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GOING FOR A *RIDENS* EVANS (LEPIDOPTERA: HESPERIIDAE: EUDAMINAE): A NEW SPECIES REARED IN AREA DE CONSERVACION GUANACASTE, NORTHWESTERN COSTA RICA

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Abstract.—*Ridens* is a genus of about 20 described species of neotropical skipper butterflies to which we add ***Ridens conservationinternationalis* Burns and Grishin, new species**. We describe it from wild-caught caterpillars, what they eat, pupae, reared adults, genitalia, nuclear and mitochondrial genomes, and the Z chromosome. The type-series of this skipper comes from mid-elevation (510–980 m) rain forest on the Caribbean slope of the Cordillera Guanacaste in northwestern Costa Rica. (One male has been taken in Darien in eastern Panama.) To date, caterpillars have been found on just three species in two genera (*Persea* and *Beilschmiedia*) of Lauraceae. The head of immature stages is unusual with respect to larval color pattern and pupal morphology. Adult facies differs from those of congeners, and male genitalia differ sharply from those of the other species of *Ridens* reared in Area de Conservation Guanacaste (ACG). Three phylogenetic trees based on genomic data show that *R. conservationinternationalis* is well-removed from described species of *Ridens* but close to a similar-looking male of an undescribed species from Peru. (Tangentially, we undo the polytypic status of *R. crison* by reinstating *R. cachinnans* as a species instead of subspecies and newly raising *R. howarthi* from subspecies to species.)

Key Words: caterpillars, facies, foodplants, genitalia, Lauraceae, mitochondrial genome, nuclear genome, phylogenetic trees, pupae, Z chromosome

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What, yet another big undescribed skipper butterfly from Area de Conservacion Guanacaste (ACG), Costa Rica? Yes, this is what you can expect when, for over 40 years, Janzen, Hallwachs, and a growing team of parataxonomists have found many thousands of Lepidoptera caterpillars on their foodplants and reared them in individual plastic bags to adults (Janzen et al. 2009, Bertrand et al. 2014, Janzen and Hallwachs 2016, 2022). Evidence that some of the reared skipper species are new combines classical taxonomic characters of adults with such life history data as ecologic occurrence, caterpillar facies, and foodplant choice—and, more recently, with molecular attributes. For example, facies and genitalia of adults but, especially, disparate caterpillar color patterns, distinguished four new species in the supposedly monotypic genus *Venada* Evans; and mitochondrial COI barcodes recognized these species after their formal description (Burns and Janzen 2005). Later, DNA barcodes were the first clue to the presence of a fifth new species of ACG *Venada* (Burns et al. 2013). Earlier, using some differences in foodplant selection and caterpillar color patterns, coupled with adult size and subtle differences in facies, Burns detected six cryptic species—going under one name, *Astraptes fulgerator* (Walch)—that barcodes, which had just been introduced (Hebert et al. 2003), not only verified but increased by four (Hebert et al. 2004); and barcode and foodplant choice revealed yet another species in 2007. Barcodes covaried with striking differences in foodplant selection to document four cryptic species of *Perichares* Scudder (Burns et al. 2008). More recently, data from Grishin's analysis of genomic DNA covaried with DNA barcode data to distinguish three cryptic species of *Udranomia* Butler that otherwise differed in little more than their ecologic preferences (Janzen et al. 2017).

In the pre-barcode year 2002, Burns compared various species of *Ridens* Evans with specimens of that genus recently reared in ACG and determined that one of the ACG species was undescribed. Since then, it has been called simply *Ridens* Burns01 in the database of Janzen and Hallwachs (2022) and in the neighbor-joining (NJ) barcode trees of the Centre for Biodiversity Genomics at the University of Guelph, Canada. Now, we need a formal designation.

Materials and Methods

Specimens of *Ridens* in the National Museum of Natural History (USNM)—which include reared material from ACG—were examined, and some of their genitalia dissected, put in 12-depression spot plates in glycerin for easy comparison (using a Leitz Wetzlar TS widefield stereomicroscope), and eventually stored in one-dram vials of ethanol. Photographic images of adults and genitalia in Figs. 1–10 were made using the Visionary Digital BK Lab System™ outfitted with a Canon 5D EOS and a Canon 100 mm macro-lens (for adults) and a Canon MP-E 65 mm macro-lens (for genitalia). A series of photographs were taken, then post-processed using Helicon Focus™ to create a single focused image. Pins and pinholes evident in the photos were removed. Forewing length was measured from base to apex with LCD screen digital calipers. DNA work and phylogenetic analyses were carried out as previously described (Li et al. 2019). Workings of the ACG Lepidoptera inventory are fully documented in Janzen and Hallwachs 2011, 2016.

