Pronophiline butterflies (Satyridae) of the three Andean Cordilleras of Colombia

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The 125 species of the satyrid butterfly tribe Pronophilini known from the three Andean Cordilleras of Colombia are listed, together with two species whose Colombian status is doubtful. The biological, ecological and biogeographical features of the tribe are described, using the listed species as examples. The features include restriction to moist conditions at high altitudes, endemism in the Cordilleras and in areas and on slopes within them, allopatic speciation and subspeciation, parapatric distributions of related species up the altitude gradients, intraspecific variation and polymorphism and apparent mimicry. The criteria used for classifying the taxa and assessing their relationships are discussed. Seventeen new species, three new subspecies and one new form are described. At the species level, 11 new synonymies are established, two synonymies are rejected, the status of 15 other taxa is revised, and 23 new combinations are made. At the generic level, two new synonymies are established, and one genus is resurrected.


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Genus Oxeosrhtus Butler ...
Genus Panyapedaliodes Forster, gen. rev ...
Genus Parapedaliodes Forster ...
Genus Pedaliodes Butler ...
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INTRODUCTION

The Colombian Cordilleras

In the southwest of the Republic of Colombia, the Andes divide into three more-or-less parallel mountain chains, or Cordilleras, which extend for hundreds of kilometres north-northeastwards. The narrowest and least high, the Western Cordillera, is separated from the main Andean backbone by the gorge of the Río Patía and from the Central Cordillera by the Cauca valley. It runs for some 600 km between 2 and 7°N, with its highest point, in the Farallones de Cali, at about 4400 m above sea-level; for most of its length, its central ridge lies above 2000 m, yet the distance between the Cauca river to its east and its western 1000-m contour is only 40–70 km.

The Central Cordillera is the main extension of the Andean backbone, with no distinct southern starting-point. For the purposes of this paper, I consider its southernmost limit to be bounded by the Juanumbu and Putumayo rivers, east of Pasto, at 1°20'N. From there it runs for about 670 km to 7°N, bounded to its west by the Cauca valley and to its east by the Magdalena valley (the two rivers being between 100 and 140 km apart). Its highest mountains are the Nevado del Huila (5750 m) and the Nevado del Ruiz (5400 m); its central ridge lies entirely above 2500 m northwards to Medellín.

The Eastern Cordillera begins as a narrow ridge, joining the Central Cordillera near its southern limit at the headwaters of the Magdalena and Caquetá rivers. The 3000-m contour is not reached for some 300 km (at 3°30'N), but northeast of this point the Cordillera broadens so that in Boyacá its 1500-m contours are separated by 180 km of higher land. Its highest peak is in the Sierra Nevada del Cocuy (5493 m), and I consider its northernmost limit to be at Ocaña (8°16'N); its overall length is therefore about 830 km. (North of Ocaña, a relatively low, narrow ridge (the Sierra de Perijá) extends to the Serranía de Valledupar, and at 7°40'N lies the southwestern extremity of the Venezuelan Cordillera de Mérida.)

The area of land lying above 2000 m in each of the Cordilleras is: Eastern, 48,300 km²; Central, 33,400 km²; Western, 10,600 km² (Adams, 1985). The approximate maximum elevations of contact between the northern Andean ranges are as follows: Western—Central Cordilleras, 1500 m; Central Cordillera—main Andean backbone, 2500 m; Eastern—Central Cordilleras, 2000 m; Eastern Cordillera—Cordillera de Mérida, 1000 m; Eastern Cordillera—Serranía de Valledupar, 1500 m.
Biology and ecology of Pronophilini

The Pronophilini Reuter (Miller, 1968) is a tribe of the Satyridae distributed from Arizona, U.S.A., to Patagonia (including the West Indies). The majority of species fly in the montane cloud-forests and above the tree-line in the Andes of Colombia, Venezuela, Ecuador, Peru and Bolivia. In Colombia, very few species occur below 1800 m; a greater number fly in the páramo above the tree-line, that is above about 3500 m; but the maximum species diversity is found at 2600–2700 m in the Andean Cordilleras (Adams, 1985). As Adams & Bernard (1977, 1979, 1981) have already pointed out, all the northern Andean species have a requirement for moist conditions, which is met in the cloud-forests and páramo by cloud immersion and rainfall almost every day for about 10 months of the year. Even within the forest, and certainly in the páramo, many species are concentrated along water-courses or in marshy terrain. The majority of the forest species are most commonly found where there are stands of Chusquea ‘climbing’ bamboos (known as “chusque” or “cañuela” by the native people), and it seems possible that this genus contains the food-plants of most of the pronophilines (see Adams & Bernard, 1981).

