagnosis. Typical forewing length: male 22 mm, female 23 mm. Males of *J. azan* differ most conspicuously from those of *J. naza* by having a more distally positioned white postdiscal band on both wings, a longer last abdominal sternite with narrower projections (Fig. 9F), narrower and more pointed upper and lower portions to the genitalic valvae, and asymmetrical lower valve portions, with the right projection being approximately half as long again as the left one (Fig. 7F). *Juditha azan* is also externally very similar to *J. molpe* and *J. caucana*, with which it has often been erroneously thought to be conspecific (e.g. Seitz, 1916–20; Stichel, 1911, 1930–31; Bridges, 1994; d’Abrera, 1994), but it may readily be distinguished by its consistently larger size (typical FW length of 22 mm instead of 17 mm), and a number of morphological characters (see the accounts of *J. molpe* and *J. caucana*). Females of *J. azan* are difficult to distinguish from those of *J. naza* based on wing pattern alone (see that species account). However, its genitalia (Fig. 11F) differ in having a corpus bursae with slightly broader and straighter signa, a considerably longer section of sclerotization at the posterior end of the ductus bursae with small lateral bumps at the anterior edge of the sclerotization, and an ostium bursae that is heavily sclerotized, prominently protruding and possesses a sharply medially indented ventral lip, as in *J. molpe* and *J. caucana*.

Both sexes of the nominotypical subspecies are distinguished from those of the remainder by always having broader postdiscal white bands on both wings, with white from cell Cu1 of the forewing band entering into the distal portion of the discal cell (typically present in males, always prominently present in females).

Taxonomy. This species was first described under the name *Papilio lamis* Stoll, 1780, but because this is a junior homonym of *Papilio lamis* Cramer, 1779 (a neotropical nymphalid now placed in *Peria* Kirby), the name *azan* Westwood, [1851] became the oldest available name for the species, and was first utilized in this context by Lamas *et al*. (1991). Although the syntype female of *J. azan* is labelled as originating from Pará in the eastern Brazilian Amazon, the phenotype it represents is actually restricted to southeastern South America. Because the types of both *azan* and *australis* clearly originated from southeastern Brazil, these are treated as synonyms.

Biology. The biology of this subspecies is undoubtedly typical for the species.

Distribution. *Juditha azan azan* ranges throughout the southeastern states of Brazil from Bahía to Rio Grande do Sul and into northeastern Argentina, although it should also occur in southern Paraguay (Fig. 15). Given the lack of specimens available for examination from the area between the lower Amazon and coastal southeastern Brazil, the northernmost limit of this subspecies is currently unclear. A female from Conceição on the upper Rio Tapajós in northern Mato Grosso is somewhat intermediate between *J. azan majorina* and *J. azan azan*, and females from western Mato Grosso and Rondônia are somewhat intermediate between *J. azan completa* and *J. azan azan*. Additional literature records include Fercal (*Distrito Federal*), Brazil (Brown & Mielke, 1967; as *J. lamis lamis*); and Misiones, Argentina (Hayward, 1973; as *Peplia lamis azan*).

Specimens examined. 77♂, 77♀. BRAZIL: *Bahía,* no specific locality, 2♀, BMNH, 1♀, MNHN; *Espírito Santo*, Linhares, 1♂, 1♀, AME (♂: DH# 2000–280; ♀: 2000–288); no specific locality, 3♂, 10♀, BMNH; *Minas Gerais*, San Jacintho Valley, Teófilo Ottoni, 1♀, BMNH; no specific locality, 1♂, BMNH; *Rio de Janeiro*, Rio de Janeiro, 16♂, 13♀, BMNH; 4♂, 6♀, MNHN, 2♂, USNM; Niterói, 1♀, MNHN; Petrópolis, 1♀, USNM; Restinga Jacarepagua, 2♂, 1♀, AME (♂: DH# 2000–282; ♀: 2000–289); Lagoa de Sacuaresma, 2♂, 1♀, BMNH; Paineiras, 1♂, BMNH; Corcovado, 1♂, 1♀, BMNH; Gavea, 1♂, 2♀, BMNH; Imbarie, 2♂, USNM; Tijuca, 3♂, 1♀, USNM (♂: DH# 1996–26; ♀: JH# SI–146); *São Paulo*, São Paulo, 2♀, BMNH; *Paraná*, Castro 6♂, 4♀, BMNH; *Santa Catarina*, Blumenau, 1♂, MNHN; no specific locality, 4♂, 2♀, BMNH; 2♂ MNHN, 1♂, 1♀, USNM, 1♂, CMNH; *Rio Grande do Sul*, no specific locality, 1♂, 1♀, MNHN; no locality data, 3♂, 4♀, BMNH, 6♂, 4♀, MNHN, 1♀, CMNH. No locality data, 10♂, 10♀, BMNH, 3♂, 4♀ MNHN, 1♀ CMNH. Mislabelled: Pará, Brazil, 1♀, BMNH.

Juditha azan majorina **Brévignon & Gallard, 1998**

(Figs 3B,C; 7F; 9F; 11F; 15)

Juditha majorina Brévignon & Gallard, 1998: 492. Replacement name for *lamis* Stoll, 1780.

= *Papilio lamis* Stoll, 1780. *In* Cramer, P.: 88, Pl. 335, Figs F,G. Type locality: Surinam. Syntype ♂(s) unknown. This names preoccupied by *lamis* Cramer, 1779.

Diagnosis. Brévignon & Gallard (1998) provided the replacement name *majorina* for *lamis*, which although unnecessary at the species level (their intention) given the availability of the name *azan*, provided a name for the widespread Guianan and Amazonian subspecies. The male of this subspecies does not differ from *J. azan completa* but differs from the nominotypical subspecies in having narrower white postdiscal bands on both wings. The female of this subspecies always has a white postdiscal forewing band that extends from the anal margin to the discal cell end and never to the costa. The female of this subspecies superficially resembles that of *Synargis palaeste* (Hewitson), which was erroneously classified as a distinct species of *Juditha* until recently (d'Abrera, 1994; DeVries, 1997; Hall, 2000) (see *History of classification* above). Females of *S. palaeste* differ externally in having two parallel submarginal rows of cream or yellow spots on both wings, with a thin red, isolated postmedial band proximally.

Biology. Brévignon & Gallard (1998) reported that in French Guiana males perch along the border of degraded habitats during the early afternoon from 2 to 4 m above the ground. They rest on the very tips of leaves with their wings spread open and chase passing conspecific or similar looking individuals.

Distribution. *Juditha azan majorina* is widely distributed throughout the Guianas and the eastern and central Amazon basin, as far south as Mato Grosso, and as far north as central Venezuela (Fig. 15). Additional literature records include Fondes Amandes and St Annes, Trinidad (Barcant, 1970; as *Peplia lamis*); and Ilha de Maracá (*Roraima*) (Mielke & Casagrande, [1992], as *J. azan lamiola* [n. n.]), 80 km N Manaus (*Amazonas*) (Hutchings, 1991; as *J. azan lamiola* [n. n.]) and Mato Grosso (north and central) (Brown, 1986; as *J. azan*), Brazil.

Specimens examined. 87♂, 96♀. VENEZUELA: *Bolívar*, Suapure, 1♀, CMNH; *Amazonas*, Yavita, 2♀, AME; Samariapo, 1♀, AME. BRAZIL: *Amazonas*, Tonantins, 1♀, CMNH; Tefé, 4♂, 1♀, BMNH, 2♀, MNHN, 1♀, CMNH, 1♂, 3♀, AME (DH# 2000–286); Humaitá, 4♂, 1♀, BMNH; Manicoré, 1♂, MNHN; Maués, 1♂, 1♀, BMNH, 1♂, MNHN; Ipiranga, 2♂, MNHN, 13♂, 4♀, AME; Manacaparú, 2♂, CMNH; upper Amazon, 1♀, MNHN; *Mato Grosso*, Cuiabá, 2♂, 3♀, BMNH; Conceição, Rio Tapajós (intergrade), 1♀, MNHN; *Pará*, Rio Tapajós, 1♂, BMNH; Óbidos, 1♂, BMNH, 2♂, MNHN, 1♀, USNM, 4♂, 3♀, AME (DH# 2000–287); Rio Curuçamba, 1♂, 1♀, AME; Taperinha, 1♂, AME; Santarém, 1♂, 1♀, BMNH; Pará, 9♂, 11♀, BMNH, 1♀, USNM; Benevides, 1♀, CMNH; Igarapé-Açu, 1♀, BMNH; *Maranhão*, Montes Aureos, 1♂, 1♀, BMNH; São Luís, 1♀, AME; ? Amazon, 2♂, 1♀, BMNH; no locality data, 1♀, BMNH. GUYANA: *Cuyuni-Mazaruni*, Kartabo, 1♀, USNM; Bartica, 1♀, USNM, 1♀, AME; *Potaro-Siparuni*, Potaro River, 4♀, AME; *Upper Demerara-Berbice*, Demerara River, 4♂, 3♀, BMNH; Mabura, 1♀, USNM; *Upper Takutu-Upper Essequibo*, Takutu Mountains, 1♀, USNM; Kanuku Mountains, Nappi Creek, 1♂, USNM (DH# 2000–90); *East Berbice-Corentyne*, Camp Jaguar, New River Triangle, 1♀, AME; no locality data, 4♂, 5♀, BMNH. SURINAM: *Paramaribo*, Paramaribo, 1♀, BMNH; *Saramacca*, Saramacca, 1♀, BMNH; no locality data, 4♂, 4♀, BMNH, 1♂, 1♀, CMNH. FRENCH GUIANA: *Saint Laurent du Maroni*, Saint Laurent du Maroni, 1♂, 4♀, BMNH, 3♂, 2♀, MNHN; Nouveau Chantier, 1♀, MNHN; *Cayenne*, Cayenne, 2♂, 3♀, BMNH, 1♀, USNM; Montsinéry, 1♀, MNHN, 1♂, USNM; Goudronville, Rivière Kourou, 1♂, 2♀, BMNH; mouth of Rivière Kourou, 2♀, BMNH; Cacao, 1♂, USNM (DH# 1996–25); Rte de L'est, 1♀, USNM; Montagnes des Singes, 1♀, USNM (DH# 1999–18); Saül, 1♀, USNM; Pied Saut, Rivière Oyapock, 1♂, CMNH; no locality data, 1♂, BMNH, 3♂, 1♀, MNHN. TRINIDAD: Tabaquite, 1♀, BMNH; Maraval, 1♂, BMNH; no locality data, 1♂, 1♀, BMNH, 1♀, AME. No locality data, 1♂, BMNH, 1♀, MNHN. Mislabelled: Chiriquí, Panama, 1♂, USNM.

