PHYLOGENY, DISTRIBUTION, AND DESCRIPTION OF A CARIBBEAN SPECIES OF *DICEPOLIA*
(LEPIDOPTERA: CRAMBIDAE)

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Abstract- *Dicepolia nigritinctalis* **sp. nov.** is described from two female specimens from eastern Cuba and Chiapas, Mexico. The new species is most closely related to *D. rufitinctalis* (Hampson) or *D. aerealis* Hayden and occurs on the northern periphery of the range of the genus. Significant range extensions are reported for other species of *Dicepolia* Snellen across central and southern Brazil. A phylogenetic analysis of *Dicepolia* with 36 morphological characters, including two quantitative characters, indicates monophyly of the Malagasy and Neotropical groups and within the latter, monophyly of the small- and large-bodied species groups.

Key words: Neotropics, distribution, phylogeny, continuous data

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INTRODUCTION

The discovery of new distribution records should follow any taxonomic revision, as revisionary diagnoses facilitate recognition and collection. In the present case, important new records of *Dicepolia* Snellen (Lepidoptera: Crambidae: Odontiinae) came to light as the revision was going to press (Hayden, 2009a). The collection of V. O. Becker includes a comprehensive representation of micro- and macrolepidoptera from across the Neotropics. The discoveries reported here include one new species of *Dicepolia* and significant range extensions for the previously described species. The species boundaries are maintained across the expanded distributions. The phylogeny of *Dicepolia* is reconstructed to facilitate the diagnosis of taxa and determine the relationships of the new species.

MATERIALS AND METHODS

Specimens and dissections are deposited in the V. O. Becker Collection (Instituto Uiraçu, Camacan, Bahia, Brazil: VOB), and two of *D. rufitinctalis* (Hampson) in the Carnegie Museum of Natural History (Pittsburgh: CMNH). Other institutional abbreviations are: BMNH, The Natural History Museum (London), CNC: Canadian National Collection (Ottawa), ZMHB: Museum für Naturkunde (Berlin). Habitus images were photographed with a Canon PowerShot Pro1 digital camera with the Super Macro function under tungsten illumination. Abdomens were macerated in hot 10% aqueous potassium hydroxide (KOH), dissected according to standard procedure (Robinson, 1976), stained with Chlorazol Black E, and embedded in Euparal. Slide numbers are listed with the author's preparation sequence (JEH) except where given new BMNH or VOB numbers. Morphological terminology follows Klots (1970) and Maes (1985). Dissections of the new species were photographed with an Olympus Q-Color 3 camera attached to a SZX7 Zoom Stereo Microsope and edited with Adobe Photoshop Elements 6.0, adjusting the resolution and rotation. Other dissections were photomicrographed with a Nikon DX1 digital camera and a Microptics Digital Imaging system (www.microptics-usa.com) and traced in ink on plastic drafting film. Images were either traced with Adobe Illustrator 8.0 (fig. 1a) or scanned and edited with Photoshop to add stipples and dashes and remove blots. Individual images were assembled in single TIFF files, resized, and lettered. Distribution maps were obtained with DIVA-GIS 7.1.6 (Hijmans, 2010) from freely distributed Americas shape files, and locality markers were added with Adobe Illustrator. The maps include previously published specimen records (Hayden, 2009a) and new records (below).

All *Dicepolia* species treated in Hayden (2009a) were included in the phylogenetic analysis, including the Malagasy *D. marginescriptalis* (Kenrick), *D. munroealis* (Viette), and *D. rufeolalis* (Mabille). The outgroups are *Hyalinarcha hyalinalis* Hampson (Papua New Guinea, JEH slides 115♂, 116♀, CNC) and *Trigonoorda* Munroe undet. sp. (JEH slides 124♂, 125♀, CNC). The thirty-six characters (Table 2) are derived from Hayden (2009a), and the matrix (Table 1) was coded with Winclada 1.00.08 (Nixon, 2002). The resulting SS file was saved as a TNT file, to which were added two continuous characters (char. 0: ratio of labial palpi length to eye diameter, and char. 1: forewing length). The data set was analyzed with TNT 1.1 (Goloboff et al., 2008, 2009) by implicit enumeration (command "ie"). Characters were equally weighted and non-additive (unordered) except the continuous characters. To explore the effects of character dependence, sets of linked characters were downweighted by the inverse of the number of characters in each set, as in DaCosta and Weller (2005). Characters and terminals were experimentally deactivated with the "cc]" and "taxcode -" commands. Bremer support values (Bremer, 1988) were calculated from exhaustive searches of suboptimal trees at incremental levels of 0.5 to 4.0 steps. The continuous characters are coded to one decimal place, and Bremer supports are expressed likewise. The synapomorphies were mapped with Winclada (fig. 3). Character states are indicated in the text by "(character:state)."

RESULTS

Dicepolia nigritinctalis Hayden, *sp. nov.*
(Figures 1, 2b)

Description: MALE: unknown. FEMALE (figs. 1a, b): general dorsal color (including frons, thorax, and wings) brownish orange (Cuba) or pale lemon yellow (Chiapas). Frontoclypeus acutely arched. Labial palpi brownish gray in color, 1.3 to 1.5 mm in length (2.3 to 2.7x ocular diameter). Ventral thorax and legs entirely white, except prothoracic leg tibia with mixed gray and white scales. Abdomen color not recorded. Male-specific external characters unknown. *Wings:* forewing length 5.0 to 6.0 mm, width 2.3 to 3.0 mm (Mexican specimen larger). Venation as described for *Dicepolia* (Hayden, 2009a), with hindwing M_2 and M_3 basally approximate, shortly stalked at base. Forewing dorsum with matte luster, brownish orange (Cuba) or pale lemon yellow (Chiapas). Basal 3/5 of costa dark gray. Transverse lines represented by scattered black or dark gray scales partly overlain by orange or yellow scales. Antemedial line faint, complete only in Mexican specimen: strongest on posterior half, extended obliquely distad from costa at 1/3 to posterior margin of cell, then straight and perpendicular to posterior margin of wing at 2/5. Postmedial line from costa at 4/5, curved around discocellar vein (closer to cell than to distal margin), then smoothly curved across CuA_2 and A_{1+2}, extended perpendicularly to posterior margin at 2/3 at level of discocellar. Distal fringe entirely dark gray. Posterior margin with a few small black scales but without tuft of black scales near antemedial line. Hindwings medially smoky bronze or translucent grayish, margins and fringe white; transverse lines absent. *Tympanal organs:* as for Neotropical *Dicepolia* species; bullae tympani not enlarged anteriad nor shallow. *Male genitalia:* unknown. *Female genitalia* (figs. 1c, d): ovipositor moderately long, length of S9 about 1.5 times depth. Ostium bursae unarmed. Colliculum twice as long as wide, without anterior extension on ductus bursae. Ductus seminalis inserted on ductus bursae just anterior of colliculum. Corpus bursae elongate, arachiform (peanut-shaped): posterior half (cervix bursae) rugose, as large as or slightly larger than smooth anterior half, separated from anterior half by very slight constriction. Corpus and ductus bursae without appendices. One signum present in middle of cervix bursae; signum smooth, entire, squarish, with lateral edges produced in two low triangular flanges or crests. Corpus bursae without field of granules. *Immature stages:* unknown.