Judged by the fact that extremely few species stray out of the forest into pasture, or even secondary scrub or partly regenerated forest, and that each species occurs within a tightly defined range of altitudes, the pronophilines are strongly sedentary and have narrow ecological niches. Two exceptions, Pedaliodes manis and Panyapedaliodes drymaea, fly commonly in pasture and along open roadsides well away from the forest. In areas where Chusquea is abundant, such as clearings and roadsides in the forest, at the forest edge (including the tree-line in some places) and along water-courses in otherwise open land, pronophilines often occur in large numbers; their neglect by collectors is due more to their generally drab coloration than to scarcity (see Brown, 1943: 92). In most areas above 2500 m, where there is cloud-forest and páramo, they are by far the commonest group of butterflies.

Some species, including many of those which are rare in collections and usually found singly in the field, spend most of their time out of reach in the forest trees or skipping around the tops of clumps of Chusquea (e.g. Junea and Mygona species, the Lymanopoda samius group, Panyapedaliodes panyasis, Pronophila bogotensis and P. orchewitsoni); but there are very few that do not, when the sun shines, temporarily join the majority of the species near ground level, and many can be baited to the ground by the use of faeces (human and dog are the best). In my experience, it is freshly emerged butterflies, possibly taking their first meal, which are particularly easily baited in this way (see under Corades chirone). Most, if not all, of the species feed on mineral and dead organic matter, finding it among leaf litter, in damp patches on roadsides, clearings or the banks of water-courses, in excrement and in rainwater and dew. At the highest altitudes, where there are often three or more days at a stretch without sun, the butterflies can survive and they then respond quickly to short sunny intervals by flying and searching for food.

In the Colombian Cordilleras, large tracts of primaeval cloud-forest still exist, in spite of the ravages of human interference and agriculture; but many are not easily accessible. Even in the best-known cloud-forest national park, Puracé in the Central Cordillera, illegal logging by peasant farmers is widespread. The
Institute for the Development of Natural and Renewable Resources ("Inderena") is quite effective at ensuring that forest is at least not removed from water-courses, so that even fairly close to Bogotá good collecting sites are still to be found. In many parts of the Central Cordillera unpaved roads have been built into the páramo, but do not cross the range yet and so are lightly populated; these allow access to rich areas of cloud-forest (for example, in the Puracé area). Natural areas of páramo—the moist or marshy moors above the tree-line—are easier to find than virgin cloud-forest.

Pronophiline butterflies could be employed by conservationists as indicators of the biological richness and importance of areas of cloud-forest and páramo; there is likely to be a strong link between pronophiline species numbers and general animal diversity, and between pronophiline species and subspecies endemism and general endemism among the fauna (Adams, 1983).

**Biogeography and endemism**

There are 125 species of Pronophilini, 10 of them with two or three subspecies, known from the Colombian Cordilleras, belonging to 24 genera. Although many species co-exist in most localities (30 were recorded between 2500 and 2700 m above San José de Isnos in the Central Cordillera), there are, within this large assemblage, ‘networks’ of closely related species, which are geographically separated from each other in two ways: 48 of the species, of nine of the genera, have allopatric close allies at similar altitudes in one or more of the other Cordilleras (including, in several cases, the slopes on the other side of the same Cordillera); no fewer than 61 species of 11 genera have parapatric close relatives occupying bands of altitudes above or below them on the same mountainsides. As pointed out by Adams & Bernard (1979, 1981) and Adams (1977, 1985), the universality of parapatric distributions within the Pronophilini seems to be unique in the animal world and its existence has been a major factor in the evolutionary radiation of the tribe. Adams (1977, 1985) has offered a theory of the origins of both the allopatric and parapatric groups of related species, based on the assumption that the Pleistocene Ice Ages induced a series of cycles of butterfly spread between, and isolation within, the northern Andean mountain ranges.

Table 1 gives examples of straightforward allopatry of close relatives which are not involved in parapatric groups. Table 2 includes examples of series of closely allied parapatric species, some of which occur ‘in parallel’, as it were, in two or more of the Cordilleras. The best examples of groups of species which exhibit both allopatry and parapatry exist within the two largest genera, Pedaliodes (40 species) and Lymanopoda (19 species), and these are shown in Table 3.

