

*Journal of the Lepidopterists' Society*  
59(4), 2005, 200–211

CLOUD FOREST BUTTERFLY FAUNA OF THE PANTEPUI – POOR OR POORLY KNOWN?  
DESCRIPTION OF NEW SPECIES AND RECORDS OF NEW GENERA OF PRONOPHILINA: *ERETRIS*  
*AGATA* AND *OXEOSCHISTUS ROMEO* (NYMPHALIDAE: SATYRINAE)

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**ABSTRACT.** Two new species of Pronophilina (Nymphalidae, Satyrinae) - *Eretris agata* and *Oxeoschistus romeo* - are described from the Guyana shield, also known as the Pantepui, a region of table mountains situated in southeastern Venezuela, northwestern Guyana and adjoining Brazil. They are only the third and fourth genera of the diverse neotropical montane subtribe Pronophilina (Nymphalidae, Satyrinae) reported for this vast biogeographical region. Their affinities are evaluated indicating close relationship with the Pronophilina of the Venezuelan Cordillera de La Costa. The current state of knowledge of the Pronophilina in the Pantepui is discussed. Low figures of diversity are interpreted as a result of isolation from the center of origins and diversity in the central Andes, and partly as a consequence of heavy undersampling.

**Additional key words:** Andes, affinities, bamboo, endemic species, Guyana shield, island biogeography, *Protopedaliodes*, species richness.

INTRODUCTION

Pantepui is a term originally proposed by Mayr and Phelps (1955) to designate the region of table mountains situated in southern Venezuela and adjacent areas of Brazil and Guyana. Even though throughout the years there were many contradictions and various definitions of Pantepui (Huber, 1987; Brown, 1979), all the authors concurred that this vast area is worth identifying as a separate biogeographical entity identified by a number of biotic (i.e. endemic taxa) and abiotic features.

Nearly a century ago, Strand (1912) described from the Pantepui the first species of butterfly belonging to the predominantly Andean subtribe Pronophilina (Miller, 1968; Adams, 1985; Pyrcz & Wojtusiak, 2002)—*Pedaliodes roraimae* (see fig. 5). His discovery passed completely unnoticed (Viloria & Pyrcz, 1995) and only recently, during the last decade, was there an increase of interest in the butterfly fauna of the Pantepui in general (Neild, 1996) and the Pronophilina in particular, resulting in the description of several new taxa. Four of them, *Pedaliodes demarmelsi* Viloria (1995), *P. chaconi* Viloria (1998), *P. terramaris* Viloria & Pyrcz (1999) and *P. yutajeana* Viloria & Pyrcz (1999) are closely related to each other and to *P. roraimae*. *Protopedaliodes kukenani*, described by Viloria & Pyrcz (1994) from the top of Kukenan and Roraima, represents a well differentiated endemic genus. Viloria & Pyrcz (1999) described a further two species belonging to this genus: one from Roraima — *Pr. ridouti*, and one from the Auyán Tepui — *Pr. profauna*. All of the species

described hitherto from the Pantepui belong to the *Pedaliodes* complex (Viloria, unpublished Ph.D. thesis). The two new species described herein belong to other genera and sections of the subtribe Pronophilina previously not reported in South America outside the Andes and their peripheral ranges (Sierra Nevada de Santa Marta, Cordillera de La Costa) — *Eretris* Thieme (1905) and *Oxeoschistus* Butler (1867). Their discovery is very significant as it emphasizes how little the Pronophilina fauna of the Pantepui is known, how much research is still to be done, and also raises interesting zoogeographical issues.

**Subtribe Pronophilina**

The genera *Eretris* and *Oxeoschistus* belong, according to Miller (1968), to the neotropical subtribe Pronophilina (considered by Harvey (1991) and Lamas *et al.* (2004) as a sub-tribe within the tribe Satyrini), an entirely neotropical section of the worldwide subfamily Satyrinae (Nymphalidae). The Pronophilina can be divided into three groups based on ecological and morphological criteria: Chileno-Patagonian (considered by Lamas & Viloria 2004) as belonging to the predominantly Australian tribe Hypocystini), Caribbean (only the genus *Calisto* Lathy) and tropical montane. The latter dominant section comprises approximately 460 species (Lamas *et al.*, 2004) distributed in the cloud forests and paramos of Central and South America. In continental Central America 18 species are restricted to the highest mountains of Panama and Costa Rica, and 10 to Guatemala and the neighboring states of Mexico. In South America, the vast majority, more than 95%,

occur in the Andes and its peripheral ranges: the Sierra Nevada de Santa Marta and the Cordillera de La Costa. Seven species are found in the highlands of southern Brazil. The second region outside the Andean Cordilleras where tropical montane pronophilines occur is the Pantepui.

The species belonging to the subtribe Pronophilina occur in well-defined and sometimes very narrow bands of altitude. Their altitudinal zonation has been attracting the attention of naturalists since the early twentieth century (Fassl, 1911, 1915 and 1918; Krüger, 1924 and 1925), and recently was more extensively discussed by Adams & Bernard (1977, 1979 and 1981), Adams (1985 and 1986) and Pycrz & Wojtusiak (1999, 2002). Endemism is also a notable feature of the Pronophilina. In each north Andean range, between 10% and 30% of taxa are endemic at the specific level (Adams, 1985). The endemism ratio is higher in most isolated units, such as the Sierra Nevada de Santa Marta, the Cordillera de Mérida and also the Pantepui. Adams (1985) concludes that the average altitude range of the endemic species in all three Colombian Cordilleras is set higher, close to the upper forest limit, than that of the non-endemic species. However, Pycrz & Wojtusiak (1999) show, based on sampling in western Colombia, that this is not always the case. The highest diversity of the subtribe is reported close to the upper forest limit, varying from range to range, but generally falling at 2600–3000m (Adams, 1985; Pycrz & Wojtusiak, 1999; 2002). Several species occur in the paramo grassland above the timberline as high as 4500m. Very few Pronophilina were reported below 1000m.

