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TWO NEW SPECIES OF *EUPTYCHIA* HÜBNER, 1818 (LEPIDOPTERA: NYMPHALIDAE: SATYRINAE) FROM THE GUIANA SHIELD, WITH NOTES ON *E. MARCELI* BRÉVIGNON, 2005 AND *E. RUFOCINCTA* WEYMER, 1911

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ABSTRACT. Two new species of *Euptychia* are described: *Euptychia audacia* Brévignon, Fratello & Nakahara **n. sp.** and *Euptychia aquila* Fratello, Nakahara & Brévignon **n. sp.** These two taxa, the recently described *Euptychia marceli* Brévignon, 2005 and *E. roraima* Nakahara, Fratello & Harvey, 2014, a quartet of *Euptychia* from the Guiana Shield region, are compared morphologically. New information on *E. marceli* Brévignon, 2005 is revealed, and the taxonomic status of *E. rufocincta* Weymer, 1911 is discussed including its possible synonymy with *E. picea* Butler, 1867.

.Additional key words: Euptychia picea, E. roraima, Euptychia audacia, Euptychia aquila, Guiana subregion

For many years, the gargantuan subtribe Euptychiina (see Lamas 2004) has been the subject of taxonomic studies. However, its taxonomy has been poorly understood because of the predominance of superficial morphological homogeneity among its members (Peña & Lamas 2005). Approximately 50 genera and more than 400 species have been recognized within this subtribe (Peña et al. 2010, Freitas et al. 2011, 2012). Regarding the classification of these species, lepidopterists usually accept and follow Lamas (2004), who retained most of the genera erected by Forster (1964). This scheme of generic classification is characterized by the lack of clearcut diagnoses. As a result, placements of taxa in these genera are usually tentative. However, because of recent work on Euptychia Hübner, 1818 including phylogenetic studies (e.g., Pulido-B. et al. 2011, Freitas et al. 2012), this genus has become one of the more well-defined and understood genera among Euptychiina. Though D'Abrera (1988) provisionally applied the name Euptychia in a very broad sense, we accept the strict definition of Forster, which restricts the genus to 18 described species (Lamas 2004, Brévignon 2005, Pulido-B. et al. 2011, Freitas et al. 2012, 2013, Neild et al. 2014, Nakahara et al. 2014).

Distributed throughout the Neotropical region, members of Euptychia are relatively small, almost all are marked prominently with ventral bands and submarginal eyespots and the great majority exhibit wing translucence. Almost all male Euptychia species that have been dissected show a conspicuous projection of the tegumen above the uncus in the male genitalia, which is possibly a diagnostic character to differentiate this genus from other genera in the subtribe (G. Lamas, pers. comm. 2008, Freitas et al. 2012, pers. obs.). The occurrence of one recurrent vein in the forewing discal cell is also considered a character shared by all Euptychia (Freitas et al. 2012, pers. obs.). These members of Euptychia also possess distinctive larval characters and use singular hostplants (DeVries 1987) for Euptychiina: Selaginellaceae (Lycopodiophyta) and Neckeraceae (Bryophyta), not seed plants which are the hostplants of most Satyrinae genera. Selaginellaceae are also the hostplants of some Oriental satyrines (Fukuda 1983), Ragadia Westwood, 1851 and Acrophtalmia C. Felder & R. Felder, 1861, but they belong to different subtribes within Satyrini (Peña et al. 2011).

Extensive fieldwork done in French Guiana in recent decades has rendered a significant increase of the

taxonomic and biological knowledge of the butterfly fauna of this country (Brévignon 1998, 2005, 2008, Brévignon & Benmesbah 2012). In a like manner, recent expeditions by the first author and partners have helped increase the knowledge of the butterflies of neighboring Guyana. This certainly applies to lowland and lower premontane Euptychiina, and particularly the genus Euptychia. From both recent (Brévignon 1998, 2005, 2008, Brévignon & Benmesbah 2012, Costa et al. [2014], Nakahara et al. 2014) and present studies (Costa et al. in prep.) including this article, there seems to be a considerable number of euptychiine species that appear to be endemic to the Guiana subregion of Amazonia; a high percentage (over 50%) of endemism has been detected for the Euptychia fauna of this region. The Guiana (or Guianan) subregion includes French Guiana, Surinam, Guyana and parts of adjacent regions of Venezuela and Brazil, and has a long historical basis for being considered a biogeographical region. According to Lim and Tavares (2012), the Guiana subregion "was first recognized as a biogeographic zone..." by Wallace (1852). We follow a modern work (Voss & Emmons 1996) that delineates the Guiana subregion as that section of Amazonia east of the Rio Negro and north of the Amazon River. The Guiana subregion coincides to a great extent with the Guiana Shield (Lim & Tavares 2012), a geological formation of ancient Precambrian basement rock. Extensive faunistic and floristic research focuses on this huge biogeographical region (e.g., Hollowell et al. 2001, Lim & Engstrom 2001) and both past and ongoing studies in numerous biological groups including Rhopalocera (e.g., Désamoré et al. 2010, Costa et al. [2014], in prep.), indicate that the Guiana subregion is a very important area for endemicity, not only for butterflies but also for many other groups of living organisms. The research of Costa et al. [2014], (in prep) focuses on the montane forests and other highland habitats of the Pantepui region where the greatest butterfly endemicity is expected, even more in its infancy is the study of butterfly endemicity of other montane forests, Amazonian forests and other lowland habitats (e.g., encompassed within savannahs) this vast biogeographical region.

Two new *Euptychia* species from the Guiana Shield region are described; both had been previously misidentified as known species.

MATERIALS AND METHODS

Identification of *Euptychia* species treated in this study was based on the information from the original descriptions (Butler (1867); Weymer (1911); Brévignon (2005); Nakahara et al. (2014)) and the examination of

type material and other specimens in public and private collections (listed below). The external morphology of the described species and congeners has been studied by the authors, by examining preserved specimens from several localities spanning their known geographical range, in order to evaluate their variation and stability of characters. Abdomens were dissected using standard techniques at the USNM, with adult abdomens being soaked in hot 10% KOH for 10-15 minutes, dissected and subsequently stored in glycerine. A Wild M5 stereomicroscope was used for male genitalia dissections at the USNM and photographed with a Canon 5D camera; a LEICA MZ 16 microscope was used for male and female genitalia dissections at the MGCL, with images of female genitalia taken by using a Canon EOS 50D and stacked by using Helicon focus 6.2.2 and Helicon Remote (ver. 3.4.14). Butterfly body morphological characters were studied under magnification using these binocular microscopes. Measurements are provided as minimum-maximum values. The terminology for genital and abdominal structures largely conforms to Klots (1956), except for the term aedeagus, where we follow Peña and Lamas (2005). Nomenclature for wing venation follows the Comstock-Needham system described by Miller (1970:44), and areas and elements of wing pattern follow that of Peña and Lamas (2005) and Neild (2008). The following acronyms and abbreviations are used throughout this paper.

