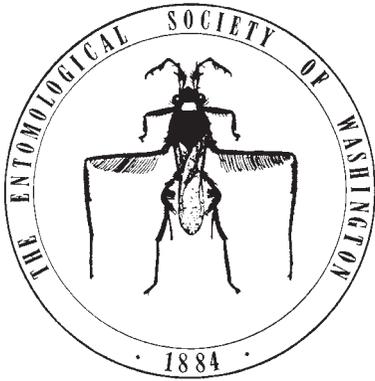


PROCEEDINGS
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ENTOMOLOGICAL SOCIETY
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**OF MANY SIMILAR SPECIES IN THE NEOTROPICAL GENUS
PORPHYROGENES (LEPIDOPTERA: HESPERIIDAE), A NEW ONE,
REPEATEDLY REARED IN COSTA RICA, IS RELATIVELY DISTINCT**

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Abstract.—Associating sexes in many species of the Neotropical hesperiid genus *Porphyrogenes* has been difficult, erroneous, or impossible, owing to their sexual dimorphism. Despite the extreme sexual dimorphism of *Porphyrogenes peterwegei* Burns, new species, full description of this rainforest skipper from Area de Conservación Guanacaste (ACG), northwestern Costa Rica, is no problem. The available sample amounts to nearly 100 reared adults, almost evenly divided between the sexes. Of these, 67 have been DNA barcoded and found to vary minimally in their COI haplotypes, with one haplotype predominating. Caterpillars and pupae consistently go through a distinctive set of developmental changes in their color patterns. Foodplant choice is conservative: of 227 immatures found in the wild, 94% were eating woody vines of the genus *Machaerium*, especially *M. seemannii* (Fabaceae), whereas 6% were feeding on the quite unrelated species *Dichapetalum morenoi* (Dichapetalaceae)—a peculiar pattern of larval foodplant selection seen in another skipper and two butterfly species in ACG. Caterpillars of *P. peterwegei* are occasionally attacked by a host-specific parasitoid (an undescribed tachinid of the genus *Siphosturmia*), which has not otherwise been encountered in 20,642 tachinid attacks on the caterpillars of >3,000 species of Lepidoptera in ACG. Morphologically, *P. peterwegei* differs significantly from its many congeners in both facies and genitalia.

Key Words: Genitalia (male and female), sexual dimorphism, caterpillars, pupae, foodplants (*Machaerium*), DNA barcodes, tachinid parasitoid

DOI: 10.4289.0013-8797.112.1.32

Speciation is kind to taxonomists when, within a bevy of similar related species, an undescribed one differs visibly from the rest. Multiple rearings and DNA barcodes become exception-

ally valuable to taxonomists when, among similar species, sexual dimorphism is so great that associating the sexes has often been incorrect or impossible. A recent detailed treatment of *Porphyrogenes* (Austin and Mielke 2008) recognizes 26 species (including

* Accepted by Robert R. Kula

the one named here), as well as three previously named but unassociated females and five unnamed unassociated females (which may or may not represent additional species). Owing, at least in part, to their late-afternoon, crepuscular, and perhaps nocturnal behavior, adults of these sizeable Neotropical skippers have always been rare in collections. Indeed, six of the nine new species of *Porphyrogenes* in Austin and Mielke (2008) are described from a single specimen, which is always male.

Porphyrogenes is known from most of Central and South America. Specific records extend from Belize (J. A. Shuey pers. comm.), Honduras, Nicaragua, Costa Rica, and Panama, to Colombia, Ecuador, Peru, Bolivia, Paraguay, and northern Argentina, and all mainland countries to the east, plus Trinidad (Austin and Mielke 2008). About three-quarters of the species occur in South America and one-third in Central America (these figures include two species attributed to both regions and exclude one species from no one knows where). Although it is not surprising that 16 of the 26 species have been found in Brazil (Austin and Mielke 2008), there are, at the very least, 12 species (two undescribed) in just the limited (and ecologically less diverse) area of French Guiana (B. Hermier in litt.). What with the similarity of many species, their excessive sexual dimorphism, and a lack of material, the geographic distribution of many described species is still nebulous, and the number of undescribed species is conjectural.

MATERIALS AND METHODS

Adult specimens used in this study have been reared from caterpillars collected during an ongoing bioinventory of Lepidoptera in Area de Conservación Guanacaste (ACG), northwestern Costa Rica (Janzen et al.