Results

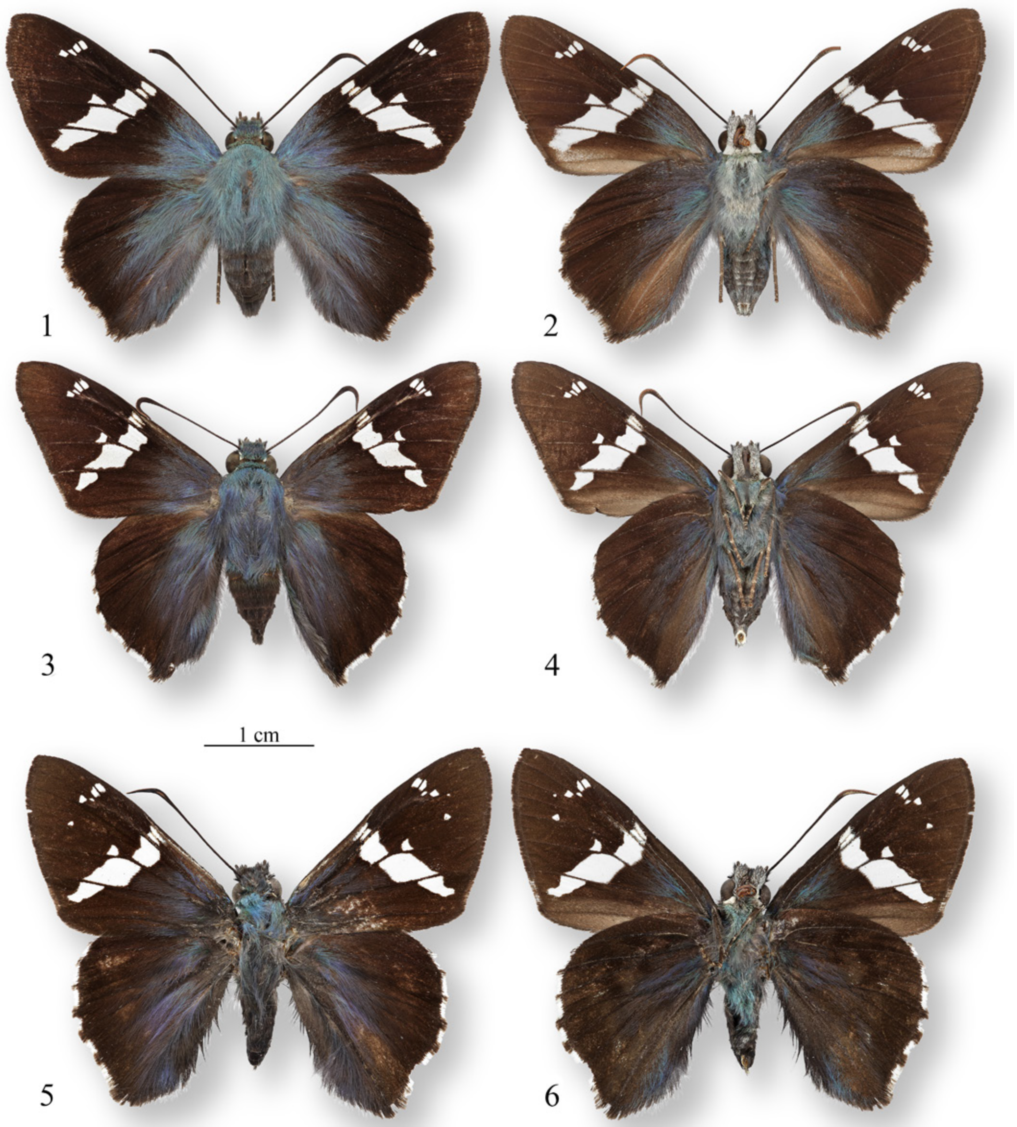
Ridens is a sizable, Neotropical, eudamine hesperiid genus of about 20 described species (Mielke 2005)—with more to come.

