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A CRYPTIC NEW *JEMADIA* (HESPERIIDAE: PYRGINAE: PYRRHOPYGINI) FROM COSTA RICA AND PANAMA WITH A SUBTLY DISTINCTIVE COMBINATION OF BLUE RAYS AND WHITE BANDS

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ABSTRACT. “We have little doubt it is rightly referred to this species,” wrote Godman and Salvin (1893: 262) about their only Panamanian specimen, a female from Calobre, in order to treat the South American *Jemadia hewitsonii* (Mabille, 1878) in their “Biologia Centrali-Americana. Insecta. Lepidoptera—Rhopalocera.” Half a century later, Evans included her in a type series of the newly described subspecies *J. hewitsonii pater* Evans, 1951, which after 50 more years Burns elevated to species status. This female is neither *J. hewitsonii* nor *J. pater*, but a new species, possibly closest to South American *Jemadia ovid* Evans, 1951, **new status**. The new Central American *Jemadia*, repeatedly reared in the Caribbean rain forest of Costa Rica’s Area de Conservación Guanacaste, is described here as *Jemadia suekentonmiller* Grishin, **sp. nov.**; and its facies, genitalia, and DNA barcodes are closely compared with those of various congeners. The twice-misplaced female is a paratype of *J. suekentonmiller* and is still the only known specimen from Panama.

Additional key words: cryptic species, biodiversity, caterpillars, skipper butterflies, genitalia, DNA barcodes, Area de Conservación Guanacaste.

Despite much work and some dedicated collecting, the Central American HesperIIDae fauna is still rich in surprises. In Nicaragua and Costa Rica, many phylogenetic groups that originated in South America currently appear to be at their northern distribution limits. Central American populations in some groups have become species that are often less common than their South American sister species and so morphologically similar to them (at least in facies) as to be cryptic (e.g., Grishin et al. 2013a).

Large series of specimens are desirable to study intraspecific variation and document interspecific differences. Abundant material from a long-term comprehensive inventory of the non-leaf miner species of Lepidoptera of Area de Conservación Guanacaste (ACG) in northwestern Costa Rica (Janzen et al. 2009, Janzen and Hallwachs 2011) is extraordinarily useful in this taxonomic effort. Because most of this material has been reared from wild-caught caterpillars, knowledge of their traits, foodplants, ecology, etc., greatly augments the usual data from adult morphology. Moreover, short

sequences (ca. 654 bp) of mitochondrial DNA coding for the C-terminal segment of cytochrome c oxidase subunit 1 (COI), and dubbed DNA barcodes, are routinely obtained for many specimens, adding molecular characters to those of morphology and biology. These DNA barcodes have been remarkable flags, both indicating possible new species and identifying recognized species (Hebert et al. 2004, Burns and Janzen 2005, Janzen et al. 2009, 2011, 2012, Burns et al. 2010, 2008, 2013, Grishin et al. 2013a, b).

While barcoding and more advanced DNA-based technologies are beginning to catch on in other areas of the Neotropics (Ratnasingham and Hebert 2007), traditional morphological comparisons are an integral part of species discovery and recognition of new ACG taxa in contrast to their closest relatives farther south. For instance, diligent and insightful analysis of facies and genitalia performed by Burns (Burns and Janzen 2001) detected a possible undescribed species of *Jemadia* E. Watson, 1893 on the basis of just three reared specimens, only one of which was male.

Comparison of over a dozen males and half a dozen females of this species available today supports Burns's conclusions. Moreover, comparison with the COI barcodes of other *Jemadia* species, many of which are South American and are from the same *Jemadia hewitsonii* species group, further strengthen the species-level status of this new taxon and place it further away from other *J. hewitsonii*-like species. Here, we formally describe this species and discuss its differences from other *J. hewitsonii* group taxa, both in facies and in male genitalia.

It should be noted that taxonomy of *J. hewitsonii* species group is currently uncertain. Further work on this group (and all Pyrrhopygini Mabille, 1877) is in progress and will soon be published by O. H. H. Mielke, E. Brockmann, and C. Mielke (pers. comm.). The purpose of this study is to describe a new species in the group and to show how to distinguish this new species from other taxa. Fortunately, the identity of taxa closest to the new species is quite clear. However, for completeness of comparison, we also illustrate facies and male genitalia of other distinct phenotypes in the *J. hewitsonii* group. Some of these taxa remain unnamed until the Mielke, Brockmann, and Mielke publication.

MATERIALS AND METHODS

Adult specimens used in this study are from the following collections: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); Natural History Museum, London, UK (BMNH); Museum für Naturkunde, Berlin, Germany (ZMHB); and American Museum of Natural History, New York, NY, USA (AMNH). All specimens reared from wild-caught caterpillars by the ACG inventory are so indicated with a specimen voucher code in the format yy-SRNP-x..., where "yy" are the last two digits of a year and "x..." is the serial number (1 to 5 digits long) of a specimen recorded for that year, e.g., 5289 or 22467. (A 6-digit code means that the adult specimen was wild-caught instead of reared.) This SRNP code can be sought on the inventory web site (Janzen and Hallwachs 2013) and soon, in general internet search engines. When they are reared, adults are on average slightly smaller than the wild-caught ones that usually populate museums.

For genitalia dissection, NVG used the following method (Robbins 1991): the abdomen was broken off, soaked for 40 minutes (or until ready) in 10% KOH at 60°C (or overnight at room temperature), dissected, and subsequently stored in a small glycerol-filled vial on the pin under the specimen. Genitalia and wing venation terminology follows Steinhauser (1981). Length measurements are in metric units and were

made from photographs of specimens taken with a scale and magnified on a computer screen. Photographs of specimens and dry genitalia were taken by NVG with Nikon D200 and Nikon D800 cameras through a 105 mm f/2.8G AF-S VR Micro-Nikkor lens; dissected genitalia were photographed in glycerol with the Nikon D200 camera without the lens and through microscopes at 2× and 5× magnifications. Images were assembled and edited in Photoshop CS5.1. Genitalia photographs were taken in several focus slices and stacked in Photoshop to increase depth of field. DNA sequences were downloaded from GenBank <<http://genbank.gov/>> or BOLD <<http://www.boldsystems.org/>>, aligned by hand since they matched throughout their length without insertions or deletions, and analyzed using the Phylogeny.fr server at <http://www.phylogeny.fr/> with default parameters (Dereeper et al. 2008). Many of these sequences have been reported in Janzen et al. (2011) and photos of specimens are available from the Area de Conservación Guanacaste (ACG) on-line database (Janzen and Hallwachs 2013) and BOLD database (Ratnasingham and Hebert 2007) to confirm or suggest identifications.

RESULTS AND DISCUSSION

Evans characterized *J. hewitsonii* by white-spotted patagia and the presence of a short discal "blue band" on the dorsal hindwing "from vein 7 [=Rs] to vein 3 [=Cu₁], placed above 2 oblique basal streaks" (Evans 1951: 52–53). This blue band, shaped more like a ray (indicated by arrows in Fig. 45), runs between the splits of two vein pairs: Rs with M₁ and M₃ with Cu₁ (yellow arrows in Fig. 45b), in most taxa spilling into the base of the cell M₃–Cu₁ (pink arrow in Fig. 45c) and possibly into the base of the cell Rs–M₁ (upper pink arrow in Fig. 45d). Evans (1951: 53) partitioned *J. hewitsonii* into five subspecies. He used the widths of the discal white band and a doublet of postdiscal spots on the forewing and the form and appearance of the submarginal band on the dorsal hindwing as the main characters to differentiate among the subspecies. The first and the northernmost subspecies, recorded from Panama, Colombia, and Venezuela, Burns later recognized as a distinct species, *J. pater* Evans, 1951, owing to the differences in genitalia valvae between it and other taxa (Burns and Janzen 2001). In a series of 73 type specimens of *J. pater* in the BMNH collection curated by Evans, only one, a female from Panama, has a shorter blue ray (running only from vein 6 [=M₁] to vein 4 [=M₃]) without either of the blue spots at the bases of M₃–Cu₁ and Rs–M₁ cells. In all other *J. pater* specimens we examined, the blue ray intrudes at least into the cell M₃–Cu₁. However, 19 ACG specimens of *Jemadia* lack

the longer blue ray characteristic of *J. pater*; instead, this ray is invariably short and limited to the spaces between veins 6 and 4 and not between 7 and 3. Therefore, these specimens, called “*Jemadia Burns01*” in Janzen et al. (2011), do not key out to *J. hewitsonii* of Evans (1951). They are described here (with the aforementioned female from Panama) as a new species proposed previously without a formal scientific name by Burns and Janzen (2001) and differing from all other *J. hewitsonii* group taxa not only by wing patterns but also by male genitalia and, where known, DNA barcodes (over 5% difference).