2009) and have been deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, District of Columbia, USA (see Type material). (In addition, seven reared adults preserved in EtOH have been deposited in the Monell Cryo Collection for Molecular and Microbial Research at the American Museum of Natural History, New York, New York, USA; three have been deposited in the Lepidoptera Tree of Life collection at the University of Maryland, College Park, USA.) The massive rearing program in Costa Rica is described in Burns and Janzen (2001), Janzen and Hallwachs (2009), and Janzen et al. (2009). Four wild-caught adults of *Porphyrogenes* have been borrowed from the Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica.

In the course of rearing enormous numbers of Lepidoptera and their parasitoids in ACG, new species have been discovered at a rate far greater than that at which they have been formally named and described. Temporary designations are needed for referring to undescribed species. When such species are thought to be very closely related to one that is already named, that name is used, but it is followed by a code with letters that denote the worker who detects two or more species instead of just one and with numbers (01, 02, 03, etc.) that arbitrarily distinguish these species—for example, *Genus species XYZ01*. When an undescribed species can be placed to genus but no further, its designation is simply *Genus XYZ01*.

Forewing length of adults was measured from base of costa to apex with a vernier caliper calibrated to tenths of a millimeter. After each measurement was recorded, the distance between caliper prongs was significantly reduced before the next specimen was measured. The measuring sequence was a



Figs. 1–4. Reared paratype male, voucher code 04-SRNP-4400 (above) and holotype female (below) of *Porphyrogenes peterwegei* from ACG, Costa Rica, in dorsal (left) and ventral (right) view; pins and pinholes artificially removed; scale bar = 1 cm.

random mix of males and females, and all but two specimens were measured on the same day. Nudum segments of the antennal club were counted with the aid of a stereomicroscope at a magnification of 40 \times . After treatment with 10% KOH, genitalia were dissected with the aid of a stereomicroscope and thereafter were kept free in glycerin. For details on the handling, comparison, and storage of unmounted genitalia, see Burns (1997). For information on methods used in DNA barcoding, see Hajibabaei et al. (2006).

RESULTS

Porphyrogenes peterwegei Burns, new species

Diagnosis.—Females of *Porphyrogenes* always have one or more forewing spots (joined, in some species, to form a transverse band), whereas males

(except for two species) are spotless. The female of *P. peterwegei* is unique in having only one spot—an outsized one in the center of the forewing (in cell CuA₁-CuA₂) (Figs. 3–4). Although females of a few other species have a similar large central spot, they also have a small distal spot (in cell M₃-CuA₁) (see figures in Austin and Mielke 2008). The male of *P. peterwegei* shares whitish wing fringes (Figs. 1–2) with just one other species, *P. stupa* Evans, which is known from a single dataless male whose ground color is virtually black with a purplish sheen, instead of dark brown as in *P. peterwegei*, and whose hind wing is broad, rounded, and lacking a tornal lobe, while that of *P. peterwegei* is narrow with a prominent tornal lobe.

Description.—*Size*: Females average larger than males. Forewing length in

mm: Male: Mean = 22.93, SD = 0.982, n = 45, Range 21.0–24.7. Female: Mean = 25.77, SD = 1.378, n = 51, Range 23.0–28.5. NB: Owing to the unnatural and inferior conditions of rearing, reared adults average smaller than wild ones; the degree of dwarfing varies, especially with respect to the stage of the caterpillar when found. The three males and four females obtained from wild-caught pupae of this species are near or at the upper end of the size range, given above, for each sex.

Number of segments in nudum of antennal club: The sexes do not differ. Mean = 29.96, SD = 1.259, n = 76, Range 27–34. The number of nudum segments is not correlated with length of the forewing.