Types: HOLOTYPE ♀: "CUBA: Col. BECKER / 71827", "CUBA: Holguin / Pin. Mayari / 640m vii.1990 / V.O. Becker", [orange label] "Comp. c/ Col. / USNM 1992 / V.O. Becker", "J.E. Hayden slide no. 617♀", "VOB 5154". PARATYPE ♀: "Col. BECKER / 109813", "MEXICO: Chia / El Chorreadero / 680m 12.vi.1997 / V.O. Becker Col.", [orange label] "Comp. c/ Tipo / USNM 1999 / V.O. Becker", "J.E. Hayden slide no. 628♀", "VOB 5155". Both deposited in VOB.

Etymology: This species is named for the uniformly dark gray distal forewing fringe, which is contrasted with the pale orange or yellow forewing ground color.

Diagnosis: Small-bodied, forewing length 5.0–6.0 mm. Dorsal color orange or pale yellow, with matte luster, not glossy. Distal fringe of forewing entirely dark gray, not white or pale. Posterior margin of forewing without scale tooth. Black scales of transverse lines partly obscured by densely packed colored scales. Hindwings smoky bronze, without trace of postmedial line. Hindwing M_2 and M_3 barely stalked, mostly approximate basally. Corpus bursae arachiform, with rugose posterior half equal to or slightly larger than anterior half and separated by slight constriction; appendices absent from corpus and ductus bursae. One smooth, squarish signum with lateral margins produced as two low flanges.

Similar species: *Dicepolia nigritinctalis* resembles *D. rufitinctalis*, *D. aerealis* Hayden, and *D. venezolalis* Hayden in size, color, and female genitalia (Hayden, 2009a). The forewing length (5.0–6.0 mm) is smaller than all but *D. rufitinctalis,* and the three species have glossy forewing maculation (*D. vaga* Hayden, *D. cuiabalis* Hayden, and some *D. roseobrunnea* (Warren) have a matte luster like *D. nigritinctalis* but are much larger in size). The newly described species does not have a tuft of black scales on the forewing posterior margin, unlike *D. rufitinctalis* and *D. aerealis*, and the forewing distal fringe is dark gray, unlike the white or pale gray fringe in the other three species. Only *D. rufitinctalis* shares the stalked hindwing M_2 and M_3. The female genitalia are distinctive: the arachiform (peanut-like) shape of the corpus bursae is intermediate between the unconstricted ovoid of *D. rufitinctalis* and the strongly constricted dumbbell of *D. aerealis* (female genitalia of *D. venezolalis* being unknown), and the posterior half is distinctly more rugose than the anterior half (9:1). The smooth, nearly circular signum with two lateral flanges, is unique in *Dicepolia*.

Distribution: Cuba: Holguín Province; Mexico: Chiapas; 640–680 m elevation. Flight period: June, July.

Remarks: Following the homologies posited in Hayden (2009a), the posterior half of the corpus bursae is interpreted to be the cervix bursae (i.e. an expanded ductus bursae), and the anterior half is the corpus bursae sensu stricto. The peanut-like shape of the corpus bursae is thought to be homologous to the dumbbell shape in *D. aerealis*, where a strong constriction separates the two halves.

The new species would run to couplet 2 in the key in Hayden (2009a). That couplet furthermore should be amended to reflect the absence of the foreleg femoral androconium in *D. aerealis:* it is present only in *D. rufitinctalis* and convergently in *D. roseobrunnea*.