Juditha azan completa (Lathy, 1904)

(Figs 3D,F; 10A–E; 15)

Nymphidium completa Lathy, 1904: 467, Pl. 27, Fig. 9. Type locality: La Merced, Peru. Syntype ♀ (2) BMNH (examined).

Diagnosis. The male of this subspecies does not differ from those of *J. azan majorina* but differs from those of the nominotypical subspecies in having narrower white postdiscal bands on both wings. The female of this subspecies is dimorphic, the first report of this phenomenon in Riodinidae. One of the morphs (approximately one in four specimens) is identical to the female of *J. azan majorina*, but the other predominant morph has a white postdiscal forewing band that extends from the anal margin all the way to the costa. This latter morph differs from the female of *J. azan azan* in having narrower white bands without white intruding into the discal cell, although certain specimens from Rondônia, Brazil, possess this last character (see below).

Biology. This species is common in Ecuador, where males perch alone or in small groups during the early afternoon along forest edges or in large forest lightgaps, along streams and on hilltops, 2–5 m above the ground.

Distribution. *Juditha azan completa* is distributed throughout the western Amazon from Colombia to Bolivia and into western Brazil (Fig. 15). Females from Rondônia are somewhat intermediate to the nominotypical subspecies, but the white bands are not as broad, especially at the base of the forewing.

Specimens examined. 41♂, 52♀. COLOMBIA: *Boyacá*, Muzo, 1♂, AME (DH# 4509); *Meta*, Río Negro, 1♀, MNHN, 1♀, USNM; *Putumayo*, San Antonio, 1♂, BMNH; Puerto Umbria, 1♂, MNHN; upper Putumayo, 4♂, 1♀, MNHN; *Amazonas*, Leticia, 1♀, AME. ECUADOR: *Napo*, Satzayacu, 1♂, JHKW; Apuya, 1♂, JHKW; Finca San Carlo, 3♀, JHKW; Limoncocha, 1♂, USNM (DH# 1999–13); *Morona-Santiago*, Bomboiza, 1♀, JHKW; no locality data, 1♂, 5♀, BMNH. PERU: *Loreto*, Río Aguas Negras, 1♀, USNM (JH# SI–147); Río Sucusari, Explornapo-ACEER, 2♂, 2♀, USNM (♂: DH# 1996–24); Balsapuerto, 1♀, BMNH; St Roque, Iquitos, 1♀, MNHN; 1♀, AME; Iquitos, 1♂, BMNH, 7♂, 4♀, MNHN; *Ucayali*, Pucallpa, 1♂, AME; *San Martín*, Chazuta, 1♂, 2♀, MNHN; Juanjui, 5♂, 8♀, MNHN; *Huánuco*, Tingo Maria, 1♂, USNM; upper Río Huallaga, 1♀, AME; *Pasco*, Río Chucharras, Río Palcazu, 1♀, BMNH; *Junín*, La Merced, 4♀, BMNH; Chanchamayo, 1♀, BMNH, 4♂, MNHN; *Madre de Dios*, Parque Nacional Manu, Pakitza, 6♂, 5♀, USNM; Reserva Tambopata, 1♂, USNM; 30 km SW Puerto Maldonado, 1♂, USNM (DH# 1996–23); 50 km WSW Puerto Maldonado, 2♀, USNM; *Cuzco*, Río Tono, 1♀, MNHN; no locality data, 1♀, BMNH. BOLIVIA: *La Paz*, Mapiri, 1♂, BMNH (JH# BM–C); *Cochabamba*, Cochabamba, 1♀, BMNH; *Santa Cruz*, Provincia Sara, 1♀, BMNH; ? Mishagoa, 1♂, MNHN. BRAZIL: *Amazonas*, São Paulo de Olivença, 2♂, BMNH; *Rondônia*, vicinity of Cacaulândia, 1♂, 1♀, USNM.

Juditha molpe (Hübner, [1808])

(Figs 3G,H; 8A; 9G; 11G; 16)

Limnas molpe Hübner, [1808]: Pl. 31. Type locality: no locality. Syntype ♂(s) and ♀(s) unknown.

= *Peplia lamis bahiana* Stichel, 1929: 23. Type locality: Bahía, eastern Brazil. Syntype ♂ (2) ZMHU (examined). Syn.n.

Diagnosis. Typical forewing length: male 17 mm, female 16.5 mm. *Juditha molpe* cannot be distinguished from *J. caucana* on the basis of wing pattern, but the two species have distinctive genitalia. The male genitalia of *J. molpe* differ by having a more bulbous base to the upper valve processes and markedly asymmetrical lower valve processes with the left portion being considerably shorter than the upper processes and the right one considerably longer (Fig. 8A,B). The eighth abdominal sternite of *J. molpe* is also typically longer, with slightly narrower and straighter projections. In the female genitalia of *J. molpe*, the sclerotized portion of the ductus bursae broadens sharply and briefly anteriorly and lacks the raised medial bumps of *J. caucana* (Fig. 11G).

Juditha molpe is geographically variable in the width of the postdiscal white bands, with all degrees of intermediates existing between the extremes. A phenotype with particularly broad bands was described as subspecies *bahiana*, which we synonymize with *J. molpe*. Females from northern Venezuela have particularly broad bands, with white that enters the forewing discal cell.

Biology. This species is common throughout its range and occurs from sea level to 1000 m. In Ecuador, males typically perch in small groups during the afternoon until 17.30 hours along forest edges and streamsides, especially in secondary growth areas. They perch on the tips of leaves with their wings half or fully open and make rapid sorties to investigate passing butterflies of a similar phenotype. Females are somewhat less frequently encountered in the same habitats, flying slowly and low to the ground throughout much of the day.

Guppy (1904) reared *J. molpe* on an unidentified species of *Cassia* (Leguminosae) in Trinidad (Appendix 4) and provided the following description of the early stages: '*Larva*. Head small and hairy. Abdomen flat slug-shaped very similar in shape and habits to the two preceding *Theope* species [*eudocia* and *foliorum*]. A pair of horn-like protuberances take the place of the club-like ones in the foregoing. Before pupating the body turns brownish. The anal segment is similar to the *Theope* larvae and there are large ants that attend and milk the larvae. These ants are solitary, are armed with a powerful pair of jaws, and when I went to remove them from the backs of the larvae, they snapped violently at the piece of wood I was holding. A pair of larvae are generally found on each plant and are to be obtained chiefly on the low-growing *Cassia* plants, chiefly through the dry season, though some are to be found at all times. *Pupa*. Very much like a piece of wood.'. Unfortunately this description is not detailed enough to ascertain whether there are any morphological differences between the early stages of *J. molpe* and its sister species *J. caucana*.

Distribution. *Juditha molpe* has heretofore been regarded as a pan-Neotropical species (e.g. Callaghan, 1982), but is actually restricted to South America, ranging from northern Colombia to southern Paraguay and Brazil (Fig. 16). It occurs entirely east of the Andes except in northeastern Colombia, where its range extends to the Sierra Nevada de Santa Marta. The boundary between the parapatric sister species *J. molpe* and *J. caucana* apparently occurs immediately to the south and west. Additional literature records include St Joseph Estate and Mayaro, Trinidad (Barcant, 1970; as *Nymphidium molpe*); and Mato Grosso (north, central and south), Brazil (Brown, 1987, as *J. molpe molpe*).