Adult Pronophilina, like other satyrines, are mostly sedentary (Adams, 1986; Pycrz & Wojtusiak, 2002) and even inside the cloud forest they are generally restricted to particular habitats (Adams, *op. cit.*). Most species show restricted vagility and even though this aspect of their behavior was not studied rigorously, field observations indicate that adults move little vertically or horizontally and keep close to their host plants or roosting places (DeVries, 1987). The biology of the Pronophilina remains largely unexplored but it appears that their larvae feed mostly on montane bamboo, in the Andes chiefly belonging to the genus *Chusquea* (Poaceae) (Schultze, 1929; Adams & Bernard, 1981; DeVries, 1987; Pycrz & Greeney, in prep.). However, Pelz (1997) reared an Ecuadorian species, *Parapedaliodes parepa* (Hewitson), on a substitute secondary grass, *Poa festuca* (Poaceae), whereas Pycrz *et al.* (1999) report that several species also use *Guadua* bamboo as their host plants. There are indications that the Pronophilina, or at least some of them, are oligophagous. In Ecuador, Pycrz (unpubl.) reared the

first to fourth instars of *Junea doraete* (Hewitson) on several different species of *Chusquea*. Bamboos are most abundant in clearings, roadsides, at the forest edge and along paths. Adults of all species of Pronophilina are attracted to decomposing organic matter, particularly to feces, carrion and rotten fruits. Therefore, the use of baited traps provides a very good method of sampling

**Consulted collections:** **BMNH:** The Natural History Museum, London, United Kingdom. **MBLUZ:** Museo de Biología de la Universidad del Zulia, Maracaibo, Venezuela. **MCC:** Mauro and Clara Costa, Caracas, Venezuela. **MIZA:** Museo de Entomología, Universidad Central, Maracay, Venezuela. **MZUJ:** Muzeum Zoologiczne Uniwersytetu Jagiellońskiego, Kraków, Poland. **SIW:** Smithsonian Institution, Washington, USA. **TWP:** Tomasz Wilhelm Pycrz, Warsaw, Poland.

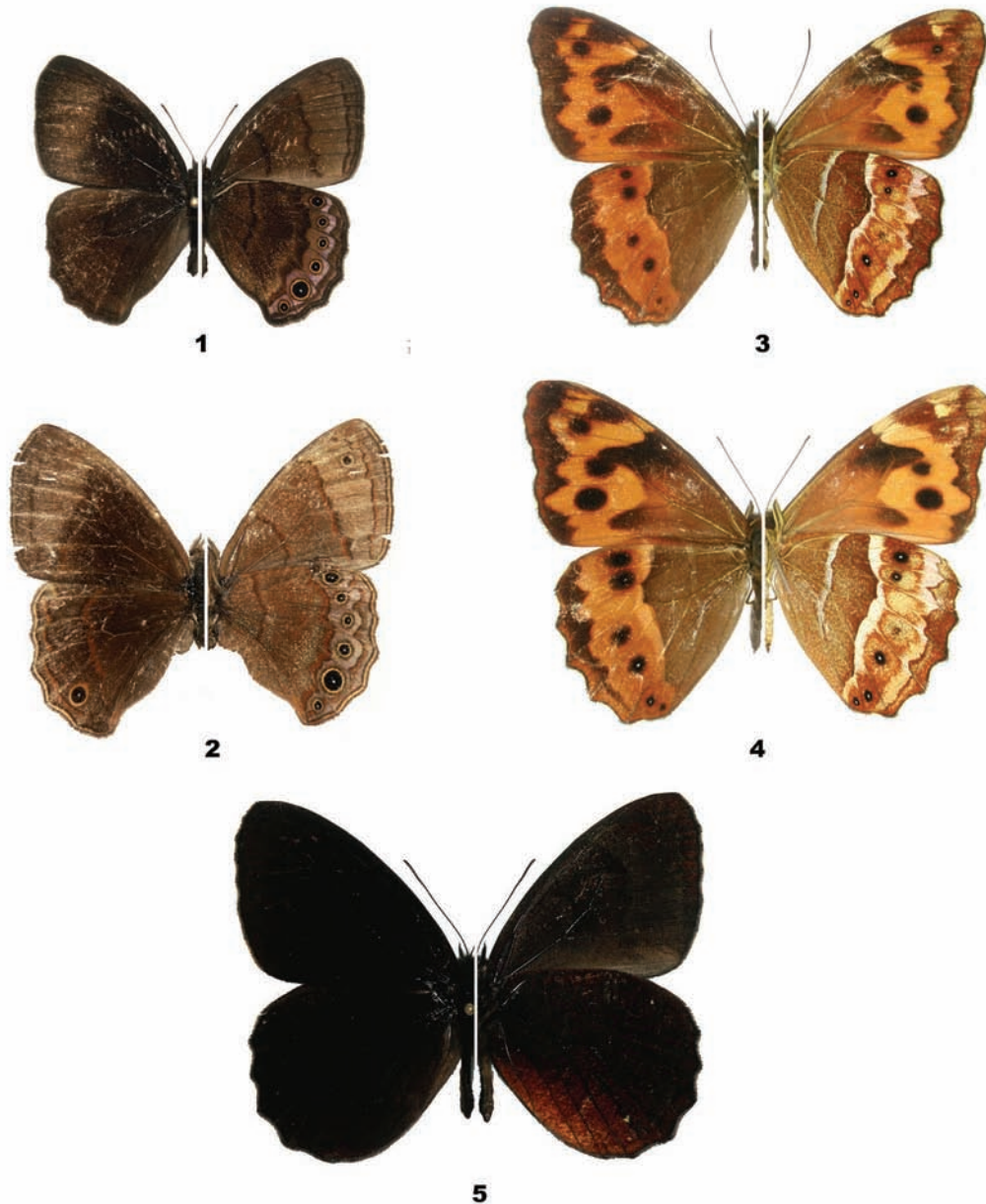
**Acronyms used:** **FW:** forewing. **HW:** hindwing. **D:** dorsal surface. **V:** ventral surface.

***Eretris agata* Pycrz,  
new species**

(Figs. 1, 2, 6, 14)

**Diagnosis:** Compared to allied species: *E. encycla* (figs. 7, 11–13, 15), *E. oculata* (fig. 16) and *E. calisto* (fig. 17)(all C. & R. Felder), the male of *E. agata* has no red markings along the VHW postmedian band's basal edge. The upperside is darker—blackish—not dark chocolate brown (which is noticeable in freshly emerged individuals). It is larger than nominotypical *E. encycla* from the Cordillera de la Costa, being approximately the size of the Cordillera de Mérida population. But *E. agata* has bigger ocelli than both and a different HW shape, somewhat ovaloid rather than squarish.

