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A NEW SPECIES OF *ERACON* (HESPERIIDAE: PYRGINAE) SUBSTANTIATED BY A NUMBER OF TRAITS, INCLUDING FEMALE GENITALIA

NICK V. GRISHIN

Howard Hughes Medical Institute and Departments of Biophysics and Biochemistry, University of Texas Southwestern Medical Center, 5323 Harry Hines Blvd, Dallas, TX, USA 75390-9050; e-mail: grishin@chop.swmed.edu

DANIEL H. JANZEN & WINNIE HALLWACHS

Department of Biology, University of Pennsylvania, Philadelphia, PA 19104; e-mails: djanzen@sas.upenn.edu, whallwac@sas.upenn.edu

ABSTRACT. A new species of *Eracon* Godman & Salvin, 1894 is described from Central America. *Eracon sarahburnsae* Grishin, **sp. nov.** differs from its South American sister species *Eracon clinias* by wing patterns, male and female genitalia, and DNA barcode. Lectotypes for *Spioniades clinias* Mabille, 1878 and *Arteurotia celendris* Hewitson, 1878, and a neotype for *Arteurotia epipola* Plötz, 1882, are designated to stabilize nomenclature and current usage of these names. The neotype designation makes *Arteurotia epipola* an objective junior synonym of *Arteurotia celendris*, and we confirm the status of *A. celendris* as a junior subjective synonym of *Spioniades clinias*.

Additional key words: cryptic species, biodiversity, caterpillars, skipper butterflies, Area de Conservación Guanacaste, Costa Rica

New data and novel methods of analysis stimulate scientific discoveries, especially at field interfaces. Comprehensive rearing inventory of the non-leaf miner species of Lepidoptera of Area de Conservación Guanacaste in northwestern Costa Rica (ACG), augmented with the analysis of their ecology and DNA barcodes (the 654 base pair region of mitochondrial DNA coding for the C-terminal segment of cytochrome c oxidase subunit 1 (COI)), has been successful in revealing a large number of undescribed Hesperiidae species (Hebert et al. 2004, Janzen et al. 2009, 2011, 2012, Burns et al. 2013, Grishin et al. 2013a, b). While some of these new species are very different morphologically from their closest relatives, e.g. *Porphyrogenes peterwegei* Burns, 2010 and the other species of *Porphyrogenes* E. Watson, 1893 (Burns et al. 2010), others are much more similar and require close scrutiny to distinguish them, e.g. species of *Venada* Evans, 1952 and *Perichares* Scudder, 1872 (Burns & Janzen 2005, Burns et al. 2008, 2013). Each of these cases benefitted from a large number of specimens reared from wild-caught caterpillars (Janzen & Hallwachs 2011) for comparative analysis and evaluation of intraspecific variation, knowledge of caterpillar morphology, food plants and other aspects of ecology, and comparison of DNA barcodes. This fertile complementary of extensive morphological, ecological and DNA data is working very well for the characterization of complex butterfly biodiversity.

Such a comparative analysis reveals new species not only within ACG, but also on a wider scale. Central American sibling species, allied to species described from South America, are revealed (Grishin et al. 2013b). Here we argue that a Central American *Eracon* at first glance similar to *Eracon clinias* (Mabille, 1878), differs from it in many aspects of morphology (including facies, male and female genitalia), as well as DNA barcodes, sufficiently to be recognized as a distinct species. Interestingly, while male genitalia appear to be more visually similar interspecifically and more variable intraspecifically in these two species of *Eracon*, female genitalia offer obvious and simple diagnostic characters for separation of the two species. It is equally pleasing to see that DNA barcodes are consistent with the species (vs. subspecies) status of the new taxon, thus complementing traditional morphological analysis.

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); and McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, FL, USA (MGCL). 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.

Standard entomological techniques were used for dissection (Robbins 1991), i.e. the distal part of adult 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 the author 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 planes and stacked in Photoshop to increase apparent depth of field. DNA sequences were downloaded from GenBank http://genbank.gov/ and BOLD database (Ratnasingham & Hebert 2007), 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 photographs of specimens are available from the Area de Conservación Guanacaste (ACG) on-line database (Janzen & Hallwachs 2013) and BOLD database (Ratnasingham & Hebert 2007) to confirm or suggest identifications.

Results and Discussion

A large-scale collecting and rearing of non-leaf mining moths and butterflies from wild-collected caterpillars in ACG produce rich datasets for the study of biodiversity (Janzen et al. 2011). These extensive datasets are particularly useful for understanding intraspecific variation and delineation of species boundaries. Augmented with mitochondrial DNA COI barcode sequences, analysis of specimens and their ecology is sensitive to discovery of sibling and cryptic species. Comparison of over 40 ACG *Eracon* reared specimens that key out to *Eracon clinias* using Evans (1953), along with South American *E. clinias* specimens, revealed that the ACG specimens were darker and with less patterned wings. Costa Rican and Panamanian wild-collected *E. clinias*-like specimens were similar to reared Costa Rican specimens (i.e. darker, less patterned) and did not match South American specimens (Figs. 1–28). These differences suggest that Central American populations could constitute a species distinct from South American populations. To address our observations further, we first stabilize the relevant nomenclature and clarify the taxonomy of the three names that could be assigned to *E. clinias*-like specimens (Evans 1953, Mielke 2005). We designate lectotypes for two of the names and a neotype for the third. This action assigns defined identities to the three names and opens a way to the description of a new species without confusion with the three existing names.

Lectotype designation for *Spioniades clinias* Mabille, 1878: The original description of *Spioniades clinias* mentions neither the number of specimens, nor their variation, and only states a single location ("E Cayenna" [possibly French Guiana]) (Mabille 1878). While it is likely that the description was written from a single specimen, it is not possible to prove it. However, to stabilize the nomenclature of *Eracon* in the light of new species described below, in particular because the original description of *S. clinias* is not sufficient to distinguish between it and the new species, it is desirable to have a single specimen as the name-bearing type. A specimen in the Natural History Museum, London, UK (BMNH) that is curated as a type of *Spioniades clinias*, comes from the Mabille collection, agrees with the original description and bears nine labels: small, round, white with red circle, printed: || Type ||, on front and handwritten: || H | 700 ||, on back; white, handwritten in red: || clinias | Mab. ||; small red stripe, no data; medium, rectangular, gray, handwritten: || = *Arteurotia* | *celendris*, Hew. ||; small, rectangular, white, printed: || Ex musæo | P. Mabille | 1923 ||; small, round, yellow, handprinted: || 78 ||; white, medium, typed: || R. Oberthür Coll. | Brit. Mus. 1931-136 ||; medium, rectangular, white, printed: || R. Oberthür Coll. | Brit. Mus. 1931-136 ||; long, white, printed: || BMNH(E) #982941 || (the last label was added by NVG during photography and inventory of this specimen), is hereby designated as the lectotype of *Spioniades clinias*. The following red label will be added to the specimen after publication of this study: || LECTOTYPE | *Spioniades clinias* | Mabille, 1-II-1878. | Pet. Nouv. Ent. 2: 201 | designated by Grishin, 2014 ||. This specimen and its labels are illustrated (Figs. 12, 26). It is a male with minimal scale loss, right antenna and tornus of left hindwing missing. This specimen

seems to be the only known syntype in collections. This lectotype is designated to ensure nomenclatural stability and avoid confusion with the new species described below. *Spioniades clinias* was transferred to genus *Eracon* (type species *Eracon biternata* (Mabille, 1889)) by Evans (1953: 36).