Ridens conservationinternationalis Burns and Grishin, new species

http://zoobank.org/66D0A292-0077-4869-B418-637E9CC9DD50

(Figs. 1–15)

Description.— *Size*: Forewing length male 21.45 ± 0.21 SE (19.6–23.0 mm, s = 0.88, n = 18); forewing length female 22.28 ± 0.23 SE (20.6–23.8 mm, s = 0.82, n = 14). (Generally, in Hesperiidae, reared adults average appreciably smaller than

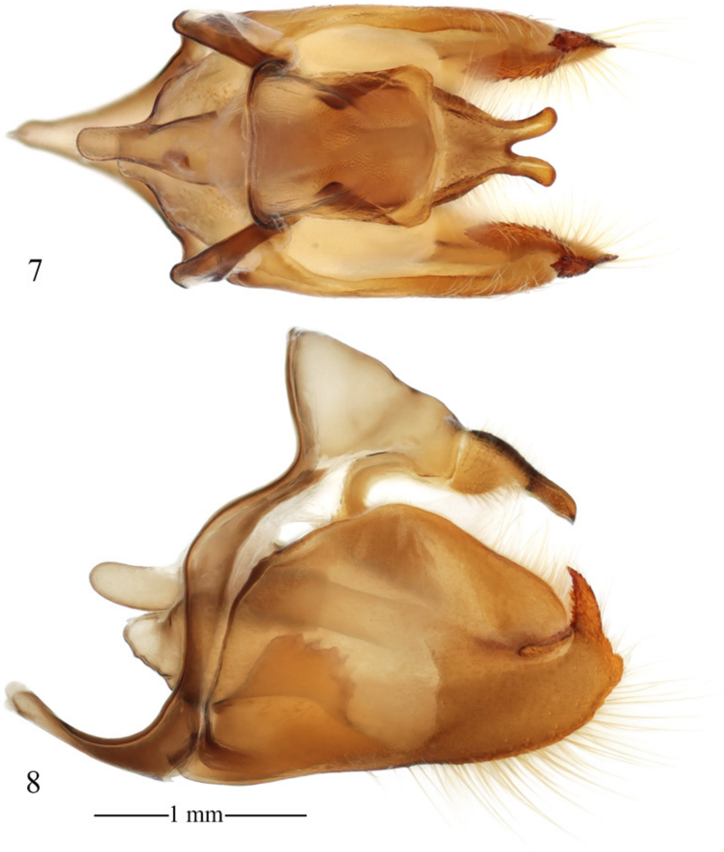


Figs. 1–6. Adults of two species of *Ridens* in dorsal (left) and ventral (right) views. 1–4, A pair of *R. conservationinternationalis* from ACG, Costa Rica. 1, 2, Female (Janzen and Hallwachs database [2022] voucher code 05-SRNP-31099). 3, 4, Holotype male (01-SRNP-9482). 5, 6, Male of unnamed close relative of *R. conservationinternationalis* from Ecuador.

wild ones, whose free-ranging caterpillars presumably have better food.)

Antenna: Shaft brown, its segments individually, but inconspicuously, marked along one side with pale yellowish to whitish scales. Club long, slender, arcuate, and sharply pointed (Figs. 1–4). Nudum 29–34 segments.

Palpus (Figs. 1–4): Third segment notably longer in females (Figs. 1, 2) than in males (Figs. 3, 4); slender, cylindrical, and porrect, with appressed, mostly light brown



Figs. 7, 8. Male genitalia of *R. conservationinternationalis* (01-SRNP-9453) (Burns genitalia dissection code X-5063); posterior end to the right. 7, Dorsal view. 8, Left lateral view (ninety-degree rotation).

scales, in sharp contrast to mixed creamy and brown, often hairlike, flaring scales of the larger second and first segments.