AMNH American Museum of Natural History, New York, USA

BMNH The Natural History Museum, London, UK LCB Lalita & Christian Brévignon collection, Cayenne, French Guiana

MB Mohamed Benmesbah collection, Plaisance-du-Touch, France

MGCL McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, Florida, USA

MNHM Museum National d'Histoire Naturelle, Paris, France

MUSM Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru

USNM National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

ZMHU Museum für Naturkunde der Humboldt-Universität, Berlin, Germany

ZSM Zoologische Staatssammlung München, Munich, Germany

DFW dorsal forewing

VFW ventral forewing

DHW dorsal hindwing

VHW ventral hindwing

Taxonomy

Euptychia audacia Brévignon, Fratello & Nakahara, new species

Figs. 1 (1-4), 2 (1-4), 3, 4 (1)

Euptychia picea; Brévignon, 1998 : 122 Euptychia sp.; Brévignon, 1998 : 123, 124 Euptychia rufocincta; Brévignon, 2005: 401: 23–26; 2008: 75, 89: 49a–c

Diagnosis. Euptychia audacia possesses a 'marcelitype' VHW ocelli pattern (based on the pattern of E. marceli); the large tornal ocellus of E. marceli is much larger, with a much wider yellow ring, compared to its large apical ocellus; it also lacks small satellite ocelli above the large tornal ocellus and below the large apical ocellus. Among described Euptychia species, E. audacia is the closest in both sexes to E. marceli, distinguished in the males by being smaller, often significantly, and slightly darker dorsally and ventrally, with the ventral brown bands less reddish. The preeminent male facies characteristic is dorsal: E. audacia males exhibit dark brown coloration in the FW apical area that largely obscures the prominent VFW apical ocellus from showing through; in E. marceli males, the DFW apical dark brown coloration is much more restricted, consequently, the prominent VFW apical ocellus is seen easily through the translucence. Female *E. audacia* are again smaller, often significantly, than E. marceli females, and their VHW large tornal ocellus is usually not as large compared to the VHW large apical ocellus as in E. marceli females, where there is always a substantial difference in size between these two ocelli. E. audacia females show slightly more DFW dark brown coloration, distally and apically, than E. marceli females, though this apical dark brown coloration is much more restricted compared to the males and does not obscure the prominent VFW ocellus from showing through the translucence, and again, the ventral brown bands are less reddish on E. audacia. Larger E. audacia and smaller E. marceli specimens can be very close, especially on worn specimens, so dissection would probably be necessary for determination. A further new species of Euptychia (see below), sympatric in the Guianan southern mountains with both E. audacia and E. marceli, also has the 'marceli-type' VHW ocelli pattern, but is very easily distinguished from *E. audacia*. Male genitalia of E. audacia n. sp. are distinguished from its congener E. marceli by the following characters: narrower and slightly curved uncus; a significant extention of the ventral margin of the tegumen is present (absent in E. marceli). Female

genitalia of *E. audacia* are distinguished from its congener *E. marceli* by the following characters: lamella antevaginalis developed, forming a plate in ventral view (not developed in *E. marceli*) (see Fig. 4). See below for male and female genitalic differences between *E. audacia* and the additional Guianan new *Euptychia* species.

Description. MALE: forewing length 16 mm

Wing shape. Forewing inner margin almost straight, outer margin almost straight, with a rounded apex. Hindwing rounded and rather elongated toward the tornus, slightly outwardly curved inner margin convex proximally to vein 3A, rounded tornus, outer margin convex, base of costa convex.

Wing venation. Forewing recurrent vein present in discal cell.

Dorsal surface of wings. Ground colour brown (R137, G98, B67), with subtle greyish overtones, slightly translucent, thus revealing dark bands and ocelli from ventral surface; apical area darker (R61, G37, B25), thus hiding preapical ocellus; fringe concolorous.

Ventral surface of wings. Ground colour brown (R178, G148, B114), lighter than dorsal surface, with five darker brown (R125, G89, B57) bands; fringe concolorous.

Forewing: a narrow band distally extended along the swollen section of subcostal vein; a regular and quite straight discal band extends from subcostal vein to just beyond vein 2A; a postdiscal band extends from the subcostal vein towards inner margin until vein 2A, in apical portion, thin and distally deviated, almost joining submarginal band, slightly broadening, thicker than discal band in its medial portion, and slightly distally deviates below Cu,; an undulating submarginal band, curved basally in each cell, extends from near apex to near tornus, gradually broadening towards vein Cu, and slightly narrowing after this vein where it is distally deviated; a dark brown, narrow and wavy marginal band extends from apex towards tornus, undulating until vein Cu, and then straight after this vein; ocellus in cell M₁ exceeding from vein M₁ and M₂ respectively, ringed in yellow and with one centered white pupil in black area; an indistinct, faint, light brown marking visible around and below the ocellus. Hindwing: a slightly regular and straight band extends from costal margin to inner margin, at base of wing; discal band of same width as that of forewing, traverses straight from costal margin towards inner margin, slightly narrower in anal portion; a postdiscal band of same width as that of forewing, extends from costal margin towards inner margin, very slightly undulating, slightly narrower in anal portion; an irregular submarginal band starts from apex and traverses along margin towards tornus, broadened and M-shaped between vein M, and Cu,; a dark brown marginal band, thin and very slightly undulated, traverses along distal margin from apex towards tornus and almost fuses to postdiscal band in cell 2A; a submarginal ocellus, smallest of three, in cell Rs, shows one centered white pupil in black area; larger ocellus in cell M₁, ventrally exceeding from vein M2, encircled by yellow ring and with one centered white pupil in black area; largest ocellus, ringed in yellow, with one centered white pupil in black area in cell Cu, exceeding from vein Cu, and Cu, respectively; an indistinct, faint, light brown marking is visible around this ocellus.

Head. Antenna light orange brown with darker base and apex, about 7 mm long; eyes entirely blackish, hairy, a fringe of creamy scales along posterior lateral edge of eye; palpus 2.5 mm long, covered with long hairy scales, creamy proximally and brownish distally; from brown.

Thorax. Dark brown dorsally, with creamy hair ventrally. Foreleg covered by long light brown hairy scales.

Abdomen. Dark orange brown dorsally, with long creamy hairy scales ventrally.