The Eastern Cordillera harbours six pairs of related species which have differentiated on the east and west slopes (all are included in Tables 1 and 3); in addition, five species have two or three subspecies within the Cordillera: Eretris porphyria, E. apuleja, Pedaliodes fuscata, P. phaea and Steroma bega. The division between the east and west slopes, however, is not clear-cut in every case: the Cocuy region in the north (east slope) has one species and two subspecies found on the west slope near Bogotá (Pedaliodes empusa, P. fuscata parapatra and E. p. porphyria); and its race of E. apuleja is referable to subrufescens, known
Table 1. Allopatric subspeciation and speciation; examples of Colombian species not involved in parapatric groups

<table>
<thead>
<tr>
<th></th>
<th>Western Cordillera</th>
<th>Central Cordillera</th>
<th>Eastern Cordillera</th>
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<tbody>
<tr>
<td>Lymanopoda</td>
<td></td>
<td>labda</td>
<td>lebbara</td>
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<tr>
<td>Pedaliodes</td>
<td></td>
<td>“pheretias”</td>
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<tr>
<td>Steroma beka</td>
<td>andensis</td>
<td>andensis</td>
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<tr>
<td>Parapedaliodes</td>
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</tr>
<tr>
<td>Pedaliodes</td>
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<td></td>
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<tr>
<td>Pedaliodes fylas</td>
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<tr>
<td>Penrosada</td>
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<td>Steremnia</td>
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</table>

Table 2. Parapatric species; some examples from the Colombian Pronophilini

<table>
<thead>
<tr>
<th></th>
<th>Lowest altitudes</th>
<th>Highest altitudes</th>
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</thead>
<tbody>
<tr>
<td>Eretris</td>
<td>calisto</td>
<td>porphyria</td>
</tr>
<tr>
<td>Mygona</td>
<td>irmina</td>
<td>propylea</td>
</tr>
<tr>
<td>Altopedaliodes</td>
<td>flavopunctata</td>
<td>reissi</td>
</tr>
<tr>
<td>Corades</td>
<td>enyo almo</td>
<td>chelonis</td>
</tr>
<tr>
<td>Corades</td>
<td>pannonia ploas</td>
<td>cistene dymanitis/chirone</td>
</tr>
<tr>
<td>Daedalma</td>
<td>dinias</td>
<td>drusilla</td>
</tr>
<tr>
<td>Junza</td>
<td>dorinda</td>
<td>doraete</td>
</tr>
<tr>
<td>Lasiosphila</td>
<td>zapatoza sombra</td>
<td>circe</td>
</tr>
<tr>
<td>Pedaliodes</td>
<td>poesia</td>
<td>phanissa</td>
</tr>
<tr>
<td>Pedaliodes</td>
<td>monis</td>
<td>manneja</td>
</tr>
</tbody>
</table>

Table 3. Allopatric subspeciation and speciation, of parapatric species; Colombian examples, the upper species occupying the upper bands of altitude in the parapatric groups

<table>
<thead>
<tr>
<th></th>
<th>Western Cordillera</th>
<th>Central Cordillera</th>
<th>Eastern Cordillera</th>
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<tbody>
<tr>
<td>Lymanopoda</td>
<td></td>
<td>huilana</td>
<td>viienteni</td>
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<tr>
<td></td>
<td>excisa</td>
<td>melia</td>
<td>lactea</td>
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<tr>
<td></td>
<td>labineta</td>
<td>excisa</td>
<td>ionitus</td>
</tr>
<tr>
<td>Pedaliodes</td>
<td>soccorae</td>
<td>phaedra</td>
<td>pallantis</td>
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<td></td>
<td>peucetas</td>
<td>peucetas</td>
<td>peucetas</td>
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<td>phrasicta</td>
<td>phrasicta</td>
<td>phrasicta</td>
</tr>
<tr>
<td>Pedaliodes</td>
<td>parranda</td>
<td>palpita</td>
<td>polusca</td>
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<tr>
<td>Pedaliodes</td>
<td>(Pollonia)</td>
<td>polusca</td>
<td>polusca</td>
</tr>
<tr>
<td>Pedaliodes</td>
<td></td>
<td>polonia</td>
<td>polia</td>
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<tr>
<td>Pedaliodes</td>
<td></td>
<td>phaeina</td>
<td>bernani</td>
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<td></td>
<td></td>
<td>phaea phaea</td>
<td>f. ochoturnia</td>
</tr>
<tr>
<td></td>
<td></td>
<td>fusca parapara</td>
<td>f. fusca</td>
</tr>
<tr>
<td>Pedaliodes</td>
<td></td>
<td>empusa</td>
<td>guicama</td>
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<tr>
<td></td>
<td></td>
<td>empusa</td>
<td>empusa/ralphi</td>
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</table>
otherwise from the Central Cordillera. The genus *Eretris* is notable for its inter-population variation, with the disjunct distributions of many of its races suggesting that similar patterns may have arisen independently in different places; the same phenomenon may have occurred to produce a Steroma species in Bolivia, flying above *S. bega andensis*, which looks similar to typical *bega* whose nearest population is in the Colombian Eastern Cordillera (see under *S. bega*).