Adult facies (Figs. 1–4): Male forewing long and narrow; outer margin straight; wings of female (Figs. 1, 2) broader and more rounded than those of male (Figs. 3, 4), as is usual in Hesperiidae. Color pattern the same in both sexes. Ground color dark brown, but body and proximal areas of both forewing and hindwing overlaid with structural blue, hairlike scales, and the blue more prominent dorsally than ventrally. Forewing, dorsally and ventrally, with broad diagonal band of six hyaline spots running from mid-costa almost to outer margin above tornus: five aligned spots in costal cell, cell Sc–R$_1$, discal cell, cells Cu$_1$–Cu$_2$, and Cu$_2$–1A+2A (the last three spots large); one small spot distally offset in cell M$_3$–Cu$_1$. Narrow diagonal band of four hyaline subapical spots in cells R$_2$–R$_3$, R$_3$–R$_4$, R$_4$–R$_5$, and R$_5$–M$_1$. Ventral forewing with wide pale strip above inner margin. Hindwing appearing spotless—except for faint, opaque, slightly darker brown spots suggesting bands ventrally—but with narrow white fringe checkered with brown (better developed in males than in females) along outer margin.

Figs. 9, 10. Female genitalia of *R. conservationinternationalis* (01-SRNP-9481) (X-5064); posterior end at the top. 9, Ventral view. 10, Right lateral view (ninety-degree rotation).

Secondary sex character (Fig. 3): Costal fold of male extending about halfway to apex of forewing, ending a bit beyond the two narrow, linear, hyaline spots, in costal cell and cell Sc–$R_{1,}$ which together form an equals sign.

Genitalia (Figs. 7–10): Male (Figs. 7, 8): Uncus divided at posterior end into narrow, terminally rounded prongs forming a shallow "V." Valva greatly and evenly humped dorsad. At its distal end, valva barely extended posterad, but with vertical, narrow, pointed, finely dentate spike, much lower at its tip than peak of valval hump; at its base, on inner side of valva, spike curves anterad into dentate, flat, medially projecting shelf. On inner side of valva, at its proximal end,

Fig. 11. Last-instar caterpillar of *R. conservationinternationalis* (01-SRNP-1474) in lateral and frontal views.

a large, wide, thin, variably dentate plate extends dorsad from base. Female (Figs. 9, 10): Lamella postvaginalis, at posterior end, well-sclerotized and notched midventrally to a variable depth up to twice that of individual in Fig. 9. At ostium bursae, variable, ventral, horizontal sclerotization (suggesting lips [Fig. 9] or a brassiere, depending on specimen and point of view); sclerotization continuing anterad, ventrally and laterally, as a short tube, dorsally incomplete and so not fully enclosing the beginning of the ductus bursae. Paired wrinkled sacs flank the posterior fourth of the bursa copulatrix.

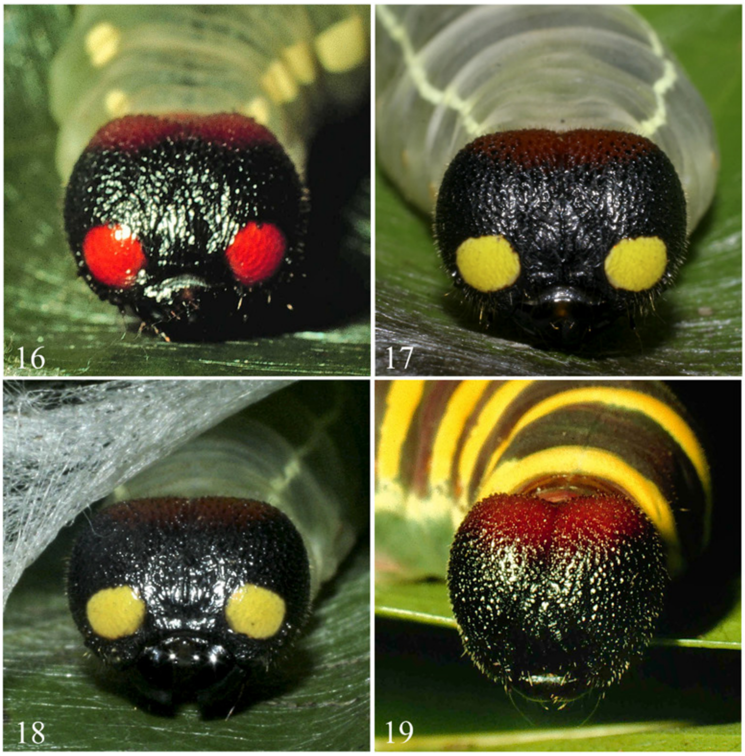
Larval facies, last instar (Fig. 11): Head dorsally rust, ventrally black, and, within the black, a lateral pair of large, pale orange, slanted, elliptical eyespots; between the rust and black, a large, central, pale orange, diamond-shaped area extending laterad almost as far as the outer ends of the eyespots. Body medium green with two dorsolateral rows of large yellow spots (one pair per segment), and heavily dotted dorsally—between the rows of large yellow spots—with small white spots. Larval head pattern unlike that of any other known hesperiid caterpillars.