Specimens examined. 281♂, 133♀. VENEZUELA: *Zúlia*, no specific locality, 1♀, AME; *Barinas*, Barinitas, 1♀, AME; *Carabobo*, Valencia, 1♀, MNHN; Las Quiguas, 1♀, BMNH; San Esteban, 4♂, 3♀, BMNH (♂: DH# 2000–86), 1♀, CMNH; Puerto Cabello, 1♀, BMNH; *Aragua*, Rancho Grande, 2♀, USNM (DH# 2000–168); *Distrito Federal*, Puerto la Cruz, 2♂, 1♀, CMNH; *Miranda*, Ocumare del Tuy, 1♀, USNM; *Sucre*, Cariaquito, 1♀, CMNH; *Bolívar*, Caicara, 2♂, 1♀, BMNH (DH# 2000–89); Suapure, 1♀, BMNH, 2♂, CMNH; *Amazonas*, San Carlos, 4♂, USNM (DH# 1999–5); Mawari-Anejidi, 1♀, AME; no locality data, 1♂, BMNH. COLOMBIA: *Magdalena*, Atánquez, 3♂, 1♀, BMNH (♂: JH# BM–5); Onaca, Sta. Marta, 2♂, BMNH; Finca Union, Río Guachaca, 3♂, BMNH (JH# BM–4); Río Don Diego, 1♀, BMNH; Cacagualito, 1♂, CMNH; Don Amo, 1♀, CMNH; *Norte de Santander*, Cúcuta, 1♂, 1♀, BMNH; 1♂ MNHN (JH# MN–1); *Vaupés*, Mitú, 1♂, AME; *Putumayo*, Jumbato, 2♂, MNHN; San Antonio, 1♂, BMNH; upper Putumayo, 3♂, 1♀, MNHN. ECUADOR: *Napo*, Pimpilala, 1♂, JHKW; Apuya, 1♂, JHKW; Tiguino, 1♀, JHKW; *Pastaza*, Puyo, 1♂, BMNH; *Morona-Santiago*, Bomboiza, 1♂, 1♀, JHKW (1♂ dissected). PERU: *Loreto*, Río Sucusari, Explornapo-ACEER, 6♂, USNM; 1♂, AME; Iquitos, 1♂, 1♀, MNHN, 1♀, FSCA; Explorama Lodge, nr Iquitos, 1♀, FSCA; Río Ucayali, 1♀, BMNH; *Ucayali*, Pucallpa, 1♂, AME; *San Martín*, Juanjui, 6♂, 3♀, MNHN; *Huánuco*, Tingo Maria, 1♀, AME; *Madre de Dios*, Parque Nacional Manu, Pakitza, 13♂, 2♀, USNM; Reserva Tambopata, 1♀, USNM; 0–3 km SW Puerto Maldonado, 1♀, AME; 10 km N Puerto Maldonado, 1♂, 3♀, USNM (♂: DH# 1999–8; ♀: 2000–169); 30 km SW Puerto Maldonado, 2♂, USNM; 50 km WSW Puerto Maldonado, 2♀, USNM; no specific locality, 1♀, MNHN; *Puno*, La Union, Río Huacamayo and Río Carabaya, 1♀, BMNH; no locality data, 2♂, USNM. BOLIVIA: *La Paz*, Coroico, 1♀, BMNH; Muchanes, 1♀, BMNH; Chulumani, 1♀, BMNH; *Santa Cruz*, Provincia Sara, 1♀, BMNH; Buena Vista, 1♂, MNHN, 1♀, CMNH; Santa Cruz de la Sierra, 1♀, CMNH; Río Yapacani, 1♀, CMNH; Cuatro Ojos, 12♂, 6♀, CMNH; Las Juntas, 5♂, 4♀, CMNH; Portachuelo, Río Palmatiles, 1♂, 2♀, CMNH; no locality data, 1♂, USNM. BRAZIL: *Amazonas*, São Paulo de Olivença, 1♂, BMNH; upper Mamoré, 1♂, 1♀, CMNH; Humaitá, 5♂, 1♀, BMNH; Manicoré, 3♂, AME; Ipiranga, 1♂, MNHN, 1♂, AME; upper Amazon, 2♂, 1♀, MNHN; *Rondônia*, vicinity of Cacaulândia, 6♂, 2♀, USNM (♀: DH# 2000–170), 3♂, AME, 2♂, FSCA; Ariquemes, 2♂, USNM; Jaru, 1♀, USNM; *Mato Grosso*, Cuiabá, 5♂, 1♀, BMNH; Alto Rio Arinos, nr Diamantino, 15♂, 5♀, USNM (♂: JH# SI–16, 17; ♀: DH# 2000–159); Baro do Bugres, 2♂, USNM; Buriti, 1♂, USNM; no specific locality, 1♀, USNM; *Mato Grosso do Sul*, Urucum, 15 mi. S Corumba, 1♀, BMNH; *Pará*, Itaituba to Óbidos, 3♂, BMNH; Óbidos, 1♀, BMNH; Rio Cury, Rio Tapajós, 2♂, BMNH; Rio Tapajós, 1♀, BMNH; Juruti, 1♂, 1♀, BMNH; Taperinha, 1♂, AME; Santarém, 1♀, BMNH, 2♂, 1♀, MNHN; Pará, 11♂, 2♀, BMNH, 1♂, CMNH; Igarapé-Açu, 1♂, BMNH; *Ceará*, no specific locality, 4♂, BMNH (JH# BM–D); *Bahía*, no specific locality, 2♂, ZMHU; *Espírito Santo*, Linhares, 4♂, 2♀, AME (DH# 2000–264); *São Paulo*, 10–20 km W Teodoro Sampaio, 1♂, USNM (DH# 1999–9); *Paraná*, Iguaçu, 1♂, 1♀, BMNH; ? Amazon, 2♂, BMNH; no locality data, 1♂, CMNH. PARAGUAY: *Concepción*, Estancia Cooper, Alto Paraguay, 2♀, BMNH; *Central*, Asunción, 1♂, BMNH; Patiño Cué, 2♂, 2♀, BMNH, 3♂, 1♀, MNHN; *Guairá*, Villarica, 6♂, MNHN; Serro Pelado, nr Villarica, 1♂, MNHN; *Caazapá*, Abai, 1♂, MNHN; ? S Paraguay, 6♂, BMNH (JH# BM–E); no locality data, 4♂, BMNH. GUYANA: *Cuyuni-Mazaruni*, Roraima, 1♀, BMNH; Carimang River, 2♂, BMNH (DH# 2000–87); Quonga, 1♂, BMNH; *Upper Takutu-Upper Essequibo*, Annai, Essequibo River, 1♂, BMNH; Essequibo River, 1♂, BMNH; ? Anna River, 1♂, BMNH; no locality data, 4♂, 3♀, BMNH, 2♂ MNHN, 1♂, 1♀, CMNH. SURINAM: *Paramaribo*, Paramaribo, 1♂, BMNH (DH# 2000–88); *Brokopondo*, Berg-en-dal, 1♂, BMNH; no locality data, 9♂, BMNH, 2♂, MNHN. FRENCH GUIANA: *Saint Laurent du Maroni*, Saint Laurent du Maroni, 2♂, MNHN; La Mana, 1♀, MNHN; 1♂, 4♀, CMNH; *Cayenne*, Cayenne, 1♂, 1♀, BMNH, 5♂, 5♀, MNHN; Pte. de Kaw, 1♀, USNM (JH# SI-141); Cacao, 1♂, USNM (DH# 1999–10); Matoury, 1♂, MNHN, 1♂, USNM (DH# 1999–7); Galion, 1♂, USNM; Montsinéry, 1♀ MNHN; Macouria, 1♂, MNHN; mouth of Rivière Kourou, 1♀, BMNH; no locality data, 2♂, 3♀, BMNH, 1♂, 1♀, MNHN. TRINIDAD: Port of Spain, 2♂, BMNH; Tunapuna, 1♂, BMNH; Fort George, 2♂, 2♀, BMNH; St Annes, 7♂, 4♀, BMNH, 1♂ MNHN; Maupertuis ridge, 1♀, BMNH; Maraval, 8♂, 1♀, BMNH, 1♂, MNHN; 6 mi. N Arima, 1♂, AME; Sans Souci Estate, Sangre Grande, 1♀, AME; Xeres Field, 1♂, USNM (DH# 1999–6); Carenage, 1♀, CMNH; no locality data, 3♂, 2♀, BMNH, 1♂, USNM. TOBAGO: no locality data, 1♀, BMNH. No locality data, 1♂, 2♀, BMNH, 5♂, 3♀, USNM. ? Pena Branca, 1♂, 1♀, BMNH. Mislabelled: Quito, Ecuador, 1♀ BMNH.