Genitalia. (three specimens prepared: vial LCB PAG 276; vial #2013-03 and #2013-04 (USNM)): uncus narrow, curved downward in lateral view, tapered posteriorly, almost evenly broad in dorsal view; tegumen dorsally flattened in lateral view, rather short conspicuous posterior projection above uncus, approximately one third length of

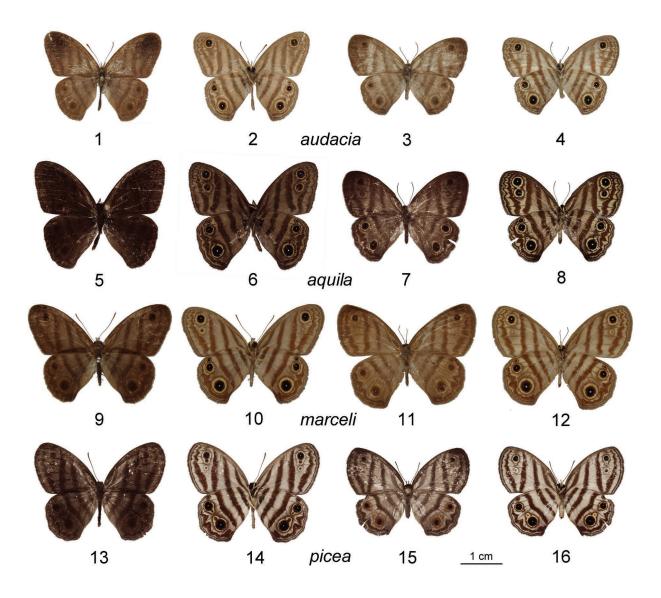


FIG. 1. E. audacia, E. aquila and E. marceli holotypes and allotypes, plus E. picea male and female form rufocincta: 1. Dorsal and 2. Ventral; E. audacia male holotype, Saiil, French Guiana 3. Dorsal and 4. Ventral; E. audacia female allotype, Saiil, French Guiana 5. Dorsal and 6. Ventral; E. aquila male holotype, E. Kanuku Mts., Guyana 7. Dorsal and 8. Ventral; E. aquila female allotype, Acarai Mts., Guyana 9. Dorsal and 10. Ventral; E. marceli male holotype, Maripasoula, French Guiana 11. Dorsal and 12. Ventral; E. marceli female allotype, Galion, Roura, French Guiana 13. Dorsal and 14. ventral; E. picea male, nr. Iquitos, Peru 15. Dorsal and 16. Ventral; E. picea female form rufocincta, Rondonia, Brazil



Fig.~2.~Male~and~female~genitalia~of~E.~audacia, E.~aquila, and~E.~marceli, with~dissected~specimens.

1-4: Euptychia audacia. 1, 2: male; 1: genitalia (PAG 276) of specimen 2, PK27 route de Kaw, Roura, French Guiana, 24-VIII-1993, n° 540, collection L. & C. Brévignon. 3, 4: female; 3: genitalia (PAG 1105) of specimen 4, Massif du Mitaraka, Borne 1, 2°13'N 54°26'30"W, 23-IX-2006, French Guiana, J.-P. Champenois leg, n° 22660 PAG 1105. 5-8: Euptychia marceli. 5, 6: male; 5: genitalia (PAG 277) of specimen 6, Galion, Roura, French Guiana, 1-V-1990, n° 559, collection L. & C. Brévignon. 7, 8: female; 7: genitalia (PAG 1104) of specimen 8, Saint-Georges-de-l'Oyapock, French Guiana, 30-V-1985, n°563, collection L. & C. Brévignon. 9-12: Euptychia aquila. 9, 10: male; 9: genitalia (PAG 1005) of specimen 10, Massif du Mitaraka, Borne 1, 2°13'N 54°26'30"W, 27.IX.2006, French Guiana, J.-P. Champenois leg, n° 22653, collection B. Hermier. 11, 12: female; 11: genitalia (PAG 1107) of specimen 12, Massif du Mitaraka, Borne 1, 2°13'N 54°26'30"W, 29.IX.2006, French Guiana, J.-P. Champenois leg, n° 22663, collection B. Hermier.

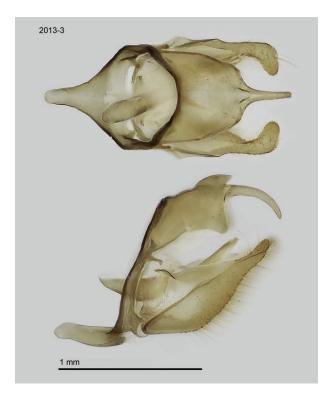


FIG. 3. Euptychia audacia male genitalia in dorsal and lateral views (DJH-2013-3) Acarai Mts./ridge, Sipu R. 2500'-3700'.

uncus, ventral margin concave, prominent projection extending ventrally from posterior margin, subtriangular and somewhat rounded in lateral view, tegumen semi-elliptic in dorsal view; vinculum fused to anterior margin of tegumen; saccus slightly rounded, almost same length as uncus, dorsally thin and evenly broad; valva sparsely hairy, posterior quarter tapered and its apex rounded, long anterior section almost parallelogram shaped, slightly narrowing posteriorly in lateral view, curved inwards at obtuse angle in dorsal view; aedeagus tubular in dorsal view, with straight and broadening anterior portion, in lateral view one third posterior narrower and positioned at approximately 30° angle, slightly broadening anteriorly, slightly longer than length of uncus plus tegumen.

FEMALE: forewing length 14.5 mm. Similar to male except as follows.

Wing shape. Forewing costa convex, inner margin almost straight, outer margin rounded; apex and tornus rounded. Hindwing rounded and less elongated than male.

Dorsal surface of wings. Ground colour brown, lighter than male (R153, G127, B92), with darker apex (R108, G78, B52) but dark brown apex coloration much more restricted than in male.

Ventral surface of wings. Ground colour lighter brown than male (R179, G158, B140), with five darker brown bands appearing more contrasted and broader than in male (R137, G106, B77).

Genitalia. (three specimens prepared: PAG 1105 LCB; SN-14-81; SN-15-24): papillae anales hairy, adorned with setae on their internal side; lamella antevaginalis sclerotized, developed, forming a plate in ventral view; weakly sclerotized 'ring' around basal side of 8th segment, less sclerotized at top, developing from lamella antevaginalis; ductus bursae very thin getting slightly broader anteriorly; corpus bursae broad with two linear signa.

Holotype. 16, French Guiana: Saül, 21.VII.1991, collection L. & C. Brévignon, n°31.

Allotype. 19, French Guiana: Saül, 21.VII.1991, collection L. & C. Brévignon, n°35.