In the Central Cordillera, quite a number of species are known only either from the Tolima area (about 4°30'N) or from the Huila area further south (2°–3°N), even though both areas have been quite well worked by Fassl, Krüger and Hardy and myself. Examples of species whose only records are from Tolima are *Lymanopoda pieridina*, *Parapedaliodes nora*, *P. margaretha*, *Pedaliodes palpita*, *P. ‘pheretias’* and *P. spina*; the list of those apparently restricted to Huila includes *Altopedaliodes flavopunctata*, *Pedaliodes phanoclea*, ‘*P.* puracana’ and *Steremnia selva*. In addition, *Eretris apuleja* and *Lymanopoda huilana* have developed separate subspecies in the two areas, the latter having two in the Tolima region, north and south of the Ibagué–Armenia divide.

Although records are, of course, incomplete, only 28 of the species are known from all three of the Cordilleras; 37 have been recorded only from the Eastern Cordillera, 18 from the Central Cordillera only, and seven from the Western Cordillera only.

Of the 52 species in the Colombian Cordilleras which are believed to be endemic to Colombia, eight fly in two or more of the ranges. Among the rest, the Eastern Cordillera claims 27, the Central Cordillera 12 and the Western Cordillera four. (The final species, *Lasiophila behemoth*, is of unknown provenance within the country.) As the total species counts from the three ranges are 87, 77 and 47, respectively, their proportions of endemic species are 31.0%, 15.6% and 8.5%. As Adams (1985) showed, there is a significant correlation between percentage endemism in a mountain range and its degree of topographical isolation from its neighbours nearer the main Andean stem (in southern Colombia). The frequencies of endemism in the Central and Western Cordilleras are also lowered by the existence of five species, endemic to Colombia, which occur in both ranges: *Lymanopoda caucana*, *Oxeoschistus pervius*, *Pedaliodes costipunctata*, *Pronophila brennus*, *Pseudomaniola pholoe* and *P. ilsa*. As far as is known, all of these except for *P. costipunctata* inhabit only the west slope of the Central Cordillera. The high degree of endemism in the Eastern Cordillera (and the differences between the faunas of its east and west slopes)—to be expected because of the relative isolation and width of the range—may be augmented by the fact that spread around its northern end is made impossible by the presence of the Sierra de Perijá and Cordillera de Mérida. Adams (1985) also demonstrated that there is a significant correlation between the total numbers of species in each of the Cordilleras and the amount of land it possesses which lies above 2000 m, the Eastern Cordillera having the greatest area and the Western the smallest of the three.

**Classification: problems and criteria**

Inter-population variation is noticeable in several pronophilines, the differences being too small to merit the creation of subspecific names, e.g. in the widespread species, *Pedaliodes poesia*, *P. antigua*, *P. peucetas* and *Pronophila archewitsoni*. Intra-population variation, on the other hand, is very restricted and
only noticeable in few of the species. In some cases, e.g. *Altopedaliodes nebris* and *Idioneurula erebioides* (both of which fly in open, marshy terrain), and *Pedaliodes ferratilis*, it takes the form of graded series of small aberrations of the typical facies. In *Pedaliodes phaedra*, there is a rare case of polymorphism, three discrete forms co-existing in the Huila region of the Central Cordillera; but only one of these, form *niphoessa*, occurs in the Tolima area. Sexual dimorphism is also very rare in the Pronophilini, notable cases being furnished by *Lymanopoda altis*, *L. panacea*, *Daedalma drusilla* and *Thiemeia phoronea*; in most species, the female (always encountered less frequently than the male) is simply larger and paler in its ground colour.