Juditha caucana **(Stichel, 1911), stat.n.**

(Figs 3I,J; 8B; 9H; 10H; 12A–P; 16)

Peplia lamis caucana Stichel, 1911: 367. Type locality: Cauca, Central Colombia. Holotype ♂ (# 3979) ZMHU (examined).

Diagnosis. Typical forewing length: male 17 mm, female 16.5 mm. The taxon *caucana* was described as, and has always been regarded as, a subspecies of *J. molpe*, even though the two taxa can not be consistently distinguished based on wing pattern. However, as *J. caucana* has distinctive male genitalia (see the account of *J. molpe* for details), we raise *caucana* to species status. The females of *J. caucana* and *J. molpe* are distinguished in the latter species account. *Juditha caucana* is also geographically variable, with the white bands becoming gradually narrower south and east of Mexico in a unidirectional cline.

Biology. *Juditha caucana* is one of the most common riodinid butterflies in Central America and occurs from sea-level to approximately 1200 m in a diversity of habitats from dry semi-deciduous to wet primary or secondary forest and even overgrown fields (Ross, 1964b; Austin *et al*., 1996; DeVries, 1997). The species is present all year, although Austin *et al*. (1996) report that in Tikal, Guatemala, it is most abundant during the early rainy season in June and July. In Ecuador, males perch along forest edges and streamsides either alone or in small groups from 12.20 to 17.45 hours. They rest both on top of and beneath leaves with their wings half or fully open 1–8 m the ground. DeVries (1997) reported both sexes visiting flowers of *Cordia*, *Croton*, *Hamelia*, *Lantana* and *Serjania*.

Females oviposit from 10.00 to 14.00 hours only on those parts of their foodplants where certain ants are present, and it seems likely that oviposition is ant-mediated (Callaghan, 1982; DeVries, 1997). DeVries *et al*. (1994) reported females in numerous cases ovipositing in the presence of *Dolichoderus* ants (Dolichoderinae), so the suggestion by Callaghan (1982) that females oviposited in the presence of *Camponotus* ants (Formicinae) may be erroneous. *Juditha caucana* utilizes a wide range of foodplants that includes nine plant families (Appendix 4). Details of the biology and morphology of the immature stages of this, the best known species in *Juditha*, are given in the introductory biology section (Fig. 12A–P).

Distribution. *Juditha caucana* occurs throughout Central America, from central Mexico to Panama, and along the western Andes, from the northern tip of the central Cordillera in Colombia to northwestern Ecuador (Fig. 16). The absence of *J. caucana* from species lists for the central-western Mexican provinces of Jalisco (Vargas *et al*., 1996), Colima (Warren *et al*., 1998) and Michoacán (a single location) (Balcázar, 1993), suggests the species does not range that far north. Meerman (1999) states *J. caucana* (as *J. molpe*) is the most common riodinid in Belize, reporting it from all five provinces of that country. Additional literature records include Jacatepec, Metates, Soyolapan El Bajo, Tuxtepec and Yetla (*Oaxaca*) (Luis *et al*., 1991; as *J. lamis molpe*), Laguna Encantada and Estación de Biológia Tropical Los Tuxtlas (*Veracruz*) (Raguso & Llorente, 1991; as *J. molpe*), Teocelo, Dos Amates, Uxpanapa (*Veracruz*), La Sepultura and Tuxtla Gutiérrez (*Chiapas*) (de la Maza, 1987; as *J. molpe*), Cuenca del Grijalva, Cuenca del Tulijá, Selva Lacandona, Macizo Central, Depresión Central and Estribaciones de los Cuchumatanes (*Chiapas*, general biogeographic zones) (de la Maza & de la Maza, 1993; as *J. lamis molpe*), Mexico; Tikal (*El Petén*), Guatemala (Austin *et al*., 1996; as *J. molpe*); El Jaral (*Santa Bárbara*), Honduras (Monroe *et al*., 1967; as *Peplia lamis molpe*); and La Selva, Chilamate (*Heredia*), Santa Rosa de Puriscal, Carillo, Desamparados (*San José*), Tortuguerro, Siquirres (*Limón*), Isla del Caño, Golfito, Llorona, Sirena, Chacarita, Río Catarata, Brujo de Buenos Aires, Quepos, Monte Verde and Carrara (*Puntarenas*), Costa Rica (DeVries, 1997; as *J. molpe*).

Specimens examined. 176♂, 165♀. MEXICO: *Veracruz*, Atoyac, 6♂, 4♀, BMNH; San Lorenzo, 1♂, BMNH; Córdoba, 2♀, MNHN, 1♂, USNM; Santa Rosa, 3♂, 3♀, USNM; Acayucan, 1♀, USNM; Motzorongo, 1♂, CMNH; Catemaco, 2♂, CMNH, 1♂, 1 ♀, AME (♂: DH# 4512); 2 mi. SE Coatzcoalcos, 3♂, 2♀, CMNH; Coatepec, 4♂, 1♀, AME; Río Tonala, Highway 185, 1♀, FSCA; 5 mi. S San José del Carmen, 1♀, FSCA; no specific locality, 1♂, AME; *Tabasco*, Teapa, 1♂, 2♀, BMNH; no specific locality, 3♂, 2♀, USNM, 1♂, CMNH; *Campeche*, 5 km W Escércega de Matamoros, 1♀, FSCA; *Quintana Roo*, Polyuc, 1♂, BMNH, 2♂, USNM; *Yucatán*, Valladolid, 2♂, BMNH; X-Can, 2♂, BMNH, 3♂, 2♀, USNM (♂: DH# 1999–1; ♀: 2000–160), 5♂, 3♀, CMNH, 1♀, AME, 5♂, 3♀, FSCA; Chichén Itzá, 1♂, 1♀, USNM, 2♂, 3♀, CMNH; Pisté, 1♀, CMNH; *Oaxaca*, Chiltepec, 2♂, CMNH, 2♂, 1♀, AME; Temascal, 1♀, AME; *Chiapas*, Palenque, 3♂, CMNH; Chajul, 1♂, AME; Yaxoquintala, 1♀, CMNH; Pichucalco, 5♂, 4♀, AME (♂: DH# 4511); S Mexico, 5♂, 3♀, CMNH; no locality data, 2♂, BMNH, 1♀, MNHN, 1♂, USNM. BELIZE: *Corozal*, no specific locality, 1♀, BMNH; *Cayo*, Camp Sibun, 1♀, USNM (DH# 2000–161); Chaa Creek, nr San Ignacio, 1♂, FSCA; *Stann Creek*, Middlesex, 1♀, CMNH; Jaguar Reserve, 1♂, 2♀, AME; *Toledo*, Blue Creek, 2♀, AME; Punta Gorda, 1♀, AME; ? Chan Chich, 1♀, AME; ? Altun Ha, 1♀, AME;? Manattee, 1♂, BMNH; no locality data, 5♂, 5♀, BMNH. GUATEMALA: *El Petén*, Piedras Negras, 1♀, CMNH; *Izabal*, Cayuga, 3♂, USNM, 2♂, 1♀, CMNH; Puerto Barrios, 1♂, 1♀, MNHN, 1♂, CMNH; Quiriguá Viejo, 4♂, 4♀, CMNH; *Alta Verapaz*, Choctún, 1♀, BMNH; Chiacám, 1♂, 3♀, BMNH; Chixoy, 1♂, BMNH; Panzós, 1♂, 1♀, BMNH; Chacoj, 1♂, 1♀, BMNH; Telemán, 1♂, 1♀, BMNH; Polochic Valley, 2♂, 7♀, BMNH; no specific locality, 1♀, BMNH; *Baja Verapaz*, Panima, 1♂, BMNH; ? Tocoy, 1♀, BMNH; no locality data, 1♀, USNM, 1♀, CMNH. HONDURAS: *Cortés*, San Pedro Sula, 2♂, 2♀, BMNH, 3♂, 2♀, USNM (♂: DH# 1999–2), 1♂, CMNH; La Cambre, 2♂, BMNH; *Atlántida*, Lancetilla, 1♀, USNM (DH# 2000–163); 18 km W La Ceiba, 1♀, USNM; no locality data, 1♀, BMNH, 3♂, USNM. NICARAGUA: *Zelaya*, Bluefields, 1♀, AME; Rama, 1♀, AME; Nueva Guinea, 1♀, AME; *Granada*, 5 km SE Granada, 2♂, 1♀, AME; no locality data, 1♂, MNHN. COSTA RICA: *Guanacaste*, Parque Nacional Santa Rosa, 5♀, USNM; 8 km NW Bagaces, 1♂, USNM; Barranca, 1♂, AME; Taboga, 6 mi. W Canãs, 1♀, FSCA; *Alajuela*, San Mateo, 1♀, BMNH, 1♀, CMNH; 11 mi. N Florencia, 2♀, CMNH; *Cartago*, Avangarez, 1♂, 1♀, USNM (♀: DH# 2000–165); *Puntarenas*, nr Esquinas, 1♂, USNM; Piedras Blancas, 1♀, USNM; Aranjuez, 1♂, BMNH, 1♂, 1♀, USNM; Rincon, 1♀, AME; Sirena, 1♂, 1♀, AME; no locality data, 1♂, BMNH. PANAMA: *Chiriquí*, no specific locality, 1♀, BMNH; *Veraguas*, Calobre, 1♀, BMNH; Santiago, 2♂, CMNH; Playa Hermosa, Isla Coiba, 1♂, USNM; Río Chagres, Isla Coiba, 1♂, USNM; Isla Coiba, 1♀, USNM; no specific locality, 2♂, MNHN; *Colón*, Santa Rita, 2♀, USNM; *Canal Zone*, Barro Colorado, 2♀, USNM, 1♂, CMNH; Madden Dam, 1♀, FSCA; Madden Forest, 1♂, 1♀, USNM (DH# 1999–3, 15); Lion Hill, 1♂, 1♀, BMNH; Colón, 2♂, 1♀, USNM; Cocoli, 1♂, 1♀, USNM, 1♀, CMNH; Farfan, 4♂, 1♀, USNM, 3♂, AME; Coco Solo, 2♂, USNM; Summit, 3♀, AME; Piña, 8♂, 13♀, AME, 2♀, FSCA; La Pita, 1♀, USNM; Gamboa, 1♂, 1♀, USNM, 2♂, 1♀, AME; Gatun, 2♂, 2♀, USNM; Bayano, 2♂, 1♀, USNM; Pedro Miguel, 1♂, CMNH; Corozal, 1♂, CMNH; no specific locality, 1♀, FSCA; *Panamá*, La Chorrera, 1♂, USNM; Isla del Rey, 1♂, 2♀, BMNH; San Miguel, Isla del Rey, 3♂, BMNH; Chepo, 1♀, USNM; Río Trinidad, 1♀, USNM; Río Torti, 1♂, USNM; *Darién*, Cerro Pirre, 1♂, USNM; no specific locality, 1♀, MNHN; no locality data, 1♂, 3♀, MNHN. COLOMBIA: *Cauca*, no specific locality, 1♂, ZMHU; *Valle del Cauca* Río Dagua, 1♂, 1♀, MNHN (♂: JH# MN–4); Yumbo, 1♂, MNHN (JH# MN–3); *Risaralda*, Santa Rita, Río Cauca, 1♀, BMNH; *Antioquia*, Valdivia, 1♀, BMNH; *Boyacá*, Muzo, 1♂, 1♀, MNHN (♂: JH# MN–2); *Cundinamarca*, Bogotá, 2♂ BMNH; El Boqueron, Río Chocho, 1♂, USNM (DH# 1999–4); *Tolima*, Río Atá, Bruselas-Planada Rd, 1♀, AME; Hare Viejo, Río Chili, 1♂, AME; ? Nueva Granada, 1♀, CMNH. ECUADOR: *Esmeraldas*, Estación Científica La Chiquita, 1♂, JHKW; La Punta, 2♀, JHKW; El Durango, 2♂, JHKW; *Imbabura*, Paramba, 1♂, BMNH. No locality data, 4♂, 2♀, BMNH, 1♂, USNM.