Jemadia suekentonmiller Grishin, **new species**

(Figs. 1–14, 45a, 46, 47a, 48a–i, 49, 50 part, 51 part)

Description: Male (n=14, Figs. 1–2, 7–10, 45a, 51 part) – holotype forewing length = 26.5 mm. Forewing triangular, no costal fold; forewing dorsally black with a diagonal discal white band broken by dark veins into 3 spots: (1) trapezoidal, narrower towards costa spot in discal cell, (2) rectangular spot with uneven edges in Cu_1 – Cu_2 cell, and (3) triangular spot with a more or less convex side in Cu_2 –2A cell, with point of this spot not reaching 2A vein; the band medium broad: 2.5–4.5 times longer than wide; a doublet of thinner than the band white postdiscal spots in cells M_2 – M_3 and M_3 – Cu_1 ; a band of four white apical spots with edges aligned along a curve in cells between veins R_3 and M_3 ; white-blue basal band; marine blue postbasal band; a doublet of marine blue elongated spots posteriad and slightly basad of white discal band; submarginal band of marine blue spots in each cell between M_2 and 2A veins, the band continuous with the white apical spots and in contact with the lower of the postdiscal white spots along vein Cu_1 ; marine blue overscaling basad near costa, towards costa from the discal white band, and distad discal cell in some specimens; ventrally similar to dorsal, but paler and more violet in background color, especially basad; basal pale band vestigial, mostly as overscaling and spots (the extreme base of the wing bluish-white); postbasal band paler (almost white), less regular and more diffuse than on the upperside; discal band continuing as bluer spots towards costa to the middle of costal cell, no doublet of marine blue spots near tornus, just some violet overscaling along vein 2A and inner margin as an extension of submarginal marine band; prominent marine blue spot distad discal cell; fringe black. Hindwing narrow, triangular, almost lobed at tornus, termen slightly scalloped between veins Cu_2 and 2A, dorsally black with two pale-blue streaks from the base along Cu_2 and 2A veins, streaks longer than half of the wing, the first streak paler, almost white; marine-blue ray narrowing from the split of veins Rs and M_1 to the split of veins M_3 and Cu_1 ; postdiscal marine blue band thinly separated into spots by darker veins, band narrowing from vein Rs to vein 2A, entering cell 2A–3A as a spot offset basad; violet spot continuous with the band in Sc+ R_1 cell; ventrally similar to dorsal, but the postdiscal marine blue band wider and from costa to anal margin; area along anal margin overscaled with marine blue; no streaks or discal ray, but the base from costa bluish-white, and two longitudinal bands (basal band paler) sometimes connected along vein 2A to form a narrow U, discal band from Sc+ R_1 vein, poorly defined in Sc+ R_1 –Rs cell in some specimens; fringe mostly black, but white mediad in cells near tornus. Head and palpi black above with white-blue spots and bands; below each palp with a wide white longitudinal band continuing on cheeks and pectus, cheeks and pectus otherwise black; antennae black, nudum dark reddish-brown, 18–20 segments (n=5), collar with four blue-white spots, tegulae black with blue-white longitudinal band; thorax above with two marine blue longitudinal bands; abdomen above black with white-blue spots on each side in tergums' anterior, beneath black, white-banded at segments; legs black with white spots and bands. **Male genitalia** (Figs. 46, 47a, 51 part) – tegumen very short, with a pair of as long as tegumen caudal

processes at the base of uncus, processes finger-shaped, directed posterodorsad; uncus more than twice longer than tegumen, dome shaped, divided into two arms, each arm thin and narrow apically and with a flat lateral lobe; gnathos poorly sclerotized and vestigial; saccus lever-shaped, directed dorsad, slightly bulbous at its apex, length as uncus; valva broad, ampulla-costa rounded, convex, without processes, but ampulla more sclerotized at the margin, cucullus more than half as long as the rest of the valva, almost rectangular, cucullus distal end is at about the same height as proximal end, cucullus dorsal margin weakly concave, finely dentate; distally, cucullus ventral margin bends dorsad almost at a right angle so that distal margin is nearly straight; sacculus as high as long, with small tooth at distal end of the dorsal margin, which is irregular and serrated anterior to the tooth; juxta very large (as long as phallobase), corner-shaped, bluntly triangular in lateral view, with several ridges; aedeagus about as long as tegumen plus uncus, boomerang-shaped, phallobase close to half of penis length, single triangular cornutus with irregular margin.

Female (n=7, Figs. 3–6, 11–14) – forewing length = 27 to 32 mm, similar to male, but larger, with more rounded, broader wings, outer margin of hindwings with a small, low lobe (absent in males) from M_2 vein to the middle of Cu_1 – Cu_2 cell, nudum 22–25 segments (n=4). **Female genitalia** (Figs. 48a–i) – lamella antevaginalis strongly sclerotized, thick, broad-M-shaped in ventral view and U-shaped in posterior view, expanding into narrowing lateral lobes; lamella postvaginalis membranous and vestigial; antrum sclerotized, slightly wider than ductus bursae; ductus bursae with a weakly bulbous sclerotized enlargement around its middle, continuous with corpus bursae, together about 4 times sterigma length.

DNA barcodes: Barcode sequence of the holotype (voucher 04-SRNP-34396), GenBank accession GU161554, 658 base pairs: AACTTTATATTTTATTTTGGAAATTGAGCAGGAATAATTGGAA CATCTCTTAGATTGCTAATTCGAAGTGAATTAGGAAGCTCCTGA ATCTTTAATTGGAGATGATCAAATTTATAATACTATTGTAAACAGC TCATGCATTTATTATAATTTTTTTTATAGTTATACCAATTATAATT GGCGGATTTGGAAATTGACTAGTCCCCCTTATATTGGGAGCA CCTGATATAGCTTTCCCTCGAATAAATAACATAAGATTTTGTT ATTACCCCTTCATTAAACCTTACTTATTTCGAAGAAGTATCGTAG AAAATGGTGCCGGAAGTGGATGAACAGTTTATCCCCCTCT CTTCATATATCGCACACCAAGGAGCTTCTGTAGATTTAGCTAT TTTTCTTTGCATTTAGCTGGAATTTTCATCAATTTTAGGAGCTA TTAACCTTTATTACAACAATTATCAATATACGAATTAACAAACCTAT CTTTTGACCAATACCATTATTTGTTTGAGCTGTAGGAATTACA GCATTATTATTACTTTTATCACTGCCGTATTAGCAGGAGCTAT TACTATATTATTAACAGATCGAAATATCAATCTCTTTTTTTGA TCCCGCTGCGAGGTGGAGATCCCATTTTATATCAACACTTATT