**Description:** **Male** (Fig. 1): **Head:** Eyes chocolate brown, lustrous, covered with dense and long setae; labial palpi covered with dark brown hair; antennae 8–9mm, orange brown, basal half covered ventrally with white scales, club only slightly thickened compared to shaft, two terminal segments black. **Thorax:** dorsally blackish brown, legs beige, tibiae covered ventrally with gray hair. **Abdomen:** dorsally and laterally blackish brown, ventrally gray. **Wings:** FW length: 22–24mm, mean: 23.2mm; n=5; apex blunt, distal margin straight. HW outer margin slightly undulated, inner margin incised below tornus. DFW ground color glossy blackish brown in freshly emerged individuals, gradually fading and becoming lighter as the wings are exposed to sunshine; distal one third with a distinctively lighter shade from costa to tornus; a nearly straight darker submarginal line running parallel to distal margin; fringes dark brown. DHW ground color same as on the FW; a very slightly lighter shade submarginally at apex, occasionally extending along submarginal area, especially in older individuals; a thin parallel undulated blackish brown submarginal line, darker than the ground color; an even thinner marginal line parallel to outer margin; fringes dark brown. VFW ground color glossy brown, lighter than on the upperside; four oblique dark brown lines, a median one, slightly arched across discal cell, a postmedian one from costa towards anal margin, fading away before touching it, nearly straight except for two curves between vein Cu1 and anal margin; a submarginal one, thinner than two basals, parallel to distal margin, slightly irregular from costa to vein M2, then nearly straight; a marginal line, very thin, parallel to the distal margin. VHW ground color from base to postmedian line dark brown, slightly suffused with tiny golden scales along inner margin and postdiscal area, which is noticeable only in freshly emerged individuals; a shallowly curved dark brown median line, darker than the ground color; a thicker chocolate brown postmedian line from costa to inner margin near tornus, roughly parallel to distal margin, slightly irregular and undulated but



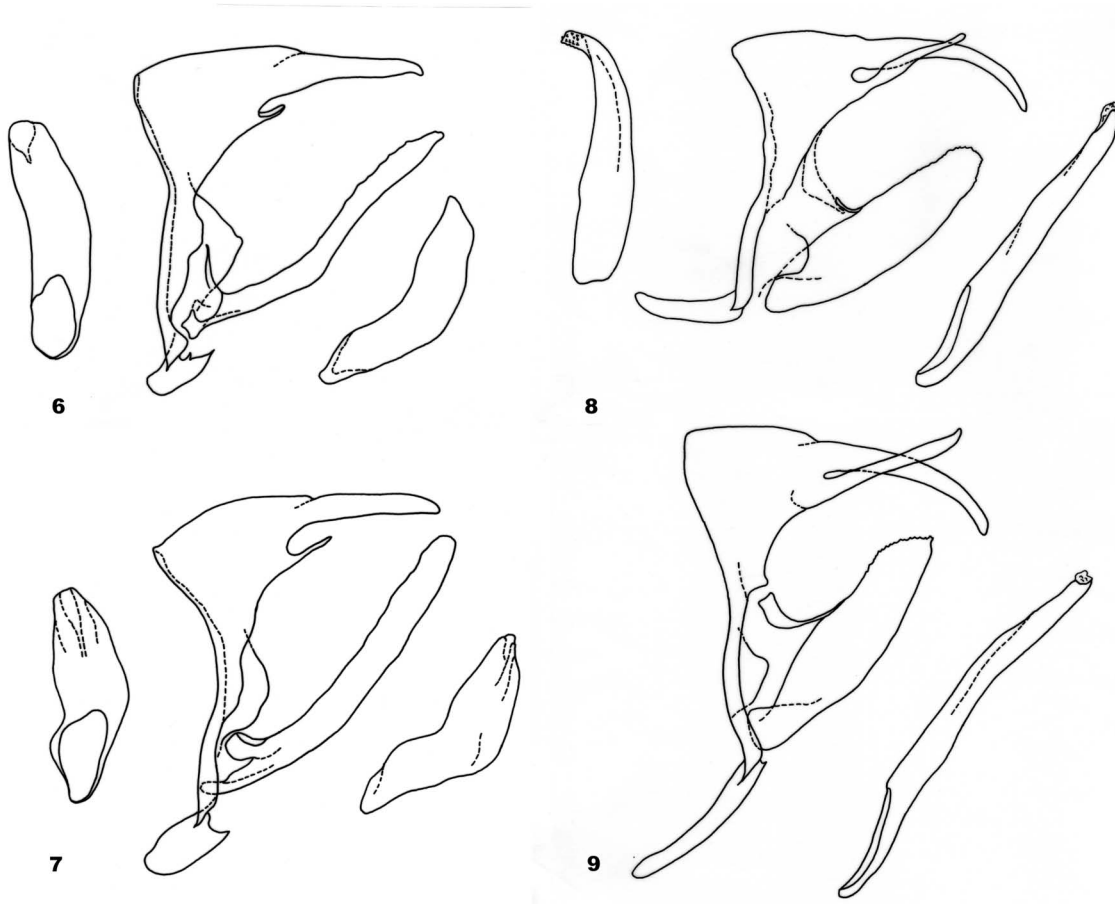
FIGS. 1–5, Some Pronophlina from the Pantepui. 1. *Eretris agata*, n. sp., male dorsum/venter; 2. *Eretris agata*, n. sp., female dorsum/venter; 3. *Oxeoschistus romeo*, n. sp., male dorsum/venter; 4. *Oxeoschistus romeo*, n. sp., female dorsum/venter; 5. *Pedaliodes roraimae* male dorsum/venter

without any deeper curves; a series of six submarginal rounded ocelli ringed with light orange and with small white triangular pupils, one in each cell from Rs–M1 to Cu2–1A, the biggest in Cu1–Cu2, the second biggest in Rss–M1, the remaining approximately the same size, half the size of the biggest, not touching the lines basad or distad of them, except the one in Cu2–1A, which crosses the submarginal line; a chocolate brown submarginal line, parallel to distal margin, thinner than the postmedian one; a thin dark brown marginal line parallel to outer margin.