Larval foodplants: Only two genera and three species in family Lauraceae are known. Species and the number of caterpillars found feeding on each, between 2000 and 2006: *Beilschmiedia brenesii* C. K. Allen 10, *Persea rigens* C. K. Allen 10, and *P. veraguasensis* Seem. 45. (No caterpillars have been found since, despite intensive search of their site and ecosystem.)

Pupal facies (Figs. 12–15): Body of an ordinary shape; tan and speckled with rusty dots. But entire anterior end of head bizarre: black and knobby, with long medial projection extending ventrad as much as anterad, and, at distal end, expanding laterad, with slight medial notch—all bilaterally symmetric.

Habitat: Mid-elevation (510–980 m) rain forest of Cordillera Guanacaste, a

Figs. 12–15. Pupa of *R. conservationinternationalis* (01-SRNP-1473) in four views. 12, Dorsal. 13, Ventral. 14, Lateral. 15, Frontal.



Figs. 16–19. Last-instar caterpillars of four species of *Ridens* from ACG, Costa Rica, in frontal view. 16, *Ridens panche* (97-SRNP-1081). 17, *Ridens biolleyi* (08-SRNP-35743). 18, *Ridens cachinnans* (09-SRNP-36708). 19, *Ridens mephitis* (93-SRNP-3068).

volcanic mountain ridge bisecting ACG roughly northwest to southeast. To date, caterpillars found only in Caribbean slope rain forest, in ACG's Sector Pitilla and Sector Rincon Rain Forest.

Geographic distribution: Northwestern Costa Rica (Area de Conservacion Guanacaste) and Panama (Darien).

Types.—Holotype male (Figs. 3, 4), voucher code 01-SRNP-9482, Costa Rica, Area de Conservacion Guanacaste, Guanacaste Province, Sector Pitilla, Sendero Mismo, lat 10.98758, long -85.41967, 680 m. Caterpillar Coll. Roster Moraga, 05/22/2001, adult eclosed 07/06/2001. Deposited in National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, with the unique identifier USNMENT 01533445. Paratypes, 17 males, 14 females, all from ACG, northwestern Costa Rica. Deposited in USNM.

Etymology.— *Ridens conservationinternationalis* named in honor of the global NGO Conservation International (https://www.conservation.org), which has for three decades been dedicated to conserving and understanding the wild tropics of the world.

Diagnostic information is in the Discussion.

Discussion

A male USNM specimen of *Ridens* from eastern Panama looks like *R. conservationinternationalis* and indicates that the species ranges well beyond ACG. Detailed label data for this individual is

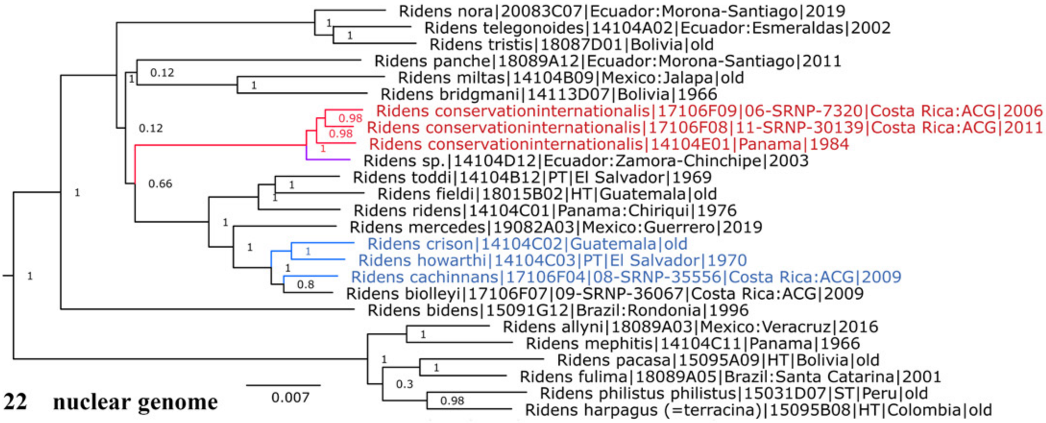
Panama, Darien, Cana [close to the border with Colombia], 1200 m, January 25, 1984, Gordon Small; DNA sample ID: NVG-14104E01, c/o Nick V. Grishin. The Panamanian specimen and two specimens from ACG cluster tightly in nuclear, Z chromosome, and mitochondrial genomic phylogenetic trees (Figs. 22–24) and reinforce the judgment that they are conspecific.