We also determined barcode sequences of 13 paratypes. Seven of them (voucher codes/GenBank accessions: 10-SRNP-103600/HM884525, 05-SRNP-31969/GU151442, 04-SRNP-32358/GU161555, 04-SRNP-30754/DQ292573, 03-SRNP-21823/DQ292574, 03-SRNP-21528/DQ292575, 01-SRNP-9029/DQ292569) are identical to that of the holotype (except that 01-SRNP-9029 has a single undetermined base pair (bp) “N” within its sequence and is lacking 102 bp from the 3' end) and others show variation within a third of a percent: 1 bp difference (145 C, not T [numbering is from 1 to 658 for the holotype as a reference]) in five sequences (09-SRNP-30034/GU649882, 05-SRNP-31086/GU150502, 04-SRNP-56811/GU150503, 02-SRNP-13059/DQ292570, 00-SRNP-4482/DQ292571), and 2 bp difference (145 C, not T and 592 T, not A) in one (96-SRNP-12846/DQ292572). Several of these sequences lack some segments at the termini. All of these 14 sequences appear monophyletic on all the trees we have seen or built, and the closest available sequence to them is that of *J. pater*, different by 23 bp, which is over 5% (Fig. 50). Additional (and updated) information and neighbor-joining trees can be retrieved by searching the BOLD database (Ratnasingham and Hebert 2007) with the holotype sequence at <http://www.boldsystems.org/index.php/IDS_OpenIdEngine>.

Types: Holotype male has the following rectangular labels: white printed & hand-printed - || Voucher: D.H.Janzen & W.Hallwachs | DB: <http://janzen.sas.upenn.edu> | Area de Conservacion Guanacaste, || COSTA RICA. | 04-SRNP-34396 ||; yellow printed - || LEGS AWAY



FIGS. 1–44. *Jemadia* specimens. 1–12. *J. suerkentonmiller* type specimens (1–2. is the holotype, others are paratypes): Costa Rica: ACC, data in text, elaborated in Janzen & Hallwachs (2013), sexes and voucher codes are: 1–2. ♂ 04-SRNP-34396; 3–4. ♀ 04-SRNP-32358; 5–6. ♀ 04-SRNP-32840; 7–8. ♂ 02-SRNP-13059 (genitalia Figs. 46i–m); 9–10. ♂ 03-SRNP-21528; 11–12. ♀ 04-SRNP-30754. Dorsal and ventral surfaces are shown on odd- and even-numbered figures, respectively. Labels are shown for some specimens between and around the views of a specimen. Labels are reduced by about 1/3 compared to specimens: smaller scale bar below one of the labels refers to labels, and larger scale bars refer to specimens. "F" indicates mirror image (left-right inverted). Pinholes and some other imperfections are digitally removed. Insets numbered with a corresponding figure number and "z" (for zoom) show the details of discal hindwing blue ray near the base of M₃-Cu₁ cell; M₃ on the right indicates where this vein reaches the edge of the inset; vertical gray bar is 1 mm; blue arrow points to an image the insert refers to, except 15z, which (for lack of space) is removed from the image of wings.



FIGS. 1–44 (continued). **13–14.** *J. suekentonmiller* paratype ♀, Panama: Calobre, leg. Arce, Godman-Salvin Collection 1912–23, BMNH(E) #1037694; **15–16.** *J. pater* [holo]type (as deduced by Mielke 2005) ♂, Colombia: Bogota region, BMNH(E) #982078; **17–18.** *J. pater* [para]type ♀, Venezuela, Hewitson Collection 79–69, BMNH(E) #1054222 (genitalia Fig. 48k); **19–20.** *J. pater* ♂ Panama: Darien Prov., Cana (Cerro Pirre), 7° 56'N 77° 43'W, 500 m, 15-Jul-1983, leg. G. B. Small, genitalia X-4830 J. M. Burns 2000 [USNM] (genitalia Fig. 47b); **21–22.** *J. ortizi* ♂ Venezuela: Mérida, S. P. Gabaldon Coll., genitalia X-4848 J. M. Burns 2000 [USNM] (genitalia Fig. 47f); **23–24.** *J. ovid* [holo]type ♂, Ecuador: Paramba, 3500 ft, Apr-1897, dry season, leg. Rosenberg, BMNH(E) #982977; **25–26.** *J. ovid* [para]type ♀, Ecuador: Paramba, leg. Rosenberg, BMNH(E) #1054224 (genitalia Fig. 48j); **27–28.** *J. ovid* ♂ Ecuador: Pichincha Prov., Alluriquín, 700 m, Aug-1973, leg. N. R. Venedictoff, genitalia X-4832 J. M. Burns 2000 [USNM] (genitalia Fig. 47g). Images of BMNH specimens on all figures are copyright Trustees of the Natural History Museum, London; used with permission.



FIGS. 1–44 (continued). **29–30.** *J. cf. albescens* Röber, 1925 ♂, Ecuador: “Environs de Loja”, 1890, E. T. Owen collection, genitalia X-4839 J. M. Burns 2000 [USNM] (genitalia Fig. 47j); **31–32.** *J. cf. albescens* ♀, Ecuador: Zamora, 3000–4000 ft, leg. O. T. Baron, BMNH(E) #1037689; **33–34.** *J. cf. albescens* ♀, Brazil: Rondônia, 62 km S Ariquemes, Fazenda Rancho Grande, 10.53°S, 62.80°W, 165 m, {19–29}-Sep-1996, leg. B. Harris, genitalia NVG121102-39 [USNM] (genitalia Figs. 48l–n); **35–36.** *J. hewitsonii* [syn]type ♂, Brazil: Amazonas, Hewitson Collection 79-69, type H 54, BMNH(E) #982976, round “Type” and square labels are shown in dorsal and ventral views; **37–38.** *J. cf. hewitsonii* ♂, Peru: Pebas, “Amazonas”, 1880, leg. M. de Mathan, BMNH(E) #1037693 (genitalia Fig. 47k); **39–40.** *J. cf. hewitsonii* ♂, Brazil: Amazonas, São Paulo de Olivença, Mar-1962, leg. J. Kesselring, genitalia vial H210 prep. S. S. Nicolay [USNM] (genitalia Fig. 47l); **41–42.** *J. cf. hewitsonii* ♂, Brazil: Matto Grosso, Cuiabá, genitalia X-4854 J. M. Burns 2000 [USNM] (genitalia Fig. 47m); **43–44.** *J. cf. hewitsonii* ♀, Bolivia: Santa Cruz de la Sierra, 1905/6, leg. J. Steinbach, BMNH(E) #1054212.

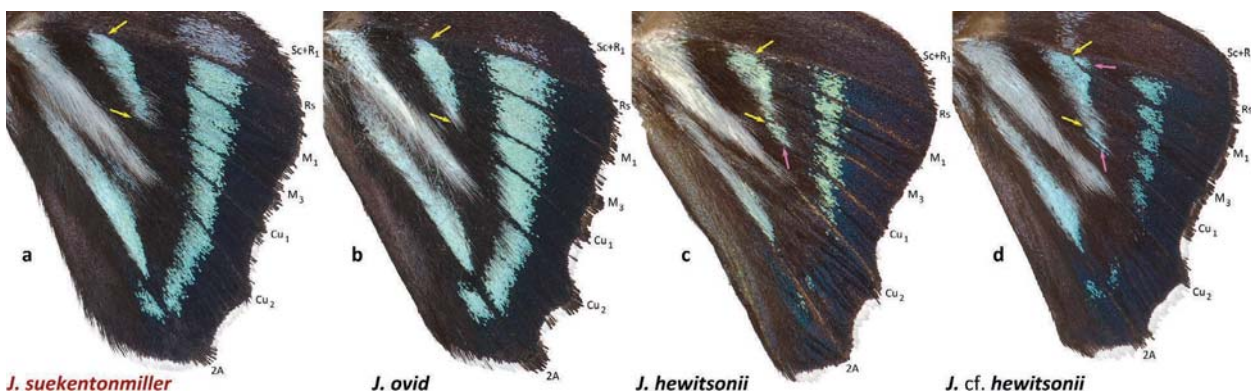


FIG. 45. Discal blue ray on dorsal hindwing of *Jemadia* males. Three observed ray types are shown: **b**, no patches of blue scales at either base of R_s-M_1 cell and M_3-Cu_1 cell (specimen Figs. 27–28); **c**, blue spot at the base of M_3-Cu_1 cell, no spot at the base of R_s-M_1 cell (specimen Figs. 35–36); **d**, blue spots at both cell bases (specimen Figs. 39–40). Veins are labeled along the outer margin. Pink arrows point at spots, yellow arrows point at the splits between R_s and M_1 veins and between M_3 and Cu_1 veins. **a**, *J. suekentonmiller* ray is of a type shown in **b**, i.e., no spots at either base (specimen Figs. 9–10). Images not to scale, but rescaled to be similar in size and are edited to digitally remove wear and imperfections in specimens.