Paratypes. 16, French Guiana: Galion, Roura, 12.VII.1990* n°543; 1Å, French Guiana: Matoury, 26.IV.1990*, n°554; 1Å, French Guiana: Mont Matoury, 19.I.2010; 16, French Guiana: Route de Kaw, pk27, Roura, 24.VIII. 1993, n°540 (genitalia dissection: PAG 276); 16, French Guiana: Route de Kaw, pk38, Roura, 19.XII.2010; 7¢, French Guiana: Saül, 15, 20, 21(3).VII.1991, 26.X, 2.XI.1999; 5°, French Guiana: Matoury, 22.XII.1985, 2.III.1986, 29.V, 12(2).VI.1990*, collection L. & C. Brévignon; 19, French Guiana: Matoury, 15.I.1987; 19, French Guiana: Mitaraka, 23.IX.2006, collection B. Hermier; 19, French Guiana: Route de Kaw, pk27, Roura, 8.VIII.1999; 1♀, French Guiana: Route de Kaw, pk32, Roura, 17.VI.2012; 19, French Guiana: Saül, 29.X.2011, collection L. & C. Brévignon. Guyana: 98, Iwokrama Rainforest Res., Iwokrama Mt. 2450–3150', 28.lll.-1.lV.2001, 4°19.82'N 58°47.91'W, Leg. S. Fratello (genitalia dissection for one male: 2013-4 Donald J. Harvey); 30, 19: Guvana: Acarai Mts./Ridge, Sipu River 2500-3000', 31.X.-10.XI.2000, 1°22.2'N 58°47.91'W, Leg. S. Fratello et al; 2d: Guyana: Acarai Mts./Ridge, Sipu River 2500-3700', 6-9.XI.2000, 1°20'N 58°57'W, Leg. S. Fratello et al (genitalia dissection for one male: 2013-3 Donald J. Harvey); 26: Guyana: Acarai Mts., Sipu River 2000-2500', 4-10.XI.2000, 1°21.3'N 58°57.4'W, Leg. S. Fratello et al; 19: Guyana: Acarai Mts., Sipu River 900-2500', 29.X.-12.XI.2000, 1°23.2'N 58°56.8'W, Leg. S. Fratello et al; 16: Guyana: Two Hat Mt., E. Kanukus, S. Rupununi, S. Slope Summit 2300-2600', 23-28.IX.2000, 3°8.8'N 59°6.9'W, Leg. S. Fratello et al; 16: Guyana: Region 9, Kanuku Mts., Nappi Mt., 2700'-3300', 03°18.8'N 59°33.9'W, 21 Feb-10 Mar 1999, leg. S. Fratello, R. Hanner, S. Hendricks, R. Williams; 29: Guyana: Region 9, Kanuku Mts., Nappi Creek, 500'–1,000', 03°N 59°34.2W, 21 Feb–10 Mar 1999, leg S. Fratello, R. Hanner, S. Hendricks, R. Williams; 16: Guyana: Region 7, Mt. Ayanganna, Kuiewa R., 2500'-3300', $05^{\circ}26.0$ 'N $60^{\circ}00.4$ 'W, 2-25 Apr 1999, leg. S. Fratello, R. Hanner, W. Prince, R. Williams; 16: Guyana: Cuyuni River, Kamaria Falls 100' 30.XI-5.XII.2000, 6°24'N 58°54.6'W, Leg. S. Fratello et al (all previous Guyana Paratypes: USNM). 16: Guyana: Bartica, B. Guiana, H. S. Parish, Joicey Bequest. Brit.Mus. 1934-120., BMNH; 2రి: Guvana: Kaieteur Falls, British Guiana, Feb.-Mar., 1936, A. Hall., BMNH; 19: Guyana: Demerara R., Crowley Bequest, 1901-78., BMNH; 19: Guyana: Carimang R., B. Guiana. H. Whitely. Godman-Salvin Coll. 1904.-1. Euptychia picea, Butl., BMNH; 19: Guyana: Br. Guiana, Parish. Ex. Grose Smith 1910. Joicey Bequest. Brit. Mus. 1934-120., BMNH

Paratypes marked with $^\circ$ show on ventral hindwing a satellite ocellus, in cell $M_{\rm a},$ of the ocellus in cell $Cu_1.$

Etymology. The specific epithet *audacia* means audacity in Latin, a quality needed to go further in the knowledge of Neotropical butterflies, especially when it concerns very common butterflies, as *E. audacia* in French Guiana. These common sibling species in less showy and popular groups have been neglected for centuries.

Distribution. Widely distributed in French Guiana and Guyana, from the northern lowlands of the coast to the southernmost mountains. In Guyana, it appears to be most common on the upper slopes and high ridges of the mountain ranges in Guyana's southern half. Guyana specimens from the Pacaraima Mts. of the Guyana tepui region are known at elevations up to approximately 900m. Though the authors know of no Surinamese specimens, based on its extensive range in French Guiana to the east and Guyana to the west, it seems probable that this taxon also occurs in Suriname. Photographic evidence of live and dry, unset specimens (A. Neild & M. Costa, pers. comm.) suggests E. audacia could occur in Venezuela: the live specimen from lowland forest near the Cuvuni River in easternmost Venezuela, close to Guyana, the unset specimens from the tepui region and at elevations above 1,000m. We sustain this affirmation also because this species has been collected on Mt. Ayanganna, Guyana, not far east of the Venezuelan border. The high Acarai Mt. ridges where some specimens were collected constitute the border between Guyana and Pará, Brazil. Euptychia audacia should occur in other localities in Pará's Acarai Mts., probably also in the mountains of Pará, Brazil adjoining Suriname, in the mountains of Amapá state,

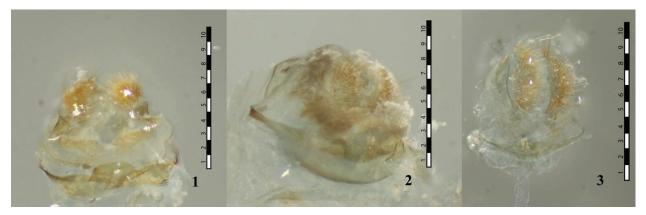


FIG. 4. Ventral view of lamella antevaginalis: 1. Euptychia audacia (SN-14-81) Relais de Patawalodge, Kaw Mountains, Cayenne, French Guiana (FLMNH voucher 191766); 2. Euptychia aquila (SN-15-23) Acarai Mts/ridge, Sipu River (USNM ENT 00233743); 3. Euptychia marceli (SN-14-79) 85km. S El Dorardo (nr Las Claritas Hotel), Bolívar, Venezuela (FLMNH voucher 191015).

