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EREBIINE AND PRONOPHILINE BUTTERFLIES OF THE SERRANÍA DEL TAMÁ, VENEZUELA-COLOMBIA BORDER (LEPIDOPTERA: NYMPHALIDAE: SATYRINAE)

TOMASZ W. PYRCZ1 AND ANGEL L. VILORIA2,3

¹ Muzeum Zoologiczne Uniwersytetu Jagiellońskiego, Ingardena 6, 30-060 Kraków, Poland; tpyrcz@yahoo.com
² Centro de Ecología, Instituto Venezolano de Investigaciones Científicas (IVIC),
Aptdo. 21827, Caracas 1020-A, Venezuela; aviloria@ivic.ve

ABSTRACT.- This is a comprehensive faunal survey of the montane subtribes Erebiina and Pronophilina (Nymphalidae, Satyrinae) in the Serranía del Tamá an Andean range situated on the border between Venezuela and Colombia in the northeastern Cordillera Oriental. Herein, 56 species are recognized and discussed. The Serranía del Tamá is a relatively low chain barely separated from the main backbone of the eastern Colombian Andes. However, its fauna contains a high percentage of taxa different at a subspecific or even specific level as compared to central or southern Cordillera Oriental fauna, particularly at higher elevations. A monobasic genus, Ianussiusa, was erected to accommodate the taxon originally described as Lymanopoda maso Godman. Six new species and thirteen new subspecies are described: Altopedaliodes tamaensis n.sp., Eretris apuleja remotissima n.ssp., Eretris porphyria recta n.ssp., lanussiusa maso santa n.ssp., Idioneurula eremita n.sp., Lasiophila circe arithmetica n.ssp., Lasiophila zapatoza elusiva n.ssp., Lymanopoda lebbaea moritzi n.ssp., Lymanopoda lecromi n.ssp., Lymanopoda samius lineana n.ssp., Oxeoschistus puerta magnus n.ssp., Pedaliodes baccara allopatra n.ssp., Pedaliodes empusa medusa n.ssp., Pedaliodes plotina ruricola n.ssp., Pedaliodes praemontagna n.sp., Pedaliodes reyi n.sp., Pedaliodes valencia n.sp., Pronophila epidipnis orcidipnis n.ssp., Steremnia pronophila fluminea n.ssp. Four new combinations are established, and two others revised; six revisions of status are made, and one status is reinstated. Additionally, two new specific synonymies are established, and sixteen lectotypes designated. The fauna of El Tamá shows few affinities with the Cordillera de Mérida, its closest eastern neighbouring range. Therefore, the importance of the Táchira Depression as the main zoogeographical barrier between them is evaluated. RESUMEN.- Se hace un inventario de las subtribus de mariposas Erebiina y Pronophilina (Nymphalidae, Satyrinae) en la Serranía del Tamá, un macizo montañoso andino situado en la frontera colombo-venezolana, en la punta noreste de la Cordillera Oriental. Se identifican 56 especies. La Serranía del Tamá es un macizo de altitudes medianas, poco diferenciado del resto de los Andes orientales colombianos. Sin embargo, su fauna de mariposas contiene un alto porcentaje de taxones diferentes a niveles subespecífico y específico, comparada con la lepidopterofauna del sur de la Cordillera Oriental, particularmente en sus mayores elevaciones. Se erigió un género monobásico, Ianussiusa, para ubicar la especie originalmente descrita como Lymanopoda maso Godman. Se describen seis especies y catorce subespecies nuevas: estos nombres en al Abstract arriba. Se establecen cuatro combinaciones nuevas, y se revisan otras dos; se hacen seis revisiones de status, y se reinstaura una. Adicionalmente, se establecen tres sinonimias a nivel específico y se designan dieciseis lectotipos. La fauna del Tamá tiene pocas afinidades con la de la Cordillera de Mérida, su vecina orográfica inmediata. Por tanto, se evalúa la importancia de la Depresión del Táchira como barrera zoogeográfica entre ambas cordilleras.

KEY WORDS.— affinities, Altopedaliodes, Altopedaliodes tamaensis n.sp., Andes, cloud forests, Corades, Cordillera de Mérida, Cordillera Oriental, Cyperaceae, Daedalma, Erebiini, Eretris, Eretris apuleja remotissima n.ssp., Eretris porphyria recta n.ssp., hostplants, lanussiusa, Ianussiusa maso santa n.ssp., Idioneurula eremita n.sp., Junea, Lasiophila, Lasiophila circe arithmetica n.ssp., Lasiophila zapatoza elusiva n.ssp., Lymanopoda, Lymanopoda lebbaea moritzi n.ssp., Lymanopoda lecromi n.ssp., Lymanopoda samius lineana n.ssp., Manerebia, Mygona, Neotropical, Norte de Santander, Oxeoschistus, Oxeoschistus puerta magnus n.ssp., Panyapedaliodes, Pedaliodes, Pedaliodes baccara allopatra n.ssp., Pedaliodes empusa medusa n.ssp., Pedaliodes plotina ruricola n.ssp., Pedaliodes praemontagna n.sp., Pedaliodes reyi n.sp., Pedaliodes valencia n.sp., Praepronophila, Pronophila, Pronophila epidipnis orcidipnis n.ssp., Pronophilina, Pseudomaniola, South America, Steremnia pronophila fluminea n.ssp., Steroma, Táchira, taxonomy, zoogeography.

The Serranía del Tamá, located on the border between the Venezuelan states of Táchira and Apure and the Colombian Department of Norte de Santander, is a medium sized, Andean chain with highest summits slightly exceeding 3600m above sea level. Its main ridge runs roughly east to west over 70 km, having a maximum width of nearly 40 km. It can be considered a continuation of the main backbone of the Colombian Cordillera Oriental, since it makes contact at altitudes over 2000m. On the other hand it is separated from the Venezuelan Cordillera de Mérida by a deep valley, traditionally called the Táchira Depression (Fig. 49).

Several parallel rivers cross the northern slopes of the range (Venezuelan side): the Río Táchira and its tributaries running north along the Colombian border finally flow into the Lake Maracaibo, while most of the remaining rivers belong to the Río Orinoco basin. The latter collects the water from the rivers Qui-

3. formerly, Biogeography & Conservation Laboratory, Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

nimarí, Negro, Frío, Colorado and Cuite, which are tributaries of the Río Uribante, while the Rio Oirá, which flows to the west along the border between the two countries falls into the Río Apure. On the southern slopes (Colombian side), the Tamá is separated from the rest of the Cordillera Oriental by the long valley of the Río Margua, tributary of the Río Arauca.

Altitudinal data of El Tamá are not accurate. Even though various Venezuelan maps indicate the Pico El Cobre (ca. 3380 m) as the maximum elevation of the range, it is almost certain that the highest peak of El Tamá is the Pico de Santo Cristo, situated on the main international ridge, at approximately 3600 m. Several other peaks reach above 3200m, i.e., the Páramo de La Revancha, the Cerro La Banderola, the Páramo del Tamá, the Cerro Babilonia, and the Páramo del Judío (or Patijudío, as it is known locally).

Local meteorological conditions are determined by the predominant tropical humid to very humid climate. It is mostly premontane and montane on the entire eastern side, within the basins of the rivers Uribante, Margua and Oirá. General conditions turn drier towards the northwest in the lower valley of the Río Táchira.

The phenomenon is easily detected when looking at the medium annual precipitation, which ranges from around 4000 mm on the southeast slopes, down to 800 mm in the northwest. In our experience, annual pattern of rain fall is more or less bimodal, the dry season lasting from between December and the beginning of May in the driest areas, but being limited to February-March in the wettest ones.

The vegetation, as usual in tropical mountains, shows a marked altitudinal zonation, with a cline towards semi-arid areas in the northwest of the range. Premontane forests cover the Quinimarí-Uribante and Margua valleys below 800m, whereas the valley of the Río Táchira is predominantly covered with deciduous premontane forests at the same elevations. Where still pristine, the entire range at 1500-2000m is naturally covered by lower montane forest, being gradually replaced by montane, cloud and elfin forests above 2500m. The tree-line, which marks the limit between cloud forests and the páramo grasslands is situated at around 3000m, except where local edaphic conditions bring it down to 2500m or even slightly below. A recent, illustrated account of the local geography and landscape descriptions of El Tamá can be found in Manara (1998).

Montane satyrine of the northern Andes: the Erebiina-Pronophilina assemblage

The tribe Pronophilini (Reuter, 1896), considered as a subfamily of the satyrids by other authors (Clark, 1947) and here as a subtribe, has been difficult to define. Miller (1968) formally retained it as a tribe, but Harvey (1991) re-worked his system and downranked it to subtribal category. Viloria (2007, this issue), determined that what was understood as the Pronophilina is actually a composition of representatives of at least three subtribes, which co-exist in the Neotropics. Thus, he proposed a redefinition of the Pronophilina based on a minimun combination of external characters that can be easily evaluated, even by a non-specialist. It became obvious that some genera formerly believed to be members of the Pronophilina were not, and a new place for them was searched for.

Morphological evidence revealed that there was no need to create new entities for the 'abnormal' Neotropical genera of high Andean and/or Fuego-Patagonian satyrines, but a need to redistribute them between two subtribes that were previously undetected in the South American continent (Erebiina Tutt and Hypocystina Miller). Thus, it became evident that South America harbors an assemblage of different satyrine subtribes, whose distribution may have very important implications for biogeography, especially because now we know that most of the tribes and subtribes within the subfamily are represented at different degrees in several continents (Viloria, 1998; but see Peña et al., 2006).

Hence, for this contribution we have decided to treat the satyrine fauna of the Serranía de El Tamá as an Erebiina-Pronophilina assemblage. Notwithstanding their actual higher systematic status, the Erebiina, the Pronophilina, and the Hypocystina can be well separated from each other using Viloria's criteria of the minimum set of characters. The other major groups of Neotropical Satyrinae, the tribe Haeterini Herrich-Schäffer, and the subtribes Euptychiina Reuter and the Parargina Tutt, still await detailed review. However, they can be separated from the main Andean-temperate assemblage on morphological (see Miller, 1968; Miller and Miller, 1997) and ecological grounds (see Adams, 1985; DeVries, 1987).

Major features of the subtribes Erebiina and Pronophilina in the Neotropics are summarized in Viloria (2007, this issue). The Pronophilina exhibit an overwhelming majority of species in the tropical Andes. Among its most speciose genera are *Pedaliodes*

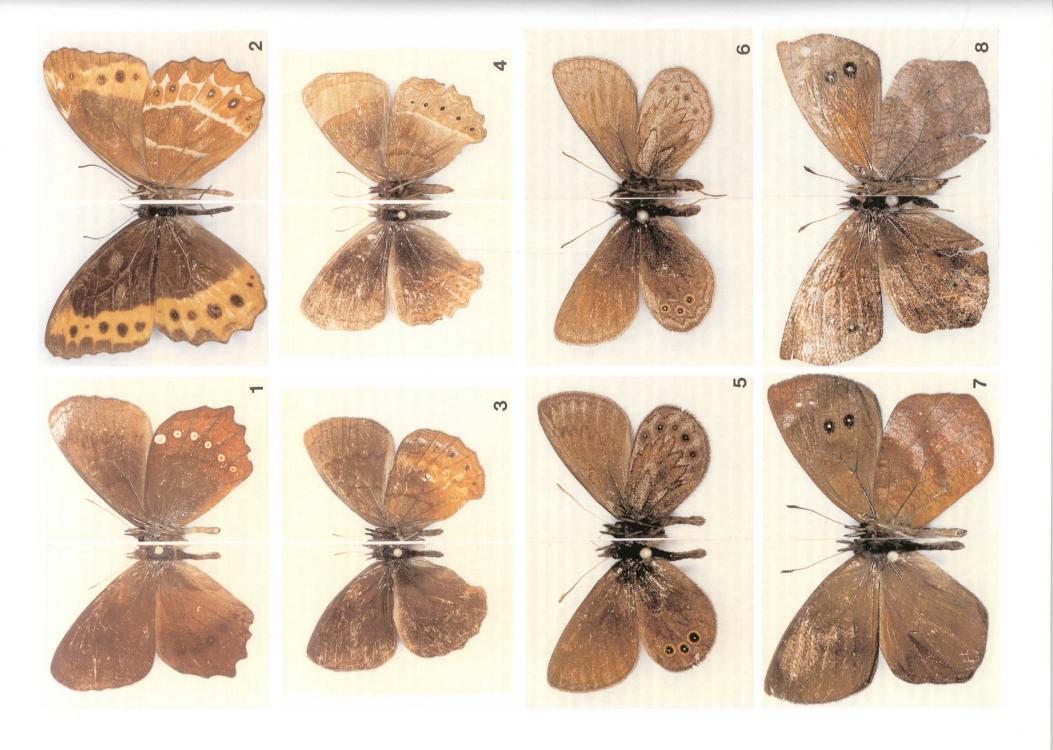
with over 230 recognized species (Viloria and Pyrcz, 2000) (242 according to Lamas *et al*, 2004), and *Lymanopoda* with about 60 species (Pyrcz *et al.*, 1999) (52 according to Lamas *et al*, 2004).

The genera of Erebiina and Pronophilina found in a typical assemblage of the northern Andes occur from approximately 800m to over 4000m, with a peak diversity between 2500m and 2900 m (Adams, 1985; Pyrcz and Wojtusiak, 1999). Local assemblages comprise between 21 species in the Venezuelan Cordillera de la Costa (Raymond, 1982; Viloria and Pyrcz, unpubl.) and the Colombian Sierra Nevada de Santa Marta (Adams and Bernard, 1977), and roughly 60 to 80 species in most of the main northern Andes. (Adams, 1985, 1986, adapted). However, the maximum species richness for the group is recorded in southern Ecuador, Peru and Bolivia. In all these areas, the local faunas of montane satyrines exceed 100 species (Pyrcz, in prep.). The isolated mountain units of the northern Andes (Sierra Nevada de Santa Marta, Sierra de Perijá, and Cordillera de Mérida) average 30%, and the main Andes approximately 15% of endemic species (Adams, 1985; Pyrcz, in prep.). Endemism ratio generally increases at higher elevations, being the highest close to the upper forest limit (Adams, 1985), but this is not always the case (Pyrcz and Wojtusiak, 1999).

Pronophilines and some erebines (*Manerebia* Staudinger) occur in well defined and sometimes very narrow bands of altitude (Adams, 1985). Their vertical zonation has attracted the attention of naturalists since the early twentieth century (Fassl, 1910, 1911, 1915, 1918; Krüger, 1924, 1925), and recently has been more extensively discussed by Adams and Bernard (1977, 1979, 1981), Adams (1985, 1986) and Pyrcz and Wojtusiak (1999).

As with many other satyrines, erebine and pronophiline butterflies are remarkably sedentary (Adams, 1986; DeVries, 1987), being generally restricted to particular habitats in the cloud forests (Adams, 1986). A high proportion of species have a limited vagility, and even though this aspect of their behavior has not been studied, simple field observations indicate that adults move little vertically or horizontally and keep close to their host plants or roosting places. The biology of the Pronophilina remains largely unexplored, but the available records reveal that their larvae feed on montane bamboo (Poaceae), chiefly of the genus Chusquea (Schultze, 1930; Adams and Bernard, 1981; DeVries, 1987; Heredia and Viloria, 2004; Viloria, 2007, this issue), but also of the genera Guadua (X. Londoño, pers. comm.) and Bambusa (Pyrcz, unpubl.). Few species seems to use other Poaceae, such as grasses (Brown, 1941; Pelz, 1997, Viloria and Pyrcz, MS), or woody cane (Miller, 1986). The use of grasses (other than primary forest bamboo) allows a few species to inhabit secondary growths and pastures at middle elevations. The most notable example of such species in El Tamá is Pedaliodes manis (C. & R. Felder), but apparently Pedaliodes plotina (Hewitson) also uses pasture grasses to some extent. Another species that almost certainly feeds on a different monocotyledoneous plant (perhaps a Cyperaceae) is Tamania jacquelinae Pyrcz, which is exclusively associated with open mid-elevation grasslands where there are no Chusquea. Recently, Pelz (1997) successfully reared an Ecuadorian species, Parapedaliodes parepa (Hewitson) in Germany on a substitution food plant, the grass Poa annua (Linnaeus) (Poaceae).

Although several pronophiline species have been included as threatened with extinction in the Red Data Book (Adams, 1983) and similar catalogues (Rodríguez and Rojas-Suárez, 1995), it seems likely that human activity may, under certain circumstances stimulate the survival and growth of some of their populations (although certainly changing natural patterns of altitudinal distri-



bution). Their main hosts, *Chusquea* bamboos (Poaceae), are invasive plant species, being more abundant in clearings, roadsides, at the forest edge, and along paths in the cloud forests. They are indeed considered synantropic plants by tropical botanists and ecologists (Cortés, pers. comm.). Andrade (1994) considers most species of Pronophilini surveyed in the Risaralda Province (Colombia) as indicators of secondary forest.

Adults of nearly all species feed on decomposing organic matter, and are heavily attracted to it, particularly animal or human faeces, carrion and rotten fruits. We have seen one high altitude species feeding on flowers of *Espeletia* in Venezuela (Viloria and Pyrcz, MS).

History of zoological research in El Tamá

To our knowledge, the first zoologist to do research in the Serranía del Tamá, was the American mammalogist Wilfred H. Osgood, who visited and collected vertebrates in the area for the Field Museum of Chicago in 1911 (Osgood, 1912), but there is no indication that he actually obtained any invertebrates. Only later in this century a number of expeditions explored the area for scientific purposes, including the study of plants (for a summary see Bono, 1996), amphibians (Rivero, 1979; Duellman, 1980; La Marca *et al.*, [1990]), reptiles (García-Pérez and La Marca, 1989; Barros *et al.*, 1996) and birds (Phelps and Phelps, Jr., 1958, 1963; Meyer de Schauensee and Phelps, Jr., 1978; Vuilleumier and Ewert, 1978; Lentino, 1988; Calchi, 1996).

Very few entomological studies have been pursued in this range (Perruolo-Laneti, [1985]; Blanco, 1987, 1988; De Marmels, 1988). The study of butterflies, including the members of the Satyrinae, started in the Tamá at the latest in 1980 with the collections of F. Romero and R. Murphy in the Mata Mula region, along the road between Bramón and Delicias (1700-1900 m). At that time, collectors from Maracay and San Cristóbal (F. Romero, J. Blanco and R. Salazar) also began to sample butterflies at lower elevations (below 1200m) in the valleys of the Río Uribante, Río Frío, and Río Negro. Later, in 1983 an expedition of the Universidad Central de Venezuela (MIZA) reached the páramo from Betania, obtaining the first sample of butterflies known from higher elevations (above 2500m). Subsequently, T. Pyrcz set up an expedition to the area of Betania in 1987, from which resulted the description of the genus Tamania (Pyrcz, 1995), hitherto the only published systematic information about the satyrine butterflies of El Tamá. More recently, the upper cloud forests of El Tamá were surveyed twice by entomologists of the MIZA, twice by A. Viloria (in 1992 and 1994, with R. Calchi, J. Camacho, and M. García from La Universidad del Zulia, MALUZ), and twice by F. Rey (Universidad Nacional Experimental del Táchira). MALUZ expeditions devoted considerable efforts to investigate the fauna of the páramo. J. F. Le Crom (Bogotá) and F. Valencia (Universidad de Pamplona) managed to explore and collect butterflies in the neighbourhood of Herrán on the Colombian slopes of the range in 1993 and 1994. Since then, F. Rey has addressed a number of efforts to collect butterflies in the upper valley of the Río Quinimarí, especially around San Vicente, an area previously unexplored by entomologists. In 1996, T. Pyrcz and A. Viloria independently conducted extensive collections of satyrines and

Fig. 1-8. 1) Ianussiusa maso santa Pyrcz & Viloria, n. ssp. (male Holotype). 2) Oxeoschistus puerta magnus Pyrcz & Viloria, n. ssp. (male Holotype). 3) Eretris apuleja remotissima Pyrcz & Viloria, n. ssp. (male Holotype). 4) Eretris porphyria recta Pyrcz & Viloria, n. ssp. (male Holotype). 5) Idioneurula eremita Viloria & Pyrcz, n. sp. (male Holotype). 6) Idioneurula eremita Viloria & Pyrcz, n. sp. (female Allotype). 7) Lymanopoda lecromi Pyrcz & Viloria, n. sp. (male Holotype). 8) Lymanopoda lecromi Pyrcz & Viloria, n. sp. (female Allotype).

other butterflies in different sectors of the region: the valley of San Vicente, El Reposo, Betania, Paramito, Cerro La Banderola, and La Línea. The result of the study of the pronophilines from all these collections is presented in this article. We have been recently informed of new butterfly captures in the area by Giovanny Fagua (Univ. Javeriana, Bogotá, Colombia, pers. comm.), but this material has not been examined for this study.

Information about representatives of other families of butterflies known in the Serranía del Tamá has been made available through the study of the material obtained by the expeditions referred to above. Thus, Neild (1996) published the updated taxonomy, distribution, and color illustrations for three nymphalid subfamilies, Rey and Pyrcz (1996) described *Catasticta revancha*, a pierid apparently endemic in the upper valley of the Río Quinimarí, and Johnson *et al.* (1997) described *Solanorum pyrczi*, a high Andean lycaenid, also restricted to this range. More recently, have appeared descriptions of three new subspecies from the range: *Catasticta uricoecheae inopa*, *C. tricolor tomasi* (Pieridae) (Wojtusiak and Rey, 1999), and *Prepona praeneste isabelae* (Nymphalidae) (Orellana, 2000).

The considerable amount of new species and subspecies described in the present paper from El Tamá mountains is the outcome of extensive comparative taxonomical studies, which document important zoogeographical differences between the fauna of this range and the rest of the Colombian Cordillera Oriental. Most species of montane Satyrinae occurring in El Tamá were described over a century ago from individuals obtained in the area of Bogotá. Even in the immediate surroundings of Bogotá this fauna is not homogenous and, as pointed out by Adams (1986), the west and east slopes faunal pools separated only by the 30 km wide Bogotá plateau differ frequently at the subspecific, and sometimes even at the specific level. Not surprisingly, in the peripheral range of El Tamá, situated 300 km northwards, faunal differences are at least as distinct as those of the southern Cordillera Oriental. Sometimes the populations found in El Tamá have differentiated morphologically from their southern allies substantially enough to treat them as distinct species. This applies basically to the species found at the highest elevations, such as the páramo or the uppermost cloud forest taxa, which are believed to have been physically isolated for the longest periods of time. In most cases the differentiation process has not achieved a full speciation, but minor morphological differences, basically in the wings' color pattern, are obvious and stable enough to attribute them a subspecific status.

Acronyms for collections consulted

AFN Collection of Andrew F. Neild, London, UK. BMNH The Natural History Museum, London, UK.

FRC Collection of Fernando Rey, San Cristóbal, Venezuela.
FRR Collection of the Romero family, Maracay, Venezuela.
JB Collection of Joffre Blanco, San Cristóbal, Venezuela.
LC Collection of Jean-François Le Crom. Bogotá, Colombi

LC Collection of Jean-François Le Crom, Bogotá, Colombia.

MALUZ Museo de Artrópodos, Facultad de Agronomía, La Universidad del Zulia, Maracaibo, Venezuela.

MBLUZ Museo de Biología, Facultad Experimental de Ciencias, La Universidad del Zulia, Maracaibo, Venezuela.

MHNUN Museo de Historia Natural de la Universidad Nacional de Colombia, Bogotá, Colombia.

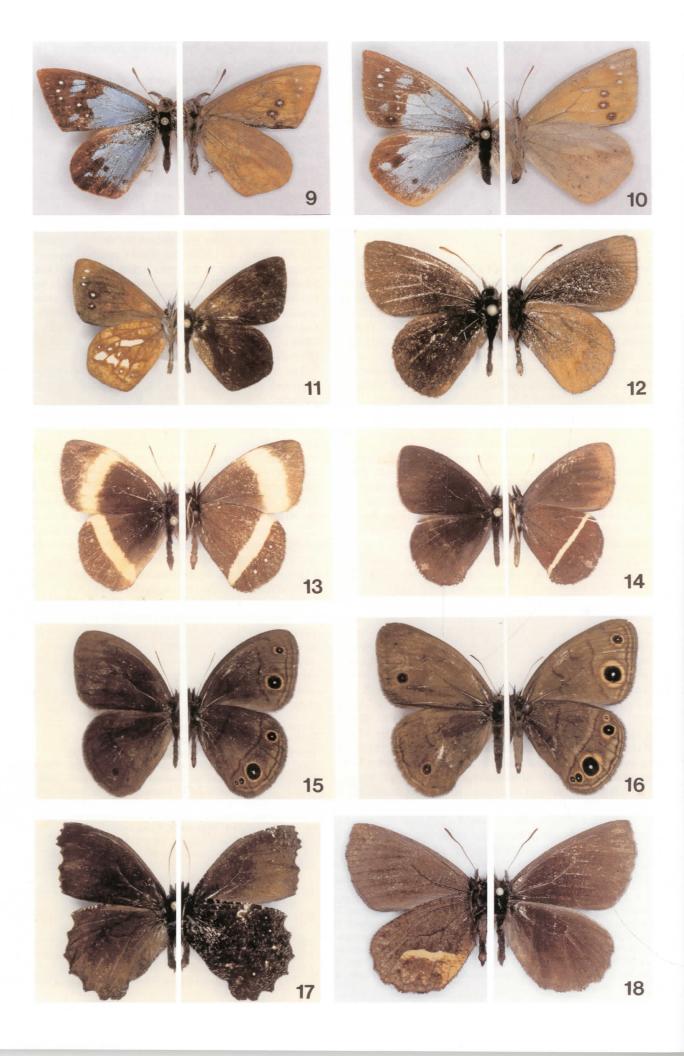
MIZA Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela.