|| FOR DNA ||; red printed - || HOLOTYPE ♂ | *Jemadia* | *suekentonmiller* | Grishin ||. Holotype data: Costa Rica: Area de Conservación Guanacaste, Guanacaste Province, Sector Pitilla, site Sendero Cuestona, 10.99455 -85.41461, 640 m, collected on 12-VIII-2004 as pupa on *Casearia arborea* (Salicaceae) by Calixto Moraga, adult eclosed 08-Sep-2004, voucher code 04-SRNP-34396. Since the holotype is from a wild-caught pupa, its size is more in line with the norm for the species, and not reduced as for most adults reared from caterpillars. **Paratypes:** 13 ♂♂ and 7 ♀♀. Costa Rica, Area de Conservación Guanacaste: Guanacaste Province, Sector Pitilla, reared from caterpillars feeding, or collected as pupae, on *Casearia arborea* (Salicaceae), plus one adult: site Estación Pitilla, 10.98931 -85.42581, 675 m: 1♂ collected as adult on 17-III-2005, voucher code 05-SRNP-31086; 1♀ collected on 16-VI-1996 as antepenultimate instar, adult eclosed on 21-IX-1996, genitalia No. X-4821 J. M. Burns 2000, voucher code 96-SRNP-12846; site Loaiciga, 11.01983 -85.41342, 445 m: 1♂ collected on 29-X-2003 as preantepenultimate instar, adult eclosed on 03-IV-2004, voucher code 03-SRNP-21528; 1♀ collected on 19-VI-2004 as antepenultimate instar, adult eclosed on 04-X-2004, voucher code 04-SRNP-33566; site Sendero Cuestona, 10.99455 -85.41461, 640 m: 1♂ collected on 08-VIII-2004 as pupa, adult eclosed on 01-IX-2004, voucher code 04-SRNP-34305; 1♀ collected on 04-II-2004 as last instar, adult eclosed on 31-III-2004, voucher code 04-SRNP-30754; site Sendero Evangelista, 10.98680 -85.42083, 660 m: 1♂ collected on 23-XI-2000 as preantepenultimate instar, adult eclosed on 10-IV-2001, genitalia No. X-5050 J. M. Burns 2001, voucher code 00-SRNP-4482; 1♂ collected on 06-I-2001 as penultimate instar, adult eclosed on 15-II-2001, genitalia No. X-5883 J. M. Burns 2004, voucher code 01-SRNP-9029; site Sendero Laguna, 10.9888 -85.42336, 680 m: 1♂ collected on 31-V-2005 as antepenultimate instar, adult eclosed on 26-IX-2005, voucher code 05-SRNP-31969; 1♀ collected on 19-V-2004 as preantepenultimate instar, adult eclosed on 12-X-2004, genitalia NVG121102-38, voucher code 04-SRNP-32840; site Sendero Memos, 10.98171 -85.42785, 740 m: 1♂ collected on 06-I-2009 as antepenultimate instar, adult eclosed on 16-III-2009, voucher code 09-SRNP-30034; 1♀ collected on 28-IV-2004 as preantepenultimate instar, adult eclosed on 15-X-2004, voucher code 04-SRNP-32358; 1♂ site Sendero Mismo, 10.98758 -85.41967, 680 m collected on 12-XI-2003 as preantepenultimate instar, adult eclosed on 31-III-2004, voucher code 03-SRNP-21823; 1♂ site Sendero Paleta, 11.00434 -85.41646, 570 m, collected on 23-VIII-2004 as pupa, adult eclosed on 30-VIII-2004, voucher code 04-SRNP-34735; 1♂ site Sendero Rotulo, 11.01355 -85.42406, 510 m, collected on 13-VII-2002 as last instar, adult eclosed on 13-VIII-2002, genitalia No. X-5884 J. M. Burns 2004, voucher code 02-SRNP-13059; 1♂ site

Sendero Trichoptera, 10.98571 -85.41869, 655 m, collected on 14-XII-2004 as antepenultimate instar, adult eclosed on 10-IV-2005, voucher code 04-SRNP-56811; 1♀ collected as adult, genitalia No. X-4822 J. M. Burns 2000, voucher code 98-RIOS-171; 1♂ Alajuela Province: Sector Rincon Rain Forest, site Leiva (Potrero Chaves), 10.939 -85.322, 433 m, collected as adult on 02-IV-2010, leg. J. D. Turner & N. Turner, voucher code 10-SRNP-103600; 1♂ Cartago Province: 3 km WNW of Grano de Oro, 9° 49' 24"N 83° 29' 06"W 1100 m, collected as adult on 15-IV-2006, leg. I. & M. Nakamura, K. Nishida & R. Alverado. 1♀ Panama: [Veraguas Province, 25 km NE of Santiago,] Calobre, [8° 16'N, 80° 49'W per Selander & Vaurie (1962)] [leg.] Arcé, specimen No. BMNH(E) #1037694.

Deposition of types: Holotype is in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Two paratypes (09-SRNP-30034 & from Panama: Calobre) are in the Natural History Museum, London, UK (BMNH). Two paratypes (04-SRNP-34305 & 04-SRNP-33566) are deposited in the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL (MGCL). One paratype (from Costa Rica: Cartago Prov.) is in Ichiro Nakamura collection. All other paratypes are in USNM.

Type locality: COSTA RICA: Area de Conservación Guanacaste, Guanacaste Province, Sector Pitilla, site Sendero Cuestona, GPS: 10.99455 -85.41461, elevation 640 m.

Etymology: Burns and Janzen (2001) wrote: "... the northernmost member of the *J. hewitsonii* species complex ... is ... in the rainforest of the ACG ... and ... more adults are desired before formal description of this apparent differentiate." The adults are now available, and this spectacular butterfly is named in honor of Susan Miller and Kenton Miller (RIP), in recognition of their 48 years of intense advocacy, planning, legitimizing, and mentoring the national parks of the world, and, specifically, recommending and planning the founding of Parque Nacional Santa Rosa in 1971 (today Sector Santa Rosa), the initial seed of Area de Conservación Guanacaste (ACG), and mentoring and inspiring Alvaro Ugalde and Mario Boza to found

the national park system of Costa Rica. Without their efforts, all known ACG forest habitat for this butterfly would long ago have been logged and agroscaped.

Distribution and phenology: Currently, this rain forest species is known from Costa Rica (Guanacaste, Alajuela and Cartago provinces) and Panama (Veraguas province), and has been reared in Costa Rica to eclose in February, March, April and August, September, October (Janzen and Hallwachs 2013), and two free-flying adults have been collected in March and April. The reasons for peaks and troughs in its phenology are unclear.