**Genitalia** (Fig. 6): Uncus stout, ended with a short hook; gnathos short, less than one-fourth the length of uncus, slat-like; valvae long and thin with a characteristic shallow curve in the middle; aedeagus tubular, simple; saccus shallow.

**Female** (Fig. 2): **Head, thorax and abdomen** as in male. **Wings:**

Wing shape as in male. FW length 23.5mm. DFW ground color dull dark brown, slightly lighter than in the male; color light brown distally from a postmedian oblique darker line running from costa to inner margin near tornus; a dark brown submarginal line, parallel to distal margin; a thin dark brown marginal line parallel to distal margin. DHW ground colour dark brown, same as in basal two-thirds of the FW; a brick-red postmedian line with a dark brown distal edge roughly parallel to distal margin from mid costa towards inner margin fading away at vein Cu2; a double dark brown and light brick-red submarginal scalloped line parallel to outer margin, fading away between vein Cu1 and tornus; a thin yellow marginal band edged basally with dark brown; a prominent oval submarginal ocellus in cell Cu1–Cu2, ringed with yellow and with a white pupil. VFW ground color medium brown, light brown distally from the postmedian line;



FIGS. 6–9. Male genitalia of Pronophilini. **6.** *Eretris agata*, n. sp. (aedeagus extracted in lateral and dorsal view). **7.** *Eretris encycla encycla* (aedeagus extracted in lateral and dorsal view). **8.** *Oxoeschistus romeo*, n. sp. (aedeagus extracted in lateral view, valva extracted in dorsal view). **9.** *Oxoeschistus puerta* sp. (aedeagus extracted in lateral view).

the pattern of dark brown lines as on the upperside but edged with crimson red, the median and submarginal ones distally, the postmedian one basally; a thin yellow marginal band, edged basally with dark brown; a small rounded subapical ocellus in cell M1–M2, ringed with yellow and with a minute white pupil. VHW ground color medium brown; the pattern of dark brown lines as in the male, except that median and submarginal ones are edged distally with a thin crimson red line, whereas the postmedian is edged basally with a band of the same colour which overshadows most of the brown; submarginal ocelli of the same size and color as in the male; a thin yellow marginal basally dusted with dark brown.

**Type material:** Holotype ♂: Venezuela, Estado Bolívar, Sierra de Lema, road El Dorado - Santa Elena de Uairén km 132, 1983, 1350–1400m, M.C. Costa *leg.*, MIZA Maracay; Paratypes: 9 ♂ and 1 ♀: same locality as the holotype, 22–23.II.2004, M.C. Costa & T. Pyrcz *leg.* (2 ♂ in MCC, 1 ♂ in BMNH, 1 ♂ in MIZA, 5 ♂ and 1 ♀ in TWP).

**Etymology:** This species is dedicated to Agata, a daughter of its discoverers Mauro and Clara Costa, Italo-Venezuelan lepidopterists from Caracas.

**Behavior:** *Eretris agata* was discovered along the El Dorado – Santa Elena de Uairén asphalt road between

kilometer 130 and 135 (figs. 19–23). All the individuals were collected along the cloud forest edge when moving from inside the forest to the roadside, apparently looking for sunning spots. Several stands of an unidentified bamboo, its most likely host plant, were found some 20–30 meters inside the forest and more individuals were observed there. They were keeping to sunny gaps, occasionally patrolling and perching on large leaves at 3–5 meters above the ground. In the same habitat another species of Pronophilina was observed, *Pedaliodes roraimae* showing similar behavior but venturing more often into open areas, as well as another cloud forest Euptychiini satyrine, *Forsterinaria* sp.

**Remarks:** The genus *Eretris* (Thieme) comprises approximately fifteen species distributed in South and Mesoamerica (Lamas, *et al.*, 2004). Three species are

found in Guatemala/Mexico and Panama/Costa Rica, and the remainder in the Andes. There has been no cladistic analysis of *Eretris*, but the genus is morphologically highly homogenous and presents several plausible synapomorphies. It can be recognized from other Pronophilina by several characters emphasized in the original generic description (Thieme, 1905), such as short antennae reaching roughly one third the length of costa and the lack of a FW upperside male androconial patch. The most outstanding feature of the color pattern are fully developed submarginal ocelli on the VHW and a rarely present vestigial M1–M2 ocellus on the VFW. The wing venation with the HW cross-vein m1–m2 bent inside discal cell is typical of the Pronophilina (Miller, 1968; Vitoria, Ph.D.). Male genitalia of *Eretris* are very particular and can be recognized by a short, flattened, singularly sculptured aedeagus, short subunci and thin slat-like non-sculptured valvae.

The systematics of *Eretris* is very demanding because the differences between most species are very subtle. Additionally there is considerable infraspecific (Adams, 1986) and individual variation. The most obvious and significant taxonomic characters in the color pattern are all on the VHW: the shape and color of postmedian, submarginal and marginal lines, the size and number of submarginal ocelli and the color between the submedial line and the anal margin.

***Oxeoschistus romeo* Pycz & Fratello,  
new species**

(Figs. 3, 4, 8)

**Diagnosis:** This species is immediately recognized from other congeners by the highly irregular shape of the FW orange band characterized by deep basal and distal intrusions compared to regular, nearly linear, edges of other related species, especially *O. simplex* Butler and *O. puerta* (Westwood) (fig. 9).

**Description: Male** (Fig. 3): **Head:** eyes blackish brown, setose; palpi white covered with black hair; antennae two fifths the length of costa, dark brown, club formed gradually, slightly thicker than shaft. **Wings:** FW length 31mm; apex blunt; distal margin slightly convex; HW outer margin scalloped. FW and HW fringes medium brown. DFW basal and postbasal area medium brown; median area crimson red progressively darkening distally; a wide, brick orange band extending from postmedian to submarginal area with an irregular basal edge and deep incursions of dark brown along costal margin in the subapical area, along vein M3 and in cell Cu2–1A, and a dentate distal edge; dark brown rounded submarginal spots M1–M2, M3–Cu1 and the largest of all in Cu1–Cu2; submarginal area dark brown becoming gradually lighter towards distal margin. DHW basal and median area medium brown; a wide brick orange band extending from postmedian to submarginal area with a nearly straight inner edge except for a shallow postdiscal incision and a dentate distal edge; a series of dark brown rounded spots situated in the middle of the band smaller than on the FW in Rs–M1, M1–M2, M3–Cu1, Cu1–Cu2 and two in Cu2–1A, all of them surrounded by a crimson red halo; submarginal area dark brown reaching distal margin from costa to vein M2; an orange marginal band from vein M2 to tornus where merging

with the postmedian orange band. VFW color pattern similar as on the upperside; median orange band slightly lighter, whitish along basal edge towards costa, subapical area along costa and inside cell R5–M1 suffused with chestnut; subapical black spot in M1–M2 with a white pupil; subapical pale yellow spot in cell R5–M1; apical and submarginal areas suffused with beige scales. VHW ground color rufous brown; median line nearly straight, from costa to vein 1A basally edged with white; a band extending from postmedian to submarginal area shaped as on the upperside, white along basal and distal end, rufous orange in the middle, and a series of six black dots with white pupils situated in the middle of the band from Rs–M1 to Cu2–1A, two in the latter, except in cell M2–M3 where instead a lighter pale yellow patch.