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Appendix 1.

List of characters for twenty-four ingroup species of *Juditha*, *Lemonias*, *Thisbe* and *Uraneis*, and outgroup *Audre domina* used in the phylogenetic analysis.

External morphology

1. *Prominent, isolated and contrasting white spot behind each chaetosema*: (0) absent; (1) present (e.g. Fig. 1L). CI = 1; RI = 1.
2. *Well defined, narrow and contrasting strip of colour along ventral surface of palpi*: (0) absent; (1) present (Fig. 1L). CI = 1; RI = 1.
3. *Tegula*: (0) same colour as thorax; (1) with a red patch along dorsal margin that contrasts with colour of thorax (e.g. Fig. 1L). CI = 1; RI = 1.
   Character 3 in Penz & DeVries (1999).
4. *Male forelegs*: (0) unicolorous; (1) striped (Fig. 1L). CI = 1; RI = 1.
5. *Two narrow and contrasting stripes on ventral surface of abdomen*: (0) absent; (1) present (Fig. 1L). CI = 1; RI = 1.
6. *Lateral, contrasted white, yellow or orange spot at base of abdomen*: (0) absent; (1) present (e.g. Fig. 1G). CI = 1; RI = 1.
7. *Contrasting lateral stripe on abdomen that becomes dorsolateral anteriorly*: (0) absent; (1) present (e.g. Fig. 1F). CI = 0.5; RI = 0.5.

8. *If contrasting lateral stripe on abdomen that becomes dorsolateral anteriorly present (7 : 1)*: (1) unicolorous (e.g. Fig. 1F); (2) vertically striped (e.g. Fig. 1H). CI = 1; RI = 1.
9. *Forewing radial vein R4 touches wing margin*: (0) before apex at costal margin; (1) after apex at distal margin (Fig. 1L). CI = 1; RI = 1.

Character state (1) was first illustrated by Stichel (1911), who used it to define his *Uraneis*. Also Character 4 of Penz & DeVries (1999).

10. *Hindwing tornus*: (0) not produced into variably elongate lobe at vein 2 A; (1) produced into variably elongate lobe at vein 2A (e.g. Fig. 1L). CI = 0.5; RI = 0.86.

Adapted from character 5 in Penz & DeVries (1999).

11. *Hindwing tornus*: (0) not produced into point at vein Cu2; (1) produced into point at vein Cu2 (e.g. Fig. 1B) (1). CI = 1; RI = 1.

Note that state (1) is variably prominent in *albinus*.

12. *Spots at base of DFW*: (0) plain and unicolorous (e.g. Fig. 1K); (1) ringed with paler scaling (e.g. Fig. 1O). CI = 1; RI = 1.
13. *If spots at base of DFW ringed with paler scaling (12 : 1), spots in males*: (1) orange (e.g. Fig. 2A); (2) white (e.g. Fig. 1O). CI = 1; RI = 1.
14. *DFW postdiscal band of male*: (0) laterally disjointed (e.g. Fig. 2A); (1) continuous (e.g. Fig. 1O). CI = 1; RI = 1.

Note that *lycorias* and *ucubis* are given a question mark (?), in the former case due to uncertainty as to whether the subapical white band is postdiscal or submarginal, and in the latter because the postdiscal markings are obscured.

15. *If DFW postdiscal band of male continuous (14 : 1), band*: (1) composed of 2 colours (e.g. Fig. 2E); (2) unicolorous (e.g. Fig. 1O). CI = 1; RI = 1.
16. *If DFW postdiscal band of male continuous and unicolorous (15 : 2), band*: (1) orange (Fig. 1L); (2) white (e.g. Fig. 1O). CI = 1; RI = 1.
17. *Submarginal spots on DHW*: (0) absent or isolated (e.g. Fig. 1D); (1) contiguous, forming a continuous 'chain-link' pattern (e.g. Fig. 1O). CI = 1; RI = 1.
18. *Dorsal coloration overlying brown/black background*: (0) white and orange (e.g. Fig. 1K); (1) white with blue iridescence (e.g. Fig. 1J). CI = 0.5; RI = 0.75.
19. *If dorsal coloration overlying brown/black background white with blue iridescence (18 : 1), blue iridescence*: (1) associated with postdiscal band only (e.g. Fig. 1J); (2) widespread on wings (Fig. 1L). CI = 0.67; RI = 0.67.
20. *White fringe on FW*: (0) not present in all of cells Cu2 to R4+5 (e.g. Fig. 1K); (1) present in all of cells Cu2 to R4+5 (e.g. Fig. 1H). CI = 0.5; RI = 0.67.
21. *DHW postdiscal band of male composed of*: (0) broad band (e.g. Fig. 1K); (1) small spots (e.g. Fig.1H); (2) absent (Fig. 1L). CI = 1; RI = 1.
22. *DHW postdiscal band of male*: (0) does not touch distal margin (e.g. Fig. 2A); (1) touches distal margin (e.g. Fig. 1E). CI = 1; RI = 1.
23. *DHW postdiscal band of male*: (0) not restricted to tornus (e.g. Fig. 1O); (1) restricted to tornus (Fig. 1E). CI = 1; RI = 1.
24. *Spots in discal cell of VFW*: (0) orange or white (e.g. Fig. 1I); (1) brown (e.g. Fig. 2O); (2) absent (e.g. Fig. 1J). CI = 1; RI = 1.
25. *Postdiscal white immediately distal to discal cell end on VFW*: (0) continuous line (e.g. Fig. 1D); (1) divided into 2 spots (e.g. Fig. 1B); (2) absent (e.g. Fig. 1J). CI = 0.5; RI = 0.8.
26. *Two spots at base of cell Cu2 on VFW*: (0) present (e.g. Fig. 1I); (1) absent (e.g. Fig. 1L). CI = 0.5; RI = 0.75.
27. *Spot in crotch of humeral vein at costal base of VHW*: (0) isolated (e.g. Fig. 1E); (1) forms part of band that extends to base of anal margin (e.g. Fig. 1I); (2) absent (e.g. Fig. 1L). CI = 0.4; RI = 0.73.
28. *Orange at base of VHW cell Rs*: (0) absent; (1) present (e.g. Fig. 1B). CI = 0.33; RI = 0.33.
29. *Submarginal spots on VHW*: (0) entire (e.g. Fig. 1D); (1) divided into 2 parallel lines of spots (e.g. Fig. 1B); (2) merged into 2 continuous parallel lines (e.g. Fig. 1J); (3) absent (e.g. Fig. 1L) (3). CI = 0.6; RI = 0.75.
30. *Orange line on vein 2A between tornal black spots of VHW*: (0) absent; (1) present (e.g. Fig. 1I). CI = 0.33; RI = 0.6.
31. *Orange line on vein M1 between apical black spots of VHW*: (0) absent; (1) present (e.g. Fig. 1I). CI = 0.5; RI = 0.5.
32. *White fringe on HW*: (0) present in all of cells Cu2 to R4+5 (e.g. Fig. 1H); (1) not present in all of cells Cu2 to R4+5 (e.g. Fig. 2O). CI = 0.5; RI = 89.