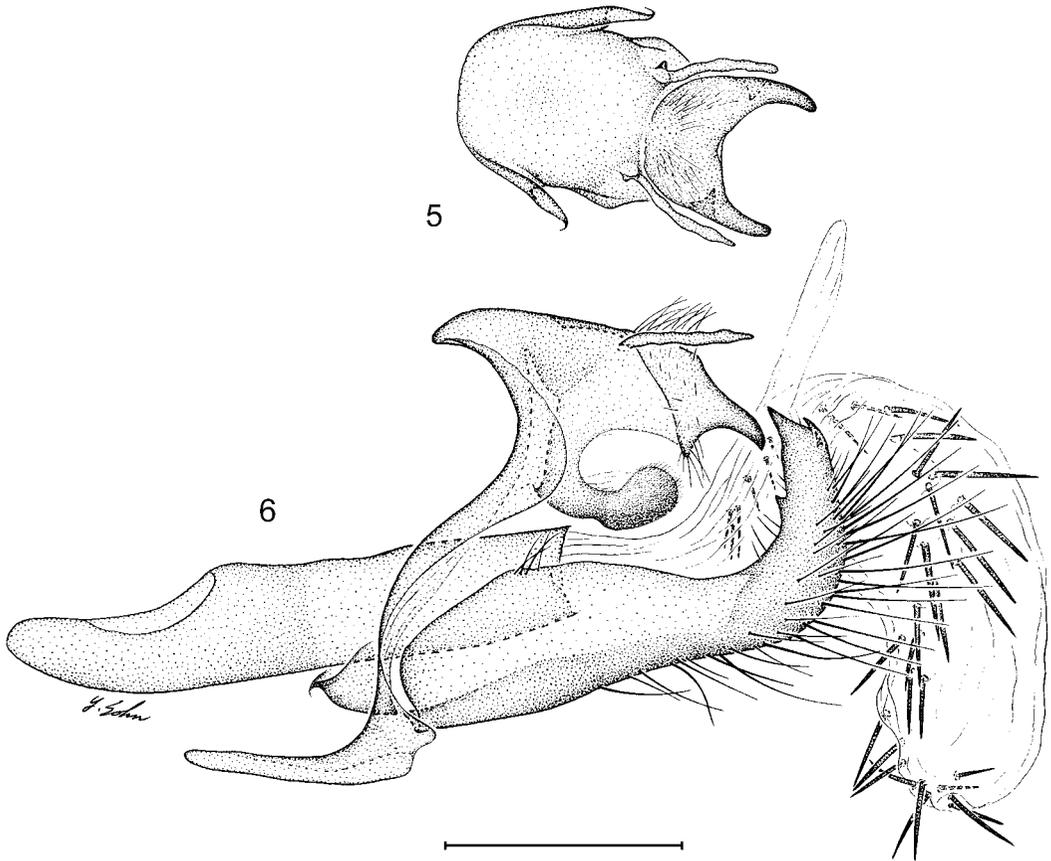
Wing shape (Figs. 1–4): Sexual dimorphism pronounced. Wings of male narrow and apically pointed; those of female broad and apically rounded. In both sexes, hind wing tornus conspicuously lobed.

Facies: Sexual dimorphism extreme. Male (Figs. 1–2): Body and wings dark brown both dorsally and ventrally, but dorsally conspicuously overscaled with dull orange on body and on about proximal half of forewing and proximal two-thirds of hind wing. Fringe along outer margin of both wings narrowly edged off-white. Hind wing with faintly suggested postmedian band of small, darker brown spots (more detectable ventrally than dorsally). Legs dull orange. Female (Figs. 3–4): Body and wings grayish brown dorsally and especially ventrally, with one huge, elliptical, hyaline spot in middle of forewing in cell CuA_1-CuA_2 . Dorsal overscaling faint greenish gray; purplish sheen distal to this overscaling, primarily on forewing (visible when viewed at certain angles). Edge of fringe along outer margin not distinctively off-white (as in male), but often

(though variably) paler than ground color, especially above tornal lobe. Hind wing postmedian band of darker spots more evident than in male, especially ventrally. More or less conspicuous pale gray, submarginal to marginal strip (interrupted by darker veins) distal to ventral hind wing spotband and contrasting with it. Similar marginal strip of still paler gray on ventral forewing. All of ventral forewing space between vein 2A and inner margin extra pale. Legs dull orange.

Secondary sex characters: Male: Forewing with costal fold. Forewing vein 2A bowed anteriorly and, along highest reaches of its arc, swollen and ventrally devoid of scales; vein 2A, from swollen stretch to base of wing, bisecting ventral speculum comprising variously modified scales. On dorsal hind wing, two conspicuous, adjacent, distally light-brown and proximally tan hair tufts arising near base of cell $Sc+R_1-Rs$ and near base of discal cell, and associated with large speculum extending from discal cell to costa. Both sexes: Ventral hind wing with deep, pale-scaled groove (most prominent proximally) in cell 2A-3A.