Lectotype designation for *Arteurotia celendris* Hewitson, 1878: The original description of *Arteurotia celendris* mentions neither the number of specimens, nor their variation, and only states a single location ("Amazons" [Brazil]) and a single collector ("Bates") (Hewitson 1878). To stabilize nomenclature of *Eracon* in the light of new species described below, in particular because the original description of *Arteurotia celendris* is not sufficient to distinguish between it and the new species, it is desirable to have a single specimen as the name bearing type. A specimen in the Natural History Museum, London, UK (BMNH) that is curated as the type of *Arteurotia celendris*, comes from the Hewitson collection, agrees with the original description and bears six labels: small, round, white with red circle, printed: || Type ||, on front and handwritten: || H | 679 ||, on back; small, round, white with red circle, printed: || Type ||, on front and handwritten: || Calendris, | Hew. ||, on back; small, rectangular, white, handwritten: || Celendris ||; large, rectangular, white, handprinted and printed: || Amazon. | Hewitson Coll. | 79-69. | Conognathus | calendris. 1 ||; small, rectangular, white, handwritten: || Amaz ||, glued to the back of the previous label; long, white, printed: || BMNH(E) #982940 || (the last label was added by NVG during photography and inventory of this specimen), is hereby designated as the lectotype of *Arteurotia celendris*. The following red label will be added to the specimen after publication of this study: || LECTOTYPE | *Arteurotia celendris* | Hewitson, IV-1878. |Ann. & Mag. Nat. Hist. (5)1: 347–348 | designated by Grishin, 2014 ||. This specimen and its labels are illustrated (Figs. 9, 23). It is a male, mounted on a minuten pin, both antennae missing and wings with glue, indicating extensive repair. Evidence at hand cannot support *Arteurotia celendris* as a biologically distinct species, and its continued treatment as a junior (by just 2 months!) synonym of *Spioniades clinias* appears reasonable at the moment (Shepard 1934, Evans 1953, Mielke 2005). The lectotype is designated to ensure nomenclatural stability and avoid confusion with the new species described below.

Neotype designation for *Arteurotia epipola* Plötz, 1882: After inspection of the original Plötz drawings, Godman (1907) concluded that *Arteurotia epipola* is a synonym of *Eracon clinias*. The original description of *Arteurotia epipola* mentions neither the number of specimens in the type series, nor the collection that contained them (Plötz 1882). Both *Spioniades clinias* and *Arteurotia epipola* were described apparently from French Guiana ("E Cayenna" and "Cayenne", respectively) within a few years of one another. Texts of both descriptions are very similar (Mabille 1878, Plötz 1882), and that of *Spioniades clinias* also lacks collection information. It is conceivable that these taxa were described from the same specimen(s). While many Plötz types (of names that he attributed to Maassen) are currently in the ZMHB collection, we were not able to locate specimens labeled as *Arteurotia epipola* types there. Only two males of *E. clinias* were found by NVG after every specimen in every Hesperiidae drawer was examined. The ZMHB card-catalogue also did not contain information about *Arteurotia epipola*. Likewise, we failed to find the Plötz illustration referred to by Godman (1907) among the copies of Plötz drawings in BMNH (drawing number 1340 for *Arteurotia epipola* apparently was not copied, as drawing 1352 follows 1339 on the next page). Therefore, the only information about *Arteurotia epipola* would be that derived from the original description (Plötz 1882: 256). The original description of *Arteurotia epipola* mentions a narrow, white, crossed by dark veins transversal band in the middle of both surfaces of the hindwing, extensive blue overscaling and a "black rear angle" on the hindwing underside (Plötz 1882). Neither the band, blue overscaling, nor the tornal hindwing dark area are pronounced in Central American specimens (Figs. 1–8, 15–22), but are very noticeable in many *E. clinias* specimens (Figs. 9–14, 23–28). Additionally, the specimens were apparently from French Guiana. This indicates to us that the name *Arteurotia epipola* should not apply to the Central American specimens and is indeed most likely a synonym of *Spioniades clinias*, as suggested by Godman (1907) and supported by all subsequent references (e.g. Draudt 1922, Shepard 1934, Evans 1953, Mielke 2005). To ensure this interpretation of the name followed in the literature for the last 105 years, thus preserving stability of nomenclature, a specimen from French Guiana, which is simultaneously the lectotype of *Spioniades clinias* (designated above), in BMNH collection (BMNH(E) #982941, Figs. 12, 26), is hereby designated as the neotype of *Arteurotia epipola*. The following red label will be added to the specimen after publication of this study: || NEOTYPE | *Arteurotia epipola* | Plötz, 1882 (Maassen in litt.). | Berl. ent. Ztschr. 26: 256 | designated by Grishin, 2014 ||. This neotype designation makes *Arteurotia epipola* a junior objective synonym of *Spioniades clinias*. We

FIGS. 1–28. *Eracon* specimens. **1–14.** dorsal and **15–28.** ventral views of the same specimens. **1, 15.** *E. sarahburnsae* holotype ♂, data in text. **2–8.** and **16–22.** *E. sarahburnsae* [USNM]: **2–4** and **16–18** are paratypes; DNA barcodes for **5–8** and **19–22** are lacking and identification is tentative. **9–14.** and **23–28.** *E. clinias*: **9, 23.** lectotype of *Arteurotia celendris* Hewitson, 1878, ♂, Brazil: Amazonas, leg. Bates [BMNH]; **12, 26.** lectotype of *Spioniades clinias* Mabille, 1878, and, simultaneously, neotype of *Arteurotia epipola* Plötz, 1882, ♂, French Guiana [BMNH] (all three designated herein). Voucher codes for ACG paratypes: **2, 16** - ♀ 05-SRNP-22120; **3, 17** - ♂ 05-SRNP-22467; **4, 18** - ♀ 05-SRNP-22121, data in text. Data for other USNM specimens: **5, 19** - ♂, Costa Rica: Limón Prov., Guapiles, May, Schaus & Barnes coll., genitalia NVG130614-44 (genitalia Fig. 29l); **6, 20** - ♀, Costa Rica: Limón Prov., Banano River, III-1907, Wm. Schaus collection; **7, 21** - ♂, Panama: Panamá Prov., Distrito de El Llano, Cordillera de San Blas, N of El Llano, ca. 330 m, 10-V-1978, leg. G. B. Small; **8, 22** - ♀, Panama: Chiriqui Prov., "Bocas del Toro", 24-III-1985, leg. G. B. Small; (continued on next page)