Diagnosis: This species belongs to *Jemadia*, because it possesses all the characters of the genus as given in the Evans identification key (1951: 3–4) and is particularly similar to other *J. hewitsonii* group taxa (all treated by Evans as subspecies). COI barcode sequences have been obtained for most species of *Jemadia*, including its type species, *Jemadia hospita* (Butler, 1877) (Fig. 50). The difference between the DNA barcodes of *J. suekentonmiller* and *J. hospita* is close to 10%, and is about the same as differences in many other *Jemadia* species pairs, e. g., *J. hospita* and *J. fallax* (Mabille, 1878) (Fig. 50). Although DNA sequence information about *Jemadia* is still very scarce, it is significant that the tree shown in Fig. 50 agrees very well with morphological evidence (Figs. 1–48, 51 and Warren et al. (2013) with photographs of other species), and that there is no indication of introgression or hybridization between species. Reliable groupings in the tree agree with the structure of Evans's (1951) identification key, e.g., all *J. hewitsonii* group taxa form a monophyletic group. Moreover, each of two pairs of species that are next to each other in his key, i.e., *J. hospita* (in which Evans included *J. pseudognetus* (Mabille, 1878) as a subspecies) plus *J. sosia* (Mabille, 1878) and *J. menechmus* (Mabille, 1878) plus *J. scomber* H. Druce, 1908, comprises sister taxa in the tree (Fig. 50).

The new species belongs to the *Jemadia hewitsonii* group by phenotype and by its position in the DNA barcode NJ tree. Taxa in this group can be distinguished from other *Jemadia* by the white-spotted collar and by the dorsal pattern of the hindwing, which consists of: (a) two pale streaks along veins Cu_2 and 2A from the base to at least half of the wing, the first streak paler and the second one bluer; (b) short discal blue ray constrained between veins Rs and Cu_1 and directed from the split of veins Rs and M_1 towards the split of veins M_3 and Cu_1 ; (c) postdiscal blue band approximately following the contour of hindwing outer margin. In other *Jemadia* species groups, either the pale streaks along veins Cu_2 and 2A are absent or short and discal ray is very long,

reaching 2A vein; or the discal ray is absent (Fig. 45).

The new species is distinguished from all other taxa in the *J. hewitsonii* group by the combination of the following characters (the first two are likely diagnostic for facies): (1) discal blue ray on dorsal hindwing is short, only between M_1 and M_3 veins, blue scales do not invade bases of cells Rs– M_1 and M_3 – Cu_1 (Fig. 45a); (2) discal white band on forewing is rather broad, 2.5–4.5 times longer than width (Figs. 1–14); (3) postdiscal blue band on dorsal hindwing is medium to broad, developed in all cells between veins Rs and 3A (Figs. 1–14); (4) cucullus distal end is at about the same height as proximal end (Figs. 46a, i, 47a); (5) cucullus dorsal margin is only slightly concave, more finely dentate; (6) cucullus ventral margin distally bends dorsad almost at a right angle and at the distal end deviates only slightly from a straight vertical line, thus cucullus appears most rectangular of all *J. hewitsonii* group species; (7) dorsolateral process (one on each side) off the distal end of tegumen is long, finger-like; (8) phallobase is short, about half of the penis length; (9) dorsal margin of sacculus near the apical tooth is dentate and irregular, not smooth and ending in a single prominent tooth; (10) saccus slightly bulbous at the apex (for genitalia characters see Figs. 46, 47a). These characters are illustrated in Fig. 51.

Interestingly, *J. suekentonmiller* shares most of these characters (all except 2, 5, 6 & 10) with *Jemadia ovid* Evans, 1951, **new status**, described as a subspecies of *J. hewitsonii* (Fig. 51). Both *J. suekentonmiller* and *J. ovid* have a short discal blue ray (character 1, Figs. 46a, b, yellow arrows) and well-defined postdiscal blue bands (character 3, Figs. 46a, b) on dorsal hindwing, cucullus distal end the same height as proximal end (character 4, Figs. 46a, g); long tegumen processes (character 7, Figs. 46a, g, pointed to by a brown arrow); short phallobase (character 8, Figs. 46a, g, measurements indicated by green marks and ratios shown in green numbers); and several teeth at the dorsal margin of sacculus (character 9, Figs. 46a, g, shown as insets “z”). Preliminary analysis of female genitalia (Fig. 48) shows that both the new species and *J. ovid* are characterized by narrower lamella antevaginalis near the antrum than that of both *J. pater* and *J. cf. hewitsonii*. While we did not obtain DNA sequences of *J. ovid*, we suspect that these extensive phenotypic similarities indicate that *J. suekentonmiller* is its Central American sister. Because of these similarities with the new species, as thus different from all other *J. hewitsonii* group taxa (*J. pater* and *J. ortizi* included), we treat *J. ovid* as a distinct species rather than a subspecies, in-line with the conclusions of Burns and Janzen (2001) who wrote: “Consideration of the color-pattern characters . . . ,