MIZPAN Muzeum i Instytut Zoologii Polskiej Akademii Nauk, Warsaw, Poland.

MNHN Muséum National d'Histoire Naturelle, Paris, France.

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

MZUJ Muzeum Zoologiczne Uniwersytetu Jagiellońskiego, Kraków, Poland.



RMA Collection of Roger Manrique, Mérida, Venezuela. RMU Collection of Raymond Murphy, London, UK.

SMTD Staatliches Museum für Tierkunde, Dresden, Germany. TWP Collection of Tomasz Wilhelm Pyrcz, Warsaw, Poland.

ZMHU Zoologische Museum, Humboldt Universität, Berlin, Germany. Other abreviations

HC Hewitson Collection, Brit. Mus. 79-69 [accession code in BMNH]. RB Rothschild Bequest, Brit. Mus. 1939-1 [accession code in BMNH].

Subtribe EREBIINA Tutt, 1896

IANUSSIUSA Pyrcz & Viloria, 2004

Ianussiusa Pyrz & Viloria, 2004:284.

Type-species: Lymanopoda maso Godman, 1905:188.

Description.- Head: eyes naked; labial palpi twice the length of head, covered with long (one third the length of palpus) dense hair-like setae, third segment short, one fourth the second; antennae to half costa, composed of 28 segments, sparsely scaled, club composed of 8-10 segments, gradual, not very prominent. Wings: (Fig. 1) forewing subtriangular, apex obtuse; hindwing kite-shaped, apex blunt, tornus angular, outer margin scalloped, more prominently in cell Cu1. Venation (Fig. 48) of forewing: Sc, R1 and R2 all independent; root of R3 nearer to root of R4 than to discal cell, root of M1 on R, same length as r-m2; m2-m3 straight; venation of hindwing: root of M1 halfway between those of Rs and M2; that of M3 halfway between those of M2 and Cu1, cross vein m1-m2 straight. Color pattern: upperside of both wings unicolorous, chestnut or brown; underside pattern composed of simple elements of ground plan and a straight row of faint whitish submarginal dots on the forewing, and in each cell a row of well-marked milky-white pupilled ocelli, roughly parallel to outer margin on hindwing. Sexual dimorphism: light, female slightly larger than male with richer, more constrasting underside pattern. The male has no apparent specialized androconial scales, particularly no scent patch (stigma) on the forewing upperside. Male genitalia: (Fig. 43) tegumen stout, uncus 3/5 of tegumen, subuncus reduced, saccus long and slender, valva of same length as tegumen and uncus, with two prominent processes, dorsal 2/3 the length of apical one, aedeagus slightly arched, 1/5 longer than valva. Female genitalia: (Fig. 46-47) bursa copulatrix roughly spherical with two thin, parallel stigmae, sinus vaginalis broad, extending to both sides of abdomen, anterior wall of sinus vaginalis sculpted with ripple-like, lightly sclerotized cuticular plates; anal papillae rounded.

Remarks.- The taxon maso was removed from Lymanopoda by Pyrcz and Viloria (2004) because it does not share the synapomorphies of the genus, specified by Pyrcz et al. (1999:497-498). These are, in the color pattern, the ocelli in cells M3-Cu1 and Cu1-Cu2 always displaced basally in relation to the remainder, the hindwing underside median band broken and displaced in the discal cell, connected to the postbasal band; in the male genitalia. a bulbous projection of the tegumen at the junction with the uncus and the absence of subunci (although a weakly sclerotized projection occurs in all species which is probably not homologous with the subunci, appearing to be a modification of the basal part of the uncus), replaced by a (usually) strongly sclerotized subscaphium; in the female genitalia, a sclerotized lamella of anal papillae on the distal part of the posterior apophysis and an accessory gland (of unknown function, probably producing an egg gluing secretion) posterior to the ostium bursae.

Fig. 9-18. 9) Lymanopoda samius lineana Pyrcz & Viloria, n. ssp. (male Holotype). 10) Lymanopoda samius lineana Pyrcz & Viloria, n. ssp. (female Allotype). 11) Lymanopoda lebbaea moritzi Pyrcz & Viloria, n. ssp. (male Holotype). 12) Manerebia pervaga Pyrcz & Viloria (male Holotype). 13) Manerebia pluviosa Pyrcz & Viloria (male Holotype). 14) Manerebia leaena gonzalezi Pyrcz & Viloria (male Holotype). 15) Manerebia mycalesoides (C. & R. Felder) (male: Sta. Ana-San Vicente, ca. 1400m, 20 Sep 1997, A. Neild leg.). 16) Manerebia mycalesoides (C. & R. Felder) (female: Táchira, vía Chorro del Indio, Loma del Viento, ca. 1400m, 19 Sep 1997, A. Neild leg.). 17) Steremnia pronophila fluminea Pyrcz & Viloria, n. ssp. (male Holotype). 18) Altopedaliodes tamaensis Viloria & Pyrcz, n. sp. (male Holotype).

Ianussiusa does not have the minimum set of characters shared by the members of the subtribe Pronophilina sensu Viloria (2007, this issue), but fits the diagnostic characters for the Neotropical Erebiini, where it is placed besides its possible sister genus Tamania Pyrcz. It is interesting to point out that the wing shape of Ianussiusa is very reminiscent of Lymanopoda caudalis Talbot & Rosenberg (from Peru), which is otherwise a typical Lymanopoda.

Ianussiusa maso santa Pyrcz & Viloria, new subsp. (Fig. 1, 43)

Lymanopoda maso Godman, 1905:188, pl. 10, fig. 9. 4 syntypes, Colombia, Frontino, BMNH, [examined].

Cheimas ? polyommatus Röber, 1927:420, 430, pl. fig. 9. Holotype male, Colombia, "SNSM", BMNH, [examined]. Synonymy established by Adams & Bernard, 1977: 271.

['Lymanopoda' maso subsp. nov. Pyrcz & Viloria, MS]; Viloria, 2000:267.
[Ianussiusa maso n. ssp., no.1093b Pyrcz & Viloria, MS]; Lamas & Viloria, 2004:215.

Diagnosis.— The new subspecies differs from the nominate as follows: upperside darker, chocolate brown instead of chestnut; underside darker; row of hindwing ocelli situated further distally from postmedian line, ocelli considerably smaller and yellow instead of milky-white, but red pupils larger. Some individuals of the nominate subspecies bear an additional ocellus on the costal margin, absent in *I. maso santa*. In the nominate subspecies there are always two ocelli in cell Cu2-1A, but only one in *I. maso santa*.

Description.– MALE: Forewing length: 21-24mm, mean: 22.95mm, n = 8. Upperside of both wings chocolate brown, basal third of forewing slightly lighter, lustrous. Forewing underside pale brown, distal half lighter, with indistinct dark brown median and postmedian lines, the latter wavy, a fine submarginal brown line, a series of yellowish submarginal dots apparent in each cell and an apex suffused with magenta. Hindwing underside reddish brown with darker, indistinct median, postmedian and submarginal lines, roughly parallel to outer margin, postmedian regular and submarginal sinuate, a series of six small postmedian yellowish ocelli, pupilled with reddish brown. Genitalia: as illustrated in Fig. 43, or described for the genus.

FEMALE: Unknown.

Material examined.— Holotype (male): Betania, Potrero, Venezuela, 2395m, 17 Aug 1996, A. Viloria, V. Carrizo, D. González [MALUZ]. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 2 males [1 wing preparation], same data; 2 males, Bosque arriba de Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo, D. González; 2 males [1 in MUSM], Selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo, J. & A. González [MALUZ]; 7 males, Bosque arriba de Betania, 16 Apr 1996, T. Pyrcz & F. Rey [TWP]; 1 male, same locality, Aug 1987, T. Pyrcz [MZUJ].

Etymology.— The name santa comes from saint (Latin, adj., fem.). Remarks.— Ianussiusa maso maso was described from the northern extremity of the Colombian Cordillera Occidental or Cordillera Central (Antioquia). Similar individuals occur in Tolima and on eastern slopes of the Andes in Ecuador (La Bonita, Baeza, Baños). The report of *I. maso* from the Sierra Nevada de Santa Marta (Adams and Bernard, 1977) is due to a mislabelled specimen collected by E. Krüger in Tolima, which served Röber (1927) as the type for his species, *Ch. polyommatus*, a synonym of *I. maso*. Subspecies santa has a very particular, slow and sturdy flight. The majority of the individuals observed in Betania were seen descending to puddle on the bank of a stream along with Lymanopoda albocincta Hewitson and Steremnia pronophila fluminea Pyrcz & Viloria, new subsp.

IDIONEURULA Strand, 1932

Idioneurula Strand, 1932:146. Type-species: Idioneura erebioides C. & R. Felder, 1867, by monotypy (replacement name for Idioneura C. & R. Felder, 1867 nec Philippi, 1865. In Verh. Zool.-bot. Ges. Wien, 15:615; However, we found that Idioneura Philippi is also preoccupied by Idioneura Selys, 1860).



Fig. 19-22. 19) Lasiophila circe arithmetica Viloria & Pyrcz, n. ssp. (male Holotype). 20) Lasiophila zapatoza elusiva Pyrcz & Viloria, n. ssp. (male Holotype). 21) Pronophila epidipnis orcidipnis Pyrcz & Viloria, n. ssp. (female Allotype).

Idioneurula eremita Viloria & Pyrcz, new sp. (Fig. 5-6, 34)

[Lymanopoda (sic) panacea (Hewitson); Manara, 1998:103 (misidentification)].
 [Idioneurula sp. nov. Pyrcz & Viloria, MS]; Viloria, 2000:267.
 [Idioneurula n. sp. Pyrcz & Viloria, MS, no. 1095]; Lamas & Viloria, 2004:215.

Diagnosis.— Differs from *I. erebioides* in the hindwing underside pattern, an invariably present zigzagging postmedian line and a series of submarginal ocelli, whereas in *I. erebioides* the pattern is indistinct, the ocelli are faint or absent, and there is a common individual form in which there are yellowish intervenous stripes.

Description.— MALE: *Head*: eyes naked, dark coffee brown; palpi three times longer than head, heavily hairy, dorsally light brown, ventrally brown; antennae reaching three fifths of costa, composed of 34 segments, light brown except for dorsal surface of club, which is chocolate brown; shaft with some brown scales on upperside and white on underside, club 2.5 times as broad as shaft, concave (spoon-shaped), with two carinae at lateral edges and another along middle of the concavity. *Thorax*: dark brown, covered with very short hair scales. *Abdomen*: dorsally and ventrally dark brown. *Wings*: forewing length: 18.5-21mm, mean: 19 mm, n = 78; hairy, dorsally lustrous reddish brown, ventrally lighter and more brilliant; forewing triangular, apex and tornus obtuse; hindwing oval, margins rounded; ground color of dorsal surface of wings brilliant brown, a bit darker at basal region, and slightly lighter and with chestnut tone in submarginal region; long and tiny chocolate brown scales flanking margins of wings; light brown faintly dusted on costal and external

margins of forewing upperside; hindwing upperside has two dark brown zig-zag lines limiting basal and distal edges of postdiscal-submarginal area, in this area a series of 3 (or 4) rounded ocelli in cells M2-M3 to Cu1-Cu2 (or Cu2-1A), the first three 1.5-2mm diameter, whilst that in Cu2-1A reduced to 1mm or less, sometimes vestigial or absent; ocelli dark coffee brown, circled by ochreous yellow and finely pupilled with white; ventral surface of wings densely covered with short hair scales, especially along margins and veins; forewing ground color brown, progresively darker towards base, discal region limited by 2 zig-zag dark brown lines, another similar separating marginal and submarginal regions; wing edges flanked with dark brown, greyish light brown dusted along space between costa and origin of radial veins, as well as subapical and submarginal regions; some sparse reddish scales on central region of wing; series of 3 (or 4) vestigial submarginal white dots in cells M1-M2 (or M2-M3) to Cu1-Cu2, sometimes surrounded by dark brown shadows (vestigial ocelli); hindwing ventral surface ground color brilliant brown, darkened at base and flanks; 3 zig-zag dark brown lines limiting the following regions: submarginal from marginal, discal from postdiscal, and subdiscal from discal, the second being more pronounced; grey scales dusted over basal, postbasal and marginal region, as well as in middle of discal region; on this part a series of 5 (or 6) ocelli from cell M2-M3 to Cu2-A1, dark brown, pupilled with white and difusely circled by brown; discal region densely dusted with reddish scales. Male genitalia: as illustrated (Fig. 34).

FEMALE: Forewing length: 17-20mm, mean: 18.09mm, n = 24. Differs from male in the following features: antennal segments: 40; wings slightly narrower; general ground color on dorsal surface of wings, lighter in distal half of wings, hindwing ocelli smaller, thickly circled by ochreous yellow; dark lines limiting both flanks of postdiscal-submarginal band more discrete. Iridiscent light brown along external margin and in apical region;

ground color of ventral surface of wings greyish light brown; forewing basically showing same design as in male but with lighter tone and without submarginal white dots; hindwing has same pattern as in male but much more faint, brown color, which is dominant in male, here displaced by greyish light brown, except for discal band, where brown still dominates; ocelli very reduced (those at extremes tend to disappear) and thickly circled by ochraceous brown.

Material examined.— Holotype (male): Páramo del Tamá, Departamento Norte de Santander, Colombia 3100-3200m, 16 Feb 1992, A. Viloria & J. Camacho *leg*. [MALUZ]. Allotype (female): Parque Nacional El Tamá, Táchira-Apure, Venezuela, 3100-3350m, 16/18 Feb 1992, A. Viloria, J. Camacho leg. [MALUZ]. Holotype desposited in MALUZ.

Paratypes: COLOMBIA: 1 male, 1 female, same data as holotype. VENEZUELA: 1 female, arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo, J. & E. González leg.; 24 males, 7 females, El Paramito, 2500-2600m, 24 Aug 1996, A. Viloria, V. Carrizo & L. E. González leg. [MALUZ]; 12 males [including 1 wing preparation], 9 females, same locality, 2500-2550m, 27 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 10 males, Betania, Paramito, 2400-2450m, 15 Apr 1996, T. Pyrcz leg, [TWP]; 12 males, 2 females [of which, 1 male and 1 female in TWP], same data as allotype [MALUZ]; 1 male, Páramo Tamá, P. N. El Tamá, 3100-3300m, 17 Apr 1996, T. Pyrcz leg. [AFN]; 1 male, cuesta de La Cueva, cerca del Picacho, 3100m, 14 Apr 1996, T. Pyrcz & F. Rey leg. [BMNH]; 6 males, 1 female: Páramo El Tamá, via La Línea, 3200-3300m, 14 Apr 1996, T. Pyrcz & F. Rey leg. [FRC]; 22 males, 3 females, same data [TWF].

Etymology .- eremita: in Latin, a hermit.

Remarks.- Mirroring the case of *Altopedaliodes tamaensis* Viloria & Pyrcz, **new sp.** and *A. nebris* (Thieme), this species is the local replacement for *Idioneurula erebioides* (C. & R. Felder), which is found in similar habitats further south. Typical individuals of *I. erebioides* are found in the region around Bogotá and in the Sierra Nevada del Cocuy.

MANEREBIA Staudinger, 1897

Manerebia Staudinger, 1897:139. Type-species Manerebia cyclopina Staudinger, 1897, by subsequent designation (Hemming, 1943:24).
Penrosada Brown, 1944:255. Type-species Lymanopoda leaena Hewitson, 1861, by original designation [synonymy in Lamas & Viloria, 2004].
Posteuptychia Forster, 1964:137. Type-species Pronophila mycalesoides C. & R. Felder, 1867, by monotypy [synonymy in Lamas & Viloria, 2004; for explanation see below under Manerebia mycalesoides (C. & R. Felder)].

The genus Manerebia was raised by Staudinger (1897) for five Bolivian and Peruvian taxa; four of them, M. cyclopina, M. cyclopella, M. cyclops, and M. typhlops, are valid species, but M. thyphlopsella is a junior synonym of Manerebia insulsa (Hewitson). Other taxa described originally in this genus are, M. nevadensis Krüger (1924) from the Sierra Nevada de Santa Marta in Colombia, M. monops Hayward (1949) from Argentina (= M. cyclopella), M. staudingeri Forster (1964) from Bolivia, and M. keradialeuka Hayward (1968) from Ecuador (= Manerebia interrupta Brown). Forster (1964) represented the figures (of the types) and discussed all Bolivian Manerebia, but did not discuss in more details the taxonomy of the genus. Miller (1968) referred to some morphological characters of Manerebia as a genus within the tribe Pronophilini. In spite of their extensive studies on north Andean Pronophilini, Adams and Bernard (1977) dealt only with M. nevadensis which they briefly compared to M. staudingeri.

The genus *Penrosada* was raised by Brown (1944) for 7 species, previously placed in *Lymanopoda: L. leaena* Hewitson, *L. apiculata* C. & R. Felder, *L. lanassa* C. & R. Felder (a possible subspecies of *Manerebia leaena*), *L. lisa* Weymer, *L. satura* Weymer, *L. cillutinarca* Weymer (a synonym of *Manerebia zoippus* H. Druce), and *L. keithi* Dyar (= *Manerebia satura* Weymer). Adams & Bernard (1979, 1981) and Adams (1986) described four further species of *Penrosada* from Colombia and Venezuela.

We have considered Penrosada as a subjective junior synonym of Manerebia because we have found no synapomorphies to distinguish it from the latter (in head and wing morphology, wing color pattern, male genitalia structure). A reading of the diagnosis of the genus Penrosada given by Brown (1944) shows that all the specified characters apply in full extent to the species of the genus Manerebia (sensu Staudinger). Namely, the wing shape (particularly anal margin of the hindwing slightly incised near anal angle), size, ground plan (generally a fully developed ocellus in Cu2-1A of both the fore and hindwing), venation pattern (hindwing crossvein m1-m2 shorter than in Lymanopoda and straight or just gently curved, and M3 much closer to Cu1 than to M2.) and color of walking legs (usually yellowish). The male genitalia structure of Manerebia (sensu Staudinger), a character particularly emphasized by Brown, is indistinguishable from Penrosada. The conspicuous oblique, straight yellow or whitish band on the hindwing underside present in most Penrosada of Brown and absent in the five original Manerebia of Staudinger is a character of secondary taxonomic value, and does not even allow to separate with confidence between species. Some species of Manerebia (sensu novum) are polymorphic and depending on the morph can have this band shortened, discontinuous or even completely absent, for example in Manerebia ignilineata (Dognin), Manerebia apiculata (C. & R. Felder), and Manerebia trimaculata (Hewitson). It is therefore only of infrasubspecific value.

The following taxa were also transferred to *Manerebia* (Lamas and Viloria, 2004): *Manerebia franciscae* (Adams & Bernard), *Manerebia inderena* (Adams), *Manerebia lanassa* (C. & R. Felder), *Manerebia levana* (Godman), *Manerebia navarrae* (Adams & Bernard), *Manerebia quinterae* (Adams & Bernard), *Manerebia reducta* (F. M. Brown).

Further details on the current arrangement of subspecies and synonyms within *Manerebia* were published by Lamas and Viloria (2004) and Pyrcz *et al.* (2006). However the genus needs revisionary studies.

Manerebia leaena gonzalezi Pyrcz & Viloria, 2006 (Fig. 14, 38)

[Manerebia sp. nov. 1 Pyrcz & Viloria, MS]; Viloria 2000:267; 2001: fig. 1. [Lymanopoda leaena Hewitson, 1861:156, pl. 9, fig. 1]. Syntype: "Ecuador, Quito, BMNH [examined].

Penrosada leaena (Hewitson); Brown, 1944:256.

[Manerebia leaena n. ssp. 1105c Pyrcz & Viloria, MS]; Lamas & Viloria, 2004:215.

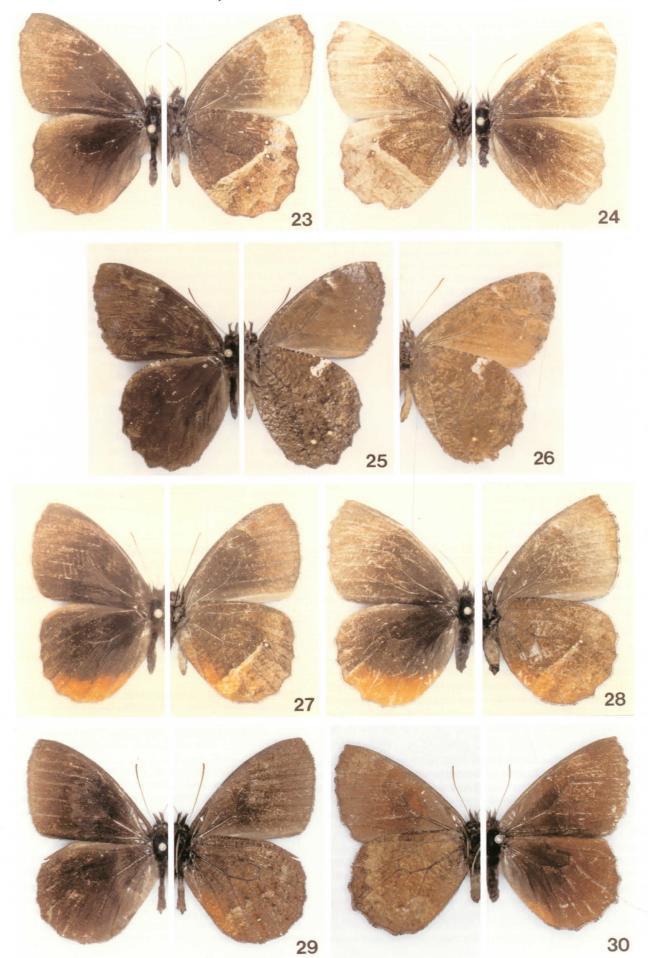
Manerebia leaena gonzalezi Pyrcz & Viloria, in Pyrcz et al., 2006:43, figs. 1E, 10C, 15.

Material examined.— Holotype male, selva nublada arriba de Betania, Venezuela, 2400-2480m, 24 Aug 1996, A. Viloria *leg*. [MALUZ].

Paratypes: COLOMBIA: 1 male, Herrán, Parque Nacional Natural El Tamá, Norte de Santander, 2500m, Dec 1993, J. F. Le Crom *leg*, [LC]. VENEZUELA: 1 male, via La Línea, 2300-2700m, 17 Apr 1996, T. Pyrcz *leg*. [TWP].

Remarks.- This species of *Manerebia* is known from a few individuals seen and collected in cloud forest at elevations between 2300 and 2700m. It flies high around bamboos (*Chusquea*) along with *Lymanopoda lebbaea moritzi*, **new subsp.**, *L. albocincta* and *Eretris porphyria recta*, **new subsp.** It is not as fast flying as most of the butterflies found with it, and infrequently descend within human reach. Despite its external appearence, which closely resembles *M. franciscae* from Mérida, and *M. inderena*, its genitalia, which are characterized by a long, arched uncus and a dentate distal half of the ampulla, indicate it is a subspecies of *L. leaena*.





Manerebia pervaga Pyrcz & Viloria, 2006 (Fig. 12, 36)

[Manerebia sp. nov. 2 Pyrcz & Viloria, MS]; Viloria, 2000:267; Viloria, 2001:

[Manerebia n. sp. 1121 Pyrcz & Viloria, MS]; Lamas & Viloria, 2004:216. Manerebia pervaga Pyrcz & Viloria, in Pyrcz et al., 2006:72, figs. 9E, F, 14H,

Material examined.- Holotype male: Parque Nacional El Tamá, Venezuela, 3100-3350m, 16/18 Feb 1992, A. Viloria & J. Camacho leg.

Paratypes: VENEZUELA: 1 male, same data [MALUZ]; 1 male, Páramo El Tamá, 2600m, 12 Feb 1983, M. Vivas leg. [MIZA]. COLOMBIA: 1 male, Páramo El Tamá vía Herrán, Norte de Santander, Dec 1993, J. F. Le Crom leg. [LC].