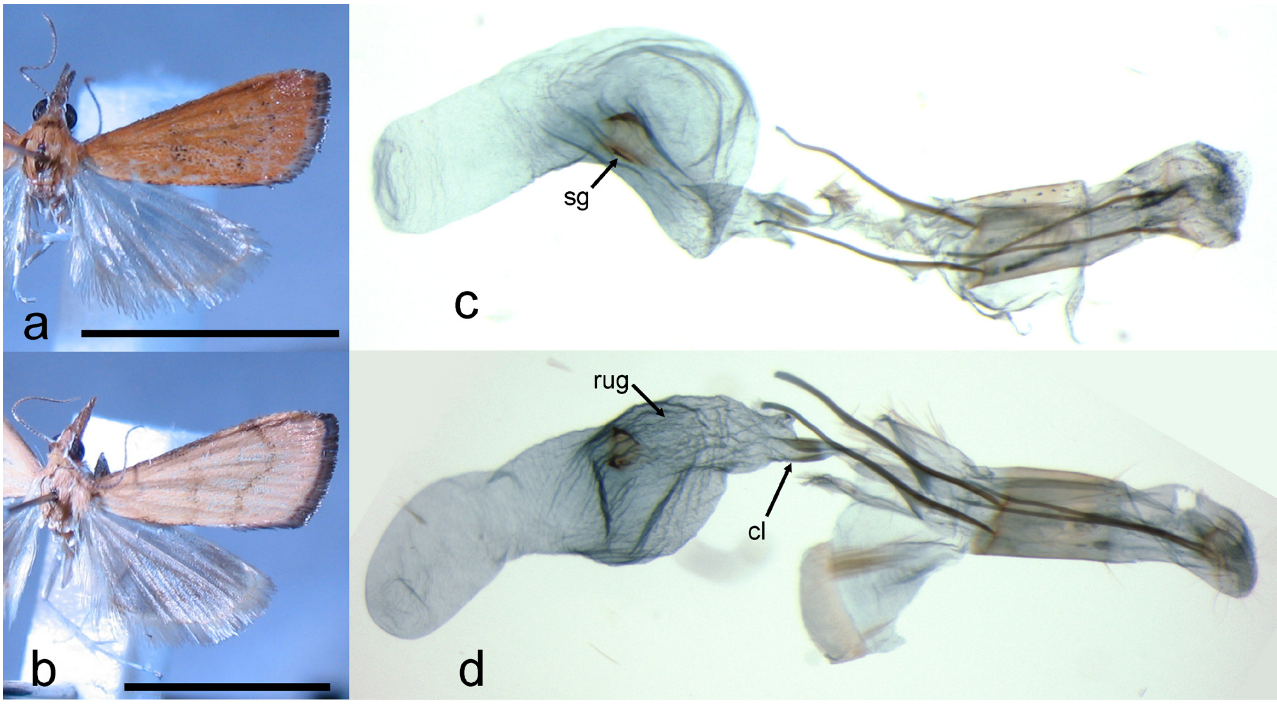

Fig. 1. *Dicepolia nigritinctalis sp. nov.*: **a)** Holotype (Cuba: Holguín) habitus (scale 5mm); **b)** paratype (Mexico: Chiapas) habitus (scale 5mm); **c)** holotype genitalia (VOB slide 5154; scale not available); **d)** paratype genitalia (VOB slide 5155; scale not available). *cl,* colliculum; *rug,* rugosities of cervix bursae; *sg,* signum.

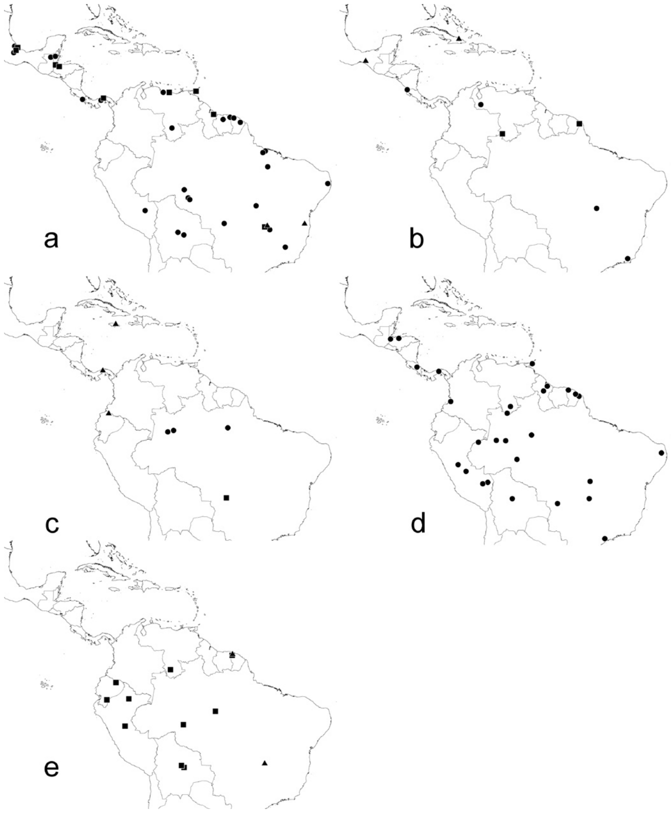

Fig. 2. Distribution of *Dicepolia* species: **a)** *D. rufitinctalis*: circles: form 1 of Hayden (2009a) (males with slender cornutus), squares: form 2 (with robust cornutus), triangles: females with elongate, centipede-like signum; **b)** small, bronzy *Dicepolia* spp.: circles: *D. aerealis*, squares: *D. venezolalis* (where locality can be determined), triangles: *D. nigritinctalis*, **c)** large-bodied *Dicepolia* spp.: circles: *D. amazonalis*, square: *D. cuiabalis*, triangles: *D. vaga*; **d)** *D. roseobrunnea*; **e)** squares: *D. artoides*, triangles: *D. bicolor*.

Species distributions

Numerous specimens of described species representing new distribution records were found in the VOB. Some represent significant range extensions across the Neotropics. No records were found for *D. amazonalis* Hayden, *D. cuiabalis, D. vaga,* or *D. venezolalis*. Specimen-level label data are as follows.

D. aerealis Hayden (fig. 2b).—**BRAZIL, GO:** 1♂: “Col. BECKER / No 21940”, “Ilha do Bananal / Goiás, BRASIL / 4-8.IX.1977 / V.O. Becker col.”, “VOB 5150”; **BRAZIL, RJ:** 1♀: “Col. BECKER / 85911”, “BRASIL: RJ / Nova Friburgo / 800m 22.i.1993 / V.O. Becker Col”, [orange label] “Comp. c/ Col. / USNM 2002 / V.O. Becker”, “VOB 5151”.

D. artoides Hayden (fig. 2e).—**BRAZIL, RO:** 4♂♂: “Col. BECKER / 62951”, “BRASIL: RO / Porto Velho / 180m 24.iv- / 12.v.1989 / V.O. Becker”, [orange label] “Comp. w. Col. / USNM 1998 / V.O. Becker”. **ECUADOR:** 1♂: “Col. BECKER / 102534”, “ECUADOR: MORONA / Gualaquiza, 900m / 19.xii.1992 / V.O. Becker Col.”, [orange] “Comp. w. Col. / USNM 1998 / V.O. Becker”.

D. bicolor Hayden (fig. 2e).—**BRAZIL, DF:** 1♂: “Col. BECKER / 58365”, “Planaltina, DF. / BRASIL - 1000m / 3.VIII.1986 / V.O. Becker col. / [on left side:] 15˚35’S / 47˚42’W”, “VOB 5149”. 1♂: same data except “58577,” “26.VIII.1986,” and [orange label] “Comp. w. Col. / USNM 1998 / V.O. Becker”, “6858.60.” (not dissected).

D. roseobrunnea (Warren) (fig. 2d).—**BRAZIL, GO:** 1♂: “Col. BECKER / 52832”, “BRASIL: GO / Goiás, 500m / 13-15.x.1984 / V.O. Becker col”; 1♂: “Col. BECKER / 64192”, “BRASIL: GO / Ilha do Bananal / 200m Rio Javaré / 14-19.ix.1985 / V.O. Becker col.”. **BRAZIL, RO:** 3♂♂: “Col. BECKER / 62341”, “BRASIL: RO / Porto Velho / 180m 24- / 30.iv.1989 / V.O. Becker”, [1 male with orange label] “Comp. w. Col. / USNM 1998 / V.O. Becker”. **COSTA RICA:** 1♀: “Col. BECKER / No 29770”, “Turrialba, Costa Rica / 600m / 25.XI.1972 / V.O. Becker col.”, [yellow label] “Comp. c/Col. / BMNH 1979 USNM 1981 / V.O. Becker”, [orange label] “Comp. w. Col. / USNM 1998 / V.O. Becker”, [orange label] “Comp. c/ Col. / USNM 2002 / V.O. Becker”, “VOB 5148” (♀). **GUATEMALA:** 4♀♀: “Col. BECKER / 125186”, “GUATEMALA: Izab. / 30km SE Morales / 700 - 1100m / 14˚50’N-88˚40’W / 1-2.viii.2000 / V.O. Becker Col.”