The USNM male *Ridens* in Figs. 5, 6 (from Ecuador, Zamora-Chinchipe, 1450 m, hilltop 1 km S Zamora, 4° 04.04’ S, 78° 57.88’ W, September 26, 2003, David H. Ahrenholz; DNA sample ID: NVG-14104D12, c/o Nick V. Grishin) clusters in all three phylogenetic trees (Figs. 22–24) with the Costa Rican and Panamanian *R. conservationinternationalis*, but less closely. We consider it a separate species because of its diverse, independent, external characters: the forewing of the Ecuadorian male is wider than those of *R. conservationinternationalis* males, and its outer margin is slightly curved instead of straight (cf. Figs. 5, 6 with Figs. 3, 4); the hindwing white fringe is wider and more strongly checkered in the Ecuadorian male; the ventral hindwing bands, which are barely perceptible in *R. conservationinternationalis*, are more evident; and the forewing has a small, hyaline, subapical spot in cell M_2–M_3 that specimens of *R. conservationinternationalis* lack (cf. Figs. 5, 6 with Figs. 1–4). Although spot expression varies intraspecifically (and sometimes extensively) in many species of skippers, in others it is so fixed that minuscule differences are taxonomically useful. For example, dorsal absence of a small forewing spot distinguishes females and most males of one of four cryptic species