Remarks.- This is the third species flying in the paramo of El Tamá with a close relative in the southern Cordillera Oriental; in this particular this is P. levana (Godman). This butterfly seems to be seasonal, and has only been found flying during the dry season, in very sunny days, high up in the páramo grasslands.

Manerebia pluviosa Pyrcz & Viloria, 2006 (Fig. 13, 37)

[Manerebia sp. nov. 3 Pyrcz & Viloria, MS]; Viloria, 2000:267. [Manerebia n. sp. 1120 Pyrcz & Viloria, MS]; Lamas & Viloria, 2004:216. Manerebia pluviosa Pyrcz & Viloria in Pyrcz et al., 2006:44, figs. 2A, 10F,

Material examined.- Holotype male: entre Betania y La Banderola, Venezuela, 2810m, 23 Aug 1996, A. Viloria leg. [MALUZ].

Paratype (male): VENEZUELA: Fundo Piedra Blanca, San Vicente de

la Revancha, 9-12 Dec 1997, F. Rey leg. [TWP].

Remarks.- This seems to be a rare insect. It flies in the same altitudinal band as Pedaliodes reyi new sp., which has a similar yellow banded pattern. We have never seen it flying during the dry season.

Manerebia mycalesoides (C. & R. Felder, 1867) (Fig. 15-16, 44)

Pronophila mycalesoides C. & R. Felder, 1867:473. Euptychia lethe Butler, [1867]a:465. Pedaliodes mycalesoides (C. & R. Felder); Thieme, 1905:69. Euptychia mycalesoides (C. & R. Felder); Weymer, 1912:224. Posteuptychia mycalesoides Forster, 1964:137, fig. 171 (male genitalia). 'Penrosada' lethe (Butler); d'Abrera, 1988:824, fig. 'Penrosada' mycalesoides (C. & R. Felder); Viloria, 2000:267. Manerebia mycalesoides (C. & R. Felder); Lamas & Viloria, 2004:215; Pyrcz et al., 2006:36, figs. 8H, I, 14D, 20.

Material examined.- VENEZUELA: 1 male, Sta. Ana-San Vicente, ca. 1400m, 20 Sep 1997, A. Neild leg.; 1 female, Táchira, vía Chorro del Indio, Loma del Viento, ca. 1400m, 19 Sep 1997, A. Neild leg. [TWP]; 1 male, Venezuela, Dyson leg. [LECTOTYPE of Euptychia lethe Butler, herein designated], 1 male, same data [PARALECTOTYPE of E. lethe Butler, herein designated]. COLOMBIA: 1 male, Bogotá, Lindig leg., Ex Felder coll., Rothschild Bequest, Brit. Mus. 1939-1 [LECTOTYPE of Pronophila mycalesoides C. & R. Felder, herein designated] [BMNH].

Figs. 23-30. 23) Pedaliodes baccara allopatra Viloria & Pyrcz, n. ssp. (male Holotype). 24) Pedaliodes baccara allopatra Viloria & Pyrcz, n. ssp. (female Allotype). 25) Pedaliodes empusa medusa Pyrcz & Viloria, n. ssp. (male Holotype). 26) Pedaliodes empusa empusa (C. & R. Felder) (male: Bogotá, Muzo, Uricoechea, Felder Colln. Lectotype of Pronophila empusa C. & R. Felder, herein designated). 27) Pedaliodes plotina ruricola Pyrcz & Viloria, n. ssp. (male Holotype). 28) Pedaliodes plotina ruricola Pyrcz & Viloria, n. ssp. (female Allotype). 29) Pedaliodes praemontagna Viloria & Pyrcz, n. sp. (male Holotype). 30) Pedaliodes praemontagna Viloria & Pyrcz, n. sp. (female Allotype).

Remarks.- Euptychia lethe Butler [1867], described from an unspecified Venezuelan locality (we suspect the Cordillera de La Costa, where it was recently collected by the junior author) represents the taxon Pronophila mycalesoides (C. & R. Felder, 1867), which was described from Bogotá (Colombia). Both types were examined by us in the BMNH, and they evidently represent the same taxon. Lamas [1997] demonstrated that the publication of the Felders predates Butler's by at least five days, therefore the valid name for this taxon, according to the principle of priority of the ICZN (1999) is P. mycalesoides. Forster (1964) erected the monobasic genus Posteuptychia for this species on the strength of its peculiar male genitalic morphology, but failed to notice that this, along with the wing color pattern and venation, corresponds very well to the genus Manerebia Staudinger. Accordingly, the monobasic Posteuptychia has to be considered a junior synonym of Manerebia (see also Pyrcz et al., 2006). Manerebia lethe seems to be a rare, localized species, but it may be overlooked by collectors. It is found in the lower cloud forest on the foothills of the Tamá range, at 1000m. Nothing was known about the behavior or ecology of this species, until Andrew Neild (pers. comm.) observed, and collected it in the Loma del Viento, State of Táchira, in 1997, where it flies in a windswept open area, associated with bamboo. The female was feeding on white flowers about one meter above ground.

TAMANIA Pyrcz, 1995

Tamania Pyrcz, 1995, Type-species: Tamania jacquelinae Pyrcz, 1995, by original designation.

Tamania jacquelinae Pyrcz, 1995

[Manerebia cyclops Staudinger; d'Abrera, 1988:825, fig. (misidentification)]. Tamania jacquelinae Pyrcz, 1995:520. Tamania jacquelineae [sic] Pyrcz; Pyrcz, 1995:520-525, fig. 1-9.

Material examined. - VENEZUELA: 2 males, 1 female, Betania, 2500m, Aug 1987, T. Pyrcz leg. [Holotype male and Paratypes, MIZA]; 2 males, same data [Paratypes, TWP]; 12 males [1 in MUSM], 1 female [in MUSM], Potrero arriba de Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 10 males [1 wing preparation], same locality, 2400-2450m, 15 Aug 1996, A. Viloria, V. Carrizo & J. González leg.; 5 males, same locality, 2350m, 16 Aug 1996, A. Viloria & V. Carrizo leg.; 1 male, Betania - El Potrero, 2395m, 17 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 5 males, 3 females, Betania - El Potrero, 2400m, 24 Aug 1996, A. Viloria, V. Carrizo & L. E. González leg.; 1 male, Potrero vía al Paramito, 2460m, 27 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 1 male, Potrero arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo & J. & A. González leg. [MALUZ]. COLOMBIA: 1 male, 1 female, Colombia, Norte de Santander, Tamá range, 2300-2400m, Dec 1993, J. F Le Crom [Paratypes,

Remarks.- This genus and species is known exclusively from El Tamá range, but we do not know as yet whether it is really an endemic in the area, or a species occurring in local populations also elswhere in the Colombian Andes. Tamania jacquelinae has some affinities with the genera Idioneurula (see Pyrcz, 1995), and Manerebia. It should be considered as a relict species. It only occurs in association with grassland, flying close to the ground. In 1996 it was found to be common in the same spot where it was discovered nine years earlier. It appears to have very strict requirements as far as its habitat is concerned and its specific host plant is most probably a Cyperaceae abundant in the area. This would be extremely unusual for middle elevation Andean satyrines. One specimen was collected in El Reposo, at a similar elevation to Betania. A few specimens were collected in Herrán,

on the Colombian side of El Tamá. *Tamania jacquelinae* flies slowly and low above grass, and is therefore very easy to catch. The females are slightly smaller and lighter than the males.

Subtribe PRONOPHILINA Reuter, 1896

ALTOPEDALIODES Forster, 1964

Altopedaliodes Forster, 1964:148. Type-species: Pronophila tena Hewitson, 1869, by original designation.

Altopedaliodes tamaensis Viloria & Pyrcz, new sp. (Fig. 18, 39)

['Altopedaliodes' sp. nov. 1 Pyrcz & Viloria, MS]; Viloria, 2000:267. ['Altopedaliodes' n. sp. Pyrcz & Viloria, MS, no. 539]; Lamas et al., 2004:207.

Diagnosis. - This species is most similar in facies to A. nebris Thieme but on the hindwing underside it has no trace of white submarginal dots and the yellow markings are larger, diffused and extend along anal margin. Description.- MALE: Head: eyes hairy, dark reddish brown with black hairs; palpi twice as long as head, dark coffee brown with black and light brown hairs, sparse white scales; antennae reaching to 2/5 of costa, shaft and ventral surface of club orange-brown, club dorsally brown, gradually formed and subcylindrical. Wings: forewing (length: 23-24.5mm, mean: 24mm, n = 4) triangular, tornus slightly obtuse, apex subtruncate; hindwing suboval, external margin softly crenate; body coffee brown, ventrally lighter. Upperside unicolorous chocolate brown, white marginal scales scattered between veins. Forewing underside ground color paler than upperside, lighter towards apical region, and in anal and costal margins; apical region marbled with chestnut and ochraceous scales. Hindwing underside ground color chocolate brown, gradually lighter towards external third of wing, entirely dusted with chestnut scales; ochraceous yellow dusted on submarginal and marginal regions, and also forming a solid but irregular wedge, whose base covers anal angle to postdiscal region of anal margin, and running through postdiscal region to vein M3, where wedge apex is truncated; reddish chestnut dusted over basal half of wedge, and more heavily on postdiscal region, beside wedge; zig-zag submarginal line of chocolate brown; vestigial postdiscal yellow dot in cell Cu2-1A; marginal scales chocolate brown, except for the white ones scattered between veins. Genitalia: as illustrated (Fig. 39).

FEMALE: Unknown.

Material examined.— Holotype (male): Páramo del Tamá, Departamento Norte de Santander, Colombia, 16 Feb 1992, 3100-3200m, A. Viloria, J. Camacho & R. Calchi *leg*.

Paratypes: VENEZUELA: 1 male, Páramo del Tamá, Parque Nacional El Tamá, Estados Táchira-Apure, 16/18 Feb 1992, 3100-3350m, A. Viloria, J. Camacho & R. Calchi *leg.*; 2 males, Cerro La Banderola, Parque Nacional El Tamá, Estados Táchira-Apure, 20 Aug 1996, 3300m, A. Viloria *leg.* [MALUZ].

Etymology. – The name of this species derives from the name of the type

Remarks.— Closely related to its allopatric ally, *Altopedaliodes nebris* (Thieme), which occurs in Cundinamarca, Cordillera Oriental, Colombia. Both *A. tamaensis* and *A. nebris* fly in open páramo above the tree line. The similarity between *A. tamaensis* and another páramo denizen found in the southern part of the Cordillera Oriental, *A. cocytia* (C. & R. Felder), is only external. They have very different male genitalia configuration, especially the aedeagus, which is stylised and relatively long in *A. tamaensis*, but broad and short in *A. cocytia*.

CORADES Doubleday, [1849]

Corades Doubleday, [1849]:115. Type-species: Corades enyo Hewitson, [1849], by monotypy.

Corades enyo almo Thieme, 1907

Corades enyo Hewitson, [1849]:117 [male, B.M. Type No. Rh 4038, Caraccas [sic], Venezuela, Dyson; lectotype designated by Viloria and Camacho (1999: 176) (examined)].

Corades envo var. almo Thieme, 1907:222.

Material examined.— VENEZUELA: 2 males, Betania, 2200-2300m, 16 Apr 1996, T. Pyrcz *leg.*; 1 male, same data, 9 Aug 1987 [TWP]. Remarks.— *C. enyo* occurs at elevations around 1600-2200m. The subspecies *almo* Thieme was described from northern Andean specimens (Colombia and Ecuador), and southern (Peru). However, between these in southern Ecuador there are least two well differentiated unnamed subspecies of *C. enyo* (Pyrcz, in prep.). The individuals found in El Tamá are phenotypically very close to central Peruvian and Bolivian specimens but are larger.

Corades chelonis rubeta Thieme, 1907

Corades chelonis var. rubeta Thieme, 1907: 223.

Material examined.- VENEZUELA: 1 male, Este de Betania, 2520-2620m, 19 Feb 1992, A. Viloria, J. Camacho, R. Calchi leg. [MALUZ]. Remarks.- This species occurs in the Cordillera de Mérida, throughout Colombia, and in eastern and southwestern Ecuador and north-easternmost Peru. In southeast Ecuador it occurs sympatrically with the closely related C. peruviana Butler. Adams (1986) claims that Peruvian specimens of C. chelonis correspond to the nominate subspecies. This is not correct. The nominate subspecies occurs only in the Colombian Cordillera Oriental. C. chelonis rubeta is distributed in the Cordillera de Mérida and El Tamá. Generally, the forewing upperside orange patch in cell M3-Cu1 is rounded in subspecies rubeta, and oval in the nominate. In rubeta, the hindwing upperside is brick rufous, slightly darker than in the nominate subspecies. The latter is also slightly larger. Thieme (1907) also points out shorter "tails" in rubeta. C. chelonis is replaced in the Cordillera de Mérida at higher elevations by an endemic species C. pax Watkins, but in El Tamá it occurs up to the timber line.

Corades medeba columbina Staudinger, 1894

Corades medeba var. columbina Staudinger, 1894: 77.

Material examined.— VENEZUELA: 5 males, Betania-El Potrero, 2400-2600m, 28/29 May 1994, A. Viloria, J. Camacho, M. García leg.; 2 males, bosque arriba de Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo, D. González leg.; 1 male, same data, 2400-2450m, 15 Aug 1996, A. Viloria, V. Carrizo, J. González leg.; 1 male, same data, 2350m, 16 Aug 1996, A. Viloria, V. Carrizo leg.; 1 male, selva nublada arriba de Betania, 2400-2480m, 24 Aug 1996, A. Viloria, V. Carrizo, L. E. González leg. [MALUZ]; 6 males, Betania, 2200-2300m, 16 Apr 1996, T. Pyrcz leg.; 1 male, same data, 15 Apr 1996; 5 males, same data, 2700m, Aug 1987 [TWP].

Remarks.— This is a widespread species ranging from Venezuela (Cordillera de la Costa) to Bolivia. The differences in the color pattern between various populations of *C. medeba* consist basically in the gradual enlargement of orange markings on the hindwing underside from north to south. In the populations found in the Cordillera de Mérida and Colombia (including El Tamá), described as *columbina*, orange markings are shaped as small, rounded spots. Specimens from Ecuadorian populations show a faint orange streak, which connects the spots to the wing base. In south Peruvian and Bolivian specimens, corresponding to the nominate subspecies, the streak and the patch merge into one, wide elongated patch. *C. medeba* is the lower representative of the parapatric duo involving *C. cybele* Butler (Adams, 1986).

Corades pannonia ploas Thieme, 1907

Corades pannonia var. ploas Thieme, 1907:212.

Material examined.— VENEZUELA: 1 female, Betania-El Potrero, 2400-2600m, 28/29 May 1994, A. Viloria, J. Camacho, M. García [MALUZ].

Remarks.— The nominate subspecies of *C. pannonia* occurs in the Cordillera de la Costa (Venezuela). *C. pannonia ploas* was described from the Cordillera Oriental (Bogotá) and it also occurs in the Cordillera de Mérida, all three Colombian Cordilleras, and in west Ecuador. *C. pannonia condorita* Lamas is found in east Ecuador and north and central Peru, while *C. pannonia albomaculata* Staudinger flies in south Peru and Bolivia. *C. pannonia* flies at lower elevations than most *Corades*, but individuals have been observed exceptionally at much higher elevations (2900m) in the Cordillera de Mérida.

Corades dymantis Thieme, 1907, new stat.

Corades cistene var. dymantis Thieme, 1907:220. Lectotype, male, Colombia, Bogotá, Nolcken, [designated by L. D. Miller (unpublished), in ZMHU] [examined].

Material examined.— VENEZUELA: 1 male, San Vicente de la Revancha, 2400m, F. Rey leg. [FRC].

Remarks.- C. dymantis Thieme and C. cistene Hewitson are sympatric in southeast Ecuador (Pyrcz, unpublished). The two species are very similar in their patterns and differ basically in that in C. dymantis the hindwing upperside patches are orange, widely separated and triangular, while in C. cistene they are brick red and form a sinuate band. The valvae of the male genitalia of C. dymantis are much more slender than in C. cistene, particularly in the northern subspecies generosa Thieme. Contrary to the opinion of Adams and Bernard (1981), the population in the Cordillera de Mérida does not belong to species dymantis, and clearly deserves a separate specific status (Pyrcz, in prep.). The populations of C. dymantis found in Colombia also vary considerably between each other. At the present it is best to treat the El Tamá population as belonging to nominate dymantis, described apparently from the west slopes of the Cordillera Oriental in the area of Bogotá. C. dymantis flies in the uppermost cloud forests, usually at elevations around 3000m, but our only specimen was collected below its normal altitude range.

Corades cybele cybele Butler, 1866

Corades cybele Butler, 1866:40, pl. 3, fig. 2.

Material examined. – VENEZUELA: 1 male, Vía El Reposo, 2700m, F. Rey *leg*. [FRC].

Remarks.— This species occurs in all three main Colombian Cordilleras, eastern Ecuador, and Peru, in high elevation cloud forests, above the life zone of its relative *C. medeba*. It was found first by Krüger (1925), then by Adams and Bernard (1977) in the Sierra Nevada de Santa Marta but has not been collected so far in the Sierra de Perijá. In northern Peru flies the subspecies *C. cybele semiplena* Thieme. In Venezuela *C. cybele* is exclusively known in El Tamá.

Corades chirone Hewitson, 1863

Corades chirone Hewitson, 1863:71, pl. 36, fig. 3.

Material examined. – VENEZUELA: 1 male, via La Línea, 2700-3000m, 17 Apr 1996, T. Pyrcz *leg*. [TWP].

Remarks.—*C. chirone* occurs in Venezuela (El Tamá), throughout Colombia and Ecuador, and in northernmost Peru (Tabaconas). This species flies in the uppermost forest close to the timber line, generally in the same habitat as *C. dymantis*.

DAEDALMA Hewitson, 1858

Daedalma Hewitson, 1858:[85]. Type-species: Daedalma dinias Hewitson, 1858, by subsequent designation (Butler, 1867b:268).

Daedalma drusilla Hewitson, 1858

Daedalma drusilla Hewitson, 1858:[86], fig. 7.

Daedalma dora Staudinger, 1897:138, pl. 5, fig. 7. Synonymy established by Adams, 1986:253.

Material examined. – VENEZUELA: 1 male, via La Línea, 2700-3000m, 17 Apr 1996, F. Rey & T. Pyrcz *leg*. [TWP]; 1 female, Betania - via Páramo El Tamá, 2425m, 16/20 Mar 1983 [MIZA].

Remarks.- This is a species restricted to the Colombian Cordillera Oriental, associated with upper cloud forests. Adams (1986) suggested that *Daedalma drusilla* replaces *D. dinias* Hewitson at higher elevations in the Cordillera Oriental. However, the latter species has not been collected so far in El Tamá range.

ERETRIS Thieme, 1905

Eretris Thieme, 1905:131. Type-species: Pronophila decorata C. & R. Felder, 1867, by subsequent designation (Hemming, 1943: 24).

Eretris porhyria recta Pyrcz & Viloria, new subsp. (Fig. 4)

Pronophila porphyria C. & R. Felder, 1867: 470. 1 male syntype, Venezuela, in BMNH, [examined].

Eretris porphyria (C. & R. Felder); Thieme, 1905:132.

[Eretris porphyria subsp. nov. 1 Pyrcz & Viloria, MS]; Viloria, 2000:267.
[Eretris porphyria n. ssp. Pyrcz & Viloria, MS, no. 639f]; Lamas et al., 2004: 208.

Diagnosis.— Eretris porphyria recta differs from the nominate subspecies as follows: hindwing underside postmedian band straight instead of slightly incurved in Cu1-Cu2; anal suffusion dirty yellow, not rufous, extending along inner edge of postmedian band from tornus to costa; silver scaling on hindwing underside and forewing underside apex more extensive; hindwing underside postmedian band less pronounced distally in cells Cu1-C2 and Cu2-1A.

Description.- MALE (Fig. 4): Forewing length: 20-22mm, mean: 20.95mm, n = 38. Upperside of both wings dark brown, lustrous, submarginal area of forewing slightly lighter, a barely visible narrow, blackish submarginal line on fore and hindwing, a fine, orange marginal line on the hindwing from vein Cu1 to tornus. Forewing underside brown, slightly lighter than on the upperside, crossed by three blackish brown roughly parallel lines, median, postmedian and submarginal, the latter sinuate, plus a fine marginal orange line; the area between postmedian and submarginal lines lighter and suffused with steely scaling in the postdiscal area near costa. Hindwing underside dark brown in basal half, steely beyond, crossed by a blackish brown median line and a series of fine chestnut bands, postmedian, submarginal and marginal, postmedian band nearly straight except for a shallow notch on vein Cu1, submarginal and marginal bands parallel and slightly sinuate, postmedian band faintly edged basally with dirty yellow, spreading over anal area; a row of five small submarginal, black ocelli, circled with chestnut and pupilled with white.

FEMALE: Similar to male but color pattern lighter on both upper and underside. Forewing length: 21-22mm, mean: 21.25mm, n = 4.

Material examined.— Holotype (male): Tamá National Park, Venezuela, 2300m, 15 Apr 1996, T. Pyrcz & F. Rey *leg*, [MIZA]. Allotype (female): Betania - El Potrero, Venezuela, 2400-2600m, 28/29 May 1994, A. Viloria, J. Camacho & R. Calchi *leg*. [MALUZ]. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 1 male, Este de Betania, 2520-2620m, 16-19 Feb 1992, A. Viloria, J. Camacho & R. Calchi leg.; 1 male, same data, 2780-2810m, A. Viloria, J. Camacho & R. Calchi leg.; 1 male, 2620-2780m, 19 Feb 1992, A. Viloria, J. Camacho & R. Calchi leg.; 3 males, Betania - El Potrero, 2400-2600m, 28/29 May 1994, A. Viloria, J. Camacho & R. Calchi leg.; 1 male, La Línea, 3100m, 30 May/2 Jun 1994, A. Viloria, J. Camacho & M. García leg.; 3 males, bosque arriba de

Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 1 male, same data, 2350m, 16 Aug 1996, A. Viloria & V. Carrizo leg.; 1 female, entre Betania y La Banderola, 2400-2600m, 23 Aug 1996, A. Viloria, V. Carrizo & A. González leg.; 1 male, 1 female, entre Betania y La Cueva, 2750m, 23 Aug 1996, A. Viloria, V. Carrizo & A. González leg.; 2 females, selva arriba de Betania, 2400-2480m, 24 Aug 1996, A. Viloria, V. Carrizo & L. E. González leg.; 8 males, selva vía al Paramito, 2400-2460m, 27 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 1 male, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo & J. & A. González leg. [MALUZ]; 6 males, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo & J. & A. González leg. [MALUZ]; 6 males, selva arriba de Betania, 2400m, viii.1987, T. Pyrcz leg.; 4 males, via La Línea, 2300-2700m, 17 Apr 1996, T. Pyrcz & F. Rey leg.; 4 males, Betania, 2200-2300m, 15-16 Apr 1996, T. Pyrcz & F. Rey leg. [1 in AFN]; 2 males, San Vicente de la Revancha, 2300-2350m, 13-14 Apr 1996, T. Pyrcz & F. Rey leg. [TWP].

Etymology.— recta, straight in Latin, after the shape of the postmedian line of the hindwing underside, which is diagnostic for this subspecies. Remarks.- Subspecies based on wing pattern can be recognised in this and the next species, even though phenotypic differences are not as obvious as in some Lymanopoda or Pedaliodes. Nominate E. porphyria probably occurs in the Chama valley in the central Cordillera de Mérida. There are several geographical subspecies in the northern Andes, some of them undescribed, and a thorough revision of E. porphyria and E. apuleja will be the subject of a separate article (Pyrcz, in prep.). It is intended to clarify the zoogeography and systematics of the genus Eretris, which has been largely misunderstood by previous authors, mainly because of the lack of good series of specimens with reliable data.

Eretris apuleja remotissima Pyrcz & Viloria, new subsp. (Fig. 3)

Pronophila apuleja C. & R. Felder, 1867:471. 1 male syntype, Colombia ("Venezuela"), in BMNH, [examined].

Eretris apuleja (C. & R. Felder); Thieme, 1905:132.

Eretris ochrea var. bogotana Krüger, 1924:25. Lectotype male, Colombia, Chipaque, [designated by Pyrcz, 1999a:233], in MIZPAN, [examined]. Synonymy established by Adams, 1986:257.

[Eretris apuleja subsp. nov. Pyrcz & Viloria, MS]; Viloria, 2000:267. [Eretris apuleja n. ssp. Pyrcz & Viloria, MS, no. 629d]; Lamas et al., 2004: 208.