D. rufitinctalis (Hampson) (fig. 2a).—**BELIZE:** 1♂: “BELIZE: Orange Walk Dist. / Rio Bravo Base Camp, / 17 Apr 1995, J.A. Shuey / Rainforest edge, / UV light. Site 413171”, “JEH Slide No. 875♂”; 1♂: “BELIZE: Toledo / Punta Gorda / H. S. Parish”, “JEH Slide No. 876♂” (CMNH). **BRAZIL, BA:** 1♀: “Col. BECKER / 106242”, “BRASIL: BA / Camacan, 600m / 15.xi.1995 / V.O. Becker Col”, “VOB 5153”. **BRAZIL, DF:** 1♂: “Col. BECKER / 56807”, “Planaltina, DF. / BRASIL - 1000m / 15.IX.1984 / V.O. Becker col. / [on left side:] 15˚35’S / 47˚42’W”; 2♂♂: same data except “56808” and one dissected, “VOB 5152”; 1♀: same data except “57862” and “25.IX.1985”. **BRAZIL, GO:** 1♀: “Col. BECKER / 48587”, “BRASIL: GO / Ilha do Bananal, Rio Javaré, 200m / 7.IX.1982 / V.O. Becker col.” **BRAZIL, MA:** 1♂: “Col. BECKER / 77278”, “BRASIL: MA / Açailandia, 150m / 19-27.xi.1990 / V.O. Becker & G.S. Dubois col.” **BRAZIL, MG:** 1♀: “Col. BECKER / No 15105”, “Sete Lagoas, MG / BRASIL - 720m / 19.VIII.1969 / V.O. Becker col.”; 1♀: same data except “No 15106”; 1♀: “Col. BECKER / No 15108”, “Sete Lagoas, MG / BRASIL - 720m / 7.IX.1969 / V.O. Becker col.”; 1♂: same data except “No 15107” and label “[orange] Comp. c/Col. / BMNH 1979/81 / V.O. Becker”; 1♀: “Col. BECKER / 59806”, “BRASIL: MG / Unaí, 700 m / 16.X.1988 / V.O. Becker col.”, “[orange] Comp. c/Tipo / USNM 1999 / V.O. Becker”. **BRAZIL, MT:** 1♂: “Col. BECKER / 93884”, “BRASIL: MT/ Chapada dos / Guimarães, 800m / 20.xi.1994 / V.O. Becker Col”. **BRAZIL, PA:** 1♀: “Col. BECKER / 53291”, “BRASIL: PA / Belém, 20m / 10-15.xi.1984 / V.O. Becker col”. **BRAZIL, RO:** 1♂: “Col. BECKER / 62941”, “BRASIL: RO / Porto Velho / 180m 24- / 30.iv.1989 / V.O. Becker”; 1♀: “Col. BECKER / 88547”, “BRASIL: RO / Cacaulândia, 140m / 15-18.x.1993 / V.O. Becker Col”.

Phylogenetic analysis

Two cladograms were found with 76.7 steps (CI = 0.60, RI = 0.65; figure 3), differing only in whether *D. nigritinctalis* is the sister species of *D. aerealis* (fig. 3a) or of *D. rufitinctalis* (fig. 3b). The new species shares with the former a uniquely constricted corpus bursae (28:1), and with the latter the uniquely stalked hindwing M_2+M_3 (9:1). For both characters, CI and RI = 1.0 in one cladogram, and CI = 0.5, RI = 0.0 in the other. The basal split in *Dicepolia* is between the clades of Neotropical (*N*) and Malagasy (*M*) species; clade *N* is poorly supported (BS = 0.3), and clade *M* is well-supported (BS = 3.9). The Neotropical clade includes two groups: the small-bodied yellowish species (clade *S*) and the generally large-bodied species characterized by an extension of the colliculum along the ductus bursae (char. 33:1, clade *C*). Characters were coded after the descriptions in Hayden (2009a) except as follows: *D. rufitinctalis* has an attenuate valve apex, and *D. venezolalis* has a rudimentary row of hairs on the A8 pleuron.

Counting all possible states that add 0 steps when applied to *D. nigritinctalis* on either tree (Hayden, 2009b), the male of the species is predicted to have genitalia generally like those of *D. aerealis* and *D. rufitinctalis*. There is less certainty about the presence of the foreleg androconium (5:0 or 1) and of the A8 pleural hair ridge (15:0 or 1), the shape of the S8 posterior edge (19:0 or 1), and the length of the phallus (short or long, 27:1 or 2).

Three nodes have Bremer support values less than 1.0: all *Dicepolia* (clade *D*), clade *N*, and clade *S*. Deactivation of the two continuous characters results in six cladograms of 64 steps, including the two original trees plus four trees (not shown) where *D. nigritinctalis* clusters with the outgroups, the

Table 1. Matrix of 36 characters for analysis with TNT. Letter substitution: A = 0 or 1, B = 1 or 2.

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&[continuous]
Trigonoorda_sp      ? ?
H_hyalinalis        ? ?
D_rufeolalis        2.2 11.4-11.9
D_marginescriptalis 2.2 13.0
D_munroealis        3.2 12.0
D_artoides          2.9-3.5 7.0-8.8
D_bicolor           1.8-2.2 6.1
D_vaga              2.0-3.3 8.6-10.8
D_roseobrunnea      1.8-2.9 7.2-10.3
D_cuiabalis         2.8 9.0
D_amazonalis        1.8 7.8-9.0
D_venezolalis       1.9-2.4 6.3-6.9
D_aerealis          1.9-2.7 6.6-8.4
D_rufitinctalis     1.6-2.6 5.1-7.2
D_nigritinctalis    2.3-2.7 5.0-6.0
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```
&[numeric]
                        5    10   15   20   25   30   35
                        |    |    |    |    |    |    |
Trigonoorda sp      0100110010000010101110000000-00010
H_hyalinalis        3110110000000110000110000000-01011
D_rufeolalis        011011001011000-1010--101201001011
D_marginescriptalis 411010000011000-0011010012????????
D_munroealis        1?1?00000011??0-10?10110120101000-
D_artoides          211011000100111110011120120111010-
D_bicolor           201000000100111110011120100111010-
D_vaga              1110110011001111100111101200-10111
D_roseobrunnea      11111100A100111110011110120101010-
D_cuiabalis         1B101100110011111001110010????????
D_amazonalis        1B101100110010111001111010????????
D_venezolalis       0B101100000011111101111111????????
D_aerealis          0110111000001111100111111210-0000-
D_rufitinctalis     0011111100001011110111111B00-0001A
D_nigritinctalis    0A1?11010000??????????????10-01010