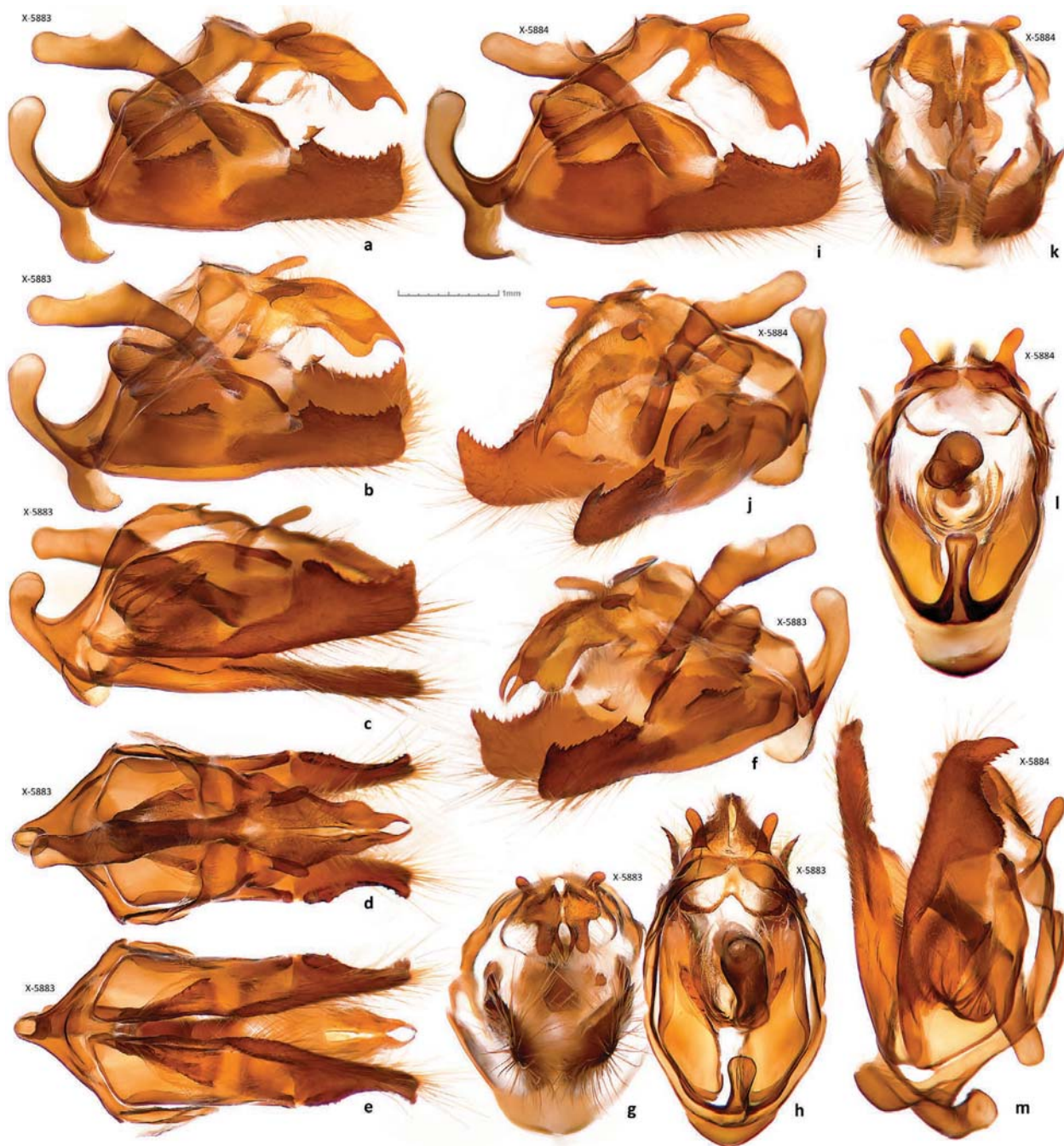


FIG. 46. Male genitalia of *Jemadia suekentonmiller*. Genital capsule of paratypes, Costa Rica: ACG, data in text. Genitalia Nos. and voucher codes: **a–h**, X-5883 J. M. Burns, 01-SRNP-9029; **i–m**, X-5884 J. M. Burns, 02-SRNP-13059 (specimen Figs. 5–6). Views: **a, i**, left lateral; **b**, dorsolateral; **c, m**, lateroventral; **d**, dorsal; **e**, ventral; **f, j**, posterolateral; **g, k**, posterior; **h, l**, anterior. Specimens are in USNM.



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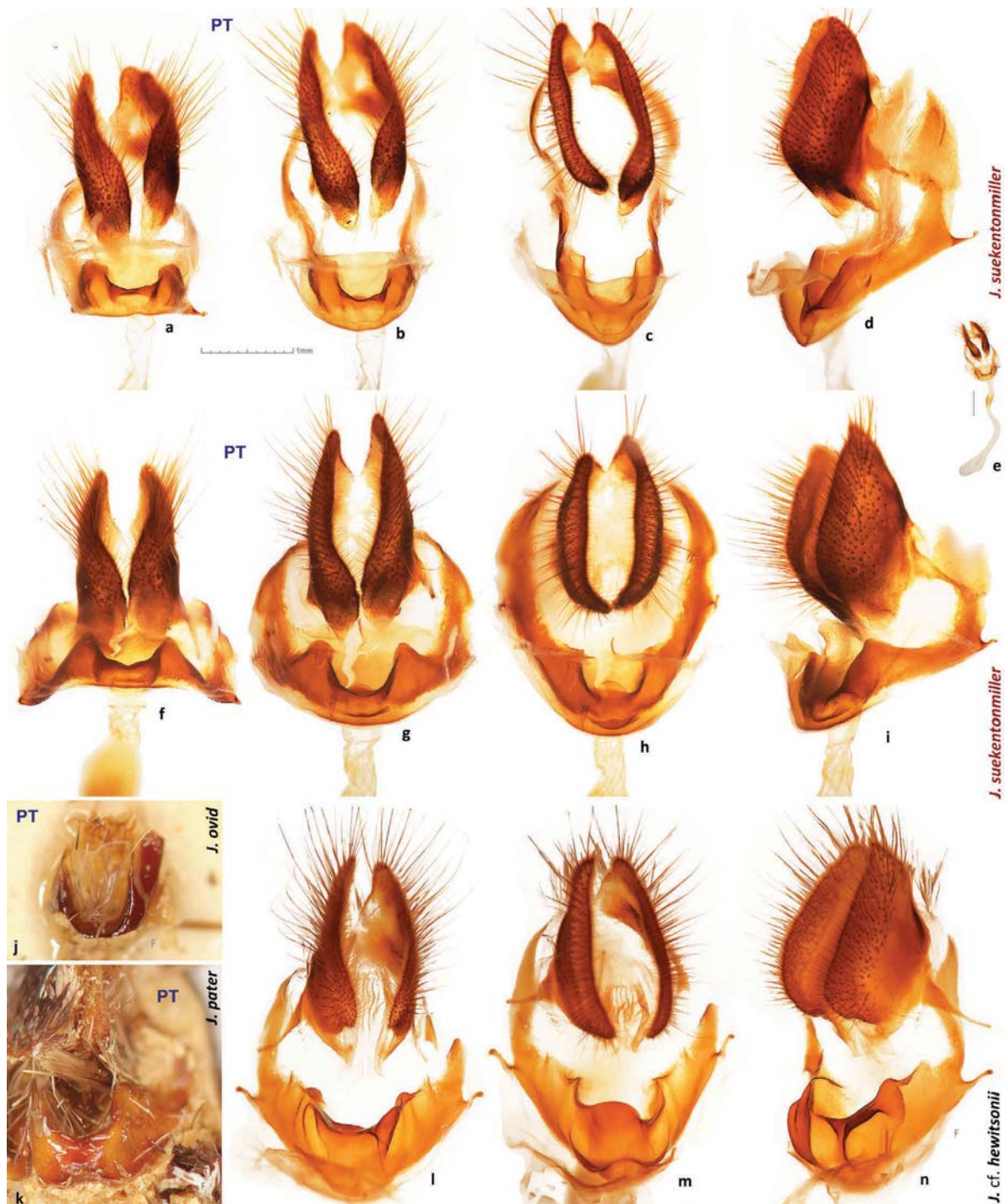


FIG. 48. Female genitalia of *Femadia hewitsonii* group species. **a–i.** *J. suekentonmiller* n. sp. paratypes, Costa Rica, ACG, data in text, genitalia Nos. and voucher codes: **a–e.** X-4821 J. M. Burns, 96-SRNP-12846 and **f–i.** X-4822 J. M. Burns, 98-RIOS-171; **j.** *J. ovid* [para]type, Ecuador: Paramba, leg. Rosenberg, BMNH(E) #1054224 (specimen Figs. 25–26); **k.** *J. pater* [para]type, Venezuela, Hewitson Collection 79-69, BMNH(E) #1054222 (specimen Figs. 17–18); **l–n.** *J. cf. hewitsonii*, Brazil: Rondônia, 62 km S Ariquemes, Fazenda Rancho Grande, 10.53°S, 62.80°W, 165 m, {19–29}-Sep-1996, leg. B. Harris, genitalia NVG121102-39 [USNM] (specimen Figs. 33–34). Views: **a, f,** ventral; **b, g, l,** posteroventral; **c, h, j, m,** posterior; **d, i, n,** ventrolateral; **k,** lateroventral; **e.** reduced image of complete genitalia, scale shows 1 mm. **j.** is dry genitalia glued to carton card; **k.** is shown in situ, the end of abdomen with genitalia exposed, others are wet preparations stored in glycerin. “F” indicates mirror image (left-right inverted). Images of BMNH specimens are copyright Trustees of the Natural History Museum, London; used with permission.