FIGS. 1–28. (Continued) *Eracon* specimens. **1–14.** dorsal and **15–28.** ventral views of the same specimens.**10, 24** - ♂, Brazil: Rondônia, vic. Caucalandia, 10.533 -62.8, 160-350 m, 9-X-1991, leg. J. Kemner, genitalia X-6056 J. M. Burns 2004 (genitalia Fig. 29q); **11, 25** - ♀, Ecuador: Orellana Prov., Yasuni Research Station, Rios Tivacuno & Tiputini, 0.675 -76.397, 220 m, 29-X-1998, leg. D. H. Ahrenholz, genitalia NVG120922-14 (genitalia Fig. 30g, h); **13, 27** - ♂, Peru: Loreto Prov., Rio Amazones, 200 m, Explorama Inn, 25 mi E Iquitos; {9-12&17-21}-IX-1990, leg. R. Leuschner, genitalia NVG130614-44 [USNM] (genitalia Fig. 29s); **14, 28** - ♀, Peru: Tambopata Prov., 30 km SW Puerto Maldonado, 300 m, 30-IV-1984, leg. S. S. Nicolay, genitalia NVG120922-13 (genitalia Fig. 30e, f). Several half-side images have been flipped and pinholes and some other imperfections have been digitally removed to emphasize actual elements of the pattern in all specimens, except for the types of *E. clinias*, *E. epipola* and *E. celendris*. Labels for primary type specimens are shown below each specimen, except for the *E. sarahburnsae* holotype where labels are also above. Labels are at 1/2 the scale. Species names for each row, names for primary types (LT - lectotype, NT - neotype, above a specimen), general locations and sexes are shown.

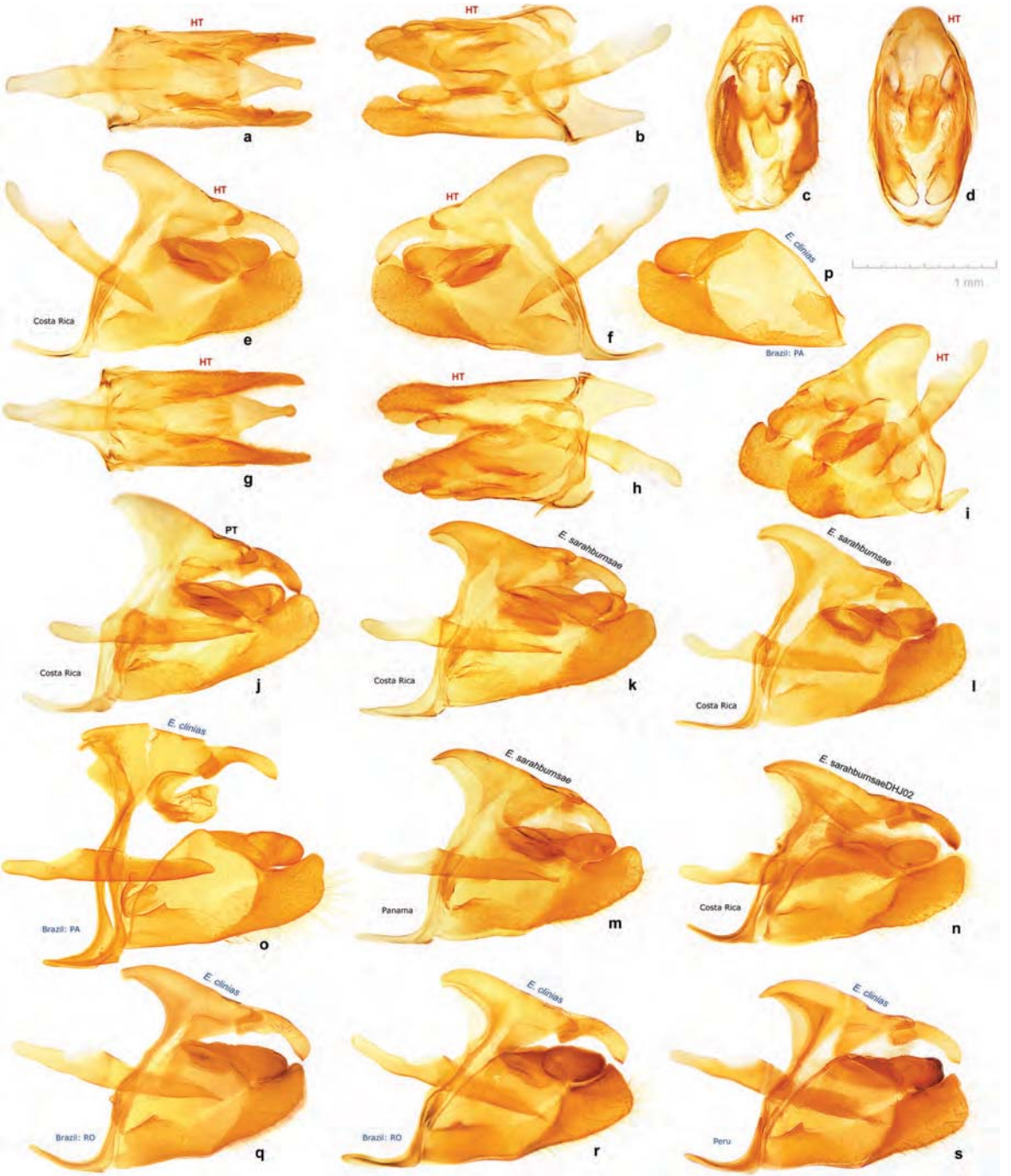


FIG. 29. Male genitalia. **a–m.** *Eracon sarahburnsae*: **a–i.** holotype, voucher code 01-SRNP-5247, genitalia X-6059 J. M. Burns 2004 (Figs. 1, 15) in several views: **a.** dorsal, **b.** right dorsolateral, **c.** posterior, **d.** anterior, **e.** left lateral, **f.** right lateral, **g.** ventral, **h.** left ventrolateral, **i.** right posterolateral; **j.** paratype, genitalia X-6058 J. M. Burns 2004, voucher code 01-SRNP-5289; **k.** genitalia X-5223 J. M. Burns 2002, voucher code 02-SRNP-7253; **l.** Costa Rica: Guapiles, May, Schaus & Barnes coll., genitalia NVG130614-44 (Figs. 5, 19); **m.** Panama: Panamá Province, 5mi N of El Llano, 9.283 -79.0, ca. 330 m, 17-V-1978, leg. G. B. Small, genitalia X-6057 J. M. Burns 2004. **n.** *E. sarahburnsae*DHJ02, genitalia X-6869 J. M. Burns 2010, voucher code 05-SRNP-1688. It has a 1.5–1.7% difference in DNA barcode from other ACG *E. sarahburnsae* specimens and may represent yet another undescribed cryptic species. **o–s.** *E. clinias*: **o–p.** Brazil: Pará, Saunders Coll., Godman-Salvin Coll. 1912-23, minislide 651, pinned under the specimen, tegumen squashed in slide preparation, interior view of left valva is shown in **p**; **q.** Brazil: Rondônia, vic. Caucalândia, 10.533 -62.8, 160-350 m, 9-X-1991, leg. J. Kemner, genitalia No. X-6056 J. M. Burns 2004 (Figs. 10, 24); **r.** Brazil: Rondônia, vic. Caucalândia, 10.533 -62.8, 160-350 m, 12-X-1991, leg. J. MacDonald, genitalia X-6073 J. M. Burns 2004; **s.** Peru: Loreto Province, Rio Amazones, 200 m, Explorama Inn, 40 km E Iquitos; {9-12&17-21}-IX-1990, leg. R. Leuschner, genitalia NVG130614-45 (Figs. 13, 27). All specimens are at USNM except **o–p**, which is in BMNH and copyright (©) Trustees of the Natural History Museum, London (used with permission).