; hold 5000; cc - 2.35;
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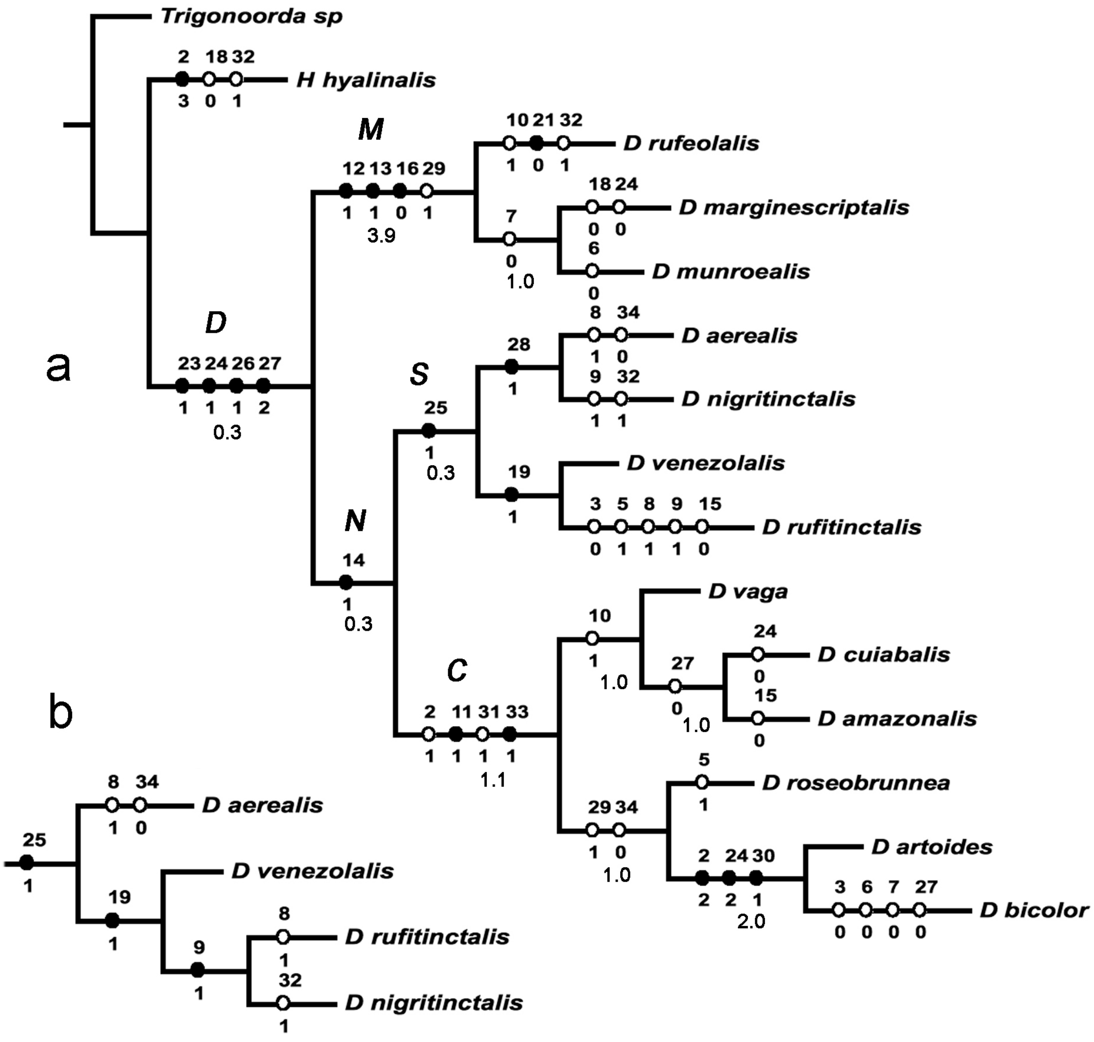

Fig. 3. Phylogeny of *Dicepolia*. **a)** tree one, **b)** clade *S* of tree two. *D, Dicepolia; M,* Malagasy species; *N,* Neotropical species; *S,* small-bodied yellowish species; *C,* species with collicular extension (33:1). Black circles: unique synapomorphies; white circles: homoplastic synapomorphies; Bremer support values below nodes.

rest of the topology being otherwise the same. Deactivation of *D. nigritinctalis* (all characters active) results in the same two trees (72.7 steps), differing only in the topology of clade *S,* and clades *D, N,* and *S* have Bremer supports of 2.0, 1.0, and 1.0 respectively. Four sets of linked characters were experimentally downweighted: characters 16–17, 29–30, and 34–35 were downweighted by 1/2, and 21–23 by 1/3. Inapplicable states were recoded as absent. The resulting two trees were the same as those from equally weighted characters.

DISCUSSION

Dicepolia nigritinctalis occurs along the northern distribution of *Dicepolia.* The species with the closest distribution is *D. rufitinctalis*, the type series of which is from Veracruz, Mexico, north of the Chiapas locality. However, the latter species is not known from the Antilles, despite its widespread continental distribution. *Dicepolia nigritinctalis* is only the second species recorded from the Greater Antilles, after the single Jamaican specimen of *D. vaga* (Hayden, 2009a). The insular specimens of both *D. nigritinctalis* and *D. vaga* do not differ from their continental counterparts in either genitalia or maculation, except the orange versus yellow variation of the former. The Cuban specimen is from Holguín Province, like the distantly related odontiine *Suinoorda maccabei* Hayden (2009b). The recent discovery of both these species underscores the need for research on Antillean Pyraloidea.

The distribution of the new species on the periphery of its closest relatives (figures 2a, b) could be explained by allopatric speciation. Biogeographic analysis was not attempted because the sympatry of other species and their widespread distribution made the delimitation of areas of endemism difficult.