Genitalia: Male (Figs. 5–6): In lateral view, body of valva (i.e., anterior two-thirds) low; distal one-third of valva (= harpe) robust (i.e., not notably narrower than adjacent part of body) and abruptly bent dorsad, nearly or quite forming right angle with body, then terminating in large, sharp, anterodorsal point and bearing some preterminal coarse teeth. Cornuti long, essentially straight, delicate spines (numbering 31, 31, 32, 32, 34 [see Fig. 6], and 36 in six individuals); in everted vesica, rather evenly and widely spaced, except for some relatively clustered proximal ones. Tegumen stocky; its delicate posterior prongs uneven in diameter, about as in Figs. 5–6 (or, in extreme case, so uneven as



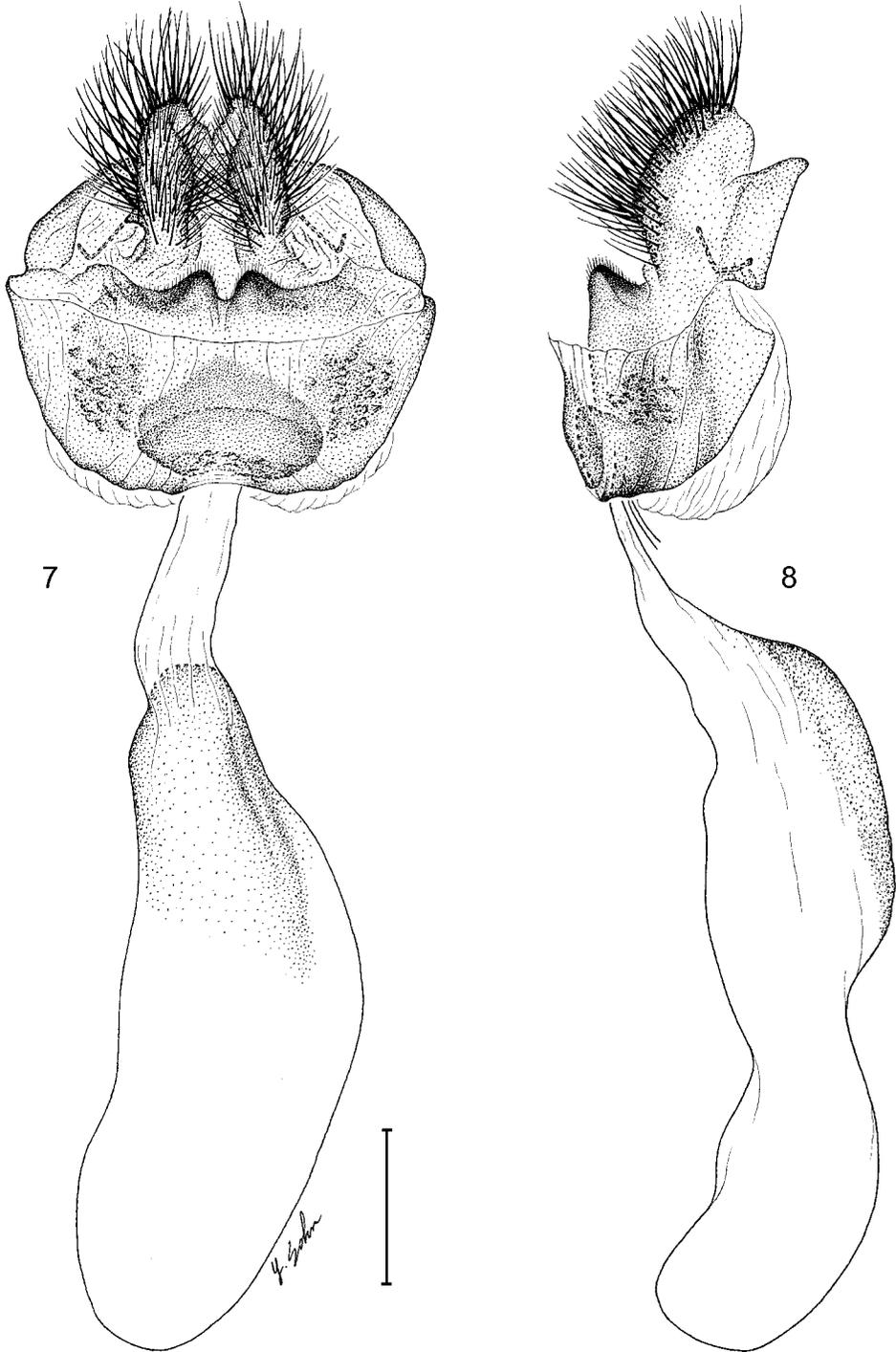
Figs. 5–6. Genitalia of paratype male of *Porphyrogenes peterwegei* (genitalia dissection code X-5235, voucher code 01-SRNP-5734) from ACG, Costa Rica; scale bar = 1.0 mm. 5, Tegumen and uncus in dorsal view. 6, Complete genitalia, with vesica everted, in left lateral view.