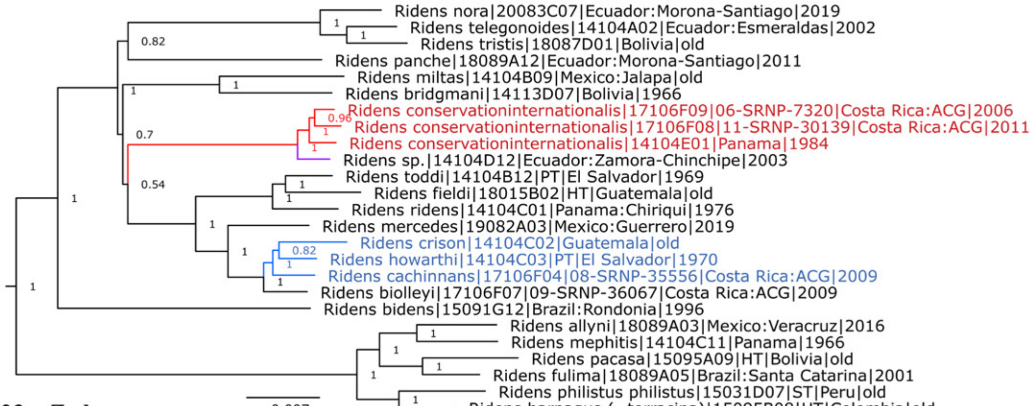

20


21

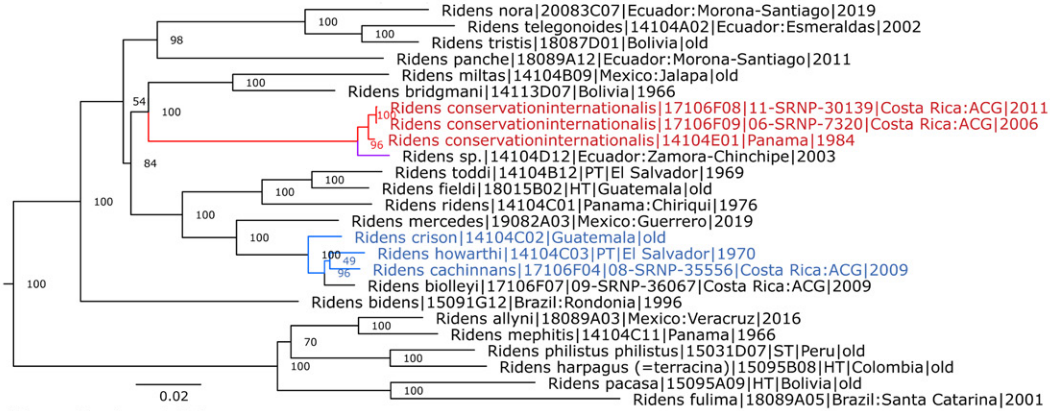
Figs. 20, 21. Pupae of two species of *Ridens* from ACG, Costa Rica. 20, *Ridens biolleyi* (00-SRNP-9259), lateral view. 21, *Ridens panche* (98-SRNP-2005), ventral view.



22 nuclear genome



23 Z chromosome



24 mitochondrial genome

Figs. 22–24. Phylogenetic trees of *Ridens* species. 22, Constructed from protein-coding regions in nuclear genome. 23, Constructed from Z chromosome. 24, Constructed from mitogenome. For each specimen in the trees, information is separated by a | into the following categories: (1) taxon name, (2) DNA sample code, (3) ACG database code (where applicable), (4) type status, if any (HT holotype, ST syntype, PT paratype), (5) locality, and (6) year of collection ("old" marks specimens that are not dated and were likely collected 100-150 years ago). (In the case of *R. harpagus*, it is the holotype of its synonym, *terracin*, that was examined.)

of *Perichares* (Burns et al. 2008); small differences in the presence, position, and size of forewing spots characterize species of *Venada* (Burns and Janzen 2005, Burns et al. 2013); and a slight difference in position and size of a small hindwing spot distinguishes species of *Udranomia* (Janzen et al. 2017).

Among species of *Ridens*, the near absence of ventral hindwing bands (Figs. 2, 4) sets *R. conservationinternationalis* apart: in nine species, pale scales mark the lower end of brown bands that are unmistakable anyway, or border their distal edge; and, in about eight species, ventral bands stand out because they are light blue or white. (Four species also have a short white band on the dorsal hindwing.) The tornal lobe of the hindwing is rudimentary in *R. conservationinternationalis* (Figs. 1–4) and about four other species, variably short but unmistakable in most species, and, in three species, hypertrophied to a short or long tail. In species with a white hindwing fringe, it is checkered in only five species (four of these with no or much reduced subapical forewing spots, two with strong edging of pale scales distad of the distal hindwing band, and one with no forewing diagonal band). On the lower half of the hindwing, between the brown band and the outer margin, three species have a large patch of pale scales, white in two of them and yellow in the other. The diagonal forewing band of hyaline spots is (when present) directed toward the outer margin above the tornus in *R. conservationinternationalis* and seven other species, but toward the tornus in seven species and toward the inner margin in four. Eight species augment subapical spots of the forewing in size and number, but five species lack them. As in *R. conservationinternationalis*, the male forewing is more often long and narrow than not. Besides its barely perceptible ventral hindwing bands, *R. conservationinternationalis* has a unique combination (Figs. 1–4) of the various varying facies characters noted above.

Male genitalia are species-specific variations on a *Ridens* theme: see illustrations in Godman and Salvin 1879–1901: pl. 75, fig. 15; Williams 1926: fig. 17; Williams 1927: figs. 19–22; Williams and Bell 1933: pl. 4, fig. 5, Williams and Bell 1934: pl. 1, fig. 13; Evans 1952: pl. 17, C.12; Steinhauser 1974: figs. 61–66; Steinhauser 1983: figs. 1, 3, 6; Freeman 1979: fig. 5; Mielke 1993: figs. 12–16; and Austin 1998: fig. 7. (Evans named genus *Ridens* in 1952, and previously its species were in the genera *Eudamus* Swainson, *Goniurus* Hübner, and *Telegonus* Hübner.) Genitalia of undiscovered cryptic species might not differ at all.