Brazil contiguous with French Guiana, in the mountains of Roraima state, Brazil adjacent to Guyana's easternmost Acarai Mts., and possibly in the tepui region of Roraima state. It could also occur in the lowlands of Amapá, Brazil which are contiguous with the French Guiana lowlands, in the lowlands of Pará, and possibly in the lowlands of Amazonas state, Brazil adjoining Pará and Roraima states.

Behavior & habitat. In French Guiana, E. audacia has been observed in primary and secondary forests, mostly during the rainy season. It occurs with equal frequency in lowland or hill forest, flying in both the morning and the afternoon with no seeming preference. In French Guiana, the phenology of E. audacia differs from that of sympatric E. marceli, which flies all year long and is sometimes frequent on hilltops early in the morning (6:30–8:00AM). During the recent Guyana expeditions undertaken by the first author and partners, far more males (n = 20) were collected compared to females (n = 4). Only one of these specimens (a male) was collected in lowland forest; one (a male) was collected on a tepuian plateau at approximately 900m, all others came from the slopes and high ridges of mountain ranges at elevations from approximately 150 to approximately 1,000m (e.g., Fig. 5). About two thirds of these specimens, all males except for one female, were collected on the high ridges of these mountain ranges above approximately 750m; three out of four females were from lower slopes, two at approximately 150-300m. These data suggest that at least in Guyana, E. audacia is more prevalent or concentrated in hill forest compared to lowland forest, the males most common on high ridges. Some other Euptychiina of different genera collected during these expeditions also followed this pattern. Whether this distribution pattern reflects hill-topping behavior by the males or an actual greater prevalence of E. audacia in Guyana at these higher elevations is a subject for future study. With three out of four females taken on lower

slopes suggests possible hill-topping behavior for this species. In Guyana, *E. audacia* seems to be predominantly a hill forest species that ranges into lower premontane forest in the mountains including the Pantepui. Typical of many Euptychiina, males perched/rested on top of leaves within one and a half meters of the forest floor, their flight not fast but erratic and their daily flight activity of substantial duration.

Euptychia aquila Fratello, Nakahara & Brévignon, new species

Figs. 1 (5-8), 2 (9-12), 4 (2), 6, 7

Euptychia picea; Brévignon, 2012: 43: 9-12; 45: 10; 49.

Diagnosis. Euptychia aquila, like E. audacia, possesses a 'marceli-type' (see above) VHW ocelli pattern. Male E. aquila are easily distinguished from sympatric E. marceli and E. audacia, and all other known Euptychia besides E. roraima, by an entirely dark brown dorsum that exhibits very little translucence. In addition, male E. aquila is darker ventrally than E. audacia and E. marceli and shares with female E. aquila a few other characters that differentiate it from E. audacia and E. marceli: there is usually a prominent second VFW apical ocellus in cell M_3 that is much less prominent and often faint in E. audacia and E. marceli; it usually has a very small satellite (sometimes extremely tiny and inconspicuous) above the VHW large tornal ocellus (sometimes contained within the yellow ring of the large ocellus) that is lacking on most E. audacia and all E. marceli; it almost always has a VFW submarginal band that angles strongly inward below vein Cu₁, this is more variable on E. marceli and E. audacia and usually does not angle inward as prominently as on *E. aquila*. Female *E. aquila*



Fig. 5. West Kanuku Mts. from Nappi Peak (approximately 1,000m), Guyana; over 30 Euptychiina species occur on these and nearby forested slopes and ridges, including *E. audacia*, *E. aquila* and probably *E. marceli*.

are similar in size to E. marceli females and usually larger than E. audacia females, and their most distinguishing character is that they possess two large distal ocelli on the DHW lacking on E. marceli and E. audacia, where the two large ventral ocelli show through the translucent wings. As noted above, E. roraima also manifests a dark brown dorsum, though it is somewhat lighter on the distal third of both the forewing and hindwing; it is equally dark ventrally compared to E. aquila but there are significant wing shape and ventral wing pattern differences between E. roraima and E. aquila elucidated in the original description of E. roraima. The male genitalia of E. aquila differ from the genitalia of E. marceli by having a slightly curved and narrower uncus; a conspicuous postero-ventral wedge-shaped projection of the tegumen; a rather triangular distal half of the valvae; an anteriorly curved aedeagus. The male genitalia of E. aquila differ from the genitalia of E. audacia by the conspicuous postero-ventral wedge-shaped projection of the tegumen being narrower and longer in *E. aquila*. The female genitalia of *E. aquila* are distinguished from

its congeners *E. marceli* and *E. audacia* by the following characters: lamella antevaginalis wide and sclerotized, shaped as a ventral escutcheon (thin and not sclerotized in *E. marceli*, not escutcheon shaped in *E. audacia*) (see Fig. 4).

Description. MALE: forewing length 17 mm.

Wing shape. Forewing inner margin almost straight, outer margin almost straight, with rounded apex. Hindwing rounded and elongated towards tornus, slightly outwardly curved inner margin convex proximally to vein 3A, rounded tornus, outer margin convex, rounded apex, base of costa convex.

Wing venation. Forewing recurrent vein present in discal cell. Dorsal surface of wings. Ground colour dark brown (R23, G18, B17), hardly translucent; fringe concolorous.

Ventral surface of wings. Ground colour dark brown, lighter than dorsal surface (R88, G58, B44), with five dark reddish brown bands (R54, G24, B18); fringe concolorous.

Forewing: a narrow band extends distally along swollen section of subcostal vein; a regular and quite straight discal band extends from subcostal vein to just beyond vein 2A; a postdiscal band, almost parallel to discal band and thicker, extends from subcostal vein and traverses towards inner margin until vein 2A, slightly broadening to end and markedly distally deviated below vein Cu₂; an undulating submarginal band extends from near apex to near tornus, gradualy broadening towards vein Cu₂ and slightly narrowing after this vein, curved basally in each cell, proximally displaced below Cu₁; narrow marginal band extends from apex towards tornus, very weakly



FIG. 6. *Euptychia aquila* male genitalia in dorsal and lateral views (DJH-2013-1) Two Hat Mt, E. Kanukus, S. Rupununi, S. Slope Summit 2300-2600'.

undulating until vein $\mathrm{Cu}_{\scriptscriptstyle 1}$ and then straight after this vein; ocellus in cell M, exceeding vein M, and M, respectively, ringed in yellow and with one centered white pupil in black area; smaller ocellus located in cell M_{\circ} , ringed in yellow and with one centered white pupil in black area; indistinct, faint, dark brown marking is visible around ocelli. Hindwing: regular band extends from costal margin to inner margin, at the base of hindwing; discal band, same width as that of forewing, traverses straight from costal margin towards inner margin, narrower in its anal portion; a postdiscal band of the same width as that of the forewing, extends from the costal margin towards the inner margin, very slightly distally curved, slightly narrower in its anal portion; irregular submarginal band starts from apex and traverses along margin towards tornus, broadened and M-shaped between vein M, and Cu,; marginal band, thin and very slightly undulated, traverses along distal margin from apex towards tornus and almost fuses to postdiscal band in cell 2A; submarginal ocellus in cell Rs, the smallest of all, shows one centered white pupil in black area; a larger ocellus in cell M, ventrally exceeding from vein M, encircled by yellow ring and with one centered white pupil in black area; largest ocellus, ringed in yellow with one centered white pupil in black area in cell Cu, exceeding from vein Cu, and Cu, respectively; a satellite minute ocellus present on the apical side of this ocellus; indistinct, faint, dark brown marking visible around this ocellus.