to suggest linked sausages). Uncus, in dorsal view, a wide U, evenly curved at bottom. Female (Figs. 7–8): Well-sclerotized sterigma surrounding midventral, paler, usually membranous area at, and posterior to, ostium bursae. Central part of lamella antevaginalis with conspicuous posterior edge forming sill of ostium bursae. Wrinkled membrane ventral to sterigma with exaggerated wrinkling laterally and sclerotized plate midventrally; sclerotized plate same width as central part of lamella antevaginalis (and directly beneath it) but extending farther posteriad. Posterior edge of lamella postvaginalis thickened, darkly sclerotized, midventrally V-

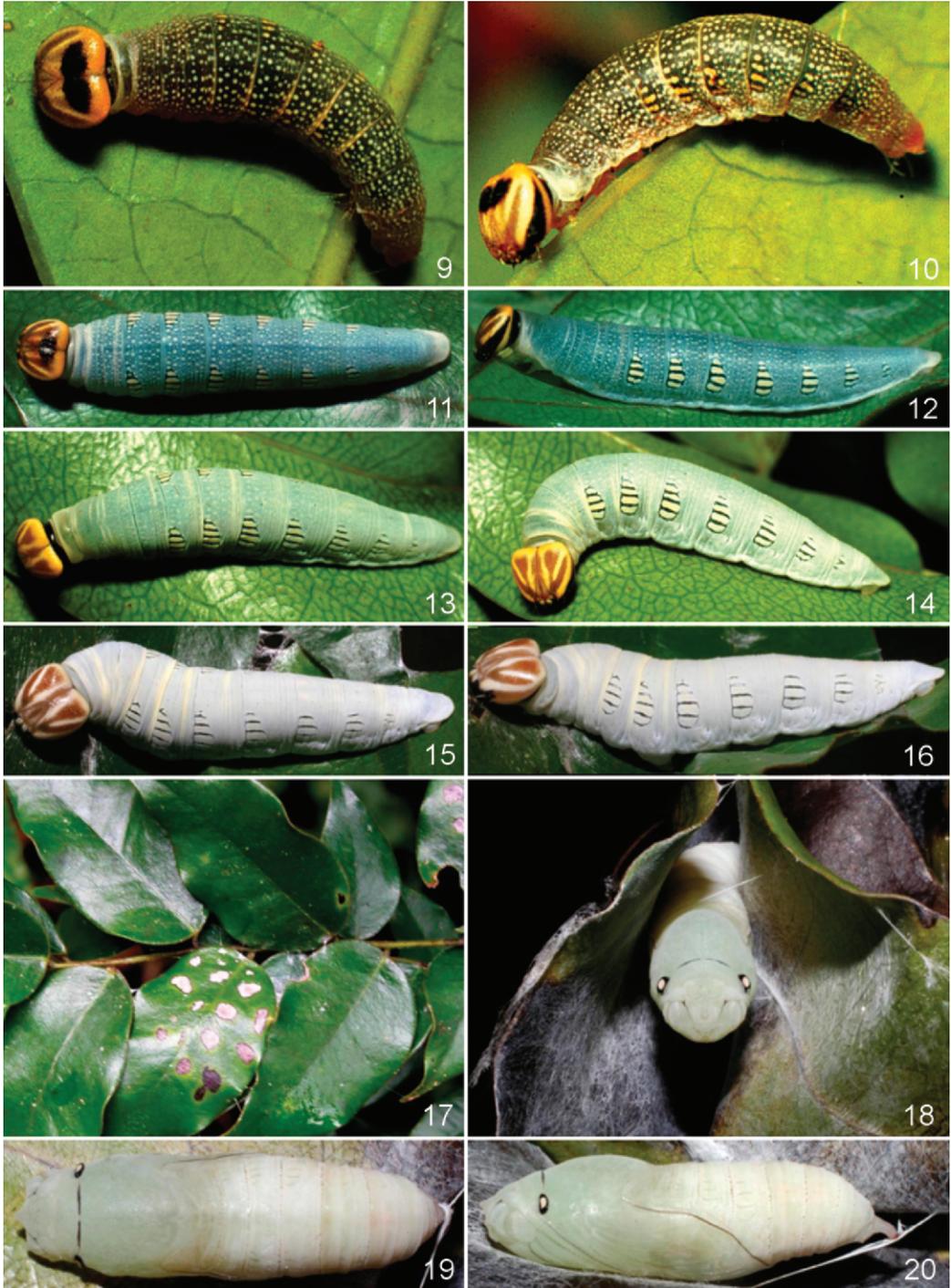
shaped, and prominently hirsute around V. Membrane of posterior 40% of corpus bursae with limited, longitudinal sclerotization suggesting trough or canoe.