FIG. 30. Female genitalia. **a–d.** *Eracon sarahburnsae*, **e–f.** *Eracon clinias*. **a–b.** Panama: Colon Prov., Nuevo Tonosi, 17-I-1980, leg. G. B. Small, genitalia NVG120922-12 [USNM]; **c–d.** paratype, Costa Rica: Guanacaste Prov., ACG, voucher code 05-SRNP-1687, data in text, genitalia NVG120922-15 [USNM]; **e–f.** Peru: Tambopata Prov., 30 km SW Puerto Maldonado, 300 m, 30-IV-1984, leg. S. S. Nicolay, genitalia NVG120922-13 [USNM] (Figs. **14, 28**); **g–h.** Ecuador: Orellana Prov., Yasuni Research Station, Rios Tivacuno & Tiputini, 0.675 -76.4, 220 m, 29-X-1998, leg. D. H. Ahrenholz, genitalia NVG120922-14 [USNM] (Figs. **11, 25**); **a, e.** complete genitalia; **b–d, f–h.** sterigma with ovipositor lobes and the last tergum; **a–c, e–g.** ventral views and **d, h.** ventrolateral view. Smaller scale bar refers to **a** & **e**.

believe that there is an exceptional need to designate the neotype to ensure nomenclatural stability by unambiguously defining this taxon and thus avoiding a possible confusion with a new species described below. The characters to differentiate this species (as defined by Plötz 1882) are discussed above and additional characters are indicated in Fig. 33 (right, for *E. clinias*).

Analysis of wing patterns, genitalia and mitochondrial DNA barcode sequences reveals that Central American E. clinias-like specimens differ significantly from South American specimens. Central American populations do not fit the above concept of *E. clinias* with its synonyms *E. celendris* and *E. epipola*, and therefore are described here as a new species, similar to, but distinct from, South American *E. clinias*.

Eracon sarahburnsae Grishin, **new species**
(Figs. 1–8, 15–22, 29a–m, 30a–d, 31, 32 part, 33 part)

Description: Male (n=20, Figs. 1, 3, 5, 7, 15, 17, 19, 21, 33 part) – holotype forewing length = 14.6 mm. *Forewing* with very narrow costal fold. Forewing dorsally dark brown with even darker areas in discal cell, base of Cu_1–Cu_2 cell and discal part of Cu_2–2A cell; discal cell with two white spots near the bases of R_2 and Cu_1 veins, elongated white spot aligned with these in Sc-R_1 cell; zigzag, ξ-shaped line of nine postmedian white spots in each cell between R_3 and 2A veins (cell Cu_2–2A with two spots), these spots nearly equidistant from each other, except the spot in M_3–Cu_1 cell closer to spot in Cu_1–Cu_2 cell than to spot in M_2–M_3 cell, spot in Cu_1–Cu_2 cell crescent-shaped. Olive and slate-colored (pale bluish) diffuse overscaling, stronger in submarginal area and forming diffuse slate-colored spot in every cell distally from the white spots. Ventrally similar to dorsal surface, but paler, without darker areas, slate-colored overscaling concentrating in submarginal spots more extensive

towards tornus. Fringe brown with pale scales mostly near apex and Cu_2–2A cell. *Hindwing* produced at the tornus, dorsally brown, with vague marginal band of pale diffuse spots, and even less defined vestigial submarginal band, slate-colored bluish overscaling, mostly of hair-like scales in distal half. Ventrally similar to dorsal surface, but the marginal band of white scales more pronounced in and posterior to discal cell, very weak to absent anterior of discal cell, slate-colored overscaling mostly in and posterior to discal cell, weaker by the margin, concentrating into inverted-V shaped submarginal spots in some cells, wing brown without overscaling near tornus. Fringe brown with pale scales in groups. *Head* and palpi brown with some olive and slate-colored scales above, slate-colored below, antennae length two-thirds of costa, mostly black, dull brown-yellow beneath near and on club, nudum red-brown, 22–23 segments (n=4), collar with olive and slate-colored scales. *Thorax* brown with some olive scales above and on the sides beneath wings, slate-colored below, including pectus, legs brown with extensive slate-colored scales. Abdomen brown above with indistinct bands of slate-colored scales at the ends of segments, slate-colored below with longer bluish scales basally and broad central brown line. **Male genitalia** (Figs. 29, 33 part) – tegumen with a pair of small caudal lobes at the base of uncus. Uncus shorter than tegumen, undivided, flattened from the sides, curved in lateral view. Gnathos shorter than uncus, arms spiculose. Saccus elongated triangular, length as uncus. Valva broad, ampulla with an oval-shaped rounded process, costa slightly concave before ampulla, cucullus broad, rounded, extending caudad beyond the process off ampulla for about half of its length. Sacculus with a poorly defined rounded tooth. Aedeagus about the length of tegumen with uncus, no cornuti, and phallobase evenly upcurved.

Female (n=13, Figs. 2, 4, 6, 8, 16, 18, 20, 22) – forewing length = 13.5 to 16 mm, similar to male, but without costal fold and with more rounded, slightly broader wings, nudum 24–25 segments (n=4). **Female genitalia** (Figs. 30, 33 part) – lamella postvaginalis about as long as wide, poorly sclerotized from half of its length near atrium, caudal margin with a broad and shallow notch in the middle. Lamella antevaginalis thin and narrow, expanding into narrow lateral lobes. Antrum weakly sclerotized, slightly wider than ductus bursae. Ductus and corpus bursae weakly separated from each other, together about four times sterigma length.

Barcode sequence of the holotype: Genbank Accession DQ292499, 651 base pairs:
AACTTTATATTTTATTTTCGGAATTTGAGCCGGAATAGTTGGA
ACATCTTTAAGTTTATTAATTCGAACTGAATTAGGTAATCCAGG
GTCATTAATTGGGGATGATCAAATTTATAATACTATTGTTACAG
CTCATGCTTTTATCATAATTTTTTTCATAGTAATACCAATTATAA
TCGGTGGATTTGGAAATTGACTTGTACCTCTTATATTAGGAGC
TCCTGATATAGCATTTCCACGAATAAATAATATAAGATTTTGAC
TTTTACCCCCTTCTTTAATATTATTAATTTCAAGAAGTATTGTT
GAAAATGGTGCAGGAACAGGTTGAACAGTTTATCCCCCTTTA
TCTGCTAATATTGCCCACCAAGGATCTTCTGTTGACTTAGCTA
TTTTTTCCTTACATTTAGCAGGAATTTCATCTATTTTAGGAGCT
ATTAATTTTATTACTACAATCATTAATATACGTATTAATAATCTTT
CCTTCGATCAAATACCTTTATTTGTTTGAGCTGTTGGAATTAC
AGCTTTATTATTACTTTTATCTTTACCTGTATTAGCTGGAGCAA
TCACAATACTTTTAACTGATCGAAATTTAAATACATCATTCTTT
GATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACA

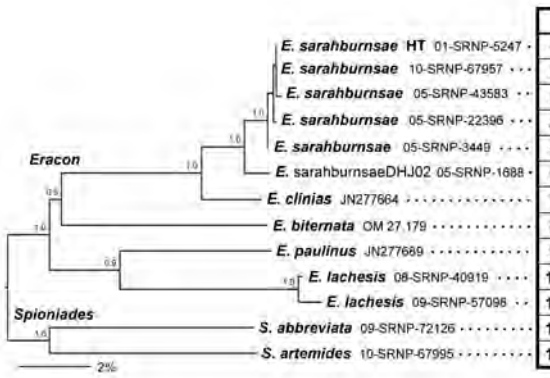
Types: *Holotype* male has the following labels: white printed & hand-printed: || Voucher: D. H. Janzen & W. Hallwachs | caterpillar (Lepidoptera) database, | Area de Conservación Guanacaste, || Costa Rica. http://janzen.sas.upenn.edu | 01-SRNP-5247 ||; white printed: || Genitalia No. | X-6059 | J. M. Burns 2004 ||; yellow printed - || LEGS AWAY | FOR DNA ||; red printed: || HOLOTYPE ♂ | *Eracon sarahburnsae* | Grishin ||. Holotype data: Costa Rica: Area de Conservación Guanacaste, Alajuela Province, Sector Rincon Rain Forest, Sendero Rincon, GPS: 10.8962 -85.27769, elevation 430 m, collected as penultimate instar by Freyci Vargas on 24-June-2001, fed on *Apeiba membranacea* Spruce ex. Benth. (Malvaceae), caterpillar prepupal date 09-July-2001, adult eclosed 26-July-2001, voucher code 01-SRNP-5247. *Paratypes*: 20 ♂♂ and 13 ♀♀, all from Costa Rica, Area de Conservación Guanacaste, reared from caterpillars feeding on *A. membranacea*. Alajuela Prov.: Sector Rincon Rain Forest: 1♂ site Sendero Rincon, 10.8962 -85.27769, 430 m, collected on 26-VI-2001 as last instar, adult eclosed on 05-VIII-2001, voucher code 01-SRNP-5289, genitalia No. X-6058 J. M. Burns 2004; site Quebrada Guarumo, 10.90445 -85.28412, 400m: 1♂ collected on 20-VII-2007 as penultimate instar, adult eclosed on 18-VIII-2007, voucher code 07-SRNP-42093; 1♂ collected on 20-VII-2007 as penultimate instar, adult eclosed on 31-VIII-2007, voucher code 07-SRNP-42094; 1♀ site Rio Francia Arriba, 10.89666 -85.29003, 400 m, collected on 03-XI-2006 as last instar, adult eclosed on 13-XII-2006, voucher code 06-SRNP-44151; site Finca Hugo, 10.88068 -85.26968, 540m: 1♀ collected on 16-X-2007 as penultimate instar, adult eclosed on 09-XII-2007, voucher code 07-SRNP-42619; 1♂ collected on 16-X-2007 as penultimate instar, adult eclosed on 06-I-2008, voucher code 07-SRNP-42620; site Finca Aurita, 10.88409 -85.25728, 460m: 1♀ collected on 05-XII-2005 as last instar, adult eclosed on 31-XII-2005, voucher code 05-SRNP-43583; 1♂ collected on 04-I-2006 as last instar, adult eclosed on 21-II-2006, voucher code 06-SRNP-40016 (Figs. 31f-i); site Palomo, 10.96187 -85.28045, 96m: 1♂ collected on 17-IX-2010 as penultimate instar, adult eclosed on 25-X-2010, voucher code 10-SRNP-67957; 1♀ collected on 17-IX-2010 as penultimate instar, adult eclosed on 05-XI-2010, voucher code 10-SRNP-67958; 1♀ collected on 23-VII-2012 as penultimate instar, adult eclosed on 04-IX-2012, voucher code 12-SRNP-68151; site Cabanya, 10.87703 -85.23077, 340m: 1♂ collected on 23-VII-2008 as penultimate instar, adult eclosed on 17-VIII-2008, voucher code 08-SRNP-41449; 1♀ collected on 23-VII-2008 as penultimate instar, adult eclosed on 23-VIII-2008, voucher code 08-SRNP-41450; Sector San Cristobal: site Puente Palma 10.9163 -85.37869, 460m: 1♂ collected on 30-III-2005 as penultimate instar, adult eclosed on 24-IV-2005, voucher code 05-SRNP-1714; 1♂ collected on 30-III-2005 as penultimate instar, adult eclosed on 01-V-2005, voucher code 05-SRNP-1713; 1♀ collected on 30-III-2005 as antepenultimate instar, adult eclosed on 13-V-2005, voucher code 05-SRNP-1687, genitalia NVG120922-15 (Figs. 30cd); 1♀ collected on 10-VII-2005 as antepenultimate instar, adult eclosed on 30-VIII-2005, voucher code 05-SRNP-3823; site Sendero Huerta: 10.9305 -85.37223, 527 m, 1♂ collected on 18-VI-2005 as antepenultimate instar, adult eclosed on 26-VII-2005, voucher code 05-SRNP-3449; 1♀ collected on 05-VIII-2005 as penultimate instar, adult eclosed on 18-IX-2005, voucher code 05-SRNP-4520; 1♀ collected on 25-XI-2005 as penultimate instar, adult eclosed on 19-I-2006, voucher code 05-SRNP-7368; 1♂ collected on 01-VII-2007 as second instar, adult eclosed on 14-VIII-2007, voucher code 07-SRNP-2980; 1♂ collected on 01-V-2009 as penultimate instar, adult eclosed on 29-V-2009, voucher code 09-SRNP-1734; 1♂ Sector Brasilia, site Gallinazo, 11.01825 -85.37199, 360 m, collected on 22-IV-2008 as antepenultimate instar, adult eclosed on 23-V-2008, voucher code 08-SRNP-65365. Guanacaste Prov.: Sector Del Oro: 1♂site Quebrada Lajosa, 11.03306 -85.42876, 400 m, collected on 30-VI-2008 as antepenultimate instar, adult eclosed on 02-VIII-2008, voucher code 08-SRNP-21838; site Margarita, 11.03234 -85.43954, 380m: 1♂ collected on 28-XI-2003 as last instar, adult eclosed on 06-I-2004, voucher code 03-SRNP-37802; 1♀ collected on 13-VI-2005 as last instar, adult eclosed on 06-VII-2005, voucher code 05-SRNP-22121 (Figs. 4, 18, 31de); 1♀ collected on 13-VI-2005 as antepenultimate instar, adult eclosed on 18-VII-2005, voucher code 05-SRNP-22120 (Figs. 2, 16); 1♂ collected on 29-VI-2005 as antepenultimate instar, adult eclosed on 03-VIII-2005, voucher code 05-SRNP-22467 (Figs. 3, 17); 1♂ collected on 24-VI-2005 as antepenultimate instar, adult eclosed on 10-VIII-2005, voucher code 05-SRNP-22396; 1♂ collected on 24-VI-2005 as antepenultimate instar, adult eclosed on 26-VII-2005, voucher code 05-SRNP-22364; Sector Pitilla, site Medrano, 11.01602 -85.38053, 380m: 1♂ collected on 05-VII-2012 as antepenultimate instar, adult eclosed on 13-VIII-2012, voucher code 12-SRNP-71669; 1♀ collected on 05-VII-2012 as preantepenultimate instar, adult eclosed on 22-VIII-2012, voucher code 12-SRNP-71670; 1♂ collected on 17-VII-2012 as preantepenultimate instar, adult eclosed on 22-VIII-2012, voucher code 12-SRNP-71781.