The exact relationship of *D. nigritinctalis* to *D. aerealis* or *D. rufitinctalis* remains ambiguous. Both relationships are supported by one unique synapomorphy: a constricted corpus bursae (with *D. aerealis*) and stalking of hindwing M_2+M_3 (*D. nigritinctalis*). For both characters, the identical values of the consistency and retention indices in either cladogram (unity when the species are grouped, and 0.5, 0.0 when not) do not suggest preference for either relationship. Additional evidence, at least from male specimens, will be required.

The two specimens of *D. nigritinctalis* are remarkably similar, despite the separation in range. They differ only in size (the Chiapas specimen being slightly larger) and maculation. The Cuban specimen is rusty orange, whereas the Chiapas specimen is pale yellow, and in the former, the transverse lines are strongly obscured by the densely packed orange scales. Insofar as the female genitalia are unknown for *D. venezolalis*, it is possible that the two species are conspecific. However, the maculation is quite different (being glossy brassy with a paler forewing fringe and more complete transverse lines), and that species as far as known is restricted to continental South America.

The new specimens of *D. rufitinctalis* vary significantly in maculation, and the genitalic variation noted in Hayden (2009a) recurs across the range. Melanic specimens are present in the VOB, and the single dissected male from Planatina, DF (VOB slide 5152) belongs to "form 2" with a robust cornutus (Hayden, 2009a). A melanic female from Camacan, Bahia (VOB slide 5153, fig. 4p) has an elongate, ribbon-like signum with numerous bilateral projections, like a centipede, unlike the short, oval signum of typical *D. rufitinctalis*; this signum was also found in a non-melanic specimen from the Federal District (Hayden, 2009a). Other specimens vary in the width and intensity of the transverse lines. *Dicepolia rufitinctalis* may comprise a species complex, but at this time, the genitalic variation cannot be associated other sources of evidence. The variation only weakly correlates with geographic distribution, except that the chilopodiform signum is known only from BA and DF, Brazil. However, the new records for *D. aerealis* and *D. bicolor* show that the species may be sympatric across broad ranges, so sympatry should not be taken as evidence against specific distinction in *Dicepolia*. Melanism and other external variation do not correlate with genitalic differences or with elevation, and as yet there is no way to associate the male and female forms. No dissected specimens show intermediate morphology, such as with cornuti or signa of intermediate size. The solution to the problem, including association of sexes, may require molecular, larval, and ecological evidence.

The similarity of the specimens across the substantially expanded ranges corroborates the species boundaries. *Dicepolia aerealis* (fig. 2b, circles) was previously known only from Costa Rica and Venezuela. The Nova Friburgo record is the second-southernmost record for any *Dicepolia*, after one specimen of *D. roseobrunnea* from São Paulo (Staudinger Collection, ZMHB; E. G. Munroe slide 3040). The specimens do not differ from northern *D. aerealis*: in addition to maculation, the male lacks the foreleg androconium found in *D. rufitinctalis,* and the female corpus bursae lacks a signum and is divided by a very narrow medial stricture. *Dicepolia bicolor* was described from St. Jean de Maroni, French Guiana (undated but before 1939, Rothschild Collection, BMNH). The new specimens from the Federal District of Brasil (fig. 2e: triangles) are identical in genitalia, and the maculation differs only in the narrower width of the pale medial fascia. As with *D. aerealis*, the similarity of specimens across the distribution confirms the species's status. The new Ecuadorean specimen of *D. artoides* is very large (forewing length 9mm, width 5mm), but the characters are otherwise the same. The results illustrate the importance of collecting across broad geographic areas.

Dicepolia (clade *D*) is diagnosed from the two outgroups by four uniquely derived synapomorphies: phallus distinctly spiralled (26:1, all species), presence of small fields of fine hairs (piluli) on posterolateral corners of male S8 (23:1, absent in *D. rufeolalis*), vinculum flat or medially emarginate (24:1, rounded or laterally angled in a few derived species), and presence of one elongate cornutus at least half the length of phallus (27:2, fig. 4j: *cr,* may be short in *D. rufitinctalis* and *D. venezolalis*, or absent in some large-bodied Neotropical species). These characters are unobserved for *D. nigritinctalis*. The most reliable of these characters is the spiralled phallus, which is present in all species and contrasts with the straight or slightly curved phallus of other Odontiinae. The forewing color (yellow, orange, rosy brown or glossy brown) also reliably distinguishes *Dicepolia* from most odontiines except the Southeast Asian *Trigonoorda* and *Irigilla* Swinhoe. The Malagasy *Dicepolia* (clade *M*) are characterized by four synapomorphies, the first three uniquely derived: saccus tympani laterally oblong (12:1) and shallow (13:1); male S8 slightly extended within A7 (by much less than width of S8) (16:0); appendix of ductus bursae present (29:1,