**Genitalia** (Fig. 8): Uncus twice the length of tegumen, hooked; gnathos two-thirds the length of uncus, curved upwards; saccus deep, slat-like; valvae approximately the same width in basal and distal part with slightly serrate distal extremity and curved inwards; aedeagus slightly longer than valvae, smooth and straight.

**Female** (Fig. 4): **Head, thorax and abdomen** similar to the male. **Wings:** FW length 33 mm; DFW and DHW similar to the male; orange band a shade lighter, pale orange. VFW similar to the male; orange band a shade lighter, pale orange; VHW similar to the male but lighter, suffused with white scales along distal edge of the submarginal line.

**Type material:** Holotype ♂: Guyana, N. slope Mt. Roraima, 2<sup>nd</sup> Camp, 1300m, 5°16N, 60° 44W, 12.III.–16.IV.2001, Romeo Williams, Wiltshire Hinds *leg.*, SIW. Paratype ♀: same data.

**Etymology:** This beautiful montane satyrine is gratefully named after Romeo Williams, a Guyanese national. A friend of the junior author, Romeo has been an indispensable team member for the recent lepidoptera expeditions to a number of Guyana's remote montane regions. Beyond these expeditions, Romeo's bush skills, work ethic and dedication have added immeasurably to numerous other biological field endeavors in Guyana's hinterlands.

**Remarks:** The genus *Oxeoschistus* Butler comprises thirteen species, including one highly polytypic species — *Oxeoschistus simplex* Westwood with five recognized subspecies. The genus *Dioriste* Thieme is considered herein as a subjective junior synonym of *Oxeoschistus* following Lamas *et al.* (in press). Accordingly, seven species of *Oxeoschistus* are found in the Andes and six in Central America. One species, *O. puerta*, is represented by separate subspecies in Costa Rica, Panama, Colombia and northern Venezuela. The genus is therefore particularly well represented in Central America, as compared to other genera of Pronophilina (except for the genus *Drucina* Butler, endemic to Central America), and the fact that there are as many species outside and within the Andes is unique for the subtribe. A few genera are represented in Central America by one or two species, rarely more (*Pedaliodes* Butler, *Pseudomaniola* Röber), and many have no representative at all, including *Corades* Doubleday, *Junea* Hemming, *Daedalma* Hewitson and *Mygona* Thieme among others.

Adult *Oxeoschistus* are recognized by large size for the standards of the subtribe, with an average FW



FIGS. 10–18. *Eretris* taxa related to *E. agata*. **10.** *Eretris encycla* ssp. (Las Golondrinas, N-W Ecuador) **11.** *Eretris encycla* ssp. (Mérida, S-W Venezuela) **12.** *Eretris encycla* ssp. (Tandapi, W Ecuador) **13.** *Eretris encycla encycla* (Colonia Tovar, N Venezuela) **14.** *Eretris agata* n. sp. (Sierra de Lema, Venezuela) **15.** *Eretris encycla* ssp. (Santa Lucía, S-W Ecuador) **16.** *Eretris oculata* (Jorge Chavez, N Peru) **17.** *Eretris calisto* (Zamora, S Ecuador) **18.** *Eretris* sp. (San Andres, S Ecuador)

length 3–3.5cm, blunt FW apex and undulate HW margins. Most species have conspicuous orange or yellow upperside markings usually shaped as a median band. VHW is characterized by usually fully developed large postmedian ocelli present in all cells (except M2–M3) in most species. Antennae are slender, approximately 2/5 of the FW length. Eyes are setose as in other Pronophilina (Viloria, Ph.D.). Male genitalia can be recognized by a long uncus, and particularly long subunci, in some species approaching the length of the uncus, elongate valvae without any secondary process and a serrate dorsal surface, deep saccus and long, straight aedeagus. Although, there was no cladistic analysis of the subtribe, these morphological characters indicate *Pseudomaniola* Röber or *Pronophila* Doubleday as possible sister genera (Pyrzcz, in prep.).

#### Affinities

Currently, there are 10 species of Pronophilina known to occur in the Pantepui. Three of them belong to an endemic genus *Protopedaliodes* (presenting several specialized morphological structures), whose affinities within the speciose *Pedaliodes* complex are unclear (Viloria, Ph.D.). Five species belonging to *Pedaliodes*—*P. roraimae*, *P. demarmelsi*, *P. chaconi*, *P. terramaris* and *P. yutajeana*— are closely related

allopatric taxa. They could eventually be considered, due to the slight morphological differences, as subspecies of *P. roraimae*. Viloria & Pyrcz (1995) discuss the affinities of *P. roraimae* and indicate that its closest ally is *P. pisonia* (Hewitson). Salient morphological similarities can be observed in the wing shape and colour pattern and more importantly in the shape of the male androconial patch and male genitalic structure (Viloria *et al.*, 2001). *P. pisonia* occurs in the Venezuelan Cordillera de La Costa and the parallel Cordillera del Interior in low elevation cloud forests, at 1200–1700m.