As for the *Ridens* species reared in ACG, the distal, shallow V-shaped division of the uncus in *R. panche* (Williams) is similar to that in *R. conservationinternationalis* (Fig. 7), except that in *R. panche* the prongs of the V hardly diverge in their proximal half so that the sides of the V are bent and the V as a whole is comparatively narrow. The V is deep and wide in many species of *Ridens*, including *R. biolleyi* (Mabille), *R. cachinnans* (Godman), and *R. mephitis* (Godman); and in *R. mephitis* the prongs diverge to their very end, whereas distally they are about parallel in the other two species. Furthermore, in *R. biolleyi* and *R. cachinnans*, the body of the valva is only a little humped, if at all, so that the long, posterior, dentate, vertical spike equals or exceeds the height of the valva; the inner side of the valva lacks both the large proximal plate and the distal dentate shelf at the base of the vertical spike; and the distal, ventral end of the valva extends posterad to some degree—sometimes so far as to form a narrow, sharply pointed spike. In *R. panche*, the posterior, dentate, vertical spike is short, and the ventrodistal end of the valva may extend a little posterad. *Ridens mephitis* lacks the vertical spike altogether, and the large proximal plate of the inner side of the valva extends anterad as well as dorsad.

Not only do the adults of *R. conservationinternationalis* and the other species of *Ridens* reared in ACG clearly differ from one another in external appearance, but so do their immature stages (Figs. 11–21); and those of *R. conservationinternationalis* (Figs. 11–15) differ markedly from the others. The head of the caterpillar, in all species, is dorsally rust-colored and ventrally black. In three—*R. panche*, *R. biolleyi*, and *R. cachinnans*—the black area has a pair of large, round, red-orange or yellow eyespots (see evolutionary analysis of larval and pupal eyespot mimicry in Janzen et al. 2010), while in *R. mephitis*, the black is plain (Figs. 16–19). But in *R. conservationinternationalis*, the middle area of the head, between the rust and black, has a large, pale orange diamond and, below that, in the black, a pair of large, light orange eyespots, which are slanted and elliptical instead of round (Fig. 11). In these species, dominant patterns on the body range from paired, dorsolateral, large round spots or longitudinal stripes to bands. The most spectacular morphologic difference is in the pupae: a slight, medial, anterior extension of the front of the head (Figs. 20, 21) becomes, in *R. conservationinternationalis*, a huge, knobby projection so unusual that it warrants depiction at four selected positions (Figs. 12–15).

To see *R. conservationinternationalis* in an evolutionary context, we included it in phylogenetic trees of the genus *Ridens* based on nuclear, mitochondrial, and Z chromosome genomic data (Figs. 22–24). All three trees agree in their terminal groupings of *Ridens* species (except for *R. panche*). Among described species of *Ridens*, *R. conservationinternationalis* lacks close relatives. It is the only species with rich dorsal (and weaker ventral) blue overscaling in a clade that includes species with diverse facies ranging from nearly black, white-fringed *R. tristis* (Draudt) (with some medial extension of white on the ventral hindwing), to brown, white-spotted *R. miltas* (Godman and Salvin), to the elaborately-patterned, semi-tailed generic type, *R. ridens* (Hewitson).

The three trees are incongruous around the diversification of this clade and weakly supported statistically. For instance, the mitogenome tree (Fig. 24) places the *R. conservationinternationalis* clade as sister to the *R. miltas* clade, an unexpected relationship, but with strong statistical support (100%); whereas nuclear and Z chromosome trees (Figs. 22, 23) group *R. conservationinternationalis* with *R. ridens* and its relatives, but with weak support (66% and 54%, respectively). The reason for the weak support is inconsistency between trees constructed from different genomic partitions due to rapid radiation around the origin of these clades and possible contribution of incomplete lineage sorting and gene exchange between these species. The extensive blue scaling of *R. conservationinternationalis* appeared independently of blue scaling in such distantly related species as *R. bidens* Austin, on the one hand, and *R. mephitis* and *R. harpagus* (C. Felder and R. Felder), on the other.

An aside: In the course of this study, we noted non-trivial genetic differentiation among the subspecies comprising *R. crison* (Godman and Salvin). This currently polytypic species is not even monophyletic in our nuclear and mitogenomic trees (Figs. 22, 24), and we take this opportunity to formally reinstate *R. cachinnans* as a species and to raise *R. howarthi* Steinhauser to the species level.

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