Table 3 demonstrates that among the groups of spatially separated, closely related species in *Lymanopoda* and *Pedaliodes*, it is mostly the uppermost members of the parapatric assemblages that have differentiated into separate species in the different mountain ranges. This is a general rule in the tribe: the higher the altitude preferences of a species, the more likely it is to be endemic, even if its relatives further down the mountainside have wide distributions.

The field data collected on the Colombian pronophilines have been of great value in reassessing taxonomic relationships. The early students of the tribe, for example Hewitson, Butler, Staudinger, Thieme and Weymer, had little besides external morphology to go on; faced with the large numbers of dark brown species, they seemed bemused at times (Hewitson managed to use the initial letter ‘p’ for 52 taxa in his all-embracing genus *Pronophila*), and they seized upon the most visible markings in determining closeness of relationship between species. Many of the groups of species, for example in Thieme’s (1905) valuable monograph on *Pedaliodes*, were founded on the basis of shared conspicuous characteristics, such as white or orange bands, or white or orange ‘wedges’ on the underside of the hindwing; and Weymer (1912) grouped the *Lymanopoda* species using their brown, white or blue upperside ground colour.

My own criteria for the natural classification of pronophilines are given below. In general, there are three taxonomic problems to be solved: first, to which genus should a species be assigned; secondly, is a taxon a species in its own right or merely a geographical race; and thirdly, what are its closest relatives within the genus?

Genera are characterized not only by wing shape and markings, but also by length of labial palpi, colour of legs, size of forelegs and shape of the male genitalia. It is at this level that genitalia are most useful in the tribe: for example, all *Lymanopoda* species (and no others) have a bulbous subuncus and all *Pedaliodes* species have a broad, contorted aedeagus. It was the presence in *Pedaliodes* of species with anomalous genitalia (mostly having a longer, straighter and narrower aedeagus) that led Forster (1964) to attempt to split away from it a number (12) of related genera. Although *Pedaliodes* itself is a very large genus (the largest in the tribe), there is considerable consistency in the species’ size, wing shape and basic underside patterns. This consistency is not so evident in the members of Forster’s 12 related genera: in some, the overlap is so extensive that synonymies have had to be made; in others, certain species can only be tentatively assigned to particular genera because of unique features of their facies and genitalia. It is probable that these evolutionary ‘offshoots’ of the main *Pedaliodes* stock have not radiated as extensively as *Pedaliodes sensu stricto*, but nevertheless have diverged considerably.
The second taxonomic problem is the decision whether to classify two similar taxa as species or subspecies. In cases where the taxa exist sympatrically or parapatrically (and I have never found a hybrid between such taxa), there can be no doubt of their specific status. Difficulties arise, however, in classifying allopatric taxa which share similar altitude preferences and behaviour patterns, and which are similar in appearance. Male genitalia are not useful, since intraspecific variation in their structure leads to overlap between species: divergence of external morphology has normally been more extensive than divergence of genital structure. An idea of the degree of morphological differences which are found between bona fide species in each genus can be gleaned from the parapatric assemblages, but it is very likely that selection for the avoidance of hybridization has forced rapid divergence between them since their parapatry was established; such selection, of course, does not occur in allopatric populations. As pointed out by Adams (1985), while allopatric relatives are assumed to share directly a single common ancestor, parapatric species, because of their supposed secondary origin, share common ancestry ‘at one remove’. If it were possible to quantify the extent of difference between pairs of taxa, and to carry out a cladistic analysis, I believe that the criteria would need to vary according to the biological, biogeographical and evolutionary circumstances. The larger genera (e.g. Lymanopoda and Pedaliodes), it may be surmised, have undergone a more rapid divergence than the smaller genera, such as Eretris, Lasiophila, Steremnia and Steroma. Allopatric populations of the former genera are more likely to have speciated, therefore, than those of the latter genera, regardless of the degree to which they have diverged morphologically. At the same time, populations found at higher altitudes are more likely to have evolved to the species level than relatives further down, because of the assumption (see Adams, 1985) that they have been isolated from one another for longer periods of time. These factors, which take into account rates of evolution and times of initial divergence, must, I believe, be superimposed on the criterion of degree of morphological dissimilarity.