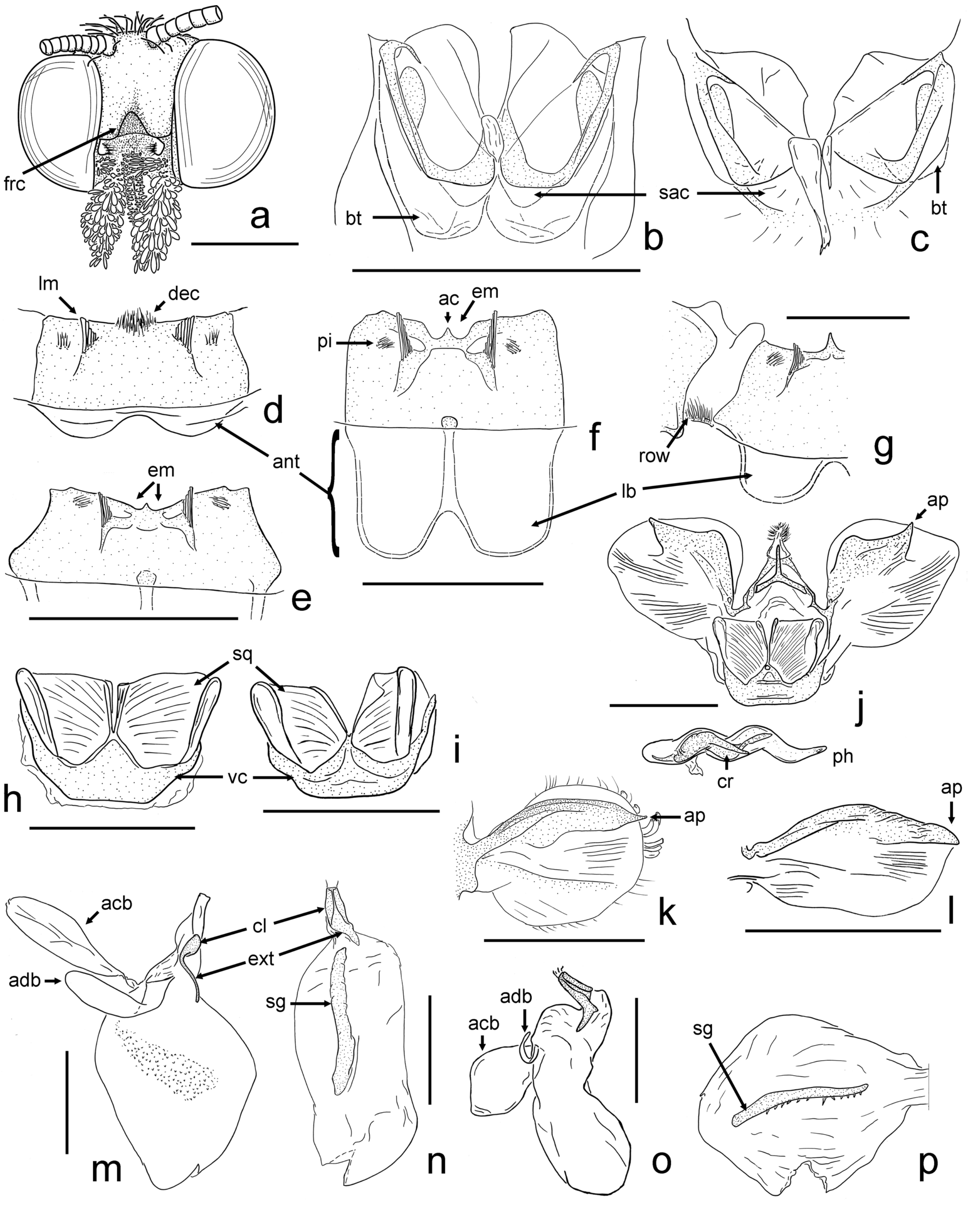

Fig. 4. Characters of *Dicepolia*. Scales = 1.0 mm (not available for *c, d, p*); numbers refer to J.E. Hayden dissections unless indicated. **a)** head, *D. rufitinctalis* (#875); tympanal organs: **b)** *D. rufitinctalis* (#876), **c)** *D. munroealis* (#288); male eighth sternites: **d)** *D. munroealis* (#287), **e)** *D. rufitinctalis* form 1 (#876), **f)** *D. rufitinctalis* form 2 (#875), **g)** *D. roseobrunnea* (#221); vinculum and squamiform structures: **h)** *D. artoides* (#80), **i)** *D. cuiabalis* (BMNH #22135); **j)** male genitalia and phallus, *D. rufitinctalis* form 2 (#247), **k)** *D. aerealis* valva (#360), **l)** *D. artoides* valva (#80); female genitalia: **m)** *D. roseobrunnea* (#223), **n)** *D. vaga* (#517), **o)** *D. artoides* (#22141), **p)** *D. rufitinctalis* (VOB #5153), chilopodiform signum. *ac,* acute medial process; *acb,* appendix of corpus bursae; *adb,* appendix of ductus bursae; *ant,* anterior portion of S8 within A7; *ap,* apex of valve costa; *bt,* bulla tympani; *cl,* colliculum; *cr,* cornutus; *dec,* deciduous hairs; *em,* submedial emarginations; *ext,* extension of colliculum onto ductus bursae; *frc,* frontoclypeal arch; *lb,* lobe of S8; *lm,* lamelliform structure; *ph,* phallus; *pi,* piluli; *row,* row of hairs on A8 pleural membrane; *sac,* saccus tympani; *sg,* signum; *sq,* squamiform structure; *vc,* vinculum.

Table 2. Characters.