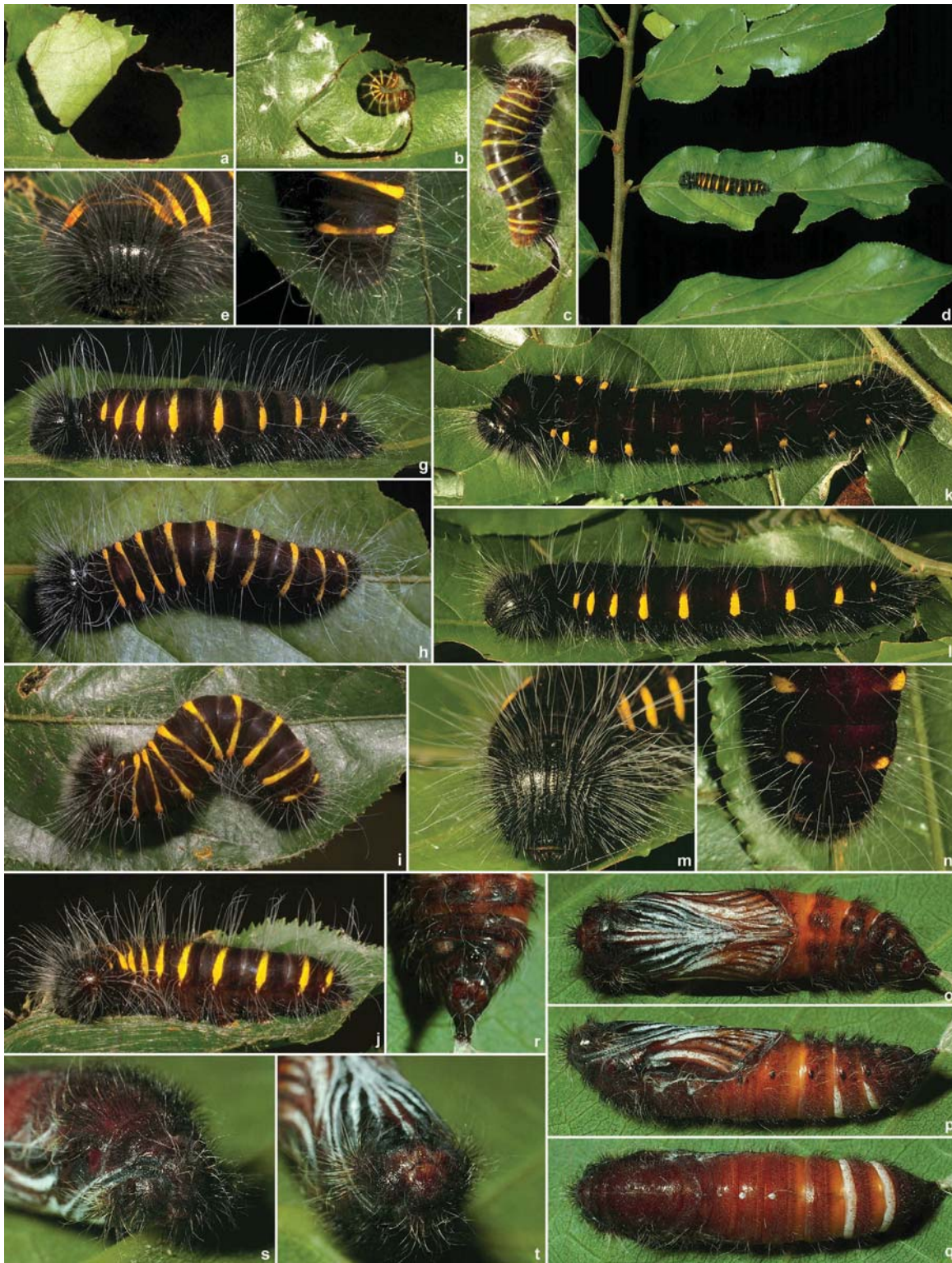


FIG. 49. Immature stages of *Jemadia suekentonmiller*. Costa Rica: ACG: **a–n**. caterpillars: **a–c**. early, **d–j**. penultimate, and **k–n**. ultimate instars; **o–t**. pupa. **a**. leaf shelter, opened in **b**; **e**, **m**. head in anterior view, posterior end in: **f**, **n**. dorsal and **r**. ventral views. Lengths of immatures: **b**. 5 mm, **c**. 8 mm, **e–f**, **i–j**. 27 mm, **d**, **g–h**. 29 mm, **k–n**. 55mm, **o–t**. 41 mm. Images **c**, **e–f**, **m–n** are magnified and **d** is reduced compared to the rest; **h** is a mirror image. Voucher codes: **a–b**, **e–f**, **i–j**. 05-SRNP-41483; **c**. 11-SRNP-31480; **d**, **g–h**. 03-SRNP-21528; **k–n**. 01-SRNP-9029; **o–t**. 02-SRNP-13059; data in text or in Janzen & Hallwachs (2013), together with additional information.

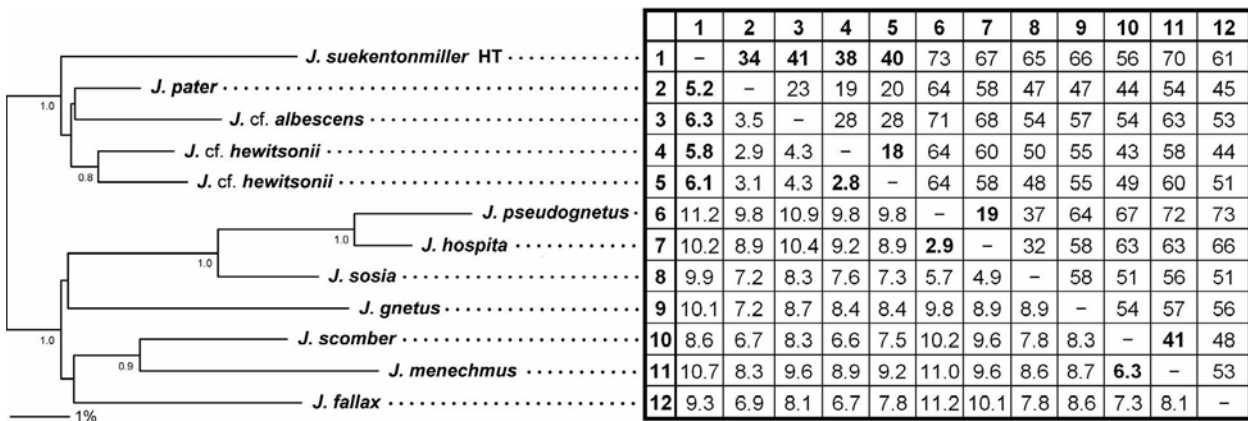


FIG. 50. DNA-derived data. DNA barcode distance matrix is shown on the right and a BioNJ (Dereeper et al. 2008) distance tree corresponding to it is on the left. The scale bar corresponding to about 1% difference is placed below the tree. Fourteen reported *Jemadia suekentonmiller* sequences (Janzen et al. 2011) are nearly identical in sequence and differ from each other by not more than 2 nucleotides (0.3%), thus only the holotype is included in the tree. All sequences used in the tree are the same length of 654 bp. Bootstrap support values of above 0.75 are shown by each node in the tree, nodes without a number represent unreliable groupings. Data for specimens: GenBank accessions, where available (two letters followed by six digits, <http://genbank.gov/>), and voucher codes (with “SRNP” from Janzen & Hallwachs (2013), others from BOLD database (Ratnasingham & Hebert 2007)) are given first: **1.** *J. suekentonmiller* holotype: GU161554, 04-SRNP-34396, Costa Rica: Area de Conservación Guanacaste, Guanacaste, Sector Pitilla, Sendero Cuestona, 10.99455 -85.41461, 640 m, collected on 12-Aug-2004 as pupa by Calixto Moraga; **2.** *J. pater*: N/A, HESP-EB 02 778, Ecuador: Pastaza, Puyo, 10 de Agosto, Palora 3, -1.5 -77.58, 1000, 19-Aug-2011; **3.** *J. cf. albescens* (*J. hewitsonii* *albescens* sensu Evans, 1951): GU662084, HESP-EB 00-402, Peru: San Martin, Rioja-Pedro Ruiz, -5.4 -77.4, 1400 m, 10-Nov-2003; **4.** *J. cf. hewitsonii*: JN278044, HESP-EB 02084, Brazil: Para, Belem, 50 km E-NO from Belem, Santo Antonio do Taua, -1.0908 -48.0745, [20–27]-Oct-2009; **5.** *J. cf. hewitsonii*: N/A, BC-OM 37.188, Brazil: Rio de Janeiro, Barra do Sao Joao, 17-Oct-1986, leg. K. Brown; **6.** *J. pseudognetus*: JGU150506, 05-SRNP-4395, Costa Rica: Area de Conservación Guanacaste, Alajuela, Sector San Cristobal, Puente Palma, 10.9163 -85.37869, 460 m, collected on 30-Jul-2005 as penultimate instar by Gloria Sihezar; **7.** *J. hospita*: HM394394, HESP-EB 00 282, Bolivia: La Paz, Caranavi-Corioco, -16.0 -67.35, 1400 m, 01-Oct-2008; **8.** *J. sosia* (sensu Evans, 1951): GU662267, HESP-EB 00 246, Peru: San Martin, “Mina de Sal”, 1900 m, 01-Jun-2007; **9.** *J. gnetus*: N/A, HESP-EB 02 624, Ecuador: Pastaza, Puyo, 10 de Agosto, -1.23 -77.52, 1000 m, 13-Jan-2011; **10.** *J. scomber*: HM394769, HESP-EB 01 028, Peru: Huanuco, Tingo Maria, -9.17 -75.59, 650 m; **11.** *J. menechmus*: HM422905, HESP-EB 00-403, Bolivia: La Paz, Caranavi, -15.5 -67.33, 750 m; **12.** *J. fallax*: GU662256, HESP-EB 00 230, Ecuador: Napo, Misahualli/Lita, -1.02 -77.4, 01-Jul-2008. The tree shown is unrooted and a confident position of the root could not be obtained. The tree is bent (i.e. the “[–]-shaped branch that does not necessarily imply the root position, is placed) to segregate *J. hewitsonii* group sequences (1 through 5) from the rest. Percent difference and the number of different nucleotides are shown below and above the diagonal in the matrix, respectively. Values corresponding to differences between sister species (two *J. cf. hewitsonii* sister species, *J. pseudognetus* vs. *J. hospita*, and *J. scomber* vs. *J. menechmus*) and between *J. suekentonmiller* and other *J. hewitsonii* group sequences are shown in bold font.