Male abdomen

33. *Eighth abdominal male sternite*: (0) produced into 2 narrow, elongate projections with soft tissue in between and laterally swollen anterior base (e.g. Fig. 5A); (1) produced into elongate, narrow and slightly bifurcate tip (Fig. 5C); (2) plain rectangle with variably shallowly indented posterior margin (Fig. 9A); (3) produced into 2 elongate approximate triangles without intervening soft tissue (e.g. Fig. 9C); (4) rectangle faintly sclerotized only at anterior base and laterally (Fig. 5D). CI = 0.8; RI = 0.93.

Adapted from character 59 of Harvey (1987).

34. *If eighth abdominal male sternite produced into 2 narrow, elongate projections with soft tissue in between and laterally swollen anterior base (33 : 0), projections*: (0) long (Fig. 5A); (1) short (Fig. 5B). CI = 1; RI = 1.
35. *If eighth abdominal male sternite produced into 2 elongate approximate triangles without intervening soft tissue (33 : 3), projections*: (1) gradually taper to point (e.g. Fig. 9C); (2) bluntly taper to point (e.g. Fig. 9F). CI = 1; RI = 1.
36. *If eighth abdominal male sternite produced into 2 elongate approximate triangles without intervening soft tissue (33 : 3), lateral margins of projections*: (1) folded over dorsally (e.g. Fig. 1C); (2) not folded over dorsally (e.g. Fig. 9H). CI = 1; RI = 1.

37. *Spines in association with eighth abdominal male sternite*: (0) absent; (1) present (e.g. Fig. 9B). CI = 1; RI = 1.

Adapted from character 49 in Penz & DeVries (1999); note they missed the presence of spines in *Juditha*.

38. *If spines present in association with eighth abdominal sternite (37 : 1), spines*: (1) coarse (e.g. Fig. 9B); (2) fine (e.g. Fig. 9E). CI = 1; RI = 1.

Male genitalia

39. *Square notch at middle of posterior margin of uncus dorsally that meets triangular tip of tegumen*: (0) absent (e.g. Fig. 5E); (1) present (Fig. 8A). CI = 1; RI = 1.
40. *Distal margin of uncus either side of central point*: (0) straight or rounded (e.g. Fig. 5E); (1) shallowly concave (Fig. 8A). CI = 1; RI = 1.
41. *Falces*: (0) shorter than tegumen and uncus combined (e.g. Fig. 8A); (1) at least as long as tegumen and uncus combined (Fig. 5G). CI = 1; RI = 1.
42. *Vinculum*: (0) complete dorsally at anterior margin of tegumen (Fig. 5E); (1) broadly incomplete (Fig. 5F); (2) incomplete for short distance in association with desclerotized section of tegumen (Fig. 8A). CI = 0.4; RI = 0.73.

Adapted from character 72 in Penz & DeVries (1999).

43. *A semisclerotized projection of annelar membrane between dorsal portions of vinculum*: (0) absent; (1) present (e.g. Fig. 7D). CI = 1; RI = 1.
44. *Vinculum*: (0) suddenly pinched or desclerotized ventrally before join with saccus (e.g. Fig. 5H); (1) of even thickness throughout or only gradually becoming narrower ventrally (Fig. 5I). CI = 0.33; RI = 0.67.
45. *Valvae*: (0) rectangular with spines at tip (Fig. 5H); (1) produced into single elongate projections with pointed tips (Fig. 5I); (2) approximate triangles with pointed tips in lateral view that have convexo-concave outer margins in ventral view (Figs 5J, 5K); (3) 'V-shaped' at tip (Fig. 7A); (4) angularly triangular in lateral and ventral view (e.g. Fig. 7C); (5) produced into 2 variably elongate projections with pointed tips (e.g. Fig. 7D). CI = 1; RI = 1.
46. *If valvae produced into 2 variably elongate projections with pointed tips (45 : 5), lower projection*: (1) symmetrical (e.g. Fig. 7E); (2) asymmetrical (e.g. Fig. 8A). CI = 1; RI = 1.

Adapted from character 89 in Penz & DeVries (1999).

47. *Teeth on valvae*: (0) present (e.g. Fig. 5H); (1) absent (e.g. Fig. 5I). CI = 0.5; RI = 0.75.
48. *Long setae on unsclerotized region between pedicel and base of valvae*: (0) absent; (1) present (e.g. Fig. 7A). CI = 1; RI = 1.

Character state (1) was first illustrated by Stichel (1911). Also Character 93 in Penz & DeVries (1999); note they erroneously report such setae in *Theope publius* and *Thysanota galena* (see text, *Characteristics of* Juditha).

49. *If long setae on unsclerotized region between pedicel and base of valvae present (48 : 1), setae*: (1) distributed continuously across relatively ill-defined area (Fig. 7A); (2) restricted to distinct raised pad (e.g. Fig. 7C). CI = 1; RI = 1.
50. *If long setae on unsclerotized pad between pedicel and base of valvae present (49 : 2), pad*: (1) narrow (2 or 3 setae wide) (e.g. Fig. 7C); (2) broad (4 or 5 setae wide) (e.g. Fig. 7F). CI = 1; RI = 1.
51. *Pedicel*: (0) not medially desclerotized and split at base (e.g. Fig. 7E); (1) medially desclerotized and split at base (Fig. 5K). CI = 1; RI = 1.

Adapted from character 50 of Harvey (1987).

52. *Aedeagus*: (0) not swollen ventrally immediately posterior to pedicel (e.g. Fig. 7C); (1) swollen ventrally immediately posterior to pedicel (Fig. 5L). CI = 1; RI = 1.

Character state (1) was first illustrated by Harvey (1987: 5.31) for *Uraneis ucubis*. Also character 81 in Penz & DeVries (1999); note we code *irenea* as state (0) instead of the state (1) coded by Penz & DeVries (1999) since its aedeagus is no broader posterior to the pedicel than it is anterior, even if posteriorly it does abruptly narrow.

53. *Everted aedeagal vesica*: (0) with single, small, medially indented rectangular sclerotized pad (Fig. 5M); (1) straight and devoid of any prominent cuticular sculpturing; (2) with single anteriorly pointing peglike cornutus (Fig. 5N); (3) with arc of spines (Fig. 5P); (4) with elongate, yellowish area of very small coarse teeth (Fig. 5O); (5) with 2 patches of very dense, fine spines (Fig. 5Q); (6) with elongate patch of spines on blind sac towards base and additional patch of smaller spines at distal tip (Fig. 5R); (7) with broadly distributed group of spines at distal tip of very long vesica (Fig. 5.); (8) sharply angled at middle and devoid of any prominent cuticular sculpturing (Fig. 5L); (9) with small, roughened, yellowish area of very small fine teeth (e.g. Figs 7E, 10E). CI = 1; RI = 1.

Note Penz & DeVries (1999) fail to show cornuti in their illustration (Fig. 16J) of the aedeagus of *caliginea* (state 5) even though they code cornuti as present in their matrix for this species. The aedeagal cornuti for *caliginea* (as *rossi*) were first illustrated by Clench (1964).

Female genitalia

54. *Signa*: (0) form invaginated sclerotized spines (e.g. Fig. 6A); (1) absent or consist of only faint sclerotization at surface of corpus bursae (Fig. 6B). CI = 1; RI = 1.
55. *If signa forms invaginated sclerotized spines (54 : 0), width*: (0) less than one-third of length (e.g. Fig. 11A); (1) more than one-third of length (e.g. Fig. 11C). CI = 1; RI = 1.
56. *Serrations along inner edge of signa*: (0) absent (e.g. Fig. 11A); (1) present (e.g. Fig. 11C). CI = 1; RI = 1.
57. *Posterior tips of signa*: (0) touch junction of ductus bursae with corpus bursae (Fig. 6A); (1) positioned at least length of opening of signa away from entrance of ductus bursae (e.g. Fig. 11A). CI = 1; RI = 1.