Diagnosis.— E. apuleja remotissima differs from the nominate subspecies in lacking the wide upperside orange suffusion and ocelli of the anal region. It has instead a chestnut mark in the anal angle. The rest of the upperside is dark coffee brown. The underside closely resembles subspecies E. apuleja altamira Adams & Bernard, but the ground color is darker; the forewing postbasal and postdiscal dark brown lines are markedly wavy, the hindwing more contrasted in color; orange-chestnut exists on the distal half of the wing; and postdiscal yellow suffusion appears only in the center of cells M2-M3, M3-Cu1, and Cu1-Cu2.

Description.- MALE (Fig. 3): Forewing length: 22-22.5mm, mean: 22.25mm, n = 3. Upperside of both wings chocolate brown, slightly lighter in submarginal area of forewing, a barely noticeable, fine marginal orange line on both wings and a small orange suffusion on tornus. Forewing underside brown, lighter than upperside, crossed by 2 dark brown roughly parallel lines, median and postmedian, the latter wavy, and two orange lines, submarginal and marginal, slightly wavy and parallel. Hindwing underside brown in basal half, suffused with light orange beyond, crossed by a series of roughly parallel bands: median, dark brown and distally edged with orange, postmedian, submarginal and marginal orange, roughly parallel, except that postmedian and submarginal converge at tornus, the area basal to submarginal band from apex to vein Cul suffused with magenta; a row of 5-6, tiny black ocelli, in cells M1-M2 to Cu2-1A, surrounded with cinnamon brown, and finely circled with dark coffee brown, all pupilled with white (the largest ca. 0.8 mm diameter). FEMALE: Unknown.

Material examined.— Holotype (male): entre Betania y La Cueva, Venezuela, 2900-3100m, 26 Aug 1996, A. Viloria, V. Carrizo & A. González *leg*. [MALUZ]. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 1 male, same data as holotype [MALUZ]. COLOMBIA: 1 male, Herrán, Parque Nacional Natural El Tamá, Dec

1993, J. F. Le Crom leg. [LC].

Etymology.- remotissima - the most remote, stressing the difficulty to obtain the few individuals known, which were flying high above tall bamboos in the uppermost forest.

Remarks.- E. apuleja is found at higher elevations than E. porphyria. It can be readily distinguished from the latter species by a russet orange suffusion on the anal half of the hindwing underside. The two species share similar flight patterns and habits. A syntype of E. apuleja apuleja (C. & R. Felder) in the BMNH (London) is labelled "Venezuela". Adams and Bernard (1981) correctly considered this as an error. The nominate subspecies occurs in the area of Bogotá, on the east slopes of the Cordillera Oriental. The population occurring in the El Tamá range belongs in a separate subspecies, as diagnosed above.

Eretris encycla (C. & R. Felder, 1867)

Pronophila encycla C. & R. Felder, 1867:472. Eretris encycla (C. & R. Felder); Thieme, 1905:133.

Material examined.— VENEZUELA: 1 male, "Venezuela", Moritz leg., Felder coll., Rothschild Bequest, Brit. Mus. 1939-1 (LECTOTYPE of Pronophila encycla C. & R. Felder, herein designated [BMNH, examined]); 1 male, same data (PARALECTOTYPE of P. encycla C. & R. Felder, herein designated [BMNH, examined]); 1 male, vía Bramón a Delicias, Mata Mula, 1850-2020m, 18 Sep 1997, A. Neild leg. [AFN]; 2 males, selva arriba de Betania, 2400-2460m, A. Viloria, V. Carrizo, A. & J. González [MALUZ].

Remarks.- E. encycla is larger and darker than two other species of Eretris reported from El Tamá. All its underside ocelli are well developed. E. encycla and E. calisto (C. & R. Felder) are possibly conspecific. Typical E. encycla occurs in the Cordillera de la Costa but the individuals found in the Cordillera de Mérida and El Tamá are almost indistinguishable from the specimens found in the type locality, except that the Andean ones are slightly larger.

JUNEA Hemming, 1964

Junea Hemming, 1964:137 (Replacement name for Polymastus Thieme, 1907 nec Claparède, 1864). Type-species: Daedalma doraete Hewitson, 1858.

Junea dorinda dorinda (C. & R. Felder, 1862)

Daedalma dorinda C. & R. Felder, 1862:427.

Daedalma emilia Butler, 1866:40, pl. 3, fig. 3. Synonymy established by Adams, 1986:260.

Polymastus dorinda (C. & R. Felder); Thieme, 1907:143. Junea dorinda (C. & R. Felder); Hemming, 1964:137.

Material examined. – VENEZUELA: 1 female, San Vicente de La Revancha, Fundo Piedra Blanca, 2350m, 26 Mar 1996, F. Rey *leg.* [AFN]; 1 male, Betania, 22 Mar 1983, 2000m, C. Vivas *leg.*; 1 male, vía La Línea, same data [MIZA].

Remarks.- This species ranges from Bolivia (subspecies whitleyi Druce) to Venezuela (exclusively in El Tamá). According to Fassl (1918) *J. dorinda* flies up to 3350m, an altitude possibly corresponding to the upper forest level. It is extremely rare in the northern Andes but in Peru, the senior author often observed hill topping males fighting for perching sites. *J. dorinda* is readily attracted to dung placed on the ground.

LASIOPHILA C. & R. Felder, 1859

Lasiophila C. & R. Felder, 1859:325. Type-species: Lasiophila cirta C. & R. Felder, 1859, by subsequent designation (Scudder, 1875:202).

Lasiophila circe arithmetica Viloria & Pyrcz, new subsp. (Fig. 19)

Lasiophila circe C. & R. Felder, 1859:326. 1 male syntype, no locality, in BMNH, [examined].

Pronophila praeneste Hewiston, 1859: pl. 2, fig. 8. Lectotype male, Colombia, New Granada, in BMNH, designated by Adams & Bernard, 1981:370, [examined].

[Lasiophila circe subsp. nov. Pyrcz & Viloria, MS]; Viloria, 2000:267. [Lasiophila circe n. ssp. Pyrcz & Viloria, MS, no. 663d]; Lamas et al., 2004:

Diagnosis.- Lasiophila circe arithmetica differs from other Colombian subspecies of L. circe in having larger forewing submarginal orange patches, and that Cu1-Cu2 is basally not restricted with black and thus is connected to the brick red median area. The pattern of the upperside of arithmetica resembles the Ecuadorian taxa, L. circe zarathustra Thieme and L. palades persepolis (Hewitson), but in zarathustra the upperside submarginal patches are of the same color as the median area, whilst in persepolis they are orange as in arithmetica but separated from median area by a wide black band.

Description.- MALE (Fig. 19): Wings: forewing length: 32-35mm, mean: 33.5mm, n = 2. Forewing upperside ground color brownish orange. Dark brown to black along marginal and submarginal areas, except for anterior half of marginal zone, which is reddish chestnut; postdiscal area lighter orange with black entering through costal and anal margins, also continuously running along all veins and forming a quadrangular spot in distal portion of cell M2-M3; two narrow, black bands flanking proximal part of cell M3-Cu1, running continuously until covering distal extremity of discal cell; triangular black spot in middle of cell Cu1-Cu2; cell Cu2-1A entirely free of black; longitudinal irregular band crossing cell Cu2-A1, and surrounding neighbouring orange portion. Hindwing upperside similar color as in nominate subspecies, but background tends to be orange in postdiscal area. Black postdiscal spots more discrete in general, that in cell M1-M2 smaller and more rounded; rest of pattern somewhat variable as in nominate L. circe. Forewing underside ground color chestnut brown, darker where visible in anterior portion of discal area, chocolate brown in posterior portion of submarginal-marginal area; apical region as in nominate L. circe but more densely dusted with white scales; continuous ochraceous yellow patch along cell M2-M3, from near extremity of discal cell towards submarginal area, running basally, in part, towards costal margin, and distally through submarginal area of cells M3-Cu1 and Cu1-Cu2; ochraceous yellow dusted in marginal area of cells M3-Cu1 and Cu1-Cu2, also forming a solid long spot in discal, postdiscal and submarginal areas of cell Cu2-1A, slightly constricted in discal area; rounded ochraceous spot in cell Cu2-A1, close to tornus. Hindwing underside similar to nominate $L.\ circe$, but more contrasted by occurrence of general dusting of light pink throughout lighter background. Yellowish submarginal dots variable in size.

FEMALE: Unknown.

Material examined.- Holotype (male): Betania-La Línea, Venezuela, 2850m, 28/29 May 1994, A. Viloria, J. Camacho & M. García leg. [MALUZ]. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 2 males, same data [MALUZ]; 1 male, Betania, via Páramo El Tamá, 2875m, 19 Mar 1983 (FWL not measured) [MIZA]; 1 male, via La Línea, 2700-3000m, 17 Apr 1996, F. Rey & T. Pyrcz leg. [TWP].

Etymology - arithmetica, a reference in Latin to the arithmetic addition of a new subspecies to the Lasiophila circe-complex.

Remarks.- L. circe arithmetica belongs in a large group, possibly monophyletic, of allopatric species and subspecies. Its immediate allopatric substitute in the central and southern Cordillera Oriental is L. circe circe C. & R. Felder. However, the color pattern of L. circe arithmetica is much more reminiscent of L. circe zarathustra Thieme, found in central Ecuador.

Lasiophila zapatoza elusiva Pyrcz & Viloria, new subsp.

Pronophila zapatoza Westwood, 1851:358. 2 male syntypes, Venezuela, Coast Range and "Bolivia", former in BMNH, [examined].

[Lasiophila zapatoza subsp. nov. Pyrcz & Viloria, MS]; Viloria, 2000:267. [Lasiophila zapatosa n. ssp. Pyrcz & Viloria, MS, no. 674f]; Lamas et al., 2004:209.

Diagnosis.- The upperside pattern of L. zapatoza elusiva differs from

subspecies L. zapatoza meridae in a slightly less reddish tone, black color on distal third of forewing slightly more spread basally, subapical and submarginal triangular patch enclosed in cell Cu1-Cu2, the latter more reduced and without orange sheen as compared to L. zapotoza meridae. Description.- MALE (Fig. 20): Forewing length: 29-32mm, mean: 30mm, n = 4. Upperside of forewing reddish in basal two thirds, submarginal and marginal area black, the border between two areas diffused, four orange subapical to submarginal patches, that in M1-M2 largest of all, elongated with a diffused outer margin, that in M2-M3 roughly square, that in Cu1-Cu2 oval and that in Cu2-1A the smallest of all, rounded, forewing fringes white in each cell. Hindwing underside reddish except for a black marginal area, 2-3mm wide, and a series of 5 roughly rounded and of same size black postmedian patches from costa to cell Cu1-Cu2, that in Cu2-1A as a minute spot, separated from black marginal area, except for that in M1-M2 which is connected to it by black venous stripes, fringes white in each cell. Forewing underside pattern reflected from the upperside but generally lighter, basal 2/3 reddish orange, marginal area paler, apex suffused with white scales. Hindwing underside reddish overcast with white scales, denser in median area, a brown median band extending from costa to discal cell, a sereis of faint postmedian brown spots, submarginal line edged basally with white from vein M3 to tornus. FEMALE. Unknown.

Material examined.- Holotype (male), Betania - El Potrero, Venezuela, 2400-2600m, 28/29 May 1994, A. Viloria, J. Camacho, M. García [MALUZ]. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 1 male, Betania, 2500m, May 1987, T. Pyrcz leg.; 1 male, same locality and collector, 2200-2300m, 15 Apr 1996; 1 male, same locality and collector, 2300-2700m, 17 Apr 1996 [TWP]. Etymology -- elusiva - a latinized name meaning elusive, something that

is difficult to obtain and tends to escape.

Remarks.- Individuals of the population discovered in El Tamá are slightly but consistently different from those of L. zapatoza meridae Adams & Bernard. However, for zoogeographical reasons we do not assign it to the latter subspecies. L. zapatoza meridae flies exclusively in the upper Chama valley, in the central Cordillera de Mérida, whereas on the outer, eastern and southern slopes it is replaced by unnamed populations related to the nominate L. zapatoza from the Cordillera de La Costa. Therefore, similar phenotypes of the Mérida and El Tamá populations can be regarded in terms of independent evolution of a similar color pattern, whereas their ranges suggest that phyletically they are definitely closer to neighbouring populations than to each other.

LYMANOPODA Westwood, [1851]

Lymanopoda Westwood, [1851]: pl. 67, fig. 6-7. Type-species: Lymanopoda samius Westwood, [1851], by monotypy.

Sarromia Westwood [1851]: pl. 67, fig. 5. Type-species: Sarromia obsoleta Westwood, [1851]. Synonymy established by Weymer, 1912.

Lymanopoda samius lineana Pyrcz & Viloria, new subsp. (Fig. 9-10, 45)

Lymanopoda samius Westwood, [1851]:402, pl. 67, fig. 6. 1 male syntype, Colombia, Bogotá, in BMNH, [examined].

[Lymanopoda caeruleata Godman & Salvin; Manara, 1998:103, 108, fig. 184 (misidentification)].

[Lymanopoda samius subsp. nov. Pyrcz & Viloria, MS]; Viloria, 2000:267. [Lymanopoda samius n. ssp. Pyrcz & Viloria, MS, no. 718b]; Lamas et al., 2004:210.

Diagnosis.- Differs from nominate subspecies in having a smaller subapical blue patch on forewing upperside, restricted to two cells; ground color darker blue, as compared to sky blue in the nominate L. samius Westwood

Description.- MALE (Fig. 9): Forewing length: 21.5-23mm, mean: 22mm, n = 6. Upperside basal two thirds dark sky blue, outer one third black, except for a postdiscal blue patch extending over 3 cells and a small isolated submarginal patch in Cu1-Cu2, 3 white subapical dots in R5-M1, M1-M2 and M2-M3 and 2 postmedian, displaced basally in relation to the remainder in M3-Cu1 and Cu1-Cu2. Hindwing upperside basal 3/4 dark sky blue, marginal area black, forming an intrusion in cell

M2-M3, 2-3 submarginal black dots in cells M3-Cu1, Cu1-Cu2 and Cu2-1A. Forewing undeside dirty yellow, slightly darker along costa and outer margin, three white subapical spots reflected from the upperside, 3 black ocelli, pupilled with white in cells M3-Cu1, Cu1-Cu2 and Cu2-1A, the latter on the tornus displaced distally in relation to remain-ing two. Hindwing underside uniform yellow with a grey overcast, with only a faint darker band extending from base of cell Cu1-Cu2 to outer margin, and a row of faint, in some individuals indistinct, submarginal black dots. Genitalia: Fig. 45.

FEMALE (Fig. 10): Forewing length: 22.5-24mm, mean 23mm, n = 2. Similar to male, but lighter in color; wings more rounded.

Etymology.— lineana derives from La Línea, or "the border-line", the name of the house of the family González in the Río Oirá, a remote locality in the páramo, just on the Colombia-Venezuela boundary.

Material examined.— Holotype (male): Páramo El Tamá, 3100-3350m, Venezuela, 16/18 Feb 1992, A. Viloria, J. Camacho & R. Calchi *leg*. [MALUZ]. Allotype (female): same data [MALUZ]. Holotype deposited in MALUZ].

Paratypes: VENEZUELA: 1 male, Cerro La Banderola, 3300m, 20 Aug 1996, A. Viloria *leg*. [MALUZ]. VENEZUELA: 4 males, 1 female, Páramo El Tamá, 3100-3300m, 17 Apr 1996, T. Pyrcz & F. Rey *leg*. [TWP]; 1 male, same data [FR].

Remarks.- It is impossible to confuse the light blue Lymanopoda samius with any other species, at least not in El Tamá and the rest of the Cordillera Oriental. L. hazelana Brown from Ecuador, which differs only by wider marginal black markings and different placement of the hindwing underside submarginal black dots, has a very distinct male genitalia, and belongs in another section of the genus (see Brown, 1943). In most of the Cordillera Oriental, L. samius flies in the upper cloud forest. However, in El Tamá it occurs exclusively in the open páramo not far away from the upper forest limit, from 3100m to at least 3300m.

Lymanopoda lebbaea moritzi Pyrcz & Viloria, new subsp. (Fig. 11)

Lymanopoda lebbaea C. & R. Felder, 1867:473. 1 male syntype, Colombia, Bogotá, in BMNH, [examined].

[Lymanopoda lebbaea subsp. nov. Pyrcz & Viloria, MS]; Viloria, 2000:267. [Lymanopoda lebbaea n. ssp. Pyrcz & Viloria, MS, no. 703d]; Lamas et al., 2004:210

Diagnosis.- The new subspecies differs from the nominate subspecies (from the region of Bogotá) in several ways. Forewing nearly perfectly triangular, with straight outer edge; slightly outcurved in nominate L. lebbaea C. & R. Felder; upperside ground color slightly darker, dark brown; ground color of hindwing underside also darker, chestnut, instead of light beige; on forewing underside, rufous suffusion restricted to basal area, whereas in nominate subspecies it extends to submarginal ocelli; black area surrounding ocelli in Cu1 and Cu2 smaller than in nominate. Description.- MALE (Fig. 11): Forewing length: 17-19mm, mean: 18mm, n = 5. Upperside chocolate brown, base of forewing lustrous and slightly lighter. Forewing underside dull brown, basal 1/3 suffused with brick red, apex chestnut, 3 subapical white dots and 2 submarginal ocelli in M3-Cu1 and Cu1-Cu2, as compared to the dots, larger, surrounded with black and displaced basally. Hindwing underside ground color ochreous; three chestnut bands, median from mid-costa to root of vein M2 and across discal cell to root of vein Cu2, postmedian from mid vein M2 to mid anal margin and submarginal from apex to vein M2 faint and parallel to outer margin, from M2 to Cu1 better marked and displaced basally from outer margin, then again from Cu1 to tornus closer to outer margin; white patch occupying whole discal cell distally from median chestnut band and a series of postmedian white patches in cells M2-M3, M3-Cu1 and Cu1-Cu2 between postmedian and submarginal chestnut bands; a series of white dots faintly edged distally with black, one submarginal in cell M1-M2, 2 postmedian in M2-M3 and M3-Cu1 and 3 submarginal in Cu1-Cu2 and a double dot in Cu2-1A.

FEMALE: Forewing length: 17-18mm, mean: 17.5mm, n=3. Female lighter in color, pale brown on forewing upperside with black ocelli pupilled with white in Cu1; rufous brown on hindwing with row of postmedian black dots; light brown on forewing underside with strong rufous suffusion basally from ocelli in Cu1 and Cu2; light beige, with

faint darker markings on hindwing.

Material examined.— Holotype (male): bosque arriba de Betania, Venezuela, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo, D. González *leg.* [MALUZ]. Allotype (female): Betania, via La Línea, 2300-2700m, 16 Apr 1996, T. Pyrcz & F. Rey *leg.* [TWP]. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 1 male, Este de Betania, 2400-2520m, 19 Feb 1992, A. Viloria, J. Camacho, R. Calchi *leg.*; 1 female, same data, 2620-2780m; 2 males, Betania-El Potrero, 2400-2600m, 28/29 May 1994, A. Viloria, J. Camacho, M. García *leg.*; 1 male, Betania, Potrero, 2395m, 17 Aug 1996, A. Viloria, V. Carrizo, D. González *leg.*; 2 males, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo, A. González *leg.* [MALUZ]; 3 males, 1 female, same data as allotype; 2 males, same data, 15 Apr 1996; 1 female, same data, 17 Apr 1996 [TWP]. Etymology.— This subspecies is dedicated to the German naturalist Karl Moritz, an early butterfly collector in Venezuela (Röhl, 1948; Viloria *et al.* 2001).

Remarks.- This species is restricted to the eastern slopes of the Colombian Cordillera Oriental (typical *L. lebbaea lebbaea*). On its western slopes, in the Cordillera Central, and along the eastern slopes of the Andes in Ecuador (south to Sierra Huacamayos) it is replaced by a close allopatric ally *L. labda* Hewitson. In El Tamá *L. lebbaea moritzi* occurs to around 2800m.

Lymanopoda ionius Westwood, [1851]

Lymanopoda ionius Westwood, [1851]:402, pl. 67, fig. 7.

Material examined.— COLOMBIA: 1 male, Herrán, Parque Nacional Natural El Tamá, Norte de Santander, 2800m, xii.1993, J. F. Le Crom *leg.* [LC]. Remarks.— This species replaces *L. lebbaea* at higher elevations on the eastern slopes of the Cordillera Oriental. Its underside pattern is variable. There are yellow and brown forms. The unique specimen collected in El Tamá does not allow us to evaluate its subspecific status.

Lymanopoda obsoleta (Westwood, [1851])

Sarromia obsoleta Westwood [May 1851]: pl. 67, fig. 5.

Lymanopoda obsoleta (Westwood); Westwood [July 1851]:402.

Lymanopoda larunda Hopffer, 1874:361. Synonymy established by Weymer, 1912:248.

Material examined.— VENEZUELA: 3 males, 1 female, bosque arriba de Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo, D. González leg.; 5 males, 1 female, same data, 2350m, 16 Aug 1996, A. Viloria, V. Carrizo leg.; 3 males, same data, 2400-2480m, 24 Aug 1996, A. Viloria, V. Carrizo, L. E. González leg.; 1 male, selva vía al paramito, 2400-2460m, 27 Aug 1996, A. Viloria, V. Carrizo, D. González leg.; 2 males, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo, J. & A. González [MALUZ]; 6 males, Betania, 2200-2300m, 15/16 Apr 1996, T. Pyrcz leg.; 3 males, Betania, Aug 1987, T. Pyrcz leg. [TWP].

Remarks.— Of all *Lymanopoda*, this is the species with the widest distribution. It occurs in the Venezuelan Cordillera de la Costa, Sierra de Perijá, and Cordillera de Mérida, and throughout the Andes south to Bolivia. *L. obsoleta* has a very wide altitudinal range, from near the upper cloud forest limit, at 3000m down to 1700m. In El Tamá it is replaced at higher elevations by the closely related *Lymanopoda lecromi* Pyrcz & Viloria, **new sp.**

Lymanopoda lecromi Pyrcz & Viloria, new sp. (Fig. 7-8, 35)

[Lymanopoda sp. nov. 1 Pyrcz & Viloria, MS]; Viloria, 2000:267. [Lymanopoda dietzi n. ssp. Pyrcz & Viloria, MS, no. 689b]; Lamas et al., 2004:209.

Diagnosis.— This species closely resembles *L. obsoleta*, from which it differs by the light golden greenish sheen on the basal 1/3 of both wings, the more intense ground color of the hindwing underside with an

ochraceous shade, absent in *L. obsoleta*, and the larger size of the forewing underside black ocelli in cells M3-Cu1 and Cu1-Cu2.

Description.- MALE (Fig. 7): Forewing length: 20.5-24mm, mean: 23mm, n = 15. Head: eyes hairy, totally brown. Palpi three times as long as head, dorsally dark brown, ventrally white with light brown and black hairs. Antennae reaching to 2/5 of costa, entirely dark-orange brown, except for external tip of club, which is orange, dorsally with white scales over distal extremity of each segment; club broad and flat, 4x as wide as shaft, more or less blunt, comprising 12-13 segments. Wings: forewing triangular, tornus relatively obtuse, outer margin slightly excavated near apex. Hindwing sub-rhomboidal, with external angle formed by extension of vein M3. Body dorsally dark brown, very hairy, with shiny reddish hairs on thorax; ventrally reddish and hairy in thorax, light brown in abdomen; legs covered with white scales, but also with light brown hairs. Upperside ground color brown, with greenish sheen on first 1/3 of both wings; basal half of forewing costal margin chestnut; vestigial subapical white dot on forewing; basal 1/3 and anal region of hindwing hairy. Forewing underside ground color brown; darker chocolate brown in anterior half of postdiscal area and posterior half of submarginal-marginal areas; apical region chestnut; subapical region finely dusted with white and yellow scales; 2 submarginal white dots in cells M2-M3 and M3-Cu1; 2 postdiscal brown ocelli, pupilled with white, in middle of cells Cu1-Cu2 and Cu2-1A, respectively. Hindwing underside ground color ochraceous brown; dark chestnut on basal 1/3 of wing, except for anal margin, and also in narrow and diffuse postdiscal band; white and light pink scales finely dusted over distal 2/3 of wing, but more towards apical angle; postdiscal series of 6 fine white dots in cells M2-M3 to Cu2-A1 (two in the latter), respectively, 2nd and 3rd closer to distal extremity of discal cell. Genitalia: as illustrated (Fig. 35).