0. Ratio of labial palpi length to eye diameter along sagittal axis (continuous).
1. Forewing length along costa (mm, continuous).
2. Forewing color: golden yellow to brownish yellow = 0; reddish orange to brown = 1; partly or completely violet-red = 2; gray = 3; pink = 4.
3. Antennal sensilla: short in both sexes = 0; male sensilla longer = 1; sensilla long in both sexes = 2. Coded as two states if only one sex known.
4. Frontoclypeal margin above proboscis: straight = 0; arched, often angulate (“^”) = 1 (fig. 4a, *frc*).
5. Foreleg androconium: absent = 0; black scales along ventral femur, opposite epiphysis = 1.
6. Forewing medial maculation: clearly lighter medial area (may be narrow), darker termen = 0; medial and postmedial / terminal areas same or similar color = 1.
7. Forewing antemedial line: absent or 1 or 2 small dots = 0; complete or at least a large spot on dorsal edge = 1.
8. Forewing scale tuft on anal margin: absent = 0; present = 1.
9. Hindwing M_2 and M_3: arising separately from cell (may be approximated) = 0; stalked = 1.
10. Hindwing postmedial line: absent = 0; present = 1.
11. Hindwing terminal area suffusion (with or without postmedial line): absent or only the very margin colored = 0; present in terminal area, comparable to width of forewing postmedial line = 1.
12. Saccus tympani, shape: deep and medially rounded (“D”) = 0 (fig. 4b); medially oblong: (“|)”) = 1 (fig. 4c).
13. Saccus tympani, posterior extension: invaginated in S2, slightly to strongly = 0 (fig. 4b); not invaginated, represented by shallow depression = 1 (fig. 4c).
14. S7 scale tuft of male: absent = 0; one medial tuft of smooth scales near posterior margin of S7 = 1. This tuft of narrow, semi-erect scales is not to be confused with the deciduous hairs on the far margin of S8 (char. 20:1).
15. A8 pleural hair row: absent = 0; present, linear in shape = 1 (fig. 4g). Reduced to a few hairs in *D. aerealis, D. venezolalis.*
16. Anterior extension of S8 within A7 (from S7-S8 membrane to anterior costa): short (extended less than half the width of S8) = 0 (fig. 4d, *ant*); long (at least half the width of S8) = 1 (fig. 4f, *ant*). This extension (underneath membrane in figs. 4d–g) is presumed to bear the insertions of genitalic retractor muscles. It varies in length, but it is always short or absent in Odontiinae that lack squamiform and lamelliform structures.
17. If S8 extended within A7 (16:1), then S8 anterior edge division: straight, mono- or weakly bilobate (length of each lobe less than half the width) = 0 (fig. 4f, *lb*); strongly bilobate (depth of each lobe at least half its width) = 1 (fig. 4g, *lb*).
18. S8 posterior median acute projection: absent = 0 (fig. 4d); present = 1 (figs. 4e, f, g, *ac*).
19. S8 posterior margin: straight across = 0 (fig. 4d, g); more or less emarginate = 1 (figs. 4e, f, *em*). The acute projection may be associated with either state.
20. Tuft of deciduous hairs on S8 posterior margin: absent = 0; present = 1 (fig. 4d, *dec*).
21. Lamelliform structures: absent = 0; present = 1 (figs. 4d–g).
22. If lamelliform structures present (21:1), their basis: sessile = 0 (fig. 4d, *lm*); on shoulders or low bumps = 1 (figs. 4e, f, *lm*).
23. If lamelliform structures present (21:1), piluli (fields of small chaetae) near posterior corners of S8: absent = 0; present = 1 (figs. 4d–g, *pi*). Among Odontiinae, these small chaetae are always absent if lamelliform and squamiform structures are absent (hence the inapplicable coding), so they may have some functional role with stridulation. However, they are absent in some cases despite the presence of the apparatus.
24. Vinculum ventral shape: round-bottomed but not medially emarginate = 0 (fig. 4i, *vc*); medially emarginate or flat = 1 (fig. 4j); flat and medially narrow, with lateral thirds distinctly angled from medial third = 2 (fig. 4h, *vc*). Synapomorphy of *D. artoides* and *D. bicolor.*
25. Apex of valve costa: not attenuate = 0 (fig. 4l); markedly attenuate, distinctly narrowing and often directed upward = 1 (figs. 4j, k, *ap*).
26. Shape of phallus: straight or slightly curved = 0; spiral or twisted = 1 (fig. 4j, *ph*).
27. Cornuti: absent, vesica bare or slightly granulose = 0; one short, less than half length of phallus = 1; one longer than half length of phallus = 2 (fig. 4j, *cr*).
28. Shape of corpus bursae: not constricted = 0; constricted like peanut or dumbbell = 1 (figs. 1c, d).
29. Appendix of ductus bursae: absent = 0; present = 1 (figs. 4m, o, *adb*).
30. If appendix of ductus bursae present (29:1), its size: normal = 0 (fig. 4m); reduced = 1 (fig. 4o).
31. Appendix of corpus bursae: absent = 0; present = 1 (figs. 4m, o, *acb*).
32. Rugose pleats on cervix bursae: absent = 0; present = 1 (figs 1c, d, *rug*).
33. Colliculum: simple, cylindrical = 0 (figs. 1c, d); with triangular extension onto ductus bursae = 1 (figs 4m, n, o, *cl, ext*).
34. Signum of corpus bursae: absent or represented by diffuse granules = 0 (figs 4m, o); present, discrete = 1 (figs 1c, 1d, 4n, 4p, *sg*).
35. If signum present (34:1), its shape: round or oval, small = 0 (figs. 1c, d); elongate = 1 (figs. 4n, p).

unknown in *D. marginescriptalis,* paralleled in three derived Netropical species). Clade *N* has the unique synapomorphy of a posteriomedial scale tuft on male S8 (14:1). Clade *S* is characterized by a valve costa with an attenuate apex (25:1, uniquely derived, not observed for *D. nigritinctalis*) and small size (forewing length 6.6–6.9 mm is optimized to the node of clade *S* in one of the cladograms, fig. 3a). The members of clade *C* share reddish orange to brown coloration (2:1, partly or completely violet-red in *D. artoides* and *D. bicolor*), hindwings with the terminal area suffused (11:1, unique and unreversed), presence of an appendix of the corpus bursae (31:1, possibly paralleled in *D. munroealis,* depending on interpretation of the two membranous appendices), and a colliculum with a triangular to elongate extension along the ductus bursae (33:1, unique and unreversed). Although these species are consistently larger-bodied than the members of clade *S,* the large size (forewing length 7.2–9.0 mm) is in fact plesiomorphic.

The two continuous characters were optimized with TNT (they are not mapped in fig. 3 because the version of Winclada used does not support continuous characters). The ratio of palp length to eye diameter (character 0) shows no evolution on either tree, with all internal nodes optimized as 2.2–2.3 mm. Forewing length (character 1) does show change, but it is counted as synapomorphic only if the ranges of the ancestral and daughter nodes do not intersect. Only two internal nodes are characterized by such gaps. The ancestral range of small-bodied clade *S,* 6.6–6.9 mm, evolves from 7.2–9.0 mm of clade *N,* but this occurs in only one tree (fig. 3a). In the other tree (fig. 3b), the range of clade *S* is 6.6–8.4 mm, due to the position of *D. aerealis*, which overlaps with the range of clade *N.* The other gap is probably trivial: 12.0 mm wing length in *D. marginescriptalis* and *D. munroealis* changes slightly from the range 11.4–11.9 mm for clade *M,* but the measurement for the two species was based on small samples.

The analysis with and without the continuous characters convincingly supports the mutual monophyly of the Malagasy and Neotropical groups. Clade *M* is strongly supported (BS = 3.9), and clade *C* moderately so (BS = 1.1). The weak Bremer support of clades *D, N,* and *S* can be explained by the variable position of *D. nigritinctalis*. When the continuous characters are deactivated, the species clusters with the outgroups in some trees. This is evidently due to the absence of information on males, because all the synapomorphies of clades *D, N,* and *S* pertain to male genitalia or androconia. The Bremer values less than 1.0 indicate that only the continuous characters matter for placement of the species. The increase of those values to at least 1.0 when *D. nigritinctalis* is deactivated indicates that those clades are generally well-supported.

Ecological information is available for only one species: *D. roseobrunnea* larvae bore in the oily seeds of *Licania* (oiticica) in northeastern Brazil, attaining pest status in the only studied case (de Oliveira, 1941). Seed-boring is known in several other tropical odontiines and appears to be general (Hayden, 2009b). In the absence of contrary evidence, its predictability in other *Dicepolia* species is not unreasonable, but knowledge of their exact ecology and behavior requires direct observation. A change in larval feeding behavior could explain the size difference that supports the clade of small-bodied species, so these species, especially the widespread *D. rufitinctalis,* should be prioritized for study. The distinct possibility of cryptic species in *D. rufitinctalis* could also be elucidated by ecological information.

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