*E. agata* presents a series of wing color pattern similarities to: *E. oculata* (C. & R. Felder) distributed along the eastern slopes of the Andes between Colombia and northern Peru, *E. calisto* (C. & R. Felder) found in central and eastern Colombia, eastern Ecuador and northern Peru and *E. encycla* (C. & R. Felder) occurring in the Venezuelan Cordillera de La Costa and Mérida, and in western Colombia and Ecuador (figs. 10–18). The VHW ocelli of *E. agata* are intermediate in size as compared to other congeners: smaller than in *E. oculata*, about the same size as in some populations of *E. encycla* (an undescribed subspecies) from the Western Cordillera in Colombia and Ecuador, and larger than in *E. encycla*. The shape

of the VHW postmedian band is most similar to *E. oculata*, less sinuate than *E. calisto* and *E. encycla*, both similar in this respect. *E. agata* has no orange or yellowish scales in the VHW anal area or basad to the postmedian line, similar to *E. encycla* (although some individuals of the nominate subspecies do have some yellow scaling) and *E. oculata*, and contrary to *E. calisto*, which always presents some yellow or orange pattern. The exclusive character of *E. agata* is that all three VHW lines are all brown, whereas in all other compared species they are crimson red. Additionally, the typical incision of the anal margin of the HW is shallower in *E. agata* than in other species, and the HW is ovaloid rather than squarish, in this respect it resembles an undescribed species of the “*calisto*” stock from southern Ecuador and northern Peru (Pyrz, in prep.). Male genitalia of *E. agata* show some similarities to *E. oculata*, especially characteristic valvae with a shallow curve in the middle and a tubular, simple aedeagus. In *E. encycla* the aedeagus is somewhat inflated in the middle and shorter. However other sclerites, tegumen, uncus, vinculum and transtilla, are nearly identical to *E. encycla* and *E. calisto*. These two species have rather long gnathi, roughly one third to half the length of uncus. The gnathi of *E. agata* are slightly shorter. On the other hand, the gnathi of *E. oculata* are rudimentary short tips, and in this respect are unique compared to other congeners.

*Oxeoschistus romeo*, as already pointed out in the new species diagnosis, basically presents all typical generic characters of the color pattern. However its DFW median orange band pattern is unique because it is modified as compared to allied species. Instead of a regular band with roughly parallel outer and inner edges, it presents an extremely irregular, erratic shape with several deep intrusions. Diagnostic features can be pointed out in the VHW pattern, especially the fact that the white-edged postmedian band is unbroken, smooth and runs roughly parallel to the outer margin. This character is found in *O. simplex* distributed throughout Colombia, *O. puerta* found in the Venezuelan Cordillera de La Costa, Mérida, Perija and northern Central and Eastern Cordillera in Colombia, and *O. duplex*. The latter is found in central (Junín, Pasco) and southern (Cuzco, Puno) Peru and Bolivia (Yungas). The male genitalia of *O. romeo* provide a series of very useful diagnostic characters. They clearly indicate *O. puerta* and *O. simplex* as the closest allies. In all these species, the gnathi are thinner than the uncus, about two-thirds its length and hooked upwards, the saccus is very long, and the aedeagus is nearly straight. The valvae of *O. simplex* are singularly serrate in the distal-dorsal one-third and occasionally present small

processes. The valvae of *O. puerta* and *O. romeo* are shorter and more compact, dorsal teeth are not as prominent and do not have any secondary process (figs. 8–9).

The above considerations indicate, the genus *Protopedaliodes* taken apart, close faunal affinities between the Pronophilina of the Pantepui and the Pronophilina occurring in the Venezuelan Cordillera de La Costa: *P. pisonia*, *E. encycla* and *O. puerta*. It is therefore sound to consider that this range was the primary source of cloud forest Pronophilina for the Pantepui. The colonization of the Pantepui might have taken place through ecological corridors across the Orinoco plains during cold glacial phases in the Pleistocene, when temperatures were 5°–9° cooler than at the present (Bush, 2002, 2004). These ecological conditions might have favored the growth of premontane forest vegetation (including *Chusquea*) at much lower elevation than currently (Cowling *et al.*, 2001); thus allowing the dispersal of pronophilines, especially the species inhabiting lower elevations (below 1500m). This scenario is plausible considering that at the southern limit of the latitudinal range occupied by the subtribe, where climate is cooler with low winter temperatures, several species of Pronophilina live in the lowlands. For example, in southern Brazil and northern Argentina *Praepedaliodes phanias* (Hewitson) occurs commonly at 200m and feeds on local *Aulonemia* sp. bamboo (Pyrz, unpubl). In south-central Bolivia, near Santa Cruz de la Sierra, a local population of *Physcopedaliodes physcoa* (Hewitson) occurs in a relictual forest at 400m. Interestingly enough, the same species is found in central Peru (Chanchamayo) at higher elevations—1200–1600m (Pyrz, unpubl.).

#### Diversity

*Eretris agata* and *Oxeoschistus romeo* represent the ninth and tenth species and only the third and fourth known genera of the subtribe Pronophilina in the Pantepui. A faunal comparison (*Appendix*) showing data from ten Andean localities gathered along altitudinal transects (only sympatric or parapatric species occurring along the same slope are considered) yields the immediate conclusion that the Pronophilina fauna of the Pantepui is extremely species poor as compared to the Andes.

The most straightforward factors responsible for this disproportion would be the lower ecological diversity and the smaller area of montane habitats in the Pantepui as compared to the Andes. Whereas in the Andes suitable habitats for the Pronophilina are found within the wide elevational belt roughly between 1000–4000m corresponding with cloud forests and paramo, in the Pantepui they are restricted by the

highest elevations of the table mountains, which is generally below 2500m, except for a few higher tepuis slightly exceeding this elevation (La Neblina, Roraima, Kukenán). In the Andes, cloud forests form a nearly continuous belt extending over 2500km along the eastern slopes from Bolivia to Venezuela, and over 1000km along the western slopes from northern Peru to northern Colombia. In the Pantepui, on the other hand, cloud forests are scattered and restricted to the slopes of isolated table mountains (Huber, 1995).

However, there are also significant differences in the observed species richness between various localities within the Andes. The index falls steadily from central towards northern Andes, from more than 100 species in southern Ecuador (Zamora) and northern Peru (Molinopampa) to 70–80 in central Colombia, and 55 in western Venezuela (El Tamá), roughly 50% of the figure in Zamora. These areas do not differ in ecological diversity and suitable habitat area (Vuilleumier & Monasterio, 1986), therefore, other factors are to be involved.