Note that *lycorias*, *hyalina*, *ucubis* and *incubus* are given a question mark (?) because, as their signa are reduced to small faintly sclerotized areas at the wall of the corpus bursae, it is not possible to determine where their posterior tips truly are.

58. *Position of signa at wall of corpus bursae*: (0) asymmetrical (Fig. 6A); (1) symmetrical (e.g. Fig. 11A). CI = 1; RI = 1.
59. *Corpus bursae*: (0) elongate (e.g. Fig. 6A); (1) spherical (Fig. 6B). CI = 1; RI = 1.

Character 26 in Penz & DeVries (1999); note we code *irenea* and *molela* as state (0) instead of (1).

60. *Posterior portion of ductus bursae, shortly before ostium bursae*: (0) not laterally compressed (e.g. Fig. 6C); (1) markedly laterally compressed (Fig. 6D). CI = 1; RI = 1.
61. *If posterior portion of ductus bursae, shortly before ostium bursae, markedly laterally compressed (60 : 1), ventral sclerotization*: (1) strong (Fig. 6D); (2) weak. CI = 1; RI = 1.
62. *Posterior sclerotized portion of ductus bursae*: (0) sclerotized dorsally (e.g. Fig. 6D); (1) not sclerotized dorsally (Fig. 6E). CI = 1; RI = 1.

Adapted from character 18 in Penz & DeVries (1999). Note that *pulcherrima* and *inambari* are given a question mark (?) due to uncertainty regarding the point when the ostium bursae becomes the ductus bursae.

63. *Posterior portion of ductus bursae immediately anterior to ostium bursae*: (0) straight or weakly bent to side (e.g. Fig. 6D); (1) strongly bent to left (Fig. 6C). CI = 1; RI = 1.
64. *Membranous portion of ductus bursae exits sclerotized portion*: (0) anteriorly (e.g. Fig. 11F); (1) ventrally (e.g. Fig. 11G). CI = 1; RI = 1.
65. *Ductus seminalis joins ductus bursae*: (0) at junction of membranous and sclerotized portions (e.g. Fig. 6E); (1) within sclerotized portion (Fig. 6D). CI = 0.33; RI = 0.82.
66. *Sclerotized junction between ostium bursae and ductus bursae*: (0) present (e.g. Fig. 6C); (1) absent (e.g. Fig. 6E). CI = 1; RI = 1.
67. *Ventral lip of ostium bursae*: (0) rounded or shallowly indented (e.g. Fig. 11A); (1) with deep 'V-shaped' indentation (e.g. Fig. 11G). CI = 1; RI = 1.
68. *Sclerotized pouch below papillae anales joined to ostium bursae by continuous sclerotized area*: (0) absent; (1) present (Fig. 6C). CI = 1; RI = 1.
69. *Ribbing in region between ostium bursae and papillae anales*: (0) absent (Fig. 6C); (1) transverse (e.g. Fig. 11F); (2) concentric (Fig. 6E). CI = 0.4; RI = 0.57.

Adapted from character 14 in Penz & DeVries (1999); note we code *irenea* and *molela* as state (1) instead of (0), and introduce state (2).

Appendix 2. Character matrix for the phylogenetic analysis.

	5 10 15 20 25 30 35 40 45 50 55 60 65
Audre domina	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
‘*Lemonias*’ *glaphyra*	0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0
‘*Audre*’ *alhinus*	0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0
Lemonias ochracea	0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 1 0 1 0 0 0 4 ? 0 0 0 0 0 0 1 0 0 0 1 0 1 0 0 0 0 0 2 0 0 0 0 1 0 1 1 0 0 0 1 0 0 0 0
Lemonias theodora	0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 2 0 2 0 3 0 0 1 4 ? 0 0 0 0 0 0 1 0 0 0 1 0 1 0 0 0 0 0 2 0 0 0 0 1 0 1 1 0 0 0 1 0 0 0 1
Lemonias albofasciata	0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 2 1 2 0 3 0 0 1 4 ? 0 0 0 0 0 0 1 0 0 0 1 0 1 0 0 0 0 0 2 0 0 0 0 1 0 1 1 0 0 0 1 0 0 0 0
Lemonias stalachtioides	0 0 0 0 0 1 1 2 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 1 0 1 0 1 0 0 0 1 ? 0 0 0 0 0 0 0 1 0 1 1 0 1 0 0 0 0 0 4 0 0 0 0 1 0 1 2 0 0 0 1 0 0 0 1
Lemonias sontella	0 0 0 0 0 1 1 2 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 1 0 1 0 1 0 0 0 1 ? 0 0 0 0 0 0 0 1 0 1 1 0 1 0 0 0 0 0 4 0 0 0 0 1 0 1 2 0 0 0 1 0 0 0 1
Lemonias caliginea	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1 ? 0 0 0 0 0 0 0 1 0 1 1 0 1 0 0 0 0 0 5 0 0 0 0 1 0 1 1 0 0 0 1 0 0 0 1
Lemonias zygia	0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 1 0 0 1 ? 0 0 0 0 0 0 0 1 0 1 1 0 1 0 0 0 0 0 3 0 0 0 0 1 0 1 1 0 0 0 1 0 0 0 1
Lemonias egaensis	0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 0 1 ? 0 0 0 0 0 0 0 1 0 1 1 0 1 0 0 0 0 0 3 0 0 0 0 1 0 1 1 0 0 0 1 0 0 0 1
Thisbe molela	0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 1 0 0 1 1 0 1 ? 0 0 0 0 0 0 0 1 0 1 1 0 1 0 0 0 0 0 6 0 0 0 0 1 0 0 0 1 0 0 1 0 0 0 1
Thisbe irenea	0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 1 0 0 0 0 2 2 0 1 0 2 0 0 0 2 ? 0 0 0 0 0 0 0 1 0 1 1 0 1 0 0 0 0 0 7 1 ? 0 0 1 0 0 0 1 0 0 1 1 0 0 1
Thisbe lycorias	1 1 1 0 0 0 0 0 0 1 0 0 0 ? 0 0 0 0 0 0 0 0 0 2 2 1 1 0 2 0 0 0 2 ? 0 0 0 0 0 0 0 1 0 0 2 0 0 0 0 0 1 1 8 1 ? 0 ? 1 1 0 0 1 0 0 1 1 0 0 0
Thisbe hyalina	1 1 1 1 1 0 0 0 1 1 0 0 0 0 0 0 0 1 2 0 0 0 0 2 2 1 2 0 3 0 0 0 2 ? 0 0 0 0 0 0 0 1 0 0 2 0 0 0 0 0 1 1 8 1 ? 0 ? 1 1 0 0 1 0 0 0 1 0 0 2
Thisbe ucubis	1 1 1 1 1 0 0 0 1 1 0 0 0 ? 0 0 0 1 2 0 2 0 0 2 2 1 2 0 3 0 0 0 2 ? 0 0 0 0 0 0 0 1 0 0 2 0 0 0 0 0 1 1 8 1 ? 0 ? 1 1 0 0 1 0 0 0 1 0 0 2
Thisbe incubus	1 1 1 1 1 0 0 0 1 1 0 0 0 0 0 0 0 1 2 0 2 0 0 2 2 1 2 0 3 0 0 0 2 ? 0 0 0 0 0 0 0 1 0 0 2 0 0 0 0 0 1 1 8 1 ? 0 ? 1 1 0 0 1 0 0 0 1 0 0 2
Juditha odites	0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 2 ? 0 0 0 0 0 0 0 1 0 0 3 0 1 1 1 0 0 0 9 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 1
Juditha pulcherrima	0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 1 3 ? 1 1 1 1 0 1 0 0 0 0 4 0 1 1 2 1 0 0 9 0 1 1 1 1 0 0 0 ? 0 0 0 0 0 0 1
Juditha inambari	0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 1 3 ? 1 1 1 1 0 1 0 0 0 0 4 0 1 1 2 1 0 0 9 0 1 1 1 1 0 0 0 ? 0 0 0 0 0 0 1
Juditha dorilis	0 0 0 0 0 0 0 0 0 0 0 1 1 1 2 1 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 3 ? 2 2 1 2 1 1 0 2 1 0 5 1 1 1 2 2 0 0 9 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 1
Juditha naza	0 0 0 0 0 0 0 0 0 0 0 1 2 1 2 2 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 3 ? 2 2 1 2 1 1 0 0 1 0 5 1 1 1 2 2 0 0 9 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 1
Juditha azan	0 0 0 0 0 0 0 0 0 0 0 1 2 1 2 2 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 3 ? 2 2 1 2 1 1 0 2 1 0 5 2 1 1 2 2 0 0 9 0 0 1 1 1 0 0 0 0 0 0 0 0 1 0 1
Juditha molpe	0 0 0 0 0 0 0 0 0 0 0 1 2 1 2 2 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 3 ? 2 2 1 2 1 1 0 2 1 0 5 2 1 1 2 2 0 0 9 0 0 1 1 1 0 0 0 0 0 1 0 0 1 0 1
Juditha caucana	0 0 0 0 0 0 0 0 0 0 0 1 2 1 2 2 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 3 ? 2 2 1 2 1 1 0 2 1 0 5 2 1 1 2 2 0 0 9 0 0 1 1 1 0 0 0 0 0 1 0 0 1 0 1

Appendix 3. List of synapomorphies for ingroup genera in the phylogenetic analysis. These are universal within the particular genus unless otherwise stated. The numbers in parentheses after each generic taxon represent the number of species it contains, and the numbers in parentheses after apomorphies refer to the character number and state in this study (see Appendix 1).