Ecological distribution: Known from ACG rainforest habitats between 95 m and 760 m. Present but scarce in intergrade between ACG rain forest and dry forest.

Larval foodplants (Table 1): Diet very restricted. Total of 213 caterpillars found feeding on seven species of *Machaerium* (Fabaceae, Fabales)—mainly *M. seemannii* Benth. and *M. acuminatum* Kunth—but 14 caterpillars found feeding on *Dichapetalum mor-*



Figs. 7–8. Genitalia of paratype female of *Porphyrogenes peterwegei* (genitalia dissection code X-5238, voucher code 02-SRNP-6579) from ACG, Costa Rica; scale bar = 1.0 mm. 7, Ovipositor lobes, sterigma, and bursa copulatrix in ventral view. 8, The same, plus part of ductus seminalis, in right lateral view.



Figs. 9–20. Caterpillars, foodplant, and pupae of *Porphyrogenes peterwegei* from ACG, Costa Rica, in dorsal (left) and left lateral (right) view. 9–10, Second instar. 11–12, Third instar. 13–14, Fourth instar. 15–16, Fifth (last larval) instar. 17, Pupal shelter on *Machaerium seemannii*. 18, Pupa in frontal view within opened shelter. 19–20, Pupa.

Table 1. Larval foodplants of *Porphyrogenes peterwegei* in Area de Conservación Guanacaste, northwestern Costa Rica, and number of wild caterpillars encountered by the bioinventory feeding on each species of plant.

Family	Species	Number of caterpillars	
Fabaceae	<i>Machaerium acuminatum</i>	26	
	<i>Machaerium falciforme</i>	1	
	<i>Machaerium floribundum</i>	3	
	<i>Machaerium kegelii</i>	1	
	<i>Machaerium salvadorensis</i>	3	
	<i>Machaerium seemanii</i>	177	
	<i>Machaerium 16556</i>	2	
	Dichapetalaceae	<i>Dichapetalum morenoi</i>	14

enoi Prance (Dichapetalaceae, Malpighiales).

Developmental times: In the rainforest environment, the duration of larval development (first through fifth instar) ranges from 90 to 100 days. Pupal development lasts 16 to 30 days. There is no evidence of pupal dormancy.

Type material.—*Holotype:* female (Figs. 3–4), voucher code 03-SRNP-6133, Rio Blanco Abajo, Sector San Cristobal, Area de Conservación Guanacaste, Alajuela, Costa Rica, 500 m, latitude 10.90037, longitude –85.37254 (USNM), collector Carolina Cano. Yellow label reads “LEGS AWAY/FOR DNA.” DNA barcode: AACCTTATATT TATTTTTGGAATCTGAGCAGGAA TAGTAGGAACTTCTCTAAGATTAC TAATTCGAACTGAATTAGGAACC CCCGGATCTTTAATTGGAGATGAC CAAATTTATAATACTATTGTTACA GCTCATGCTTTTATTATAATTTT CTTTATAGTTATACCTATTATAAT TGGAGGTTTTGGAAATTGACTAG TTCCTTAATACTGGGAGCTCCTG

ATATAGCATTCCCCGAATAAATA
ATATAAGATTTTGATTATTACCCC
CTTCTTTAACTCTTTTAATTTCAAG
AAGAATTGTAGAAAATGGTGACG
GTACAGGTTGAACTGTATACCCC
CCTTTATCATCAAATATTGCTCATC
AAGGATCTTCTGTTGATTTAGC
AATCTTTTCTCTACATCTTGCAGG
TATTTCTTCAATTTTAGGAGCTATT
AATTTTATTACTACAATTATTAATAT
ACGAATTAACAATTTATCTTTTGA
CCAAATACCTCTATTTGTTTGAGC
AGTAGGAATTACAGCTTTATTATTA
TTATTATCATTACCAGTTTTAGCTG
GTGCAATTACTATACTTTTAACTGA
TCGAAATTTAAATACTTCATTTTTT
GATCCTGCTGGAGGAGGTGATCCT
ATTTTATC.

Paratypes: 45 males, 50 females, ACG, Costa Rica (USNM). For more detail, see Janzen and Hallwachs (2009).

Etymology.—This skipper is named in honor of Peter Wege of Grand Rapids, Michigan, whose extraordinary generosity has (1) significantly increased the size of ACG and permanently secured thousands of hectares of *P. peterwegei* rainforest habitat, (2) stimulated conservation overall by supporting the founding of the Costa Rican Ministry of Environment and Energy in 1986–1990, and (3) advanced the mission and deeds of DNA barcoding.