Head. Antenna about 7.5 mm long, dark brown dorsally with base of antennomeres and tip of the club orange, orange ventrally; eyes entirely dark red brown with black hair; palpus 2.5 mm long, covered with long hairy scales cream at base and blackish distally.

Thorax. Dark brown dorsally with multicolored long hairy scales (green, yellow, orange, red), more densely on its anterior portion near head, with light brown hairy scales ventrally.

Abdomen. Brown dorsally, darker on first three segments with long multicolorous hair on the first segment, with long creamy hair scales ventrally.

Genitalia. (three specimens prepared: vials # PAG 1005 (LCB); vial #2013-01 and #2013-02 (USNM)): uncus rather narrow, curved downward in lateral view, tapered posteriorly, evenly broad in dorsal view; tegumen dorsally convex, somewhat rectangular in dorsal view; posterior projection of the tegumen visible above uncus, approximately one fourth length of uncus, ventral margin concave with conspicuous postero-ventral projection wedge-shaped, subtriangular, with rather tapered distal edge in lateral view; vinculum fused to anterior margin of tegumen; saccus rather angular, almost same length as uncus, dorsally broad, shrinking progressively anteriorly; valva sparsely hairy, posterior fifth triangular with pointed apex, middle section broadest, anterior section tapered, hooked right-angled inwards forming a boot-shape in dorsal view; aedeagus tubular, strongly curved in its anterior quarter in lateral view, and uniform width in its posterior three quarters.

FEMALE: forewing length 15 mm. Similar to the male except as follows:

Wing shape. Forewing costa convex, inner margin almost straight, outer margin rounded, apex and tornus rounded. Hindwing rounded and less elongated than male.

Dorsal surface of wings. Ground color much paler brown than the male (R172, G155, B137), both wings translucent. Hindwing with two large, yellow-ringed, white-pupiled black ocelli in the distal third of the wing, one in apical area, the other in tornal area.

Ventral surface of wings. Ground color lighter brown than dorsal ground color and much paler than male (R173, G161, B138), bands lighter than those of male (R157, G130, B84), in other respects wing pattern very similar to male except size difference between the large HW tornal ocellus, and the larger HW apical ocellus, not as significant as in male.

Genitalia. (two specimens prepared: PAG 1107 LCB; SN-15-23): Papillae anales hairy, adorned with setae on their external side; lamella antevaginalis sclerotized and developed, shaped as a ventral escutcheon, forming a sclerotized 'ring' around basal side of 8th segment; ductus bursae not sclerotized, thin, getting progressively broader anteriorly; corpus bursae long with two linear signa.

Holotype. 1₫, Guyana: Two Hat Mt. E. Kanukus, S. Rupununi, S. Slope 1200–2300', 23–28.IX.2000, 3°8.8'N 59°6.9'W, Leg. S. Fratello et al (USNM)

Allotype. 1° , Guyana: Acarai mts./ridge, Sipu R. 2500–3700', 6–9.XI.2000, $1^{\circ}20'$ N 58°57'W, Leg. S. Fratello et al (USNM)

Paratypes. FW length: 12δ , 16–19mm, 11 $^{\circ}$, 15–19mm. 4δ : Guyana: Two Hat Mt, E. Kanukus, S. Rupununi, S. Slope Summit 2300-2600', 23-28.lX.2000, 3°8.8'N 59°6.9'W, Leg. S. Fratello et al (genitalia dissection for one male: 2013-1 Donald J. Harvey); 50: Guyana: Acarai Mts./ridge, Sipu River 2500–3000', 31.X.-10.XI.2000, 1°22.2'N 58°57.9'W, Leg. S. Fratello et al (genitalia dissection for one male: 2013-2 Donald J. Harvey); 16, 19: Guyana: Acarai mts./ridge, Sipu R. 2500–3700', 6–9.Xl.2000, 1°20'N 58°57'W, Leg. S. Fratello et al (genitalia dissection: SN-15-23); 19: Guyana: Region 9, Kanuku Mts., Nappi Mt., 1500'-2700', 03°18.8 59°33.9'W, 21 Feb-10 Mar 1999, leg. S. Fratello, R. Hanner, S. Hendricks, R. Williams; 19: Guyana: Region 9, Kanuku Mts., Nappi Mt., 1000'-1500', 03°19.5'N 59°33.5W, 21 Feb–10 Mar 1999, leg S. Fratello, R. Hanner, S. Hendricks, R. Williams (all previous Guyana Paratypes: USNM); 39: Guyana – Brit. Guiana: Kutari Sources. Jan–Feb. 1936. G.A. Hudson. B.M. 1936-360. (BMNH); 26: French Guiana: Massif du Mitaraka, Borne 1, 2°13'N 54°26'30"W, 20, 27.IX.2006, J.-P. Champenois leg, n°22653, 22654, collection B. Hermier (genitalia dissection for one male: PAG 1005); 39: French Guiana: Massif du Mitaraka, Borne 1, 2°13'N 54°26'30"W, 26, 28, 29.IX.2006, J.-P. Champenois leg, n°22661, 22662, 22663, collection B. Hermier (genitalia dissection for one female: PAG 1107); 19: French Guiana: Massif du Mitaraka, Sommet en cloche, 2.233848 / -54.46057, 22-III-2015, M. Benmesbah (MNHM); 19: French Guiana: Massif du Mitaraka, Sommet en cloche, 2.233848 / -54.46057, 22-III-2015, M. Benmesbah (MB).

Etymology. *aquila*, is the feminine form of the Latin masculine adjective aquilus, meaning dark colored, thereby corresponding with the Latin feminine noun *Euptychia*. Male *E. aquila* have the darkest

dorsal surface of any known *Euptychia*, entirely dark brown with only very slight translucence. The male ventral surface is also darker than almost all other *Euptychia*.