coupled with comparison of . . . genitalia . . . , suggests that several closely related species, rather than subspecies, comprise a *Jemadia hewitsonii* species complex.”

The new species can be distinguished from *J. ovid* by its wider forewing discal band, whose width in *J. ovid* is less than a quarter of its length (character 2, Figs 1–14 vs. 23–28, *ovid* also has a very narrow, mostly streak-like, in males, postdiscal doublet of spots, Fig. 51); narrower postdiscal blue band on hindwings and this band is the broadest in *J. ovid* of all *J. hewitsonii* group taxa; less concave and finer dentate dorsal margin of cucullus, which is deeply concave and distally coarser dentate in *J. ovid* (character 5, Figs. 47a, g, h, i); cucullus being more rectangular in shape rather than more rounded distally in *J. ovid* (character 6, Figs. 47a, g, h, i); saccus looking more bulbous apically, but appearing narrower in *J. ovid* (character 10, Figs. 47a, g, insets “s”).

The next closest species is *J. pater*, which is probably sympatric with *J. suekentonmiller* in Panama (Fig. 51). These two species share the width of the discal forewing white band (not as narrow as in *J. ovid*, character 2, Figs. 1–14 vs. 15–20); cucullus ends being at about the same height (character 4); and slightly bulbous saccus (character 10, Figs. 46a, b, insets “s”). However, seven remaining characters differ between them. Notably, *J. pater* has longer discal blue ray on dorsal hindwing (between veins Rs and Cu₁) and narrower postdiscal blue band; more concave and coarsely dentate dorsal margin of cucullus; more rounded distal end of cucullus, almost turning anteriorly at the distal end; shorter process on tegumen; longer phallobase; and smooth dorsal margin of saccus (Figs. 15–20, 48b–e). Recently described *J. ortizi* Orellana, [2010] is very similar to *J. pater* (Fig. 51), but is characterized by darker palpi and foretarsi (Fig. 22), which are white in *J. suekentonmiller*;



FIG. 51. Visual keys to species in the *Jemadia hewitsonii* group. **a.** *J. suekentonmiller* (paratypes, genitalia are of a different specimen); **b.** *J. ovid*; **c.** *J. pater*; **d.** *J. ortizi*; **e.** *J. cf. albescens*; **f.** *J. hewitsonii* (wings and head are of a syntype); **g.** *J. cf. hewitsonii*. Only dorsal side of wings is shown (males), inset shows ventral side of head and chest (not of the same specimen for **c**). Lateral view of male genitalia is illustrated below the wings (not the same specimens for **a** and **f**). Wings are to scale, genitalia are scaled approximately to match each other in size. Aedeagus for **d** and right valva for **f** are shown detached. Two characters deemed to be most reliable in separating *J. suekentonmiller* are in red font. Wing patterns and genitalia are variable, therefore not all characters shown may hold in all specimens.

even more concave than in *J. pater* distal margin of cucullus, whose distal end is higher than the proximal end (Fig. 48f); and saccus that is even more bulbous at its apex (Fig. 48f inset "s"). Therefore *J. ortizi* appears to be even more distinct from the new species than is *J. pater*.

Other taxa in the *J. hewitsonii* group and unnamed phenotypes, differ by a larger number of characters, both in facies and genitalia, and are illustrated in Figs. 29–44, 45c–d, 47j–m, 48i–n, 50 (part), 51 (part) for comparison. Their taxonomy remains uncertain to us, but interesting differences in genitalia are observed, including, among others, the shape of cucullus and proportions of penis (compare Figs. 47j, k, l, and m), and sacculus dorsal margin (pointed at with pink arrow in Fig. 47). Interestingly, the proportions of penis (with shorter phallobase) are similar to those of *J. suekentonmiller* in some of these taxa (e.g., Fig. 47l). Further work on this group is in progress (O. Mielke, E. Brockmann, and C. Mielke, pers. comm.).

Immatures and foodplants (Fig. 49): In ACG, and probably elsewhere, *J. suekentonmiller* is highly host-specific, with all 68 wild-caught caterpillars having been found feeding on mature foliage of ACG rain forest *Casearia arborea* (Salicaceae). While these caterpillars were 1–4 m above the ground, there may be some in higher foliage not inspected for caterpillars. All *C. arborea* inspected for these caterpillars were growing on road-forest or abandoned pasture-forest edges, a microhabitat that is a facsimile of the margins of natural disturbance sites. While ACG is rich in species of *Casearia*, thousands of caterpillar capture records indicate that *J. suekentonmiller* eats only this one, and does this almost entirely in one band of intermediate elevation rain forest about 25 km long and 1–2 km wide, from the area of Estacion Biologica Pitilla in Sector Pitilla to Estacion Caribe in Sector Rincon Rain Forest (see Sector maps at <http://www.acguanacaste.ac.cr/>).

The first instar caterpillars are parasitized by an undescribed likely host-specific species of *Ogmoelachertus* Schauff, 2000 (Hymenoptera: Eulophidae), and the 2nd–4th instar caterpillars are parasitized by an undescribed likely host-specific species of *Casinarina* Holmgren, 1859 (Hymenoptera: Ichneumonidae). The last instar caterpillars are parasitized by an undescribed species of ACG rain forest *Houghia* Coquillett, 1897 (Diptera: Tachinidae) that specializes in attacking Pyrrhopygini.

The striking black and yellow ringed-to-dotted caterpillar color pattern (Fig. 49) places this hairy caterpillar among a large complex of similarly-colored mimics being described and analyzed elsewhere, in the same spirit as those with false eye spots (Janzen et al.

2010). The semi-hairy pupa ornamented with dark colors and fragmented white waxy overlay, standard for ACG Pyrrhopygini pupae, rather than the false eye spots commonly encountered decorating other ACG Hesperidae pupae (e.g., Janzen et al. 2010), is probably mimicking a rotting and fungus-rich pupa, the consumption of which would be decidedly hazardous to the health of a foraging bird.

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