Deposition of types: The holotype is in the National Museum of

FIG. 31. Immature stages of *Eracon sarahburnsae*. **a–o** caterpillars, ultimate instar; **p–s** pupa; in dorsal (**b, e, i, o, s**), dorsolateral (**a, d, h, j–l, n**), ventral (**q**), ventro-lateral (**r**) and dorso-anterior (**m, p**) views, caterpillar heads in approximately anterior view are shown in **c, f,** and **g**. Larval skin with a head capsule is visible in **p** and **s**. All specimens are from Costa Rica: Area de Conservación Guanacaste (Janzen & Hallwachs 2013), voucher codes for them are: **a–c** - 06-SRNP-42043; **d–e** - 05-SRNP-22121 (paratype); **f–i** - 06-SRNP-40016 (paratype); **j–m** - 05-SRNP-22393; **n–o** - 07-SRNP-42141; **p–s** - 06-SRNP-43593, data in text and additional information is available from Janzen & Hallwachs (2013). Some specimens lacking DNA barcodes (**a–c** & **j–s**) may be *Eracon sarahburnsae*DHJ02.

Natural History, Smithsonian Institution, Washington, DC (USNM). Two paratypes (05-SRNP-3449 & 05-SRNP-43583) are deposited in the Natural History Museum, London, UK (BMNH). Two paratypes (05-SRNP-22396 & 05-SRNP-22120) are deposited in the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL (MGCL). All other paratypes remain in USNM.

Specimens excluded from the type series: Three specimens from Costa Rica: ACG (voucher codes 05-SRNP-1688 (♂), 09-SRNP-40707 (♀) & 12-SRNP-68843 (♀) (Janzen & Hallwachs 2013), baptized with the interim name *Eracon clinias*DHJ02 in Janzen et al. (2011), corrected to *Eracon sarahburnsae*DHJ02 here, since they are not *E. clinias*), which otherwise would be identifiable as *E. sarahburnsae* by wing patterns and genitalia, differed by 1.3%–1.7% in their DNA barcode sequence from other *E. sarahburnsae* specimens and therefore are excluded from the type series. These three specimens sharing the same DNA barcode sequence may represent another cryptic *Eracon* species or extreme variation of the barcode. More specimens with this DNA barcode sequence are needed to assess morphological variation, and evaluate their taxonomic status. Therefore, only specimens with a known barcode matching the holotype of *E. sarahburnsae* (termed *Eracon* cliniasDHJ01 in Janzen et al. 2011) were used as paratypes. The following 11 ♂♂ and 8 ♀♀ without sequenced DNA barcodes possess the morphological (and where available) food plant characters of *E. sarahburnsae* and are tentatively assigned to this species, but are also excluded from the type series: Costa Rica, Area de Conservación Guanacaste, reared from caterpillars feeding on *Apeiba membranacea* (Malvaceae): Alajuela Prov.: Sector Rincon Rain Forest: 1♂ site Sendero Rincon, 10.8962 -85.27769, 430 m, collected on 20-V-2002 as second instar, eclosion date lost, genitalia No. X-5223 J. M. Burns 2002, voucher code 02-SRNP-7253 [USNM]; 1♂ site Vado Rio Francia, 10.90093 -85.28915, 400 m, collected on 09-IX-2006 as last instar, adult eclosed on 29-IX-2006, voucher code 06-SRNP-43416 [MGCL]; site Sendero Llano, 10.90276 -85.28996, 400 m: 1♂ collected on 27-IX-2006 as antepenultimate instar, adult eclosed on 22-XI-2006, voucher code 06-SRNP-43702 [MGCL]; 1♀ collected on 27-IX-2006 as antepenultimate instar, adult eclosed on 08-XI-2006, voucher code 06-SRNP-43703 [MGCL]; 1♀ site Montanya Figueres, 10.88367 -85.29081, 460 m, collected on 25-



	1	2	3	4	5	6	7	8	9	10	11	12	13
1	650	0	1	1	1	10	**24**	70	72	81	84	84	83
2	0	654	1	1	1	10	**24**	70	73	81	84	84	83
3	0.2	0.2	654	2	2	11	**24**	71	73	81	84	85	83
4	0.2	0.2	0.3	633	1	11	**24**	70	71	80	83	83	81
5	0.2	0.2	0.4	0.2	549	7	**19**	58	58	65	65	70	73
6	1.5	1.5	1.7	1.7	1.3	654	**23**	67	72	81	82	80	85
7	**3.7**	**3.7**	**3.7**	**3.8**	**3.5**	**3.5**	654	69	70	75	80	85	80
8	10.8	10.7	10.9	11.1	10.6	10.3	10.6	654	80	74	77	82	79
9	11.1	11.2	11.2	11.2	10.6	11.0	10.7	12.2	654	**58**	**59**	83	92
10	12.5	12.4	12.4	12.7	11.8	12.4	11.5	11.3	**8.9**	654	5	85	80
11	12.9	12.8	12.8	13.1	11.8	12.6	12.2	11.8	**9.0**	0.8	654	88	85
12	12.9	12.8	13.0	13.1	12.8	12.3	13.0	12.5	12.7	13.0	13.5	654	69
13	12.8	12.7	12.7	12.8	13.3	13.0	12.2	12.1	14.1	12.2	13.	10.6	654