The decrease in species richness is more radical in the peripheral ranges of the northern part of the continent, the Venezuelan Cordilleras de Mérida, Perijá and La Costa, and the Colombian Santa Marta range. Sharp diversity break-downs correspond with several topographical and ecological barriers. A very important one is the so-called Táchira depression, a deep valley separating the Colombian Cordillera Oriental from the Cordillera de Mérida (Vuilleumier & Ewert, 1978; Pycz & Vilorio, in press). Other barriers include: the Valle del César separating Perijá from the Sierra Nevada de Santa Marta (Adams, 1985) and the Lara plateau separating the Cordillera de Mérida from the Cordillera de la Costa (and the parallel, low Cordillera del Interior). The fauna of the Cordillera de la Costa (awaiting monographic treatment, Pycz *et al.*, in prep.) accounts for 24 species of Pronophilina, less than half of that of El Tamá, and merely one fourth of the species-rich southern Ecuador. This yields the conclusion that these barriers act as a 'filter' for the dispersal of pronophilines from the center of diversity in the main Andes (corresponding with the putative center of radiation of the subtribe, situated in the central Andes between Ecuador and Bolivia, Pycz, in prep.) into peripheral ranges.

The tepuis are separated from the already impoverished Cordillera de La Costa by vast lowlands, the Orinoco plains (300–400km) and from the Eastern Cordillera by the upper Llanos (>500km). If a simple area/distance from source calculation is carried out according to the classical island geography model (MacArthur & Wilson, 2001), a dramatic decrease in the

Pantepui is to be expected.

Low diversity figures for the Pantepui may also be partly a consequence of the severe undersampling of this region. Admittedly, the sampling for pronophiline butterflies in the Pantepui has so far been negligible. The few specimens collected throughout the years are an outcome of random or even casual collecting, either by scientists other than entomologists (usually geologists, botanists or ornithologists who most frequently visited the region), or tourists. The reasons for this poor knowledge of the Pronophilina fauna in the Pantepui are multiple. First of all, Venezuelan authors (DeMarmels *et al.*, 2003) point out that the region is very remote and difficult and costly to reach. It certainly is true in the case of the summits of the most remote tepuis such as La Neblina, Tapirapécó, Duida or Marahuaca. These tepuis can be accessed easily only by helicopter. Otherwise, a long arduous expedition is necessary usually entailing canoeing for several days and many days of jungle trekking. Both ways are very costly, which is a very strong barrier for any biological research. However, the few tepuis situated in the eastern part of the Guayana highlands, especially Roraima, Kukenan, Auyan and a handful of other smaller table mountains, are relatively easy and inexpensive to reach. As a matter of fact, one of the new species described herein was collected in the area called La Escalera, along the asphalted main road leading from Km. 88 to Santa Elena de Uairén, which is crossed daily by dozens of vehicles!

La Escalera can be considered as the only relatively well sampled area within the entire Pantepui. In the local cloud forest at 1300–1400m only two species of Pronophilina were documented—*Pedaliodes roraimae* and *Eretris agata*, and a third—*Oxeoschistus romeo*—is likely to occur. The question arises: is the reported diversity low in relative terms as compared to the Andes? Not necessarily, considered that we are discussing diversity at 1300–1600m. As already stated, the highest diversity of the subtribe in the Andes falls at elevations between 2500 and 3000m (Adams, 1985; Pycz & Wojtusiak, 1999, 2002). Below 1600m diversity is at its lowest. For comparison, in the Andean Western Cordillera in Colombia—Tambito (Pycz & Wojtusiak, 1999) and Ecuador—Las Golondrinas (Pycz & Wojtusiak, in prep.), where total species richness along sampled elevational gradients (1600–2500/2600m) exceeds 60, only three species were reported below 1600m. Interestingly enough, they are representatives of three genera reported from La Escalera: *Pedaliodes phrasiclea* Grose-Smith, *Eretris depressissima* Pycz and *Oxeoschistus simplex* (Butler), which underlines a structural similarity to the Pantepui fauna at a similar





FIGS. 19-23. Type locality of *Eretris agata*, new species. **19.** *Chusquea*? sp. bamboo in a forest clearing. **20.** Bamboo node detail. **21.** *Chusquea*? sp. bamboo, likely host plant of *E. agata*. **22.** Young *Miconia* sp. (Melastomataceae). **23.** Swampy forest with bamboo clumps

altitude.

There are sight reports of further species and genera of Pronophilina in the Pantepui by experienced lepidopterists. Mauro Costa (pers. comm.) observed for a while an individual butterfly, which he identified as *Lasiophila* or *Mygona*, as he was able to notice its diagnostic pattern of the HW underside. This observation took place on the above-mentioned road at Km 130 (1400m). Andrés Orellana (pers. comm.) observed for some time a butterfly on the summit of Roraima, brown with some golden sheen, which he believes could have been a *Lymanopoda* Westwood (a species rich Andean genus of the subtribe Pronophilina).

The junior author has participated in two large-scale expeditions to major Guyana tepuis in the Pakaraima Mts: Mt. Wokomong (ca. 1675m) in November 1993 and Mt. Ayanganna (ca. 2050m) in April 1999. During the Mt. Wokomong expedition, approximately one week was spent at an elevation between ca. 1425m–1575m with plenty of bright sunshine. Even though a medium-sized bamboo was very common along the summit ridge (ca. 1575m), no pronophilines were captured or definitively seen. On the Mt. Ayanganna expedition there was the same result, with a little over a week spent at elevations (ca. 1375m–1675m) where at least some pronophilines were expected. Again there was plenty of brilliant sunshine, but on Mt. Ayanganna, bamboo did not seem common on the small part of this huge mountain massif that we explored. It was disappointing that we spent no time collecting on the summit plateau (ca. 2050m). On a previous botanical expedition, botanist Terry Henkel reported seeing dark medium-sized butterflies common on the summit plateau when the sun was shining. Were these pronophilines, and if so, could they differ from species on the not too distant Mt. Roraima?

All this emphasizes an urgent need for well-organized sampling and thorough research of the cloud forest butterfly fauna of this extremely interesting region of South America. There is little interest among local entomologists in promoting and carrying out research, and especially field work, in this part of Venezuela. Unfortunately, when it comes to foreigners, the restrictions imposed by Venezuelan laws (these laws having as their primary goal the protection of the environment and native Amerindian culture) in recent years, have practically created such bureaucratic obstacles that permits are nearly impossible to obtain rendering any investigation very difficult (see Viloría & Pyrcz, 1999 comments on this issue).