FEMALE (Fig. 8): Forewing length: mean: 23-26.5mm, 24mm, n = 5. Differs from male in having more apiculate forewing, with very convex external margin, and remarkable excavation near apex. Hindwing external margin excavated between apex and angle in vein M3. Body less hairy and paler. Upperside ground color paler; forewing bearing one subapical translucent window (ca. 1.2 mm diameter) in cell M2-M3; postdiscal series of 3 tiny white dots in cells M3-Cu1 and Cu2-1A, respectively, that in Cu1-Cu2 closer to discal area. Forewing underside ground color pale light brown; basal half of wing reddish chestnut; suffusion of dark chocolate brown towards postdiscal area; 2 postdiscal dark coffee brown ocelli, which are pupilled with white in cells Cu1-Cu2 and Cu2-1A respectively; similar one, but smaller, in Cu2-A1 near tornus. Hindwing underside basically showing same pattern as in males, but basal and postdiscal area pale brown, the rest light pinky brown, dusted with pale brown; pair of white dots prevails near anal angle in cell Cu2-A1; postdiscal series of vestigial white dots in cells Cu1-Cu2 and Cu2-1A, respectively, finely circled with dark brown.

Material examined.— Holotype (male): Este de Betania, Venezuela, 2750-2810m, 16/19 Feb 1992, A. Viloria, J. Camacho & R. Calchi *leg*. [MALUZ]. Allotype (female): same data, 2520-2620m, 19 Feb 1992. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 1 male same data as holotype; 2 males, same data as allotype; 3 males, via La Línea, 2600-2900m, 30 May 1994, A. Viloria, J. Camacho & M. García leg.; 1 male, same data, except for 2400-2600m, 28/29 May 1994; 1 male, Cerro La Banderola, 3000-3200m, 20 Aug 1996, A. Viloria leg. [MALUZ]; 5 males, 1 female, Betania, 2200-2300m, 15/16 Apr 1996, T. Pyrcz & F. Rey leg.; 3 females, via La Línea, 2300-2700m, 17 Apr 1996, T. Pyrcz & F. Rey leg. [TWP] and [LC, 1 male].

Etymology.— This species is dedicated to Jean François Le Crom, a French lepidopterist who lives in Bogotá. He significantly contributed in the preparation of this paper and has always been very helpful in the course of our research on the subtribe Pronophilina.

Remarks.— L. lecromi belongs in a group of closely related species, represented in the Cordillera de Mérida by four allopatric species, L. dietzi Adams & Bernard, and three undescribed ones. Lymanopoda lecromi most closely resembles a new species found in the uppermost forest of the opposite side of the San Cristóbal valley, in El Batallón mountain range. Its southern replacement is L. altis Weymer, quite dissimilar in facies but sharing with L. lecromi and L. dietzi the same characters of male genitalia structure. They are also related to L. maletera Adams & Bernard from the Sierra de Perijá.

Lymanopoda albocincta albocincta Hewitson, 1861

Lymanopoda albocincta Hewitson, 1861:157, pl. 9, fig. 5.
Lymanopoda issacha Butler, 1870:26. Synonymy established by Adams & Bernard, 1979:107.

Material examined.— VENEZUELA: 1 female, San Vicente de La Revancha, Fundo Piedra Blanca, 2350m, 26 Mar 1996, F. Rey leg.; 1 male, vía Bramón a Delicias, Mata Mula, 1850-2020m, 18 Sep 1997, A. Neild leg. [AFN]; 1 male, 1 female, Betania-El Potrero, 2400-2600m, 28/29 May 1994, A. Viloria, J. Camacho, M. García leg.; 1 male, bosque arriba de Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo, D. González leg.; 2 males, same data, 2400-2450m, 15 Aug 1996, A. Viloria, V. Carrizo, J. González leg.; 2 males, same data, 2350m, 16 Aug 1996, A. Viloria, V. Carrizo leg.; 3 males, same data, 2400-2480m, 24 Aug 1996, A. Viloria, V. Carrizo, L. E. González leg.; 2 males, selva vía al paramito, 2400-2460m, 27 Aug 1996, A. Viloria, V. Carrizo, D. González leg. [MALUZ]; 22 males, Betania, 2200-2300m, 15-16 Apr 1996, T. Pyrcz & F. Rey leg.; 1 male, Betania, Aug 1987, T. Pyrcz leg. [TWP].

Remarks.— It is one of the most widely distributed species of *Lymanopoda*, known between the Venezuelan Cordillera de la Costa and central Peru. In the El Tamá range it is found down to 1900m.

MYGONA Thieme, 1907

Mygona Thieme, 1907:162. Type-species: Pronophila prochyta Hewitson, 1862, by original designation.

Mygona irmina (Doubleday, [1849])

Pronophila irmina Doubleday, [1849]: pl. 60, fig. 2. Oxeoschistus irmina (Doubleday); Butler, 1867b:268. Mygona irmina (Doubleday); Thieme, 1907:167.

Material examined.— VENEZUELA: 2 males, bosque arriba de Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo, D. González leg.; 1 male, same data, 2400-2480m, 24 Aug 1996, A. Viloria, V. Carrizo, L. E. González leg.; 1 male, same data, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo, J. & A. González [MALUZ]; 3 males, 1 female, Betania, 2200-2300m, 16 Apr 1996, T. Pyrcz leg.; 1 male, Vía Delicias, 1800m, Jun 1982, F. Rey leg. [TWP].

Remarks. – *Mygona irmina* occurs in the Cordillera de la Costa in Venezuela, the Sierra de Perijá, the three Colombian Cordilleras, and northeast Ecuador.

OXEOSCHISTUS Butler, 1867b

Oxeoschistus Butler, 1867b:268. Type-species: Pronophila puerta Westwood, 1851, by original designation.

Oxeoschistus puerta magnus Pyrcz & Viloria, new subsp. (Fig. 2)

Pronophila puerta Westwood, 1851:358; male syntype?, "Colombia", in BMNH, [examined].

[Oxeoschistus simplex subsp. nov Pyrcz & Viloria, MS (misidentification)]; Viloria, 2000:267.

[Oxeoschistus puerta n. ssp. Pyrcz & Viloria, MS, no. 756i]; Lamas et al., 2004:211.

Diagnosis.— Differs from the nominate subspecies, and from *O. puerta fuscus* R. Krüger, by its considerably larger size; forewing length: 33-36 mm, mean: 35mm, n = 8 (*O. puerta simplex* Butler, forewing length mean: 31mm). Upperside postmedian-submarginal bands lighter, light yellow orange, as compared to dull orange in nominate and fuscous in *fuscus*, and only slightly narrowed in subapical area, in this respect resembling *O. puerta isolda* Thieme. Submarginal dark brown rounded spots bigger.

Description.—MALE (Fig. 2): Upperside basal two thirds of both fore and hindwing dark brown, a wide light orange postmedian to submarginal band on both wings, slightly widening towards hindwing tornus, enclosing

a row of dark brown oval patches, one in each cell, of approximately same size except for tiny patches in cell M2-M3 of forewing and a double spot in cell Cu2-1A of hindwing, marginal area dull brown from apex to tornus on forewing and from apex to cell M3-Cu1 on hindwing. Forewing underside pattern reflected from the upperside with some variation, lighter, orange band fades in the subapical area, discal cell and apex dusted with brick red and marked with two whitish subapical streaks, ocelli in cells M1-M2 and M2-M3 white pupilled. Hindwing underside russet brown, with a straight whitish submedian band from costa to vein 1A, and a postmedian to submarginal white band, straight from costa to M3, then angled inwards toward basal side of tornal ocellus, with basal margin slightly irregular, and distal strongly concave in each cell, enclosing a series of black ocelli ringed with russet brown and pupilled with white, one in each cell except at costa, in cell Cu2-1A two ocelli, and the ocellus in cell M2-M3 lacking black.

FEMALE: Differs from nominate subspecies in same respect as male, but larger (forewing length: 37mm), and color of postmedian band lighter. **Material examined.**— Holotype (male): Táchira, Delicias, Venezuela, 1000m, Mar 1987, [coll. unknown] [MALUZ]. Allotype (female): Mata Mula, via Delicias, Venezuela, 1800m, 04 Nov 1988, R. Murphy *leg*. [TWP]. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 1 male, Delicias, Tachira State, Mar 1987, A. Neild *leg*.; 1 male, vía Delicias, El Tamá, Táchira, Coll. A. Neild (donated by the Mattei brothers, no data supplied); 2 males, San Vicente de La Revancha, Fundo Piedra Blanca, Sierra de El Tamá, Táchira, 2350m, 26 Mar 1996, F. Rey *leg*.; 1 female, vía Delicias, P. N. El Tamá, Táchira, ca. 1700m, [no date], F. Rey *leg*. [AFN]; 1 male, Mata Mula, via Delicias, 1800m, Jun 1982, F. Romero Jr. *leg*.; 2 males, same locality and collector as allotype, Mar 1987; 2 males, same data, Apr 1987; 1 male, same data, May 1987; 2 males, same data, Jun 1987 [TWP].

Etymology.- magnus - big in Latin, for its large size as compared to other subspecies.

Remarks.- Oxeoschistus puerta embraces a group of 10 known subspecies (see arrangement in Lamas et al., 2004). Typical O. puerta flies in the Venezuelan Cordillera de la Costa (not in "Colombia" as type label indicates); O. puerta isolda is restricted to the Chocó region of western Colombia and Ecuador. O. puerta simplex seems to occur in all three Colombian Cordilleras and in Ecuador (east of the Chocó). There is also an undescribed subspecies of O. puerta endemic in the Sierra de Perijá (Viloria, in prep.). Subspecies duplex Godman and submaculatus Butler & Druce fly in Bolivia and Costa Rica, respectively.

PANYAPEDALIODES Forster, 1964

Panyapedaliodes Forster, 1964:157. Type-species: Pronophila panyasis Hewitson, 1862, by original designation.

Muscopedaliodes Forster, 1964:153. Type-species: Pedaliodes muscosa Thieme, 1905. Synonymy established by Adams, 1986:275.

Panyapedaliodes panyasis (Hewitson, 1862)

Pronophila panyasis Hewitson, 1862:7, pl. 3, fig. 22. (1 male, [Venezuela], HC, BMNH Type No. Rh 3970, LECTOTYPE, herein designated, [BMNH, examined]).

Pedaliodes panyasis (Hewitson); Butler, 1868:179. Panyapedaliodes panyasis (Hewitson); Forster, 1964:157.

Material examined.— VENEZUELA: 2 males, Este de Betania, 2400-2520m, 19 Feb 1992, A. Viloria, J. Camacho & R. Calchi *leg.*; 1 male, selva vía al Paramito, 2400-2460m, 27 Aug 1996, A. Viloria, V. Carrizo & D. González *leg.* [MALUZ].

Remarks.— This species occurs in the three main Andean Cordilleras of Colombia and the Venezuelan Cordillera de Mérida. Its type locality is possibly the Cordillera de la Costa, where numerous individuals have been collected recently: there is an illustration of the species in Raymond (1982), most possibly of a specimen from the coastal range of Venezuela. Old records for Peru and Bolivia refer to different but related species. *P. panyasis* is found in the middle elevation cloud forests from around 2200m

up to 2600m.

Panyapedaliodes jephtha (Thieme, 1905)

Pedaliodes jephtha Thieme, 1905:84, pl. 2, fig. 18. (1 male, Colombia, Antioquia, LECTOTYPE, herein designated [BMNH, examined]).

Muscopedaliodes jephtha (Thieme); Forster, 1964:154, fig. 185 (male genitalia).

Panyapedaliodes jephtha (Thieme); Adams, 1986:277.

Material examined.— VENEZUELA: 1 male, San Vicente de la Revancha, 2350m, F. Rey *leg.* [FRC]; 1 male, entre Betania y La Línea, 2600-2900m, 30 May 1994, A. Viloria, J. Camacho & M. García *leg.* [MALUZ].

Remarks.— This species has a wide but apparently localized distribution. It occurs in middle elevation cloud forests from Venezuela (Cordillera de Mérida) south to Ecuador.

Panyapedaliodes tomentosa (Weymer, 1912), comb. rev., stat. rev.

Pedaliodes tomentosa Weymer, 1912:255, pl. 54, row b.

Material examined.— VENEZUELA: 1 male, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo, J. & A. González *leg*. [MALUZ]; 2 males, via La Línea, 2300-2700m, 17 Apr 1996, T. Pyrcz *leg*.; 1 male, Paramito, 2350-2450m, 18 Apr 1996, T. Pyrcz & F. Rey *leg*. [TWP].

Remarks.—Adams' (1986:278) synonymy of *P. tomentosa* with *P. silpa* (Thieme) [Lectotype: male, Bolivia, La Paz [?], Cillutincara, 3000m, Jan 1896, Garlepp; designated by G. Lamas, 1994 (ZMHU, unpublished), examined], is herein rejected. *P. silpa* occurs in Peru and Bolivia and is clearly not conspecific with the Colombian *P. tomentosa*. This species is known to us from all three Colombian Cordilleras. Fassl (1918) and Adams (1986) reported it from the Central and Oriental Cordilleras. Recently, the senior author of this paper collected it on western slopes of the Cordillera Occidental (Pyrcz & Wojtusiak, 1999).

PEDALIODES Butler, 1867b

Pedaliodes Butler, 1867b:267, fig. 1 (venation). Type-species: Pronophila poesia Hewitson, 1862, by original designation.

Pedaliodes poesia (Hewiston, 1862)

Pronophila poesia Hewitson, 1862:6, pl. 3, fig. 19. (1 male, New Granada, HC, BMNH type No. 3952, LECTOTYPE, herein designated [BMNH, examined]).

Pedaliodes poesia (Hewitson); Butler, 1867b:267.

Pronophila phanaraea Hewitson, 1868:179. Synonymy established by Thieme, 1905:52, 53. (1 female, Ecuador, HC, BMNH type No. Rh. 3953, LECTO TYPE, herein designated [BMNH, examined]).

Material examined.— VENEZUELA: 1 male, vía Bramón a Delicias, Mata Mula, 1850-2020m, 17 Feb 1995, F. Rey leg. [AFN]; 2 males, bosque arriba de Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 1 male, same locality, 2350m, 16 Aug 1996, A. Viloria & V. Carrizo leg.; 1 male, entre Betania y La Banderola, 2400-2600m, 23 Aug 1996, A. Viloria, V. Carrizo & A. González leg.; 3 males, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo, J. & A. González leg. [MALUZ]; 2 males, Betania, 2200-2300m, 15 Apr 1996, T. Pyrcz & F. Rey leg. [TWP].

Remarks.- This species is distributed from Venezuela to Peru, demonstrating a noticeable variation in the extent of white markings of the hindwing underside between populations. The individuals from the Colombian Cordillera Oriental and El Tamá are generally the brightest, and also the largest of all. *Pedaliodes poesia* is replaced in the Sierra de Perijá by a close ally, *P. suspiro* Adams & Bernard, by *P. leuchocheilus* Godman & Salvin

in the Sierra Nevada de Santa Marta, and by the endemic *P. japhleta* Butler across the Chama valley in the Cordillera de Mérida. *P. poesia* flies in lower and middle elevation cloud forest. Adams' altitudinal data (Adams, 1986) are the most accurate, 2250-2650m for the Cordillera Oriental of Colombia, though it is occasionally found below 2000m.

Pedaliodes manis (C. & R. Felder, 1867)

[Pronophila pisonia Hewitson, var.; Hewitson: 1862:7, pl. 3, fig. 20]. [Pronophila ereiba C. & R. Felder, var.; C. & R. Felder, 1867:469].

Pronophila manis C. & R. Felder, 1867:469. (1 male, Bogotá, Uricoechea, Felder Colln. [Rhop. Slide No. 11668], LECTOTYPE, herein designated [BMNH, examined]).

Pedaliodes manis (C. & R. Felder); Butler, 1868:174.

Pedaliodes pisonia f. manis (C. & R. Felder); Weymer & Maassen, 1890:100 [in part misidentification]

Pedaliodes pisonia (Hewitson) var. manis (C. & R. Felder); Thieme, 1905: 72, 73-74.

Pedaliodes pisonia manis (C. & R. Felder); Beebe, 1951:9.

Material examined.- VENEZUELA: 1 male, San Vicente de la Revancha, Fundo Piedra Blanca, 2350m, 25 Feb 1998, F. Rey leg. [AFN]; 2 males, bosque arriba de Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 2 males, same locality, 2400-2450m, 15 Aug 1996, A. Viloria, V. Carrizo & J. González leg.; 1 male, same locality, 2350m, 16 Aug 1996, A. Viloria & V. Carrizo leg.; 1 male, Betania - Potrero, 2395m, 17 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 1 female, El Paramito, 2500-2600m, 24 Aug 1996, A. Viloria, V. Carrizo & L. E. González leg.; 4 males, selva nublada arriba de Betania, 2400-2480m, 24 Aug 1996, A. Viloria, V. Carrizo & L. E. González leg.; 4 males, selva vía al Paramito, 2400- 2460m, 27 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 6 males, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo & J. & A. González leg. [MALUZ]; 12 males, 1 female, San Vicente, 2300-2350m, 12/16 Apr 1996, T. Pyrcz & F. Rey leg.; 6 males, vía Delicias, 1800--2100m, 4 Nov 1988, R. Murphy leg.; 2 males, Betania, 9 Aug 1987, T. Pyrcz leg.; 3 males, same data, Oct [19]90, [F. Rey] leg.; 9 males, Betania, 15/16 Apr 1996, T. Pyrcz & F. Rey leg. [TWP].

Remarks.- Pedaliodes manis occurs from Costa Rica (including the Venezuelan Andes and the Cordillera de la Costa) to Bolivia. Records from the Pantepui (d'Abrera, 1988) are misidentifications of P. roraimae Strand. The Bolivian and north Peruvian individuals are somewhat distinct in color pattern and wing shape (more scalloped hindwings), but their male genitalia show no significant variation. P. manis occurs in open areas such as pastures and can occasionally be seen quite far from the nearest forest. Its altitudinal range depends largely on suitable biotope, and therefore any placement of P. manis within any group of species replacing each other along an elevational gradient appears unjustified (see Adams and Bernard, 1981). P. manis occurs as high as 2800m and down to 1000m. It can be recognized from the locally sympatric P. montagna (throughout the Andes), and P. pisonia (in the Venezuelan Cordillera de la Costa), by closely examining the shape of the scent patches in males. The females, lacking this sexual character of the males, are obviously much more difficult to distinguish from each other.

Pedaliodes pisonia (Hewitson, 1862)

Pronophila pisonia Hewitson, 1862:6-7, pl. 3, fig. 21. (1 female, Venezuela, pur. From Dyson, 46-75, BMNH type No, Rh. 3965, lectotype designated by Viloria et al, 2001 [BMNH, examined])
Pedaliodes pisonia Hewitson; Butler, 1867b:267.

Material examined.— VENEZUELA: 1 male, Fundo Piedras Blancas, Edo. Táchira, 2200m, [no date], F. Rey [TWP].

Remarks.- The recognition of this species in the El Tamá region is based on a single specimen whose identity we give here with

reserve. Recently (Viloria *et al.*, 2001), it was suggested that typical specimens of *P. pisonia* have been obtained exclusively in the Cordillera de La Costa and the Serranía del Interior (Venezuela). Good series of individuals from Andean localities need to be studied in great detail.

Pedaliodes montagna Adams & Bernard, 1981, stat. rev.

[Pedaliodes manis (C. & R. Felder) var. meridensis Staudinger, in litt.] nomen nudum.

Pedaliodes montagna Adams, & Bernard, 1981:345, 361-362, figs. 8 (male genitalia), 21. (1 male, Cordillera de Mérida, S. of Mérida, La Montaña, 2450-2550m, 19 Aug 1977, M. J. Adams, holotype [BMNH, examined]).

Material examined.- VENEZUELA: 3 males, 1 female, Betania - El Potrero, 2400-2600m, 28/29 May 1994, A. Viloria, J. Camacho & M. García leg.; 7 males, bosque arriba de Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 1 male, same locality, 2400-2450m, 15 Aug 1996, A. Viloria, V. Carrizo & J. González leg.; 4 males, same locality, 2350m, 16 Aug 1996, A. Viloria & V. Carrizo leg.; 2 males, 1 female, Betania - El Potrero, 2395m, 17 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 1 male, entre Betania y La Banderola, 2400-2600m, 23 Aug 1996, A. Viloria, V. Carrizo & A. González leg.; 3 males [1 in MUSM], selva nublada arriba de Betania, 2400-2480m, 24 Aug 1996, A. Viloria, V. Carrizo & L. E. González leg.; 2 males, selva vía al Paramito, 2400-2460m, 27 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 3 males, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo & J. & A. González leg. [MALUZ]; 1 male, Betania, 2500m, Aug 1987, T. Pyrcz leg.; 1 female, Betania, 16 Apr 1996, T. Pyrcz & F. Rey leg.; 1 female, same data, 1/28 Feb 1996; 9 males, 1 female, San Vicente de La Revancha, 2300-2350m, 12/16 Apr 1996, T. Pyrcz & F. Rey leg. [TWP].

Remarks.- Pedaliodes montagna was described as an endemic species of the Cordillera de Mérida. Adams and Bernard (1981) pointed out that it is the local, allopatric replacement of *P. manneja* Thieme (which only flies in the Venezuelan Cordillera de la Costa and the Sierra de Perijá). In our opinion *P. montagna* from the Cordillera de Mérida is superficially and structurally indistinguishable from the specimens from El Tamá and many other localities from Colombia to Bolivia.

Pedaliodes praemontagna Viloria & Pyrcz, new sp. (Figs 29-30, 40)

[Pedaliodes sp. nov. Pyrcz & Viloria, MS]; Viloria, 2000:267. [Pedaliodes n. sp. Pyrcz & Viloria, MS, no. 907]; Lamas et al., 2004:213.

Diagnosis.- This species shows considerable individual variation, which makes its identification against other similarily marked species, particularly in collections, rather difficult. It can be separated fairly easily from P. montagna and P. manis, both flying at lower elevations, by the shape of the forewing upperside scent patch. This is larger and does not extend along veins Cu1, Cu2 and 1A as compared to P. manis and P. montagna. Description.- MALE (Fig. 29): Head: eyes hairy, reddish brown with black hairs. Palpi twice as long as head, dark brown with black and brown hairs. Antennae reaching to first half of costa, shaft and club or angebrown, without scales, club formed gradually, subcylindrical. Thorax: dorsally dark shiny brown, thickly hairy with reddish hairs; ventrally light brown. Wings: forewing length: 24-28mm, mean: 26.98mm, n = 52. Forewing triangular, tornus only slightly obtuse. Hindwing suboval, external margin softly crenate. Upperside ground color dark shiny brown, slightly lightened towards marginal area of forewing. Lustrous, dense discal-postdiscal androconial patch. Basal half and anal region of hindwing densely hairy. Forewing underside ground color chocolate brown, slightly lighter towards submarginal and marginal regions. Chocolate brown scales finely dusted over apex. Hindwing underside ground color chocolate brown, but gradually chestnut from postbasal region towards external margin, except for veins, which are entirely covered by chocolate scales. Reddish suffusion extending from anal margin towards inner part of wing. Yellow scales finely dusted over reddish surface of anal region, but more densely shown in postdiscal area, forming a diffuse wedge. Series of postdiscal white dots in each of cells M1-M2 to Cu2-1A, those in Cu1-Cu2 and Cu2-1A rather distinct (ca. 0.5mm diameter), the remainder vestigial. Genitalia: as illustrated (Fig. 40).

FEMALE (Fig. 30): Forewing length: 26mm, mean: 26mm, n = 2. Differs from male in having more crenate external margins of both wings; paler upperside groundcolor; reddish brown suffussion in anal region; white marginal scales between veins. Underside ground color olivaceous brown. Forewing with central suffusion of chocolate brown, as well as in apex and outer margin. Chocolate brown scales dusted over postdiscal area, chestnut on both sides of discal area, including part within distal half of discal cell. Hindwing heavily dusted with chocolate brown all over its surface, except for postdiscal-submarginal area, where brown scales are dispersed; slight reddish tone in anal margin area, with few orange and yellow scales. Two vestigial submarginal white dots in cells Cu1-Cu2 and Cu2-1A, respectively.

Variation.— Males are very variable in hindwing underside pattern, where yellow scales could be almost imperceptible or even absent.

Material examined.— Holotype (male): Este de Betania, Venezuela, 2780-2810m, 16/19 Feb 1992, A. Viloria, J. Camacho & R. Calchi leg.[MALUZ]. Allotype (female): same data, 2620-2780m, 19 Feb 1992 [MALUZ]. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 10 males, same data as holotype; 3 males, same data as allotype; 1 female, same data as holotype, 2520-2620m; 1 male, same data as allotype except for 2520-2620m; 28 males, Betania La Línea, 2800m, 28/29 May 1994, A. Viloria, J. Camacho & M. García leg.; 7 males, via La Línea, 3100m, 30 May/2 Jun 1994, A. Viloria, J. Camacho & M. García leg.; 1 male, entre Betania y La Banderola, 3000-3100m, 23 Aug 1996, A. Viloria, V. Carrizo & A. González leg.; 1 male, entre Betania y La Cueva, 2900-3100m, 26 Aug 1996, A. Viloria, V. Carrizo & A. González leg. [MALUZ]; 3 males, Betania, 2200-2300m, 16 Apr 1996, T. Pyrcz & F. Rey leg.; 12 males, vía La Línea, 2700-3000m, 16 Apr 1996, T. Pyrcz & F. Rey leg. [TWP].