DISCUSSION

DNA barcodes.—In all, 67 specimens of *P. peterwegei* have been barcoded. Individual variation in their barcodes is minimal, and the DNA sequence of the holotype is, by far, the commonest. The fact that both males and females have identical COI haplotypes is, of itself, sound evidence that, despite disparate outward appearances, they belong to one and the same species.

Natural history.—Independent evidence from numerous rearings makes the same point. Caterpillars with the same foodplants, the same behavior, and the same color patterns that change the same way in the course of larval and pupal development (Figs. 9–16, 18–20) have produced nearly equal numbers (52 males, 60 females) of the two sexes, which look so different from each other as adults (Figs. 1–4).

Although the bioinventory of ACG Lepidoptera and their parasitoids began in 1978, it was not until 2000 that an adult of *P. peterwegei* was successfully reared. (One caterpillar had been found in 1995 and another in 1998; both died of disease.) This lag was due, in large part, to the inventory's early emphasis on dry forest habitats—but also to the caterpillars' construction of unusually cryptic shelters. The flimsy shelter of a sizable caterpillar is hard to spot because, in most cases, its occupant has lightly silked together one or two leaves whose small and numerous leaflets are close-set and more or less overlapping anyway (Fig. 17). Pupation takes place within the larval shelter (Fig. 18).

Why *P. peterwegei* is limited to rain forest is not entirely clear. Its known larval foodplants (Table 1) are seven species of woody vines in the leguminous genus *Machaerium* (especially *M. seemannii*), plus, infrequently, the quite unrelated species *Dichapetalum morenoi*, all of which grow in ACG rain forest. On the one hand, neither *Machaerium* nor *Dichapetalum* occurs in ACG cloud forest. On the other hand, two of the rainforest foodplants (*M. acuminatum* and *M. kegelii* Meisn.) are present in ACG dry forest as well, along with a common, but unused, dry-forest congeneric tree (*M. biovulatum* M. Micheli). That *M. biovulatum* is a tree and all other ACG species of *Machae-*

rium are vines is probably irrelevant. Because *P. peterwegei* caterpillars have occasionally been found feeding on four of the viny species of *Machaerium* in the intergrade between ACG rain and dry forest, they may eventually be discovered eating *M. biovulatum* at the wet margin of its dry-forest distribution. Regardless of that possibility, one wonders why *P. peterwegei* does not exploit *M. acuminatum* and *M. kegelii* more fully by spreading into ACG dry forest—at least temporarily, during the six-month rainy season.

Machaerium is in the family Fabaceae in the order Fabales, and *Dichapetalum* is in the family Dichapetalaceae in the order Malpighiales. Although these orders are broadly related phylogenetically, each relates more closely to a few other orders (Stevens 2001); each comprises such a great diversity of taxa that the extremely limited foodplant selection of *P. peterwegei* may well stem from one or more similar or identical chemical cues having arisen independently in *Machaerium* and *Dichapetalum*. In the ACG bioinventory, *P. peterwegei* shares an emerging pattern—with *Astraptus enotrus* (Stoll) (Hesperiidae), *Morpho amathonte* Deyrolle, and *M. helenor* (Cramer) (Nymphalidae)—in which a species not only specializes on an array of closely related foodplants (in this case, species of the genus *Machaerium*) but also eats one to three species in the genus *Dichapetalum*.

In ACG, the caterpillar of *P. peterwegei* shares its primary foodplant, *M. seemannii*, with the caterpillars of *Telemiades nicomedes* (Möschler) (Hesperiidae), *Morpho amathonte*, *M. helenor*, and *M. granadensis* C. Felder and R. Felder (Nymphalidae), *Hapigia repandens* Schaus DHJ02 and *Antaea lichyi* Franclemont (Notodontidae), *Oxidercia toxea* (Stoll) DHJ01 (Noctuidae), and four species of Stenomatininae (Janzen

and Hallwachs 2009). None of these caterpillars are common enough to compete significantly with *P. peterwegei*, and none share parasitoids with *P. peterwegei*.

Like most species of ACG caterpillars, the caterpillar of *P. peterwegei* is attacked by parasitoids that are host-specific. Of the 227 wild-caught caterpillars found to date, one was attacked by an extreme generalist tachinid fly (*Patelloa xanthura* (Wulp) DHJ01, voucher code 02-SRNP-33798); 11 were attacked by a medium-sized, undescribed tachinid (*Siphosturmia* Wood02) that apparently attacks no other species of ACG caterpillar (out of 20,642 tachinid attacks of ACG caterpillars of more than 3,000 species of Lepidoptera).