FIG. 32. 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 2% difference scale bar is placed below the tree. The first sequence is that of the *Eracon sarahburnsae* holotype. All distinct haplotypes of *E. sarahburnsae* are included. The sequence of 05-SRNP-3449 is significantly shorter than the rest (549 vs. about 654 nucleotides), which accounts for anomalous statistics in the matrix. *Eracon sarahburnsae* DHJ02 is one of the three specimens with identical barcodes that tree away from other *E. sarahburnsae* specimens, and called *Eracon clinias* DHJ02 in Janzen et al. (2011). They may represent yet another undescribed cryptic species. Bootstrap support values are shown by each node in the tree (except within the cluster of almost identical *E. sarahburnsae* sequences) and ACG voucher codes (with SRNP, Janzen & Hallwachs 2013), GenBank accessions (with JN, http://genbank.gov/), or Olaf H. H. Mielke collection voucher code (with OM) are indicated for each sequence. Bootstrap values near and below 0.5 may correspond to incorrect topology, thus the precise phylogenetic position of *E. biternata* within *Eracon* is not confidently resolved (i.e. only trichotomy of the *E. clinias*, *E. biternata* and *E. paulinus* groups is confidently supported). The *Eracon* tree was rooted with *Spioniades abbreviata* (Mabille, 1888) and *Spioniades artemides* (Stoll, 1782) sequences. Percent difference, the number of different nucleotides and sequence length are shown below, above and on the diagonal of the matrix, respectively. Values corresponding to differences between sister species (*E. sarahburnsae* vs. *E. clinias* and *E. paulinus* (Stoll, 1782) vs. *E. lachesis* (Dyar, 1918)) are shown in bold face font. *E. clinias* and *E. paulinus* specimens are males and are from Brazil: Pará, Belem and *E. biternata* is a female from Brazil: Rondônia, near Cacaulândia, Fazenda Rancho Grande, 21-VII-1991, leg. Mielke & Miers. All other specimens are from Costa Rica, Area de Conservación Guanacaste, data in text and in Janzen & Hallwachs 2013.

VIII-2006, adult eclosed on 12-X-2006, voucher code 06-SRNP-43125 [MGCL]; site Finca Aurita, 10.88409 -85.25728, 460m: 1♀ collected on 08-VI-2006 as second instar, adult eclosed on 22-VII-2006, voucher code 06-SRNP-42043 [Tree of Life Database] (Figs. 31a-c); 1♂ collected on 08-VI-2006 as second instar, adult eclosed on 20-VII-2006, voucher code 06-SRNP-42042 [MGCL]; 1♀ site Finca Hugo, 10.88068 -85.26968, 540 m, collected on 25-VII-2007 as antepenultimate instar, larva died of disease, discarded, voucher code 07-SRNP-42141 (Figs. 31n–o); 1♂ site Sendero Tucan, 10.90424 -85.2712, 410 m, collected on 19-IX-2006 as second instar, pupa died of disease, discarded, voucher code 06-SRNP-43593 (Figs. 31p-s). 1♂ Guanacaste Prov.: Sector Del Oro, Margarita, 11.03234 -85.43954, 380 m, collected on 24-VI-2005 as antepenultimate instar, larva died of disease, discarded, voucher code 05-SRNP-22393 (Figs. 31j-m). Costa Rica: Limón Prov.: 1♂ Guapiles, May, Schaus & Barnes coll., genitalia NVG130614-44 [USNM] (Figs. 5, 19, 29l); 1♀ Banano River, III-1907, Wm. Schaus collection [USNM] (Figs. 6, 20); 1♂ Manzanillo - Gandoca Trail, up to 9.6089 -82.6431, 13-IX-2004, [Ichiro Nakamura collection]. Panama: 1♀ Chiriqui Prov., "Bocas del Toro", 24-III-1985, leg. G. B. Small [USNM] (Figs. 8, 22); Colon Prov.: 1♀ east of Colon, Santa Rita Ridge, 9.367 -79.717, 460 m, 5-I-1969, S. S. Nicolay [USNM]; 1♀ Nuevo Tonosi, 17-I-1980, leg. G. B. Small, genitalia NVG120922-12 [USNM] (Figs. 30a,b); Panamá Prov.: 1♂ Barro Colorado Island, 50 m, [eclosed] 15-III-1988, N. Greig, rearing #137 (P. DeVries), dissection GTA#10192 [MGCL]; 1♂ Distrito de El Llano, Cordillera de San Blas, N of El Llano, ca. 330 m, 10-V-1978, leg. G. B. Small [USNM] (Figs. 7, 21); 1♂ 5mi N of El Llano, 9.283 -79.0, ca. 330 m, 17-V-1978, leg. G. B. Small, genitalia No. X-6057 J. M. Burns 2004 [USNM] (Fig. 29m).

Type locality: COSTA RICA: Area de Conservación Guanacaste, Alajuela Province, Sector Rincon Rain Forest, site Sendero Rincon, GPS: 10.8962 -85.27769, 430 m.

Etymology: The name of the species honors Sarah Burns, the wife of Dr. John M. Burns, Curator of Lepidoptera (emeritus) Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC. John has identified and curated more than 17,000 reared and DNA barcoded ACG inventory specimens of Hesperiidae, within which this species and these specimens are embedded. Sarah shares John's passion for Hesperiidae and has helped him in all possible ways throughout his career. The name is a feminine noun in the genitive case.

Distribution and phenology: Currently, the species is known from Costa Rica (Alajuela, Guanacaste, Limón Provinces) and Panama (Chiriquí, Colon, Panamá Provinces), and has been reared in Costa Rica to eclose in all months of the year except March and June (Janzen & Hallwachs 2013). Free-flying adults have been encountered by other collectors in January, March, May and September.

Diagnosis: Evident similarities to South American *E. clinias* place the new species in *Eracon*. The combination of: (a) presence of a costal fold in males (vestigial in some specimens); (b) a hyaline spot over the cell spot mid costa; (c) lack of conspicuous dark