Distribution. At present known from three mountain ranges in southern Guyana, the Kanukus, both East and West, and Acarais, most specimens from the upper slopes and high ridges, 700m-1,150m, and a single specimen from mountains near the Kamoa River, approximately 700m, and in French Guiana in the extreme south of the department, in the Tumuc-Humac Mounts. The high Acarai Mt. ridges where some specimens were collected constitute the border between Guyana and Pará, Brazil. Its range should include other higher mountain ranges in southernmost Guyana (e.g., Wassarai and Kamoa Mts.), the mountains of southern Surinam, other localities in Pará's Acarai Mts., and the mountains of Amapá and Roraima states, Brazil, adjacent to the Guianan southern mountains. Approximately one week of collecting in two seasons: March-April and November, on the high slopes and ridges in Guyana's Iwokrama Mts. (approximately 110k north of the Kanuku Mts., highest summits approximately 925m), has not yielded this species.

Behavior & habitat. All known specimens of E. aquila are from hill to lower premontane forest (e.g., Fig. 5); none are known from lowland forest, which has been extensively collected in both Guyana and French Guiana (although in southern Guyana and French Guiana, where *E. aquila* has been found, the flatlands have been much less sampled than in northern regions). Present evidence strongly suggests that E. aquila is a hill-lower premontane species restricted to the Guianan southern mountains. In Guyana's Acarai Mts., which are higher than the Tumac-Humac Mounts of French Guiana, E. aquila is found, besides lowland hill forest, in lower premontane forest at approximately 1,000m and somewhat higher. In Guyana, 10 out of 11 males and two out of five females were collected on the highest slopes and summit ridges of the East Kanuku Mts. (700–800m) and Acarais (750–1,150m). Whether these records entail male hill-topping behavior is subject to further investigation. The lowest recorded elevation for Guyana specimens, a female from the West Kanukus, is 300–450m. Guyana specimens were all probably collected in the low understory within a couple of meters of the forest floor.

DISCUSSION

Both *E. audacia* and *E. aquila* are described in this genus due to their morphological resemblance to *E. marceli* and some other *Euptychia*. The placement of these new species in the genus *Euptychia* is reinforced by the presence of a projection of the tegumen above the uncus; as mentioned above, this character is thought to be a possible diagnostic character that differentiates this genus from other genera in this subtribe (Freitas et al. 2012). Whether this genitalic structure is a unique trait for *Euptychia* will be ascertained when all Euptychiina, including many undescribed taxa, are dissected. It is worth noting that this structure varies widely among known *Euptychia*, as



FIG. 7. Euptychia aquila male from the Tumuc-Humac Mts., French Guiana, the only known *E. aquila* specimen manifesting a satellite ocellus below the large VHW ocellus. This is a good example of the type of individual variation seen in *Euptychia* ventral ocelli patterns even among taxa like *E. aquila*, where this pattern is uniform to a large degree.

the drawings in Forster (1964) reveal, also comparing the modest projection of E. audacia and E. aquila with the very long projection of E. cesarense Pulido, Andrade, Peña & Lamas, 2011 (Pulido-B. et al. 2011). In addition, the presence of a recurrent vein in the FW discal cell in both new species should support their placement in *Euptychia*, as mentioned above this trait is also thought to be a shared character for Euptychia (but as mentioned before, broader study is needed including whether this character is unique to Euptychia). Early stage biology would also reinforce the placement of E. marceli, E. audacia and E. aquila in the genus *Euptychia*. Although hostplants and early stages are known for several Euptychia species (Singer et al. 1983, DeVries 1987, Beccaloni et al. 2008, Brévignon 2008), the early stage biology of the majority of taxa is presently unknown, especially regarding Amazonian species (Beccaloni et al. 2008, Brévignon 2008). The majority of Euptychia taxa with known nonseed hostplants and early stages possess whitish phenotypes (one taxon with white females, grayish males): E. mollina Hübner, 1818 and a few similar taxa (Beccaloni et al. 2008, Brévignon 2008). Euptychia insolata Butler & Druce, 1872 is one of only two Euptychia with a known nonseed hostplant, manifesting a quite different phenotype, and notable that it alone has been recorded feeding on bryophytes (Neckeraceae). This taxon (resident in south Central America and northwestern

South America) resembles the allopatric E. marceli, E. audacia and E. aquila, most similar to E. marceli. Euptychia insolata has a marked marceli-type VHW ocelli pattern; its tornal ocellus is notably large for a small butterfly and the larger apical ocellus is smaller than on *E. marceli*, resulting in a great difference in size considering these two ocelli. E. insolata exhibits a striking sexual dimorphic coloration, males are brown and females whitish, in addition to other subtle external differences. E. aquila is sexually dimorphic regarding coloration as well but in a different manner, males are dark brown dorsally, females a translucent light brown. The male genitalia of *E. insolata* are similar to those of E. marceli, E. audacia and E. aquila but with some obvious distinctions: absence of the conspicuous postero-ventral projection of the tegumen present in E. audacia and E. aquila; shape of the valvae. We assume E. marceli, E. audacia and E. aquila are by varying degrees closely related to E. insolata and infer they should also utilize nonseed hostplants, possibly bryophytes.

Concerning facies solely, E. audacia closely resembles E. marceli in many respects, though usually obviously smaller. E. aquila resembles E. marceli as well, especially females, but less closely than does E. audacia: for males, particularly because of the dark brown dorsum and darker brown venter; for females in possessing two DHW ocelli. The male genitalia of E. audacia and E. aquila possess a conspicuous posteroventral projection of the tegumen, a significant character that is lacking in *E. marceli*. This character is also found in at least four other *Euptychia* species: two Guianan species, the recently described E. neildi Brévignon, 2005 (Brévignon 2008: fig. 52) and E. roraima (Nakahara et al. 2014: fig. 3); the wide ranging E. mollina and E. hannemanni Forster, 1964, a taxon known from a restricted range (both figured in Forster 1964: p. 81). Whether this character is more prevalent in Guianan species and whether it is an important character for determining relationships in the genus, should be elucidated when a complete generic revision is undertaken including many undescribed species. It is noteworthy that E. roraima, though possessing unique facies, beyond the shared conspicuous postero-ventral projection of the tegumen, also has male genitalia very similar to E. audacia and E. aquila, and is perhaps closely related to them. As already related previously, it is also possibly deserving notice that this taxon is a very dark Euptychia, akin to E. aquila in this respect. The relationships among E. marceli, E. audacia, E. aquila and E. roraima will hopefully be discerned in this future generic revision, though the strong male genitalic and phenotypic evidence presently infer the



Fig. 8. $Euptychia\ picea$ female form rufocincta illustration from Weymer (1911).

possible close relationship of *E. aquila* and *E. roraima*.