The body of well grown caterpillars of *P. peterwegei* is “moldy white,” with a lateral series of black-bordered “stacked windows” (Figs. 13–16)—a color pattern that is more or less apparent in *Bungalotis quadratum* (Sepp), *B. diophorus* (Möschler), *B. midas* (Cramer), *Nicephellus nicephorus* (Hewitson), and *Ocyba calathana* (Hewitson) (Hesperiidae). *Porphyrogenes peterwegei* differs from these five species in, e.g., its choice of foodplants, the number of windows in the side stack, and details of color and pattern of a prominently striped head (see images in Janzen and Hallwachs 2009). Although these five species, which are closely related, are also related to *Porphyrogenes*, it is not yet known if the larval similarities reflect a common origin or parallel evolution (or both).

Caterpillars with their seemingly ostentatious white color are probably mimicking caterpillars killed by white moldy fungi, which, in turn, defend their food by producing secondary compounds highly toxic to vertebrates (e.g., Janzen 1977). Because ACG skipper caterpillars leave their shelters

to eat chiefly at night, they are usually seen when exploring diurnal vertebrate predators open their shelters—and then, if moldy or moldy-looking, are probably bypassed. Presumably, the pale pupae (Figs. 18–20) in larval shelters are likewise mimetically defended against visually-orienting vertebrate predators.

No free-living adults of *Porphyrogenes* have been encountered in ACG during 40 years of random insect observation by Janzen and Hallwachs—no doubt a consequence of these skippers’ late-day to at least late-twilight period of activity (and possibly to some activity far above-ground in the canopy, although such behavior has never been documented). A lone male specimen dated January 1984 likely came from diverse lepidopteran material taken in a light trap.

Taxonomic tangentialia.—The known range of *P. peterwegei* is moderately increased by a male in the INBio collection with the following label data: Estación Quebrada Bonita, R. B. Carara, Prov. Puntarenas, Costa Rica, 50 m, agos 1993, R. N. Guzmán. Identification of this worm, wild-caught specimen included genitalic examination (J. M. Burns genitalic dissection X-6353).

In a brief account of *P. peterwegei* under the heading “*Porphyrogenes* undescribed species,” Austin and Mielke (2008) refer to the “genitalia (Fig. 152) of an apparent male of this species” from Finca Hamadryas, Ciudad Colon, Costa Rica, 15 September 1998, dissection GTA # 13917. The genitalia in figure 152 are not those of *P. peterwegei* (they may be those of yet another undescribed species of *Porphyrogenes*), and figures 83 and 84 in Austin and Mielke (2008) show dorsal and ventral facies of this misdetermined individual.

Caterpillars of *P. spina* Austin and Mielke (described from two adult males

from Panama) have been found twice in ACG rain forest: once feeding on *M. seemannii*, the favored foodplant of *P. peterwegei*, within a few meters of caterpillars of that species; once on *M. cobanense* Donn. Sm. (see images of *P. spina* in Janzen and Hallwachs 2009). These are the only two species of *Porphyrogenes* known from ACG. However, Austin and Mielke (2008) record two more species, *P. omphale* (Butler) and *P. speciosus* Austin and Mielke, from Costa Rica; another two, *P. glavia* Evans and *P. spoda* Evans, from Panama; and one, *P. sula* (Williams and Bell), from Honduras. Moreover, their records of *P. zohra* (Möschler) include Honduras, Nicaragua, and Venezuela. The occurrence of this last taxon in Costa Rica is no longer implied but real, thanks to three males in INBio (J. M. Burns genitalia dissections X-5032, X-5240, and X-6354). In light of all these records and the scarcity of wild-caught adults, there are probably more than two species of *Porphyrogenes* in ACG.

ACKNOWLEDGMENTS

Our thanks to Donald Harvey for dissecting genitalia, Young Sohn for drawing two of them (Figs. 5–8), Karie Darrow for photographing adults (Figs. 1–4) and numbering plates, Mehrdad Hajibabaei for DNA barcoding, Bernard Hermier for sharing his extensive knowledge of *Porphyrogenes*, Sarah Burns for helping with various tasks, ACG parataxonomists for finding and rearing the caterpillars and parasitoids, and John Shuey and an anonymous reviewer for useful information. This study was supported by the National Museum of Natural History Small Grants Program to JMB; and by U.S. National Science Foundation grants BSR 9024770 and DEB 9306296, 9400829, 9705072, 0072730, and 0515699, and grants from Guanacaste

Dry Forest Conservation Fund and ACG to DHJ.

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