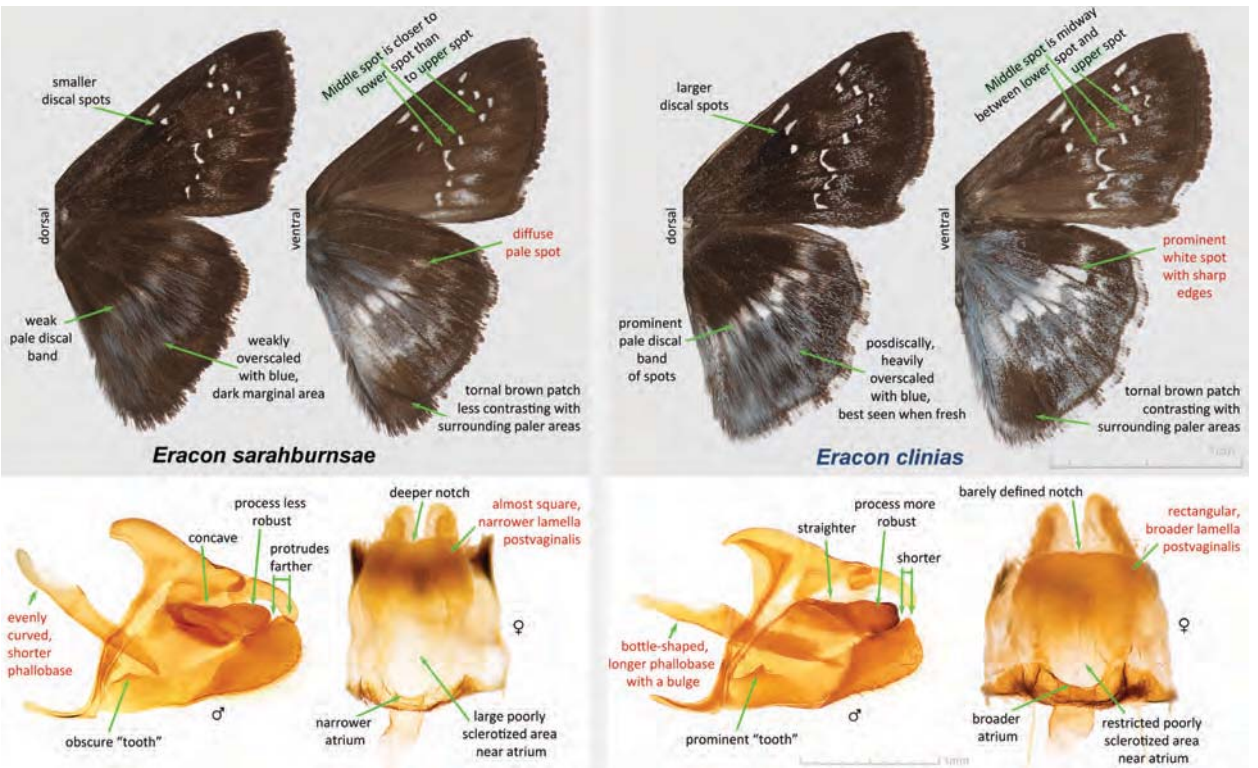


FIG. 33. Visual keys to species in the *Eracon clinias* group. *Eracon sarahburnsae* is in the left panel and *Eracon clinias* is in the right panel. Dorsal and ventral aspects of each species as exemplified by males are shown above on the left and right of the species name, respectively. Genitalia are shown below, male on the left and female on the right. Characters deemed to be most reliable in separating the species are in red font.

bands on dorsal hindwing; (d) lack of a defined black ocellus on dorsal forewing cell; (e) wings, especially hindwings with some pale-bluish scaling, differentiates *E. sarahburnsae* and *E. clinias* from all other known species of *Eracon*.

E. sarahburnsae is distinguished from *E. clinias* by the following characters (Fig. 33): (1) ventral hindwing base of cell Rs-M_1 has white scales mixed with brown scales forming a diffuse spot, vs. white spot with clearly defined edges in *E. clinias*; (2) ventral hindwing brown tornal area less contrasting with the surrounding pale-bluish background than that in *E. clinias*; (3) dorsal and ventral hindwing with more restricted areas of pale-bluish overscaling and weaker defined discal band of white spots than those in *E. clinias* fresh specimens; (4) on the fore wing, the white spot in the cell M_3–Cu_1 cell is closer to the white spot in cell Cu_1–Cu_2 than to the spot in cell M_2–M_3, vs. spot in the cell M_3–Cu_1 cell, which is further from the white spot in cell Cu_1–Cu_2 than from the spot in cell M_2–M_3, or positioned half way between the two spots in *E. clinias*; (5) female genitalia with lamella postvaginalis narrower (i.e. more elongated along anterior-posterior axis), with deeper notch on the distal margin, less sclerotized in the anterior half (antrum and areas around less sclerotized than those in *E. clinias*, antrum is relatively narrower (Fig. 30)); (6) male genitalia (differences are more subtle) with cucullus protruding further back from the obtuse process off the ampulla than in *E. clinias*, costa slightly concave near ampulla vs. almost straight in *E. clinias*, with process of the ampulla less robust, slightly smaller and narrower than that in *E. clinias*, a small tooth-like projection at the base of the valva off sacculus, which is well-developed in *E. clinias*, rounded and almost lacking; phallobase relatively shorter with evenly curved ventral side vs. longer and bottle-shaped with a broad but definitive bulge in *E. clinias* (Fig. 29). Characters (1) and (5) are most readily observed in distinguishing the two species (Fig. 33). Variation of male genitalia characters in both *Eracon* species can be assessed in Fig. 29. Additional illustrations of male and female genitalia of *E. clinias* are published by Austin (1997). Barcode sequences of the two species differ by about 3.5% (Fig.32). *E. clinias* is currently known only

from South America (Ecuador, Peru, the Guianas, northern Brazil); *E. sarahburnsae* is known only from Costa Rica and Panama.

Immatures (Fig. 31) and foodplants: All ACG rearings of E. *sarahburnsae* are from caterpillars feeding on mature leaves of the secondary forest rain forest tree, *Apeiba membranacea* (Malvaceae). Its absence from any other food plants in among the tens of thousands of other ACG Hesperiidae caterpillars found and reared (Janzen et al. 2011) suggests that it is a specialist on this species of tree. However, in places where ACG rain forest grades into ACG dry forest, *Apeiba membranaceae* is parapatric with *Apeiba tibourbou* (Malvaceae) its dry forest analogue, and it is possible that *E. sarahburnsae* may also feed on this second species of *Apeiba*.

Ecology: *Eracon sarahburnsae* is clearly a denizen of ACG lowland to intermediate elevation rain forest, as is its food plant. While the inventory has found and attempted to rear over 90 caterpillars of *E. sarahburnsae*, we have never seen an adult in nature. However, the inventory has not made an explicit effort to locate all food sources for adult butterflies in any part of ACG. Being reared, adults are on average slightly smaller than wild caught adults. Only three of the wild-caught caterpillars were parasitized—two by an undescribed species of *Hyposoter* Forster, 1869 (Ichneumonidae: Campopleginae) and one by an unidentified tachinid fly.

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We are indebted to the ACG parataxonomists for finding and rearing the caterpillars; to ACG for providing a place for them to work and rear caterpillars; to the Biodiversity Institute of Ontario at the University of Guelph, Canada, as well as BOLD of iBOL (http://www.boldsystems.org/) for sequencing and analyzing the DNA barcodes. We are grateful to Robert K. Robbins, John M. Burns, and Brian Harris (National Museum of Natural History, Smithsonian Institution, Washington, DC), David Lees and Blanca Huertas (Natural History Museum, London, UK), Andrew D. Warren and Andrei Sourakov (McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL), Wolfram Mey (Museum für Naturkunde, Berlin, Germany), Andrew Johnston, David A. Grimaldi, and Suzanne Rab Green (American Museum of Natural History, New York, NY) for granting access to the collections under their care and stimulating discussions; to John M. Burns for first identifying the ACG *Eracon* as *Eracon* nr. *clinias*; to Donald Harvey (National Museum of Natural History, Smithsonian Institution, Washington, DC) for preparations of genitalia from the John M. Burns X-series; to Ernst Brockmann for DNA barcode sequences of *Eracon clinias* and *E. paulinus*; to Olaf H. H. Mielke for discussions and legs of *Eracon biternata* used to obtain its DNA barcode; to Bernard Hermier for many enlightening discussions, and numerous suggestions; Andrew D. Warren for insightful discussions and specimen data; and two anonymous reviewers for helpful comments and corrections. The study has been supported (DHJ and WH) by U.S. National Science Foundation grants BSR 9024770 and DEB 9306296, 9400829, 9705072, 0072730, 0515699, and grants from the Wege Foundation, International Conservation Fund of Canada, Jessie B. Cox Charitable Trust, Blue Moon Fund, Guanacaste Dry Forest Conservation Fund, Area de Conservación Guanacaste, Permian Global, USNM/Smithsonian and the University of Pennsylvania.

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