Until it was described by the third author (Brévignon 2005), E. marceli had been misidentified as E. picea for many years. In fact, Guianan Euptychia specimens misidentified as E. picea in the BMNH (photos provided by A. Neild, pers. comm.), including specimens collected over a hundred years ago, represent E. marceli, E. audacia, E. aquila and at least one other undescribed Euptychia and no true E. picea. Most astounding of these embedded species in the BMNH collection are three E. aquila females collected in 1936 from the Kutari Sources, British Guiana, as it was assumed that this species was unknown until collected recently in very remote, little-or-never explored mountain ranges in southern Guyana (Kanuku and Acarai Mts.) and southern French Guiana (Tumuc-Humac Mts.); the Kutari Sources are in the easternmost district of Guyana's Acarai Mts., very close to the border of Surinam, an area expected to be part of this taxon's range and also very remote.

Even after the description of *E. marceli*, the confusion has persisted in museum collections, SF separating *E. marceli* from *E. picea* very recently in three major museum collections, AMNH, USNM and MGCL, with the differentiation of these two taxa ongoing at the BMNH (A. Neild, pers. comm.). Comparing the respective VHW ocelli pattern of each taxon actually accounts for a very easy separation of the two (see Fig. 1). The large tornal ocellus of *E. marceli* is much larger, with a much wider yellow ring, compared

to its large apical ocellus; on E. picea, the large tornal and large apical ocellus are usually much closer in size and the yellow ring around the tornal ocellus is hardly wider than the yellow ring around the apical ocellus. Euptychia picea also has a small satellite ocellus above the large tornal ocellus and usually has a small satellite ocellus below the large apical ocellus; E. marceli lacks these VHW satellite ocelli. The VHW ocelli pattern just described for E. marceli is the so-called marceli-type pattern described above. As noted above, both E. audacia and E. aquila possess this marceli-type ocelli pattern, though the size difference between the large tornal and apical ocelli and greater width of the tornal ocellus yellow ring is not as prominent on these two new species, especially in the females, and to an even lesser degree, especially for female E. aquila; in addition, E. aquila usually has a very small to tiny satellite ocellus above the VHW large tornal ocellus and rarely, E. audacia also does. Because of the long historic confusion concerning these taxa, it is worth noting that there are a small number of undescribed taxa that could be confused with E. marceli, E. audacia and female E. aguila; specimens representing these taxa were shared with us by our colleagues or uncovered during our own research. Among them are some small Euptychia, like E. audacia, whose males are indistinguishable dorsally from this species, and some Brazilian lower Amazonian specimens seemingly important to understanding the relationship of *E. marceli* and *E. picea*.

On the Identity of *Euptychia rufocincta* Weymer, 1911 and a Possible Future Neotype Designation

Further confusion concerning the Guianan 'marcelitype' species resulted from the poor condition, missing specimens, and mistakes concerning E. picea form rufocincta (Weymer 1911) type material. In 1911, Weymer described rufocincta as a form of E. picea based on a specimen he presumed was from Surinam. A notable feature of this form rufocincta and the reason for this appellation, is the presence of two rufous rings on the DHW, these rings surrounding the two large VHW ocelli showing through the DHW translucence (Fig. 1 (15)); this notable feature is clearly mentioned in the original description and also figured in that work (Weymer 1911) (Fig. 8). Form rufocincta was raised to species rank by Lamas (2004), and has been treated as a species by several authors (e. g. Pulido-B et al. 2011). However, the syntypes of *E. rufocincta* have not been found yet, and a putative type specimen illustrated in Warren et al. (2014) is a specimen in ZSM, which had erroneously been labelled as 'paratype' by Forster (G. Lamas, pers. comm.). In addition, there is no evidence

that this specimen was actually examined by Weymer, especially because the dorsal hindwing rufous rings are hardly evident on this specimen. In addition, our examination of Euptychia specimens photographed at the ZMHU and ZSM did not result in the discovery of the syntype of E. rufocincta. These facts and subsequent confusion resulted in tentatively using the name E. rufocincta for the taxon now being described as E. audacia, when describing E. marceli (Brévignon 2005). Analysis done during work on this present manuscript has shown that E. rufocincta is actually female E. picea, concerning certain Amazonian populations of E. picea, a conclusion probably reached by other researchers as well and seeming close to Weymer's original intent when he described *E. picea* form rufocincta. Regarding these populations of E. picea, the main reason for this conclusion is that only male E. picea and female E. rufocincta have been found in the collections we studied and their ventral patterns correlate extremely well. What is currently considered E. picea includes populations whose females lack the dorsal rufous rings (A. Neild and K. Willmott, pers. comm.). Until the Amazonian E. picea complex is studied further, we decided it is prudent to not synonymize E. rufocincta with E. picea at this time. There remains the possibility that in the future, the name rufocincta might be used for certain populations of E. picea, at least to the level of subspecies. In addition, a future neotype designation for E. rufocincta might preclude further confusion concerning this 'taxon'.

Also in question is the provenance of Surinam for both E. picea form rufocincta given in the original description and the false 'type'; as extensive collecting in French Guiana and Guyana has never produced any E. picea, and no other similar looking specimens are known from Surinam (H. Gernaat, pers. comm.), the only logical conclusion is that Surinam is a mistaken locality for this taxon. Present evidence points to E. picea having a widespread Amazonian distribution outside the Guiana subregion, probably allopatric to E. marceli, E. audacia and E. aquila, all sympatric in the Guianan southern mountains, E. marceli and E. audacia sympatric widely elsewhere in the Guianas, and all three taxa probably endemic to the Guiana subregion. Beyond the French Guiana localities given for E. marceli in the original description (Brévignon 2005) and additional French Guiana localities, E. marceli is found widely in Surinam and Guyana and has been collected in eastern Venezuela not too distant from Guyana (A. Neild, pers. comm.); as in E. audacia, there is the possibility that *E. marceli* is more widespread in the Guiana subregion.

CONCLUSION AND FUTURE RESEARCH

Mainly because of recent extensive collecting efforts in French Guiana and Guyana, three distinct Guianan Euptychia species long hidden among museum specimens of E. picea have been discerned: first E. marceli (Brévignon 2005) and now E. audacia and E. aquila. With this progress comes many additional questions that will hopefully be answered with subsequent research. Outside the scope of this manuscript but of interest to the authors, is the relationship of the aforementioned *E. insolata* and the undescribed species with E. marceli, E. audacia and E. aguila. The description of these undescribed taxa by our colleagues and one of us (SN) will differentiate them from known taxa and represent another advance. We look forward to the morphological, genetic and early stage biology studies, larger in scope, that will clarify relationships and increase ecological knowledge concerning these attractive small denizens of Neotropical rainforest understories.

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