#### ACKNOWLEDGEMENTS

The senior author would like to thank Mauro and Clara Costa for their outstanding help in Venezuela and Dr. Janusz Wojtusiak (Kraków) for kindly supporting throughout the years his research on the Pronophilina. The 2004 trip to Venezuela was made possible thanks to an internal grant of the Zoological Museum of the Jagiellonian University in Kraków, Poland (BW/2003). The Mount Roraima ornithology expedition was largely funded through a National Geographic Research and Exploration Grant. The Smithsonian Institution Division of Birds graciously allowed lepidoptera collecting on their expedition. Christopher Milensky, Museum Specialist in the Division of Birds, facilitated this effort and made sure the specimens and data returned to the Smithsonian. Chris, Wiltshire Hinds, a University of Guyana Biology Student at the time, and Romeo Williams all did some lepidoptera collecting, with Romeo and Wiltshire doing the bulk of this. Dr. Scott Miller, then Chairman of the Smithsonian Entomology Department, made Smithsonian personnel and equipment available for the photos. Dr. Patricia Gentili-Poole, Museum Specialist, took the excellent digital photos. The authors would like to thank Dr. Keith Willmott (BMNH) for performing genitalic dissections and drawing the male genitalia of *O. romeo*.

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*Received for publication 16 October 2004; revised and accepted*

**Appendix:** Pronophilini species richness in 11 localities along altitudinal transects

Genera	San Lorenzo	Colonia Tovar	Manaure	La Culata	Betania	Choa Chi	Puracé	Runtún	Zamora	Molino-pampa	Roraima
<i>Arhuaco</i>	1	0	0	0	0	0	0	0	0	0	0
<i>Cheimas</i>	0	0	0	1	0	0	0	0	0	0	0
<i>Corades</i>	4	3	4	6	7	7	7	8	10	8	0
<i>Daedalma</i>	0	0	0	0	1	2	2	3	3	3	0
<i>Drucina</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Junea</i>	0	0	0	0	1	2	2	2	2	2	0
<i>Apexacuta</i>	0	0	0	0	0	0	1	1	1	2	0
<i>Lasiophila</i>	1	1	1	1	2	3	3	3	4	4	1?
<i>Mygona</i>	0	1	1	1	1	2	2	2	2	2	0
<i>Oxeoschistus</i>	0	1	1	1	1	2	2	2	2	3	1
<i>Pseudomaniola</i>	1	1	1	1	2	1	1	1	4	4	0
<i>Pronophila</i>	2	2	3	2	3	3	3	4	6	5	0
<i>Thiemeia</i>	0	1	0	0	0	0	0	1	1	1	0
<i>Pedaliodes</i> <sup>°</sup>	7	8	12	15	19	29	34	32	42	42	1
<i>Paramo</i>	1	0	0	0	0	0	0	0	0	0	0
<i>Dangond</i>	0	0	1	0	0	0	0	0	0	0	0
<i>Redononda</i>	0	0	0	1	0	0	0	0	0	0	0
<i>Protopedaliodes</i>	0	0	0	0	0	0	0	0	0	0	2
<i>Eretris</i>	1	1	3	2	3	6	5	5	5	5	1
<i>Lymanopoda</i>	2	2	6	5	6	10	9	10	10	10	1?
<i>Manerebia</i>	1	1	2	2	4	4	3	4	7	6	0
<i>Steroma</i>	1	1	1	1	1	1	1	1	2	3	0
<i>Steremnia</i>	0	0	0	0	1	2	3	3	5	5	0
<i>Diaphanos</i>	0	0	0	1	0	0	0	0	0	0	0
<i>Idioneurula</i>	0	0	0	0	1	1	0	0	0	0	0
<i>Ianusiusa</i>	0	0	0	0	1	0	1	1	0	0	0
<i>Tamania</i>	0	0	0	0	1	0	0	0	0	0	0
Total species	<b>22</b>	<b>24</b>	<b>35</b>	<b>37</b>	<b>55</b>	<b>75</b>	<b>79</b>	<b>83</b>	<b>107</b>	<b>105</b>	<b>5 (7)</b>
Total genera	<b>11</b>	<b>12</b>	<b>12</b>	<b>14</b>	<b>17</b>	<b>15</b>	<b>16</b>	<b>17</b>	<b>16</b>	<b>16</b>	<b>4 (6)</b>

<sup>°</sup> *Pedaliodes sensu lato*

Localities co-ordinates and faunal data source:

- San Lorenzo: Colombia, Sierra Nevada de Santa Marta, north slopes, 11°08'N 74°03'W (Adams & Bernard, 1977)
- Manaure: Colombia, Serranía de Perijá, west slopes, 10°23'N 72°58'W (Adams & Bernard, 1979; Viloría, Msc. thesis, unpubl.)
- La Culata: Venezuela, Cordillera de Mérida, Sierra de la Culata, southeast slopes, 8°41'N 71°08'W (Adams & Bernard, 1981; Pyrcz & Wojtusiak, 2002)
- Colonia Tovar: Venezuela, Cordillera de La Costa, north slopes, 10°26'N 67°15'W (Raymond, 1982; Pyrcz, in prep.)
- Betania: Venezuela, Cordillera Oriental, Sierra del Tamá, north slopes, 7°27'N 72°26'W (Pyrcz & Viloría, in press)
- Choachi: Colombia, Cordillera Oriental, Cundinamarca, east slopes, 4°33'N 73°57'W (Adams, 1986; Pyrcz, 1999)
- Puracé: Colombia, Cordillera Central, Cauca, east slopes, 2°22'N 76°16'W (Adams, 1986; Pyrcz, 1999)
- Runtún: Ecuador, Cordillera Oriental, Tungurahua, north slopes, 1°25'S 78°25'W (Pyrcz et al. 1999; Pyrcz & Viloría, 1999, Pyrcz, 2000, unpubl.)
- Zamora: Ecuador, Cordillera Oriental, Nudo de Sabanillas, east slopes, 3°58'S 79°03'W (Pyrcz et al. 1999; Pyrcz & Viloría, 1999, Pyrcz, 2000, in press)
- Molinopampa: Peru, Cordillera Oriental, Chachapoyas, southeast slopes, 6°10'S 77°34'W (Pyrcz, 2004)