Etymology.- praemontagna, litterally means before or below the mountain, premontane.

Remarks.- The type series comes from a single area of cloud forest on the trail between the village of Betania and the páramo de El Tamá where it is locally abundant on sunny days. Only one specimen came to a trap baited with rotten banana placed in the spot for two weeks. This species belongs to the complex of Pedaliodes ferratilis Butler, and may be the same one reported as such by Adams (1986) from the Sierra Nevada del Cocuy and the Cordillera Oriental (whose individuals, examined by us in the BMNH, were not included in the type series). The population from El Tamá is well distinct in facies from Adams' specimens of 'P. ferratilis' from the Cordillera de Mérida. The complex, which comprises several species found from Venezuela to Bolivia, is taxonomically very difficult, with very few morphological and structural characters to explore. What is beyond doubt is that the true Pedaliodes ferratilis is an insect of large size (much larger that the individuals of the reputed north Andean populations), which is only known to the authors from Peru.

Pedaliodes proerna proerna (Hewitson, 1862)

Pronophila proerna Hewitson, 1862:9, pl. 4, fig. 29. (male, Colombia, Bogotá, pur. from Stevens, 56-142, Hewitson Coll., LECTOTYPE, herein designated, [BMNH, examined]).

Pedaliodes proerna (Hewitson); Butler, 1867b:267.

Material examined.— VENEZUELA: 1 male, via Delicias, ca. 1700m, [no date], F. Rey leg. [AFN]; 1 male, selva nublada arriba de Betania, 2400-2480m, 24 Aug 1996, A. Viloria, V. Carrizo & L. E. González leg.; 1 male, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo & J. & A. González leg. [MALUZ]; 3 males, 2 females, Betania, 2200-2300m, 16 Apr 1996, T. Pyrcz & F. Rey leg.; 2 males, 2 females, same locality, 2700m, Aug 1987, T. Pyrcz [TWP].

Remarks.- *Pedaliodes proerna* has been largely misidentified by all consulted authors. This includes Adams (1986), particularly the populations he found in the Central and Occidental Cordilleras,

where P. proerna is sympatric or parapatric with several barely marked dark brown Pedaliodes, some of them then undescribed. Adams (1986) points out correctly that the individuals from the Cordillera Oriental have a white-speckled wedge. The largest individuals, with the largest white wedge, occur in the Upper Chama Valley (Cordillera de Mérida) and belong to the subspecies P. proerna fumaria Thieme. However, what was overlooked by Adams is that P. proerna is obviously polymorphic, at least in the Cordillera Oriental population, including El Tamá. Our material from El Tamá shows that there is huge variation in the color and shape of the hindwing underside anal wedge. Such variation is not common for the genus Pedaliodes. Males which are closest to the type have a relatively short whitish wedge, wavy or v-shaped on its basal edge. Other specimens have a straight inner edge, and longer and better marked wedge; some lack any white anal speckling at all, but have a well defined straight postmedian line; and others have the same shape of the anal wedge as typical but with a brick-red overcast. These red specimens were misidentified partially by Adams (1986, and pers. comm.) with P. praemontagna. All these specimens belong definitely in P. proerna as they share the same wing shape, upperside color, scent patch and male genitalia. In females polymorphism is less obvious. Pedaliodes proerna is a representative of the lower cloud forest pronophiline fauna. It occurs in Betania at around 2200-2300m, but it flies down to 1500m on the eastern slopes of the Cordillera de Mérida.

Pedaliodes phoenissa (Hewitson, 1862)

Pronophila phoenissa Hewitson, 1862:9, pl. 4, fig. 30. (male, Bogotá, pur. From Isaacson, 43-2, BMNH Type No. 3984, LECTOTYPE, herein designated [BMNH, examined]).

Pedaliodes phoenissa (Hewitson); Butler, 1867b:217.

Pedaliodes prytanis (Hewitson) f. phoenissa (Hewitson); Weymer & Maassen, 1890: fig. 14.

Pedaliodes phanissae [sic] (Hewitson); Apolinar, 1914:15.

Pedaliodes prytanis (Hewitson) var. phoenissa (Hewitson); Gaede, 1931:503.
Pedaliodes phoenisca [sic] (Hewitson); Forster, 1964:167, fig. 232 (male genitalia).

Material examined.— VENEZUELA: 1 male, Betania - El Potrero, 2600m, 28/29 May 1994, A. Viloria, J. Camacho & M. García leg.

Remarks.- This species is apparently confined to the Colombian Cordillera Oriental and the Sierra de Perijá. Given that the hindwing whitish anal streak in this and other allied species tends to vary in length, *P. phoenissa* may be at times difficult to identify in the field. The angular and acute forewing apex of *P. phoenissa* is diagnostic. It is surely not conspecific with *P. prytanis* as was suggested first by Weymer & Maassen (1890) and then by d'Abrera (1988); for its genital armature clearly indicates that it belongs in a different section of the genus (see also Adams and Bernard, 1979). Part of the life cycle of this butterfly was described by Schultze (1930).

Pedaliodes empusa medusa Pyrcz & Viloria, new subsp. (Fig. 25)

Pronophila empusa C. & R. Felder, 1867:468. (1 male, Bogotá, Muzo, Uricocchea, Felder Colln., RB, LECTOTYPE, herein designated [BMNH, examined], Fig. 26).

[Pedaliodes empusa subsp. nov. Pyrcz & Viloria, MS]; Viloria, 2000:267. [Pedaliodes empusa n. ssp. Pyrcz & Viloria, MS, no. 814b]; Lamas et al., 2004:211.

Diagnosis.— Differs from individuals of other subspecies, including the nominate (Fig. 26), in that the underside is much more dusted with whitish and silver scales on the whole surface of hindwing, and on the apical area and along the outer margin of the forewing. The white costal

streak on the hindwing underside is well marked, rather wide and enters cell M1-M2. In some well-pigmented specimens the costal streak on the forewing is also well marked and extends as far as on the hindwing.

Description.— MALE: Forewing length: 25–26mm, mean = 25.60mm, n = 9. Upperside dark chocolate brown, forewing fringes white in each cell, scent patch 3-4mm wide, roughly rectangular, not extending along veins. Forewing underside dull dark brown, suffused with magenta scales in the subapical area and along upper half of outer margin, apex dark brown, a pale yellow costal postdiscal streak reaching cell M1-M2. Hindwing underside pattern marble-like, a dark chocolate brown ground color liberally dusted with whitish or light grey scales, a whitish median costal streak extending to vein M1.

FEMALE: Forewing length: 26mm, n = 1. Slightly paler on both upper and underside. White speckling barely visible, but hindwing costal streak well marked.

Material examined.— Holotype (male): Cerro La Banderola, Venezuela, 3300m, 20 Aug 1996, A. Viloria *leg*. [MALUZ]. Allotype (female): Páramo El Tamá, Venezuela, 3100-3350m, 18 Feb 1992, A. Viloria, J. Camacho & R. Calchi *leg*. [MALUZ]. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 3 males, same data as allotype; 1 male, Páramo El Tamá, 3150m, 26 Aug 1996, A. Viloria, V. Carrizo & A. González *leg.*; 2 males, entre Betania y La Línea, 2800m, 30 May 1994, A. Viloria, J. Camacho & M. García leg. [MALUZ]; 2 males, Páramo El Tamá, 3100-3300m, [T. Pyrcz] *leg.*; 8 males, 1 female, Páramo Tamá, 3100-3300m, 17 Apr 1996, T. Pyrcz & F. Rey *leg.* [TWP].

Etymology.— Medusa, the Greek mythological monster with snakes instead of hairs; from whose blood Pegasus, the winged horse, originated. The name is applied just as an euphonic combination with *empusa*.

Remarks. This is a very interesting uppermost forest species occurring in the Colombian Cordillera Oriental (E. Krüger has been the only one to collect it in the Central Cordillera, see: Pyrcz, 1999b). Reports of P. empusa from Bolivia and Peru (Forster, 1964) are misidentifications of an undescribed species (Lamas and Viloria, MS). Pedaliodes empusa does not exist in the Sierra de Perijá nor the Cordillera de Mérida. It forms a complex of highly divergent populations distinguishable by a series of stable morphological and anatomical characters (size, markings, scent patch size and shape, and even male genitalia). Two of them are differentiated enough to be recognised as separate species, P. guicana Adams, and P. ralphi Adams. Currently, a study is being carried out (Pyrcz, in prep.) in order to appreciate actual phyletic relationships within the P. empusa-complex. Pedaliodes empusa medusa, endemic in El Tamá, is only found in the open páramo not far above the upper cloud forest limit.

Pedaliodes baccara allopatra Viloria & Pyrcz, new subsp. (Fig. 23-24)

Pedaliodes pausia (Hewitson) form baccara Thieme, 1905:105, pl. 3, fig. 35.
(1 male, Columbia, [18]87, K.[albreyer], Lectotype designated by Lamas 1994 (unpublished) [ZMHU, examined]).

Pedaliodes baccara baccara Thieme; Pyrcz, 1999b:360.

[Pedaliodes baccara subsp. nov. Pyrcz & Viloria, MS]; Viloria, 2000:267.
[Pedaliodes baccara n. ssp. Pyrcz & Viloria, MS, no. 791b]; Lamas et al., 2004:211.

Diagnosis.— Differs from *Pedaliodes baccara baccara* Thieme (= *Pedaliodes fuscata parapatra* Adams, **new syn.**, holotype in BMNH examined) in being darker and having a shiny upperside, with a darker distal third of the wings. The underside color pattern is close to that of the nominate subspecies, but in general is much darker. The hindwing shows no yellow in the postdiscal area, but a narrow whitish suffussion in the basal border of the postdiscal band; the ocelli are reduced in size and brightness.

Description.— MALE (Fig. 23): Forewing length: 22-27mm, mean = 25.47mm; n = 38. Upperside chocolate brown, distal half of forewing slightly lighter. Forewing underside brown in basal two thirds, light brown dusted with white scales from postmedian to submarginal line, marginal area chocolate brown at apex, gradually lightening and merging into basal lighter area before tornus. Hindwing underside chocolate brown in basal two thirds, light brown suffused with whitish and pale yellow scales from

postmedian to submarginal line, sandwiching an indistinct yellowish postmedian wedge widening gradually from vein M2 to anal margin, postmedian line starting at costal margin at right angle, reaching vein M1, then gently bent distally to vein M2, then straight to mid anal margin, submarginal line irregular, incurved in each cell. A row of white dots, that in cell M1-M2 on postmedian line, that in M2-M3 slightly diplaced distally and that in Cu1-Cu2 half way between postmedian and submarginal lines.

FEMALE (Fig. 24): Forewing length: 24-28mm, mean = 25.81mm, n = 8. Same basic differences in wing pattern between males of this subspecies and those of *P. baccara baccara* are found between females.

Material examined.— Holotype (male): bosque arriba de Betania, Venezuela, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo & D. González *leg*. [MALUZ]. Allotype (female): bosque arriba de Betania, Venezuela, 2400-2450m, 15 Aug 1996, A. Viloria, V. Carrizo & J. González *leg*. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 3 males [1 in MUSM], same data as holotype; 2 males, same data as allotype; 4 males, 1 female, Este de Betania, 2400-2520m, 19 Feb 1992, A. Viloria, J. Camacho & R. Calchi leg.; 1 male, 1 female, same data, 2620-2780m; 15 males, 3 females, Betania -El Potrero, 2400-2600m, 28-29 May 1994, A. Viloria, J. Camacho & M. García leg.; 1 male, arriba de Betania, 2600m, 20 Aug 1996, A. Viloria leg.; 3 males, 1 female, entre Betania y La Banderola, 2400-2600m, 23 Aug 1996, A. Viloria, V. Carrizo & A. González leg.; 1 female, selva arriba de Betania, 2400-2480m, 24 Aug 1996, A. Viloria, V. Carrizo & L. E. González leg.; 2 males [1 in MUSM], selva vía al Paramito, 2400-2460m, 27 Aug 1996, A. Viloria, V. Carrizo and D. González leg.; 4 males, 1 female, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo & J. & A. González leg. [MALUZ]; 1 male, Quebrada Betania, 2500m, iv.1996, F. Rey leg. [FR]; 1 male, 2 females, Betania, viii.1987, [T. Pyrcz] leg.; 3 males, 1 female, Betania, 2200-2300m, 16 Apr 1996, T. Pyrcz & F. Rey leg.; 3 males, vía La Línea, 2300-2700m, 17 Apr 1996, T. Pyrcz & F. Rey leg. [TWP].

Etymology – allopatra is the latinization of allopatric, by definiton, the condition of a biological entity that occupies an exclusive separate country or area of distribution.

Remarks.- Adams considered P. baccara Thieme to be a Colombian form of *Pedaliodes pausia* (Hewitson), but our studies show that P. pausia is a Bolivian species, whilst what Adams considered to be P. pausia in Colombia is actually Pedaliodes plotina lucipara Weymer, new comb., stat. rev. The lectotype of Pedaliodes baccara Thieme from Antioquia, Colombia, is in the ZMHU, and it is identical to the holotype of P. fuscata parapatra Adams (described from Boyacá, Colombia), therefore the latter is a junior subjective synonym of P. baccara Thieme. It is worth noting that the type series of P. fuscata parapatra in the BMNH contains many specimens of a similar, but not closely related, undescribed species, that flies sympatrically with P. baccara in the El Arenal region, Cordillera Oriental. Pedaliodes baccara baccara is distributed in all three Colombian Cordilleras, and the new subspecies seems to be endemic in El Tamá. They all fly at relative middle elevations (around 2400-2700m) in very dense cloud forests.

Pedaliodes reyi Viloria & Pyrcz, new sp. (Fig. 31-32, 41)

[Pedaliodes sp. nov. 2 Pyrcz & Viloria, MS]; Viloria, 2000:267. [Pedaliodes n. sp. Pyrcz & Viloria, MS, no. 919]; Lamas et al., 2004:213.

Diagnosis.— Similar to *Pedaliodes cesarense* Adams & Bernard, differing from it in the following respects: the forewing upperside postmedian band is sandy yellow, or very light orange, broader than in *P. cesarense* Adams & Bernard, as broad as in *P. zuleta* Adams & Bernard, but contrary to it, it does not broaden on the costa; the band is wavier basally, more curved on the costa, reaching or almost reaching the outer edge of the discal cell. The forewing scent patch is larger, contiguous to the yellow band. The hindwing upperside postmedian band is similar to *P. cesarense*, but consistently different in color (lighter); the bands on the underside are lighter than in *P. cesarense* or *P. zuleta. Pedaliodes reyi* differs from *Pe*-



Fig. 31-33. 31) Pedaliodes reyi Viloria & Pyrcz, n. sp. (male Holotype). 32) Pedaliodes reyi Viloria & Pyrcz, n. sp. (female Allotype). 33) Pedaliodes valencia Pyrcz & Viloria, n. sp. (male Holotype).

daliodes bernardi Adams as follows: in *P. bernardi* the forewing upperside postmedian bands are very faint and darker on the hindwng, as in *Pedaliodes ochrotaenia* (C. & R. Felder), **stat. rev.** Additionally in *P. bernardi* and *P. ochrotaenia*, the hindwing upperside postmedian bands fade before reaching the anal margin, and their distal edges are diffused. On the forewing upperside the postmedian bands do not reach the costa. The scent patch of *P. ochrotaenia* is much smaller than that of *P. reyi.*

Description.— MALE (Fig. 31): Forewing length: 24-29mm; mean: 26.95mm, n = 42. Head, thorax and abdomen dark brown, abdomen ventrally beige. Eyes dark chocolate brown, hairy; labial palpi greyish covered with dull brown hair, twice as along as head; antennae chestnut, club gradually formed, reaching to half costa. Wings: Forewing apex acute in appearance due to slightly concave outer margin between apical angle and vein M1. Fringes brown and pale

orange, longer on veins. Upperside forewing basal and medial areas to postdiscal line, dark brown; a postdiscal pale orange band, 5-6mm wide, from costa to anal margin, roughly parallel to outer margin, dentate basally between veins. Hindwing basal ground color dark brown as on forewing, a postdiscal pale orange band, 3-5mm wide, narrowing and bending sharply distally on vein M2, distally dentate. Underside forewing postmedian and submarginal lines reflect pattern from upperside, area basally and distally from postdiscal band slightly lighter and paler than on the upperside, dull brown, chocolate brown dusted with lighter scales on apex and greyish beige between postmedian band and submarginal line on costa. Hindwing postdiscal and submarginal lines reflect pattern from upperside; area basal and distally from postdiscal band brown, speckled with dusty yellow scales towards outer margin, postdiscal band creamy-yellow, pale creamy-yellow gradually more dusted with brown scales towards outer margin; series of four or five whitish dots bordered with brown, one each in cells Rs-M1 to Cu1-Cu2, that in M3-Cu1 the smallest. Genitalia: as illustrated (Fig. 41).

FEMALE (Fig. 32): Forewing length: 28mm, n = 1. Similar to male, but forewing band broader.

Material examined.— Holotype (male): Este de Betania, Venezuela, 2810-2950m, 16/19 Feb 1992, A. Viloria, J. Camacho & R. Calchi *leg*. [MALUZ]. Allotype (female): Fundo Piedra Blanca, San Vicente de la Revancha, Venezuela, 2300m, 20-28 Dec 1997, F. Rey [TWP]. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 8 males, same data; 1 male, same data, 2780-2810m; 22 males, entre Betania y La Línea, 2800m, 30 May 1994, A. Viloria, J. Camacho & M. García leg.; 3 males, Cerro de La Banderola, 3000-3200m, 20 Aug 1996, A. Viloria leg.; 1 male, entre Betania y La Banderola, 3000-3100m, 23 Aug 1996, A. Viloria, V. Carrizo & A. González leg.; 1 male, same data, 2900m; 5 males [1 in MUSM], entre Betania y La Cueva, 2900-3100m, 26 Aug 1996, A. Viloria, V. Carrizo & A. González leg. [MALUZ]; 1 male, via La Línea, 2700m, 14 Apr 1996, F. Rey leg. [FR]; 8 males, vía La Línea, 2700-3000m, 17 Apr 1996, T. Pyrcz & F. Rey leg. [TWP]; 1 male, same data [AFN].

Etymology.— This species is dedicated to our friend, companion, and colleague Fernando Rey, from San Cristóbal, Venezuela.

Remarks.—Pedaliodes reyi belongs in the P. phaea-species group, where most species are characterized by conspicuous postmedian orange or yellow bands. It is most related to Pedaliodes cesarense from the Sierra de Perijá, and to Pedaliodes bernardi from the Sierra Nevada del Cocuy. It is a beautifully marked Pedaliodes. Its wide oblique upperside bands make it unlikely to confuse with any other species in the field, except with the much less common Pedaliodes valencia, new sp., which flies above it in a different, very narrow altitudinal zone. P. reyi occurs in the upper cloud forest almost to the forest limit, from around 2700-3000m. It is locally sympatric with P. praemontagna and also partially perhaps with P. valencia, new sp., and parapatric above P. baccara allopatra. Within its elevation range, it is quite common, although it is difficult to catch because of its wary and fast flight.

Pedaliodes valencia Pyrcz & Viloria, new sp. (Fig. 33, 42)

[Pedaliodes sp. nov. 3 Pyrcz & Viloria, MS]; Viloria, 2000:267. [Pedaliodes n. sp. Pyrcz & Viloria, MS, no. 944]; Lamas et al., 2004:213.

Diagnosis.— This species is readily distinguished from other similarly patterned *Pedaliodes* by the distinctive light dirty orange color of the upperside median bands.

Description.— MALE (Fig. 33): Forewing length: 23-24mm; mean = 23.33mm; n = 3. Head, thorax and abdomen uniform dark brown, abdomen only ventrally beige. Eyes hairy; labial palpi twice as along as head; antennal club gradually formed, antennae reaching to half costa. Wings: Forewing apex acute in appearance due to slightly concave outer margin between apical angle and vein M1. Fringes brown and whitish, longer on veins, particularly on hindwing. Upperside forewing basal and medial areas to postdiscal line, dark brown; area between postdiscal and submarginal lines light dirty orange, forming a 5-6mm wide band, lighter basally, especially towards anal margin, sharply defining postdical line; postdiscal line running from costa to anal margin, parallel to outer margin, slightly dentate basally between veins; submarginal line less contrasting, fading in apical area, then appearing as a delicately wavy line running from distal margin, and bending towards tornal angle on vein 1A + 2A;

marginal area brown, slightly paler than median area ground color. Hindwing basal ground color dark brown as on forewing, lighter towards postdiscal line, especially on anal margin; area between postdical and submarginal lines light dirty orange, as on forewing, 3-5mm wide, lighter basally, whitish on postdiscal line, sharply defining postdiscal line; postdiscal line running at right angle from mid costa, and bending sharply distally before reaching vein M1, then following delicately wavy, running parallel to outer margin; submarginal line less sharply defined, displaced basally, particularly on veins M2 and M3, fading, indistinguishable on tornus; marginal area brown, as in median area. Underside forewing postmedian and submarginal lines pattern reflected from upperside, edges more distinctly marked than on recto on their overall length, because of more contrasting dark brown color of median and marginal areas, and pale yellow of postmedian area; postmedial yellowish area dusted with brownish scales towards submarginal line anterior to vein Cu1, particularly heavy in subapical area and costal margin; four white dots, bordered with dark brown on submarginal line one each in cells R4-R5 to M2-M3. Hindwing postdiscal and submarginal lines pattern reflected from upperside; basal, medial, and submarginal areas brown, liberally speckled with dusty yellow scales, more densely only on medial line, which is visible from mid costa into middle of discal cell, basally displaced in discal cell; postdiscal line sharply defined, edged distally with pale creamy-yellow, this color gradually more dusted with brown scales towards submarginal line, making submarginal line barely distinguishable, particularly on tornus; series of four or five whitish dots bordered with brown one in each of cells Rs-M1 to M3-Cu1, that in M2-M3 the smallest. Genitalia: as illustrated (Fig. 42).

FEMALE: Unknown.

Material examined. – Holotype (male): Parque Nacional Natural El Tamá, Norte de Santander, Colombia, 3200m, 22 Dec 1993, J. F. Le Crom *leg*. [MHNUN]. Holotype deposited in MHNUN.

Paratypes: COLOMBIA: 2 males, same data [1 in LC, 1 in TWP]. **Etymology**.— This species is named in honour of Juan Valencia of the University of Pamplona, an entomologist who works on the butterfly faunas of the province of Norte de Santander.

Remarks.– *Pedaliodes valencia* is a scarce species. *Pedaliodes valencia*, *P. wilhelmi*, and *P. thiemei* Staudinger are the uppermost representatives of their respective parapatric groups of species in their areas of distribution, being forest-paramo ecotone denizens. Whereas *P. valencia* seems to be restricted to El Tamá, there is no apparent allopatric counterpart for *P. thiemei* in the remainder of the Cordillera Oriental.

Pedaliodes plotina ruricola Pyrcz & Viloria, new subsp. (Fig. 27- 28)

Pronophila plotina Hewitson, 1862:4, pl. 2, figs 9, 10. (1 male, Venezuela, [Coast Range], HC, BMNH Type No. Rh. 4003, LECTOTYPE, herein designated [BMNH, examined]).

[Pedaliodes plotina subsp. nov. I Pyrcz & Viloria, MS]; Viloria, 2000:267. [Pedaliodes plotina n. ssp. Pyrcz & Viloria, MS, no. 896f]; Lamas et al., 2004: 213.

Diagnosis.— P. plotina ruricola differs from other subspecies in its darker brown upperside ground color; the hindwing anal area suffusion is brick red, not orange as in the nominate subspecies or rufous-orange as in P. plotina rapha Butler or P. plotina pharnaspes (Hewitson), stat. rev. The anal suffusion extends from the anal margin to cell M3-Cu1, always broader than in P. plotina rapha, but is narrower than in the nominate subspecies; the basal edge of the suffusion is usually straight, not parallel to the outer margin as in the other subspecies known; moreover veins crossing the suffused area are not outlined with black; the extent of the brick red anal suffusion is much more constant in size than in the Cordillera de Mérida populations.