Taxon	Synapomorphies
glaphyra + *albinus* group [2]	● Hindwing tornus produced into a point at vein Cu2 [11 : 1] (e.g. Fig. 1B) ● Orange present at base of VHW cell Rs [28 : 1] (e.g. Fig. 1B) (also present in *L. caliginea* and *L. zygia*) ● An orange line present on vein M1 between apical spots of VHW [31 : 1] (e.g. Fig. 1I) (also present in *T. molela*) ● Posterior portion of ductus bursae immediately anterior to ostium bursae strongly bent to left [63 : 1] (Fig. 6C) ● A sclerotized pouch present below papillae anales joined to ostium bursae by a continuous sclerotized area [68 : 1] (Fig. 6C)
Juditha Hemming, 1964 [8]	● Spots at base of DFW ringed with paler scaling [12 : 1] (e.g. Fig. 2O) ● Spots in discal cell of VFW brown [24 : 1] (e.g. Fig. 2O) ● White fringe on HW not present in all of cells Cu2 to R4 + 5 [32 : 1] (e.g. Fig. 2O) (also not present in *L. theodora* and *L. albofasciata*) ● Long setae present on an unsclerotized region between pedicel and base of valvae [48 : 1] (e.g. Figs 7A, 10A–D) – first illustrated by Stichel (1911); also character 93 in Penz & DeVries (1999) ● Everted vesica of aedeagus contains a small, roughened, yellowish, semisclerotized patch composed of very small spines [53 : 9] (e.g. Fig. 7E) ● Posterior tips of signa positioned at least length of opening of signa away from entrance of ductus bursae [57 : 1] (e.g. Fig. 11A) ● Ductus seminalis joins ductus bursae at junction of membranous and sclerotized portions [65 : 0] (e.g. Fig. 6C) (also present in *T. hyalina, T. ucubis* and *T. incubus*)
Lemonias Hübner, [1807] [8]	● Eighth abdominal male sternite produced into an elongate, narrow and slightly bifurcate tip [33 : 1] (e.g. Fig. 5C) (not present in *ochracea*, *theodora* and *albofasciata*; also present in *T. molela*) ● Vinculum of approximately even thickness or only gradually becoming narrower ventrally [44 : 1] (Fig. 5I) (not present in *ochracca, theodora* and *albofasciata*; also present in *T. molela* and *T. irenea*) ● Posterior portion of ductus bursae, shortly before ostium bursae, markedly laterally compressed [60 : 1] (Fig. 6D)
Thisbe Hübner, [1819] [6] = *Uraneis* Bates, 1868	● Hindwing tornus produced into a variably elongate lobe at vein 2A [10 : 1] (e.g. Fig. 1K) (also present in *L. zygia* and *L. egaensis*), adapted from Penz & DeVries (1999) ● Dorsal coloration overlying brown/black background white with blue iridescence [18 : 1] (e.g. Fig. 1J) (not present in *lycorias*) ● Eighth abdominal male sternite a plain rectangle with a variably shallowly indented posterior margin [33 : 2] (Fig. 9A) (not present in *molela*; also present in *J. odites*) ● Posterior sclerotized portion of ductus bursae not sclerotized dorsally [62 : 1] (Fig. 6E), adapted from Penz & DeVries (1999)

Appendix 4. A list of all rearing records for *Juditha*, giving the species (where known), genus and family (*sensu* Gentry, 1993) of hostplant, genus and subfamily of attending ant where known, the location and bibliographic reference. Note that for some records, the name of the *Juditha* taxon differs from that given in the original publication. A question mark (?) indicates that the identity of a *Juditha* taxon is uncertain without a definite rearing location. An asterisk (*) beside a hostplant indicates that eggs were laid on or near membracids and larvae may be carnivorous (see text).

Juditha taxon	Plant taxon	Attending ant taxon	Location	Reference
odites praeclarum	Bombacaceae			
	* *Pseudobombax septenatum*	*Dolichoderus* (Dolichoderinae)	Panama	DeVries *et al*., 1994
	Moraceae			
	* *Ficus* sp.	*Dolichoderus* (Dolichoderinae)	Panama	DeVries *et al*., 1994
	Olacaceae			
	* *Heisteria cocinna*	*Dolichoderus* (Dolichoderinae)	Panama	DeVries *et al*., 1994
dorilis	Bombacaceae			
	* *Ochroma lagapus*	*Dolichoderus* (Dolichoderinae)	Costa Rica	DeVries *et al*., 1994
molpe	Leguminosae			
	Cassia sp.	Unidentified	Trinidad	Guppy, 1904
caucana	Caesalpiniaceae			
	Bauhinia sp.	*Camponotus* (Formicinae)	Colombia	Callaghan, 1982
	Capparaceae			
	Capparis sp.	Unidentified	Panama	Mallet *in* Harvey, 1987
	Dilleniaceae			
	Doliocarpus sp.	*Dolichoderus* (Dolichoderinae)	Panama	DeVries *et al*., 1994
	Tetracera sp.	*Dolichoderus* (Dolichoderinae)	Panama	DeVries *et al*., 1994
	Leguminosae			
?	*Acacia* sp.	Not stated	Not stated	DeVries, 1997
	Calliandra globerrima	*Camponotus* (Formicinae)	Colombia	Callaghan, 1982
	Cassia biflora	*Dolichoderus* (Dolichoderinae)	Panama	DeVries *et al*., 1994
?	*Cassia fruticosa*	Not stated	Not stated	DeVries, 1997
	Inga pezizifera	*Dolichoderus* (Dolichoderinae)	Costa Rica	DeVries *et al*., 1994
	Inga sp.	*Dolichoderus* (Dolichoderinae)	Panama	DeVries *et al*., 1994
	Inga vera	Not stated	Costa Rica	Janzen & Hallwachs, 2000
?	*Lonchocarpus* sp.	Not stated	Not stated	DeVries, 1997
	Pithecellobium longifolium	Not stated	Costa Rica	Janzen & Hallwachs, 2000
?	*Pithecellobium* sp.	Not stated	Not stated	DeVries, 1997
	Senna hayesiana	Not stated	Costa Rica	Janzen & Hallwachs, 2000
	Malpighiaceae			
	Heteropterys laurifolia	Not stated	Costa Rica	Janzen & Hallwachs, 2000
	Stigmaphyllon lindenianum	*Dolichoderus* (Dolichoderinae)	Costa Rica	Longino *in* Harvey, 1987
	Stigmaphyllon sp.	*Dolichoderus* (Dolichoderinae)	Panama	DeVries *et al*., 1994
	Ochnaceae			
	Ouratea luceus	Not stated	Costa Rica	Janzen & Hallwachs, 2000
	Passifloraceae			
	Passiflora adenopoda	*Dolichoderus* (Dolichoderinae)	Costa Rica	DeVries *et al*., 1994
	Passiflora coriaceae	*Dolichoderus* (Dolichoderinae)	Costa Rica	Mallet *in* Harvey, 1987
	Passiflora pittieri	*Dolichoderus* (Dolichoderinae)	Costa Rica	Longino *in* Harvey, 1987
	Passiflora pittieri	Not stated	Costa Rica	Thomas, 1990
	Passiflora vitifolia	*Dolichoderus* (Dolichoderinae)	Costa Rica	Longino *in* Harvey, 1987
	Passiflora vitifolia	*Dolichoderus* (Dolichoderinae)	Panama	Mallet *in* Harvey, 1987
	Passiflora vitifolia	*Dolichoderus* (Dolichoderinae)	Panama	DeVries *et al*., 1994
	Sapindaceae			
	Cardiospermum sp.	*Dolichoderus* (Dolichoderinae)	Belize	DeVries *et al*., 1994
	Paullinia bracteosa	*Dolichoderus* (Dolichoderinae)	Panama	DeVries *et al*., 1994
	Serjania mexicana	*Dolichoderus* (Dolichoderinae)	Panama	DeVries *et al*., 1994
	Simaroubaceae			
	Simaba cedron	*Dolichoderus* (Dolichoderinae)	Costa Rica	Longino *in* Harvey, 1987
?	*Picramnia* sp.	Not stated	Not stated	DeVries, 1997