Description.— MALE (Fig. 27): Forewing length: 24-28mm; mean 26.02mm; n = 22. Upperside of both wings chocolate brown, slightly lighter in distal one third of forewing, hindwing anal area suffused with brick red. Forewing underside dark brown in basal two thirds, light brown in distal one third, distally from postmedian line, slightly dusted with reddish scales, a faint whitish costal postdiscal streak, apex russet brown. Hindwing underside chocolate brown in basal two thirds. Slightly lighter brown from postmedian to submarginal line, forming a yellowish

postmedian wedge widening gradually from vein M2 to anal margin, median line starting at mid costa at right angle, reaching vein M1, then gently bent distally to vein M2 and following straight as a postmedian line to mid anal margin, submarginal line wavy, anal margin suffused with brick red, only one well developed submarginal white dot in M2-M3, the remainder vestigial or absent.

FEMALE (Fig. 28): Forewing length: 24-28mm, mean = 26.4mm, n = 5. Slightly paler than male, but same differences from other subspecies. **Material examined.**— Holotype (male): Betania, Potrero, Venezuela, 2395m, 17 Aug 1996, A. Viloria, V. Carrizo & D. González *leg*. [MALUZ]. Allotype (female): Bosque arriba de Betania, Venezuela, 2400-2450m, 15 Aug 1996, A. Viloria, V. Carrizo & J. González *leg*.

[MALUZ]. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 2 males, 1 female, bosque arriba de Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 4 males [1 in MUSM], same data as allotype; 1 male, 1 female, same locality, 2350m, 16 Aug 1996, A. Viloria & V. Carrizo leg.; 3 males. same data as holotype; 4 males, entre Betania y La Banderola, 2400--2600m, 23 Aug 1996, A. Viloria, V. Carrizo & A. González leg.; 4 males, 1 female, selva arriba de Betania, 2400-2480m, 24 Aug 1996, A. Viloria, V. Carrizo & L. E. González leg.; 1 male, 1 female, selva vía al Paramito, 2400-2460m, 27 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 2 males, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo & J. & A. González [MALUZ]; 1 male, San Vicente de La Revancha, Funda [sic] Piedra Blanca, 2350m, 24 Feb 1998, F. Rey leg. [AFN]; 2 males, vía Delicias, 1900m, Dec 1984, leg. F. Romero Jr.; 1 male, same locality and collector, 19 Jan 1993; 5 males, same locality, 04 Nov 1988, R. Murphy leg.; 4 males, San Vicente de la Revancha, Fundo Piedra Blanca, 2350m, 17 Mar 1995, F. Rey leg.; 4 males, same locality, 12 Apr 1996, T. Pyrcz & F. Rey leg.; 3 males, same locality and collectors, 13 Apr 1996; 1 male, same locality and collectors, 14 Apr 1996; 1 male, same locality and collectors, 16 Apr 1996; 6 males, 1 female, Betania, 2300m, 16 Apr 1996, T. Pyrcz & F. Rey leg.; 1 female, same data; 1 female, vía Delicias, 04 Nov 1988, R.Murphy leg. [TWP]. Etymology.- ruricola is a name originally conceived to stress the fact that this subspecies occurs mostly in rural areas, where the original forest habitat has been altered by humans.

Remarks.- The pattern of subspecies of Pedaliodes plotina is complex and its understanding requires thorough sampling. Adams and Bernard (1981) considered that nominate P. plotina occurs in the Cordillera de la Costa, Sierra de Perijá and the Colombian Cordillera Oriental, and that in the Cordillera de Mérida it is replaced by P. plotina rapha, with which they synonymized Hewitson's P. pharnaspes and Grose-Smith's P. plotinella. As a matter of fact P. plotina rapha is known so far only from forested areas in the upper Chama Valley, while in southern slopes of El Batallón region and the Santo Domingo Valley flies a subspecies more similar to the nominate P. plotina. In the area of San Eusebio and La Culata we detected populations corresponding morphologically to P. plotina pharnaspes, characterized by the larger and lighter orange anal suffusion. We have examined few specimens from the Sierra de Perijá, which obviously represent another, undescribed subspecies (Viloria, in prep.). Adams and Bernard (1981) records of this species from the northern Cordillera Oriental are of another undescribed subspecies. In the area of Bogota it is replaced P. plotina lucipara Weymer. Individuals of Pedaliodes plotina ruricola from El Tamá occur in secondary forest or grassland areas, usually flying along with P. manis over marshy meadows and roadsides along forest edge. It is very abundant in its habitat thoughout the year.

Pedaliodes polla Thieme, 1905

[Pronophila imeria C. & R. Felder, in litt.] nomen nudum. [Pedaliodes poluscina Staudinger, in litt.] nomen nudum.

Pedaliodes polusca (Hewitson) var. polla Thieme, 1905:103. (male, Colomb.-[ia], paramos, [18]95, Lectotype designated by G. Lamas, 1994 (unpublished) [ZMHB, examined]).

Pedaliodes polusca (Hewitson) f. polla Thieme; Weymer, 1912:258.

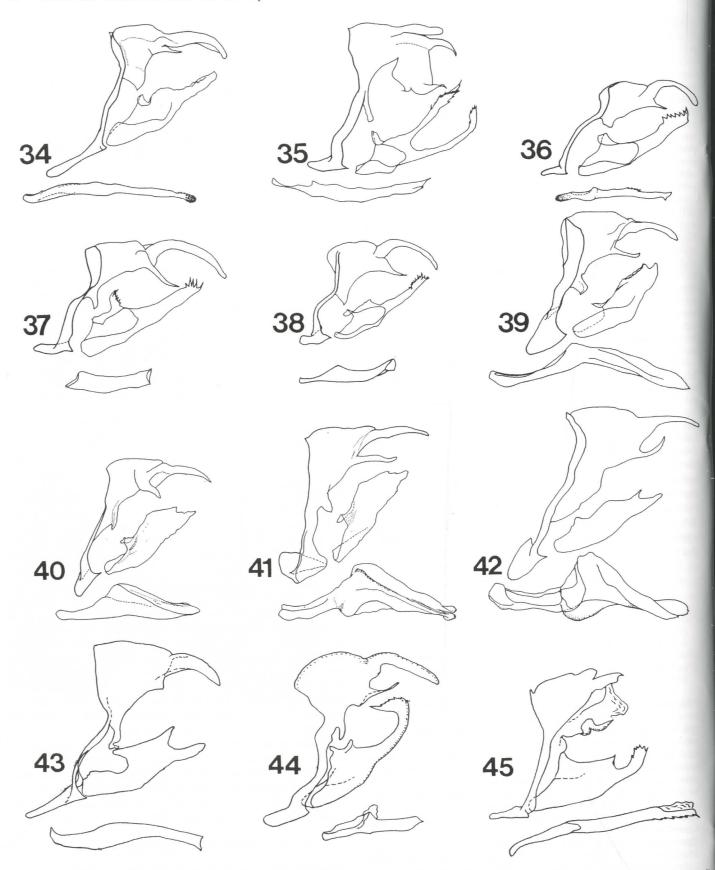


Fig. 34-45. Male genitalia of satyrine butterfly species: 34) *Idioneurula eremita* Viloria & Pyrcz, n. sp. 35) *Lymanopoda lecromi* Pyrcz & Viloria, n. sp. 36) *Manerebia pervaga* Pyrcz & Viloria. 37) *Manerebia pluviosa* Pyrcz & Viloria. 38) *Manerebia leaena gonzalezi* Pyrcz & Viloria. 39) *Altopedaliodes tamaensis* Viloria & Pyrcz, n. sp. 40) *Pedaliodes praemontagna* Viloria & Pyrcz, n. sp. 41) *Pedaliodes reyi* Viloria & Pyrcz, n. sp. 42) *Pedaliodes valencia* Pyrcz & Viloria, n. sp. 43) *Ianussiusa maso santa* Pyrcz & Viloria, n. ssp. 44) *Manerebia mycalesoides* (C. & R. Felder). 45) *Lymanopoda samius lineana* Pyrcz & Viloria, n. ssp. 45)

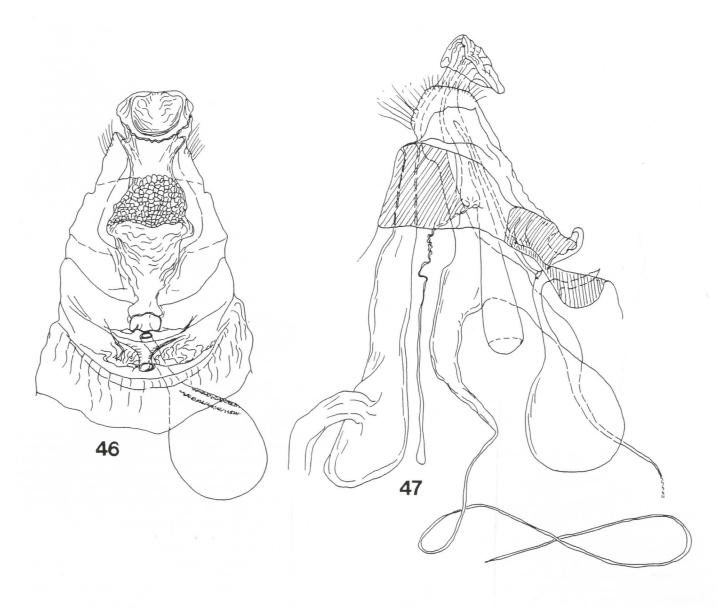


Fig. 46-47. Female genitalia of Ianussiusa maso maso (Godman): 46) ventral view. 47) lateral view.

Pedaliodes polla Thieme; Fassl, 1910:118, 132.

Material examined.- VENEZUELA: 3 males, Este de Betania, 2620-2780m, 19 Feb 1992, A. Viloria, J. Camacho & R. Calchi leg.; 3 males, entre Betania y La Línea, 2600-2800m, 30 May 1994, A. Viloria, J. Camacho & M. García leg.; 1 male, entre Betania y La Banderola, 2400-2600m, 23 Aug 1996, A. Viloria, V. Carrizo & A. González leg.; 1 male, entre Betania y La Cueva, 2750m, 26 Aug 1996, A. Viloria, V. Carrizo & A. González leg.; 1 female, El Paramito, 2500-2600m, 24 Aug 1996, A. Viloria, V. Carrizo & L. E. González leg. [MALUZ]; 2 males, vía La Línea, 2700-3000m, 17 Jun 1996, T. Pyrcz & F. Rey leg. [TWP]. Remarks.- This taxon was described from specimens collected on the eastern slopes of the Cordillera Oriental, in the region of Bogotá. The individuals found in El Tamá, when compared to those from Bogotá, are generally larger with brighter hindwing underside ochreous markings and with a somewhat more sinuate postmedian band. However, given the considerable complex variation of local populations of this species across the Andes from Venezuela to Ecuador, we refrain from naming a separate subspecies. The individuals found in the Cordillera de Mérida are indistinguishable from those in El Tamá.

Pedaliodes polusca (Hewitson, 1862)

Pronophila polusca Hewitson, 1862:10, pl. 4, fig. 31. (male, Bogotá, pur. from Stevens, LECTOTYPE, herein designated [BMNH, examined]).
Pedaliodes polusca (Hewitson); Butler, 1867b:267.

Material examined.— 1 male, Herrán, Norte de Santander, Colombia, 2800m, Dec 1993, J. F. Le Crom *leg*. [LC].

Remarks.- This species occurs throughout the northern Andes from Ecuador to Colombia, and Venezuela (El Tamá), except in the Colombian Cordillera Occidental, where it is replaced by *P. parranda* Adams, in the uppermost cloud forest.

Pedaliodes porina (Hewitson, 1862), comb. rev.

Pronophila porina Hewitson, 1862:9, pl. 4, fig. 28. (male, [Bolivia], HC, LECTOTYPE, herein designated [BMNH, examined]).

Pedaliodes porina (Hewitson); Butler, 1867b:267.

Physcopedaliodes porina (Hewitson); Adams, 1986:308.

[Pedaliodes porina n. ssp. Viloria & Pyrcz, MS, no. 906b]; Lamas et al., 2004: 213.

Material examined.— VENEZUELA: 1 male, Mata de Mula, 1900m [no date] [RMA].

Remarks. Pedaliodes porina seems to have a very wide, nearly Panandean, but localized, distribution, with various subspecies ranging from Bolivia to Venezuela (El Tamá). In many localities [confirmed in Peru and Bolivia], it seems to occur sympatrically with similar species, namely *Corderopedaliodes corderoi* (Dognin) comb. rev., stat. rev. (male, Riv. Numbala, 1889, Ex coll. Dognin 1921, presented by J. J. Joicey, Esq. Brit. Mus. 1931-29, LECTO-TYPE of Pedaliodes corderoi Dognin, herein designated [BMNH, examined]) which Adams (1986) incorrectly synonymized with P. porina, and Pedaliodes palaepolis (Hewitson) stat. rev. (male, Bolivia, HC, BMNH Type No. 3998, LECTOTYPE of *Pronophila* palaepolis Hewitson, herein designated [BMNH, examined]) (= Tisiphone lyssa Burmeister). Pedaliodes porina is apparently rare in Colombia. Adams (1986) mentions only one specimen collected in this country, in the Department of Santander. Similarily, only one male specimen has been collected so far in El Tamá range, on the road to Delicias at around 1800m. Known elevation data indicate that P. porina occurs in low elevation cloud forests, most of which have been largely destroyed below 2000m for coffee plantations in El Tamá. Our specimen represents a new subspecies with the white forewing band twice as broad as the one in typical P. porina (which was probably described from Bolivia). We decide not to name this new subspecies until further material for study is available.

PRAEPRONOPHILA Forster, 1964

Praepronophila Forster, 1964:182-183. Type-species: Pedaliodes emma Staudinger, 1897, by original designation.

Praepronophila perperna perperna (Hewitson, 1862)

[Dasynympha euchares Moritz, in litt.] nomen nudum (synonymy given by Viloria et al., 2001).

Pronophila perperna Hewitson, 1862:16-17.

Pronophila satyroides C. & R. Felder, 1867:469-470 (synonymy given by Butler, 1868: 173).

Pedaliodes perperna (Hewitson); Butler, 1867b:267.

[Pedaliodes mycalesoides (C. & R. Felder); Grose-Smith & Kirby, [1895]: 10-11 (misidentification), pl. 2, fig. 3] nomen nudum.

Praepronophila perperna (Hewitson); Adams, 1986:309.

Remarks.— One male of this unmistakable pronophiline species has been observed very closely by T. Pyrcz on July 2000, in the forests of Paramillo (1100m), a property of the Universidad Nacional Experimental del Táchira (UNET), near San Cristóbal. Although it has not been collected, its presence in the El Tamá region had always been presumed by us, due to its continuous distribution from the Cordillera de La Costa (Venezuela) along the lower cloud forests of the Andes of Venezuela and Colombia. There is also a Mesoamerican population (DeVries, 1987), which possibly belongs to a different subspecies (Viloria, unpubl.).

PRONOPHILA Doubleday, [1849]

Pronophila Doubleday, [1849]: pl. 60, fig. 1-3. Type-species: Pronophila thelebe Doubleday [1849], by subsequent designation (Butler, 1867b: 266).

Pronophila unifasciata bogotensis Jurriaanse, 1926

Pronophila unifasciata Lathy, 1906:77. Holotype male: Ecuador, in BMNH, [examined].

Pronophila bogotensis Jurriaanse, 1926:51 [not examined].

Material examined.— VENEZUELA: 1 male, Mata Mula, 1800-1900m [FFR].

Remarks.- Pronophila bogotensis Thieme was considered a subspecies of P. unifasciata Lathy by Pyrcz (2000). This taxon

has often been confused, as pointed out by Adams & Bernard (1981), with *P. thelebe* Doubleday, a species restricted to the Venezuelan Cordillera de La Costa. *Pronophila unifasciata bogotensis* is characterized by three to four well developed forewing upperside subapical white patches, and it flies in the central Cordillera de Mérida at elevations between 1900m and 2200m. In the northern (Yacambú) and eastern Cordillera de Mérida (Santo Domingo Valley), and the Sierra Nevada de Santa Marta (Colombia), occurs the subspecies *donachui* Adams & Bernard, in which the forewing subapical patches are grey and barely visible. *Pronophila unifasciata donachui*, comb. rev., occurs at lower elevations, around 1400-1600m, and occasionally down to 800m (Krüger, 1924). In El Tamá, *P. unifasciata bogotensis* has been found so far only in the area of Mata Mula on the road to Delicias.

Pronophila epidipnis orcidipnis Pyrcz & Viloria, new subsp. (Fig. 21-22)

Pronophila epidipnis Thieme, 1907:204. 7 syntypes (males): Venezuela, Mérida, in collections Staudinger [ZMHU, 3 males examined] and O. Thieme [whereabouts unknown].

[Pronophila epidipnis subsp. nov. Pyrcz & Viloria, MS]; Viloria, 2000:267. [Pronophila epidipnis n. ssp. Pyrcz & Viloria, MS, no. 1036f]; Lamas et al., 2004:214.

Diagnosis.— As in the nominate subspecies from Mérida, *P. epidipnis orcidipnis* has only a faint lightening of the dark brown color on the forewing upperside subapical area, contrary to *Pronophila epidipnis orchewitsoni* Adams & Bernard, stat. rev., in which white, greyish or bluish patches are always present. Compared to the nominate subspecies, this new subspecies has a slightly more marked orange patch on the forewing underside, basal to the Cu2-M3 ocellus, about the same size as in *P. epidipnis orchewitsoni*; the hindwing underside ground color is dull grey, and the markings are even less contrasting than in nominate *P. epidipnis*; the median and submarginal bands are very faint; the postmedian ocelli are not ringed with black as in *P. epidipnis orchewitsoni*. Contrary to *P. epidipnis epidipnis*, the hindwing apical margins not rufous but grey as in the remaining color.

Description.— MALE (Fig. 21): Forewing length: 38-39.5mm, mean 38.75mm, n = 10. Upperside blackish brown, except for faint greyish lightening on forewing subapical area. Forewing underside blackish brown, greyish brown at base and in apical area, whitish subapical patches dusted with grey, on costa in cells R5-M1, M1-M2, M2-M3 and along outer margin in cells M2-M3 and M3-Cu1, a row of four black ocelli, concave basally, pupilled with sky blue and that in M3-Cu1 edged basally with a subtriangular orange patch. Hindwing underside greyish brown with an indistinct darker pattern at base, median band and along outer margin at apex and with an S-shaped row of large postmedian ocelli, faintly showing from ground color, those in Cu1-Cu2 and a double ocellus in Cu2-1A pupilled with a tiny blue dot.

FEMALE (Fig. 22): Forewing length: 38mm. Differs from nominate subspecies and from subspecies *orchewitsoni* in same respects as male, preserving main female features of the species, basically lighter colors of upperside and chestnut suffusion of hindwing underside.

Material examined.— Holotype (male): Tamá National Park, Betania, Venezuela, 13/15.04.1996, T. Pyrcz & F. Rey *leg*. [MALUZ]. Allotype (female): same data as holotype [TWP]. Holotpe deposited in MALUZ.

Paratypes: VENEZUELA: 7 males, via La Línea, 2520-2620m, 19 Feb 1992, A. Viloria, J. Camacho & R. Calchi leg.; 1 male, bosque arriba de Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 1 male, selva arriba de Betania, 2400-2480m, 24 Aug 1996, A. Viloria, V. Carrizo & L. E. González leg.; 5 males, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo & J. & A. González leg.; 5 males, selva vía al Paramito, 2400-2460m, 27 Aug 1996, A. Viloria, V. Carrizo & D. González leg. [MALUZ]; 1 male, Betania, viii.1987, T. Pyrcz leg.; 2 males, via La Línea, 2300-2700m, 13/15 Apr 1996, T. Pyrcz & F. Rey leg.; 5 males, Betania, 2300-2400m, 13/15 Apr 1996, T. Pyrcz & F. Rey leg.; 2 males, Betania, 2300-2400m, 16 Apr 1996, T. Pyrcz & F. Rey leg.; 1 TWP].

Etymology.- The name of this taxon is an arbitrary compound word of

the existing subspecific names *orchewitsoni* and *epidipnis*, and reflects the intermediate systematic position of the new subspecies.

Remarks.- Adams & Bernard (1981) correctly observed that male genitalia of Pronophila have no particular features which allow easy recognition of species, and even less so between subspecies. The population found in El Tamá seems to be a link, in geographical and morphological terms, between P. epidipnis epidipnis Thieme, described from the Venezuelan Cordillera de Mérida and P. epidipnis orchewitsoni Adams & Bernard, reported from Colombia and Ecuador. This is the main reason why we downrank the latter to subspecies status. The type locality of P. epidipnis is "Mérida, Venezuela", or more specifically the upper Chama river valley. There are problems with the identification of the type locality of orchewitsoni. Even though this taxon was described in a paper dealing with the tribe Pronophilini in the Perijá range, the holotype was chosen, quite unfortunately, by Adams and Bernard (1979) to be a specimen from the Godman & Salvin collection (examined by us in the BMNH) without other data than "Colombia". Paratypes have been selected from many localities in the Colombian Cordillera Occidental (Frontino) and Cordillera Oriental, the Sierra de Perijá, and eastern Ecuador. Adams and Bernard (op. cit.) did state that there is "variation in the brightness of forewing markings" and actually point out that the specimens from the Sierra Nevada del Cocuy are the darkest and those from Perijá the brightest of all, however they did not name any subspecies. In our experience, the differences between the populations of what Adams and Bernard (1979) considered as P. orchewitsoni are evident, consistent, and show a geographical pattern, with no individual, infrasubspecific variations. In order to stabilize the name orchewitsoni we establish its type locality as Frontino (Antioquia), the same data as for one of the paratypes from the Godman & Salvin collection designated by Adams and Bernard (1979). This subspecies then occurs in the Colombian Cordillera Central, and southern part of the Cordillera Oriental, but also along the eastern slopes of the Andes in Ecuador, where the color pattern of individuals correspond, still with minor infrapopulation differences, to the original description of P. orchewitsoni. The populations found in the Colombian Cordillera Occidental, south-western Ecuador, Sierra de Perijá and the northern portions of the Cordillera Oriental (Sierra Nevada del Cocuy, El Tamá) are differentiated enough to be treated each as three separate subspecies of P. epidipnis. Pronophila epidipnis replaces P. unifasciata bogotensis at higher elevations in El Tamá and the Cordillera de Mérida (Adams and Bernard, 1981), and P. orcus (Latreille) on the western slopes of the Cordillera Occidental in Colombia (Pyrcz and Wojtusiak, 1999). It can be observed flying high in the canopy and settling on twigs, but spends most of the time in the understorey, and, as in most Pronophilina, it can be baited on the ground with faeces or rotten fruits. In El Tamá, P. epidipnis orcidipnis is quite common along the lower part of the trail to La Banderola.

Pronophila orcus orcus (Latreille, [1813])

Satyrus orcus Latreille, [1813]:72; 1817: pl. 35, figs. 1, 2.

Satyrus orchamus Godart, [1824]:486. Synonymy established by Thieme, 1907: 202.

Taygetis orcus (Latreille); Westwood, 1851:357.

Pronophila porsenna Hewitson, 1862:12, pl. 5, fig. 34. Synonymy established by Thieme, 1907:202.

Pronophila orcus (Latreille); Thieme, 1907:202.

Material examined. – VENEZUELA: 13 males, Betania-El Potrero, 28/29 May 1994, A. Viloria, J. Camacho, M. García *leg*. [MALUZ].

Remarks.— This is a widespread species, but with several

geographical subspecies. The population from El Tamá appears to be similar to the nominate subspecies (Pyrcz, 2004). It flies at lower to medium elevations in the cloud forest. We found it in the Betania area only in 1994.

PSEUDOMANIOLA Röber, [1889]

Pseudomaniola Röber, [1889]:222. Type-species Daedalma pholoe Staudinger, 1887, by subsequent designation (Hemming, 1943:23-24).

Pseudomaniola phaselis phaselis (Hewitson, 1862)

Pronophila phaselis Hewitson, 1862:14, pl. 6, fig. 7. Catargynnis phaselis (Hewitson); Thieme, 1907:152. Pseudomaniola phaselis (Hewitson); Adams, 1986:311.

Material examined.— VENEZUELA: 6 males, Mata de Mula, 1700-1800m [FFR]; 1 female, Estado Táchira, Hacienda Pánaga, Apr 1989, 800m, F. Rey *leg*. [TWP].

Remarks.- This fairly polytypic species has a very wide Pan-Andean distribution (Cordillera de la Costa and Sierra Nevada de Santa Marta to Bolivia), but its range is disjunct (Pyrcz, 2004). It seems to be absent from many areas. It occurs in lower cloud forests. In El Tamá it has been reported from Mata Mula at around 1800m. One record from the valley of San Cristóbal (Hacienda Pánaga, 800m) is reliable but very unusual.

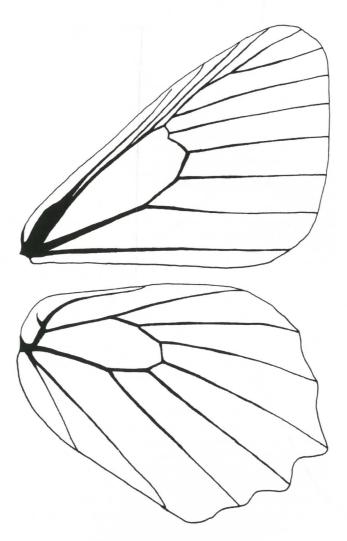


Fig. 48. Wing venation of male Ianussiusa maso maso (Godman).

Pseudomaniola loxo (Dognin, 1891)

Oxeoschistus loxo Dognin, 1891:132.

Pronophila sagartia Grose-Smith, 1900: pl. 1, fig. 2. Synonymy established by Thieme, 1907:155.

Daedalma bronza Weeks, 1901:355; 1905: pl. 35. Synonymy established by Thieme, 1907:155.

Catargynnis loxo (Dognin); Thieme, 1907:155. Pseudomaniola loxo (Dognin); Adams, 1986:312.

Material examined.— VENEZUELA: 1 male, selva arriba de Betania, 2400-2480m, 24 Aug 1996, A. Viloria, V. Carrizo & L. E. González *leg*. [MALUZ]; 1 female, San Vicente de la Revancha, 2350m, 17 Mar 1995, F. Rey *leg*. [TWP].

Remarks.—This species occurs in the three Colombian Cordilleras -contrary to the opinion of Adams (1986) who thought it is confined to the Central and Oriental Cordilleras-, but also in Ecuador. It has a relatively wide altitudinal range, being reported from elevations between 2000m (Tambito, Cordillera Occidental, Pyrcz and Wojtusiak, 1999) and 2900m (Fassl, 1918).

STEREMNIA Thieme, 1905

Steremnia Thieme, 1905:137. Type-species: Steremnia rugilas Thieme, 1905 (by subsequent designation, Brown, 1941:433).

Steremnia pronophila fluminea Pyrcz & Viloria, new subsp. (Fig. 17)

Steroma pronophila C. & R. Felder, 1867:475.

[Sterennia pronophila subsp. nov. Pyrcz & Viloria, MS]; Viloria, 2000:267. [Sterennia pronophila n. ssp. Pyrcz & Viloria, MS, no. 1070b]; Lamas et al., 2004:215.

Diagnosis.— Larger than the nominate subspecies. Upperside slightly darker brown, although variable. Underside also darker, silver scaling on hindwing indistinct, submarginal yellow dots fainter.

Description.— MALE (Fig. 17): Forewing length: 20.5-2 mm; mean: 21.45mm; n=33. Upperside of both wings uniform blackish brown, lustrous, forewing fringes white in each cell. Forewing underside dark chocolate brown dusted with sparse whitish and black scales at apex, a series of three to four submarginal white dots, one each in cells R5-M1 to M2-M3. Hindwing underside black speckled liberally with white scales, especially along outer margin, a white sinuate streak at mid costa reaching vein M2, a row of pale yellow submarginal dots apparent in each cell, in Cu2-1A faint.

FEMALE: Unknown.

Material examined.— Holotype (male): Betania - El Potrero, Venezuela, 2400-2600m, 28/29 May 1994, A. Viloria, J. Camacho & M. García *leg*, [MALUZ]. Holotype deposited in MALUZ.

Paratypes: VENEZUELA: 3 males, bosque arriba de Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo & D. González leg.; 1 male, same locality, 2400-2450m, 15 Aug 1996, A. Viloria, V. Carrizo & J. González; 1 male, same locality, 2350m, 16 Aug 1996, A. Viloria & V. Carrizo leg.; 1 male, Betania, El Potrero, 2395m, 17 Aug 1996, A. Viloria, V. Carrizo & D. González; 5 males, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo & J. & A. González leg. [MALUZ]; 1 male, Betania, P. N. El Tamá, 2200-2300m, 16 Apr 1996, T. Pyrcz leg. [AFN]; 30 males, Betania, P. N. El Tamá, 2200-2300 m, 15-17 April 1996, T. Pyrcz leg.; 1 male, via Delicias, 1900m, May 1986, F. Romero leg. [TWP].

Etymology.— fluminea, latin adjective from fluminis, river. Most individuals were observed and collected on a river bank.

Remarks.- Steremnia pronophila pronophila (C. & R. Felder) occurs in the Colombian Cordillera Oriental, whereas S. selva Adams flies in the Cordillera Central, and Ecuador. Adams (1986) reports it from upper cloud forests and forest-páramo ecotone. However, in El Tamá S. pronophila fluminea flies at much lower elevations and is particularly abundant at 2200-2300m. Most individuals were collected while mud puddling on a river bank in Betania along with L. albocincta and I. maso santa. The population of El Tamá differs consistently from the nominate subspecies occurring in the southern part of the Cordillera Oriental in

Colombia, not only in its ecology and behavior but also on morphological ground, as briefly stated above. The specimen curated in the type collection in the BMNH under *S. pronophila*, and bearing the label "type" does not correspond to the original description of Felder's *S. pronophila*, but represents *Steremnia selva* Adams.

STEROMA Westwood, [1850]

Steroma Westwood, [1850]: pl. 66, fig. 6. Type-species: Steroma bega Westwood, [1850], by monotypy.

Steroma bega Westwood, [1850]

Steroma bega Westwood [1850]: pl. 66, fig. 6.Steroma zibia Butler, 1870:23. Synonymy established by Adams and Bernard, 1979:117.

Material examined.— VENEZUELA: 1 male, Este de Betania, 2780-2810m, 16/19 Feb 1992, A. Viloria, J. Camacho & R. Calchi *leg.*; 7 males, Betania - El Potrero, 2400-2600m, 28/29 May 1994, A. Viloria, J. Camacho & M. García *leg.*; 4 males, bosque arriba de Betania, 2400-2500m, 14 Aug 1996, A. Viloria, V. Carrizo & D. González *leg.*; 1 male, same locality, 2400-2450m, 15 Aug 1996, A. Viloria, V. Carrizo & J. González *leg.*; 1 male, same locality, 2350m, 16 Aug 1996, A. Viloria & V. Carrizo *leg.*; 1 male, entre Betania y La Cueva, 2600m, 26 Aug 1996, A. Viloria, V. Carrizo & A. González *leg.*; 3 males, selva nublada arriba de Betania, 2400-2480m, 24 Aug 1996, A. Viloria, V. Carrizo & L. E. González *leg.*; 1 male, selva vía al Paramito, 2400-2460m, 27 Aug 1996, A. Viloria, V. Carrizo & D. González *leg.*; 4 males, 1 female, selva arriba de Betania, 2400-2460m, 28 Aug 1996, A. Viloria, V. Carrizo & J. & A. González *leg.* [MALUZ].

Remarks.— This taxon was considered by Weymer (1912), Brown (1943), and Adams and Bernard (1981) as conspecific with *S. andensis* C. & R. Felder. The latter replaces *S. bega* on the western slopes of the Cordillera Oriental, and southwards to Bolivia. This taxonomic treatment is consistent with that of other allopatric duos, which have similar distribution patterns in the northern Andes, and morphological differences (such as *Lymanopoda lebbaea* and *L. labda*, *Steremnia selva* and *S. pronophila*). *Steroma bega* has a particularly wide altitude range, being found from 2000m up to the upper cloud forest limit.

DISCUSSION

From the biogeographical standpoint, the main achievement of this survey is that it provides data for assessing the so-called Táchira Depression, the valley separating the Andean Cordillera Oriental from the Cordillera de Mérida, as a distributional barrier. The Táchira Depression is only about 20 km wide at 2000m and the two ranges meet at 1000m. Still, it is the lowermost point within the whole Andes between Venezuela and southern Chile. Prior to this study, comprehensive faunal data on high elevation butterflies were available only for the Cordillera de Mérida (Adams and Bernard, 1981; Pyrcz and Wojtusiak, 2002) but there were barely any data for El Tamá (Pyrcz, 1995; Rey and Pyrcz, 1996; Johnson et al., 1997; Wojtusiak and Rey, 1999; Orellana, 2000). The importance of the Táchira Depression as a biogeographical barrier for other Andean organisms was demonstrated for high altitude birds (Vuilleumier and Ewert, 1978; Vuilleumier, 1984) and páramo plants (Cuatrecasas, 1979). This study shows that it also plays an important role in shaping diversity and structure of the satyrine faunas.

Species Richness (Table 4)

The most immediate observation is that there are approximately 32% more montane satyrine species in El Tamá - 56, than in the

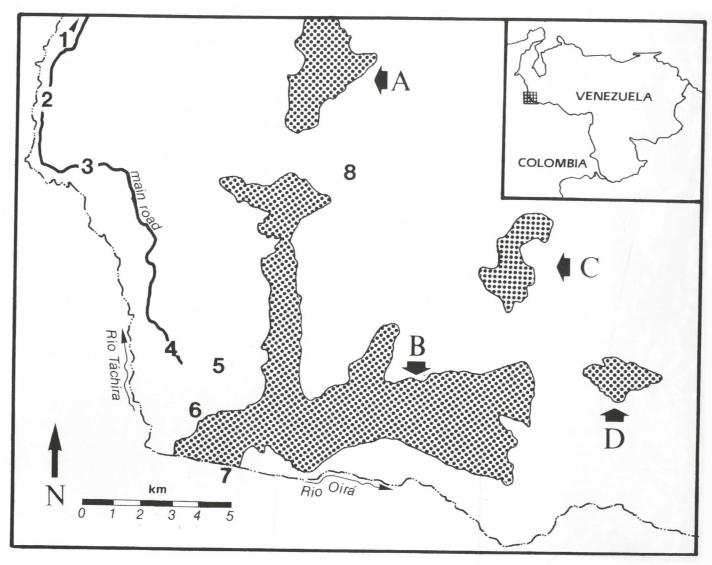


Fig. 49. Schematic of the region of the Serranía del Tamá (Venezuela and Colombia). A, B, C, D represent páramo land (above 3000m). A: Páramo Revancha, B: Páramo de El Tamá, C: Serranía de Santa Bárbara, D: Páramo Judío, 1: Road Delicias-Bramón, 2: Delicias, 3: Villa Páez, 4: Betania + selva arriba + El Potrero, 5: El Paramito, 6: via La Línea + Picacho de la Cueva del Oso + Cerro La Banderola, 7: La Línea, 8: San Vicente de La Revancha (from PDVSA, Hoja No. NB 18-4, Mosaico Semicontrolado).

neighboring Cordillera de Mérida - 38 (all figures refer to potential altitudinal transects covering the whole altitudinal range of the tribe, thus do not include allopatric species; see Pyrcz, 2004). The decrease in the number of species on the north side of the Táchira Depression is not an isolated geographical accident but a step in a more general pattern, which is a steady reduction of species richness from south to north (Table 4). In fact, there are nearly three times as many species of erebiines and pronophilines in El Tamá as in the most northernly Andean peripheral Sierra Nevada de Santa Marta - 25 (Adams and Benard, 1977) and as in the Cordillera de La Costa - 21 (Viloria and Pyrcz, unpublished data). On the other hand, there are still much fewer species in El Tamá compared to other Colombian ranges - 75 species on the east slopes of the Cordillera Oriental of the Andes in the area of Bogotá (Adams, 1986; modified), and 78 species on the east slopes of the Cordillera Central in the Puracé range (Adams, 1986; Pyrcz, 1999a, 1999b). The species richness further increases towards the south, reaching 82 species in east Ecuador, Tungurahua (Pyrcz, unpublished data), and over 100 species in Zamora, south-east Ecuador (Pyrcz, unpublished data). The relatively low

diversity of montane satyrines of the Venezuelan ranges was explained in terms of their isolation from the main Andean block (Adams, 1985; Pyrcz and Wojtusiak, 2002), where the bulk of radiation of the group, especially the Pronophilina, has occurred. It can also be related with other factors, both physical (area of montane habitats) and ecological (habitat diversity). However, the explanation for huge differences in the species richness of the subtribe Pronophilina within the main Andean chain is less straightforward.

FAUNAL AFFINITIES

Genera (Tables 1, 3)

From among 20 genera of Erebiina and Pronophilina in El Tamá, 17 are Intertropical Panandean, that is to say, they occur at least from Colombia to Bolivia. Within the erebiines, one genus found in El Tamá, *Tamania*, is apparently endemic. The genus *Ianussiusa* has apparently a disjunct distribution. It has not been reported from the remaining areas of the Cordillera Oriental but it is known to occur in the Cordillera Central (Tolima) and in east Ecuador (Napo). The third erebiine genus with a restricted

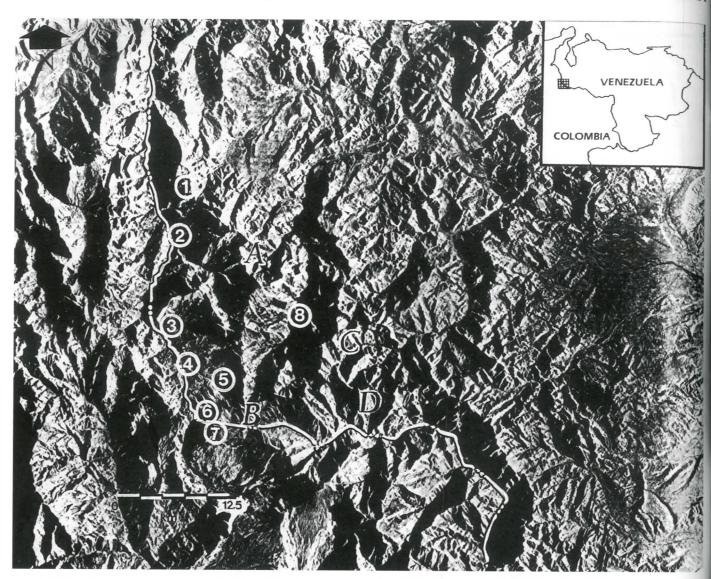


Fig. 50. Aerial photograph of the region of the Serranía del Tamá (Venezuela and Colombia) (like Fig. 49). A, B, C, D represent páramo land (above 3000m). A: Páramo Revancha, B: Páramo de El Tamá, C: Serranía de Santa Bárbara, D: Páramo Judío, 1: Road Delicias-Bramón, 2: Delicias, 3: Villa Páez, 4: Betania + selva arriba + El Potrero, 5: El Paramito, 6: via La Línea + Picacho de la Cueva del Oso + Cerro La Banderola, 7: La Línea, 8: San Vicente de La Revancha (from PDVSA, Hoja No. NB 18-4, Mosaico Semicontrolado).

range, *Idioneurula*, is endemic in the Colombian Cordillera Oriental. For four Panandean pronophiline genera – *Junea*, *Daedalma, Steremnia* and *Altopedaliodes* (the latter, possibly paraphyletic) – the El Tamá range is the northernmost limit of their distribution. About half of the genera known in El Tamá extend into the Cordillera de Mérida. On the other hand, the fauna of Mérida comprises three pronophiline genera (*Redonda* Adams & Bernard, *Cheimas* Thieme and *Steromapedaliodes* Forster), and one erebiine genus (*Diaphanos* Adams & Bernard), which are all endemic and do not occur south of the Táchira Depression (Table 1). All of them occur in the forest-páramo ecotone or above the tree line (Table 3).

Species

El Tamá shares 47 species with the southern Cordillera Oriental. Ten species found in El Tamá are not known to occur in the Bogotá area. On the other hand, the fauna of the southern Cordillera Oriental (both east and west slopes) comprises an additional 22 species, which have not yet been reported from El Tamá. Some of these could eventually be found in this range and

their absence in our check-list is probably due to insufficient sampling rather than to their actual distribution, particularly: Daedalma dinias Hewitson, Junea doraete (Hewitson), Lymanopoda viventieni (Apolinar), Mygona propylea (Hewitson), Pedaliodes phrasicla (Hewitson), and Pedaliodes phrasiclea Grose-Smith. 27 species known in El Tamá occur in the Cordillera de Mérida (Table 2).

Subspecies

Twenty six species (46.4% of the local fauna) are represented by the same subspecies in El Tamá and the Bogotá area (Corades enyo almo, C. medeba columbina, C. pannonia ploas, C. dymantis, C. cybele, C. chirone, Daedalma drusilla, Junea dorinda, Lymanopoda ionius, L. obsoleta, L. albocincta, Mygona irmina, Panyapedaliodes panyasis, P. jephtha, Praepronophila perperna perperna, Pronophila unifasciata bogotensis, Pseudomaniola loxo, Steroma bega, Pedaliodes poesia, P. manis, P. montagna, P. praemontagna, P. proerna proerna, P. phoenissa, P. polusca, and P. polla). The status of the Colombian subspecies of P. porina is in need of revision.

Table 1. Similarity ratio between mountain ranges for satyrine butterfly genera (n/Nt; where n is the number of shared genera, and Nt is total number of genera found in both ranges).

	Tamá	Mérida	Bogotá	Zamora
Tamá	1			
Mérida	0.54	1		
Bogotá	0.81	0.52	1	
Zamora	0.90	0.47	0.89	1

Table 2. Similarity ratio between mountain ranges for satyrine butterfly species (n/Nt; where n is the number of shared species, and Nt is the total number of species found in both ranges).

	Tamá	Mérida	Bogotá	Zamora
Tamá	1			
Mérida	0.40	1		
Bogotá	0.54	0.17	1	
Zamora	0.18	0.07	0.21	1

Table 3. Andean genera of Satyrinae with restricted distribution occurring in the Serranía de El Tamá and the Cordillera de Mérida; their habitats and ranges.

Genus	Tamá	Mérida	Habitat	Range
Ianussiusa	+	-	Mid-elevation cloud forest	El Tamá-Ecuador
Idioneurula	+	-	Páramo	El Tamá-Bogotá
Tamania	+	-	Mid-elevation grassland	El Tamá
Altopedaliodes	+	-	Páramo	El Tamá-Bolivia
Daedalma	+	-	Upper and uppermost cloud forest	El Tamá-Bolivia
Junea	+	-	Upper and uppermost cloud forest	El Tamá-Bolivia
Steremnia	+	-	Mid-elevation, upper forest and páramo*	El Tamá-Bolivia
Diaphanos	-	+	Páramo	Mérida
Cheimas	-	+	Forest-páramo ecotone	Mérida
Redonda	-	+	Páramo	Mérida
Steromapedaliodes	-	+	Forest-páramo ecotone	Mérida

^{*} Several species of *Steremnia* occur in páramo but the only representative of this genus in El Tamá is a middle to upper elevation cloud forest species.

Table 4. Species richness of montane pronophiline butterflies in some Andean ranges (species richness along potential altitudinal transects).

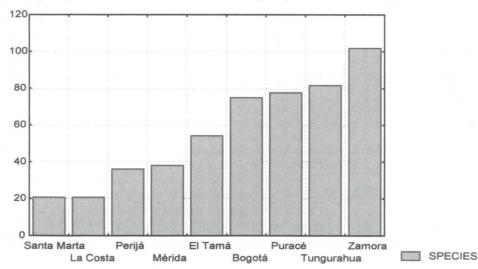


Table 5. List of the montane satyrine butterflies (Erebiina and Pronophilina) of the Serranía del Tamá (Venezuela and Colombia), with their ranges of altitudinal distribution.

Tribe	Species	Altitudinal range (m above sea level)	
Erebiina Tutt	Ianussiusa maso santa Pyrcz & Viloria	2395-2500	
	Idioneurula eremita Viloria & Pyrcz	2400-3350	
	Manerebia leaena gonzalezi Viloria & Pyrcz	1850-2700	
	Manerebia mycalesoides (C. & R. Felder)	1400	
	Manerebia pervaga Viloria & Pyrcz	2600-3350	
	Manerebia pluviosa Viloria & Pyrcz	2810	
	Tamania jacquelinae Pyrcz	2300-2500	
Pronophilina Reuter	Altopedaliodes tamaensis Viloria & Pyrcz	3100-3350	
	Corades chelonis rubeta Thieme	2520-2620	
	Corades chirone Hewitson	2700-3000	
	Corades cybele Butler	2700	
	Corades dymantis Thieme	2400	
	Corades enyo almo Thieme	2200-2300	
	Corades medeba columbina Staudinger	2200-2700	
	Corades pannonia ploas Thieme	2400-2600	
	Daedalma drusilla Hewitson	2425-3000	
	Eretris apuleja remotissima Pyrcz & Viloria	2900-3100	
	Eretris encycla (C. & R. Felder)	1850-2460	
	Eretris porphyria recta Pyrcz & Viloria	2200-3100	
	Junea dorinda dorinda (C. & R. Felder)	2000-2350	
	Lasiophila circe arithmetica Viloria & Pyrcz	2700-3000	
	Lasiophila zapatoza elusiva Pyrcz & Viloria	2200-2700	
	Lymanopoda albocincta Hewitson	1850-2600	
	Lymanopoda ionius Westwood	2800	
	Lymanopoda lebbaea moritzi Pyrcz & Viloria	2300-2780	
	Lymanopoda lecromi Pyrcz & Viloria	2200-3200	
	Lymanopoda obsoleta (Westwood)	2200-2500	
	Lymanopoda samius lineana Pyrcz & Viloria	3100-3350	
	Mygona irmina (Doubleday)	1800-2500	
	Oxeoschistus puerta magnus Pyrcz & Viloria	1000-2350	
	Panyapedaliodes jephtha (Thieme)	2350-2900	
	Panyapedaliodes panyasis (Hewitson)	2400-2520	
	Panyapedaliodes tomentosa (Weymer)	2300-2700	
	Pedaliodes baccara allopatra Viloria & Pyrcz	2200-2780	
	Pedaliodes empusa medusa Pyrcz & Viloria	2800-3350	
	Pedaliodes manis (C. & R. Felder)	1800-2600	
	Pedaliodes montagna Adams & Bernard	2300-2600	
	Pedaliodes phoenissa (Hewitson)	2600	
	Pedaliodes pisonia (Hewitson)	2200	
	Pedaliodes plotina ruricola Pyrcz & Viloria	1900-2600	
	Pedaliodes poesia (Hewitson)	1850-2600	
	Pedaliodes polla Thieme	2400-3000	
	Pedaliodes polusca (Hewitson) Pedaliodes porina (Hewitson)	2800	
		1900	
	Pedaliodes praemontagna Viloria & Pyrcz Pedaliodes proerna proerna (Hewitson)	2200-3100	
	Pedaliodes reyi Viloria & Pyrcz	1700-2700	
	Pedaliodes valencia Pyrcz & Viloria	2300-3200	
	Praepronophila perperna perperna (Hewitson)	3200	
	Pronophila epidipnis orcidipnis Pyrcz & Viloria	1100	
	Pronophila orcus orcus (Latreille)	2300-2700	
	Pronophila unifasciata bogotensis Jurriaanse	2400	
	Pseudomaniola loxo (Dognin)	1800-1900 2350-2480	
	Pseudomaniola phaselis phaselis (Hewitson)	800-1800	
	Steremnia pronophila fluminea Pyrcz & Viloria	2200-2600	
	Steroma bega Westwood	2350-2810	

Fifteen species (26.7% of the local fauna) are represented in El Tamá and the Cordillera de Mérida (Chama valley) by the same subspecies (C. enyo almo, C. chelonis rubeta, C. medeba columbina, C. pannonia ploas, Eretris encycla, Lymanopoda obsoleta, L. albocincta, Mygona irmina, Panyapedaliodes panyasis, P. jephtha, Praepronophila perperna perperna, P. unifasciata bogotensis, Steroma bega, Pedaliodes manis, and P. montagna).

These figures emphasized not only the stronger biogeographical affinity between the Serranía de El Tamá and the Cordillera Oriental, but also the relevance of the Táchira Depression in the lowering of the affinities between the former range and the Cordillera de Mérida.

ENDEMISM

The El Tamá range harbors only one endemic genus so far, Tamania. There are overall 9 endemic species, which represent 16.07% of the total number of local species. This figure is lower than in the Cordillera de Mérida (37.83%), but approximately the same as in other main Andean localities in Colombia and Ecuador (Adams, 1985; Pyrcz, 2004). Three endemic species occur in the páramo, Idioneurula eremita, Manerebia pervaga, and Altopedaliodes tamaensis; three in the uppermost forest, Manerebia pluviosa, Pedaliodes reyi and P. valencia; one in mid-elevation forest, Lymanopoda lecromi; and one in mid-elevation grassland, Tamania jacquelinae. No endemic species occur in El Tamá below 2600m (except where páramo populated by endemic species descends to 2500m). Four endemic species have their sister species in the central or southern Cordillera Oriental, while one of them (P. valencia), curiously enough, seems to be more closely related to the species occurring exclusively in the Colombian Cordillera Central (P. wilhelmi Pyrcz). One endemic (L. lecromi) is replaced by a very close ally on the oposite side of the Táchira Depression (Lymanopoda sp. nov., Viloria and Pyrcz, in prep.), while two have no close relatives at all (T. jacquelinae and M. pluviosa).

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