The final question concerns the assessment of relationships between species, particularly in the large genera. It is immediately clear from the study of parapatric groups that conspicuous markings and even wing shape are not always useful indicators of relationship. For example, Pedaliodes phrasiola, with a unicolorous dark brown upperside, is parapatric below P. peucestas, which has an oblique white band across its forewing; above that in the Central Cordillera, P. phaedra has a white (or yellow) patch on its hindwing as well. The upperside ground colours of the three parapatric Lymanopoda species in the Eastern Cordillera (east slope)—L. samius, L. ionius and L. lactea—are blue, brown and white, respectively. The apex of the forewing is of a different shape in the three Mygona species which replace each other up the altitude gradient—M. irmina, M. propylea and M. orsedice. In all such cases, and in allopatric butterflies, it is the basic pattern of the underside of the species, including the numbers and positions of inconspicuous patches and dots, which best characterize their closeness of relationship. It is assumed that the upperside patterns, visible only when the butterflies are flying or sunning themselves, are signals, both intraspecific and interspecific; the underside patterns, primarily designed for camouflage or disguise, are far less subject to fast evolutionary change. The male genitalia are useful here as well, related species within genera sharing similar genital features, sometimes indistinguishable from one another.
At the other end of the scale are the cases of the failure to diverge in closely related but distinct species and convergence of pattern in unrelated species. There are two cases of pairs of virtual sibling species in the Colombian Cordilleras: Pedaliodes manis and P. manneja, and Steremnia pronophila and S. selva. Although there are very slight morphological distinguishing characteristics, manis and manneja can only be securely told apart apart by their genital structure, and pronophila and selva by their habitat and locality. The former pair represents a rare example of strong genital divergence between parapatric relatives (perhaps because of their facial similarity?); the latter pair are separated both geographically and ecologically. Both help to demonstrate that extent of speciation is not necessarily related directly to degree of external morphological divergence.

Morphological convergence has been quite widespread in the Pronophilini. Where convergence of conspicuous upperside markings is not involved, e.g. between the sympatric species Pedaliodes proerna and P. obscura which have almost no markings on their dark brown wings, it can be assumed that selection for effective camouflage has led to the independent evolution of similar underside patterns; the same could be said of the numerous species which share white, yellow or chestnut-brown ‘wedges’, or white costal streaks, on their underside hindwings (or even of Lymanopoda albocincta and L. altis, which fly together and share a white band crossing the underside of the hindwing, unusual in the genus). In cases where unrelated sympatric species have converged in their upperside markings by diverging from the pattern found in most of their relatives, mimicry may be inferred. Clear beak-marks that I have found on at least three individuals of two species (Lymanopoda altasella Adams & Bernard in the Sierra de Perijá and Pedaliodes polusca) provide the only evidence that some pronophilines might in some way be unacceptable to potential bird predators. I believe that Batesian or Müllerian mimicry is a more likely explanation than ‘arithmetic mimicry’ (see Vane-Wright, 1976), since pronophilines do not congregate together and densities are surely never high enough to confuse a predator by ‘weight of numbers’. Examples of such convergence are provided by Pedaliodes peucestas, P. pylas and Lasiophila prosymna in the Central Cordillera, and Physopedaliodes praxithea and Panyapedaliodes philia. Lasiophila prosymna is the only member of its genus with a white oblique forewing band and P. pylas is most closely related to the orange-banded group of Eastern Cordilleran species which includes P. phaea; both P. praxithea and P. philia have an oblique orange forewing band, unique in their respective genera. Another case was reported from the Venezuelan Andes by Adams & Bernard (1981).

MATERIAL AND LITERATURE EXAMINED

The list that follows, of 125 species known from the three main Colombian Cordilleras, has been compiled from the following sources.
(1) The collections made by Mr G. I. Bernard and myself in 1977 from four sites in the Eastern Cordillera:
   (a) East slope—southern Sierra Nevada del Cocuy, near El Arenal (Boyacá, about 30 km south of the Nevada) (2300–3400 m);
   (b) East slope—above Guasca, northeast of Bogotá in Cundinamarca (3150–3350 m);
(c) West slope—below Arcabuco, on the road to Moniquirá in Boyacá (2250–2650 m);
(d) West slope—above Zipaquirá, on the road to Pacho in Cundinamarca (3100–3300 m).

(2) The collections made by Mr P. J. Hardy and myself in 1979, above Zipaquirá, Cundinamarca, and at four sites in the Central Cordillera (all on the east slope):
(a) Above Ibagué to the northwest, on the slopes of the Nevado del Tolima (1950–3000 m);
(b) Above Cajamarca to the south, in Tolima (2250–3600 m);
(c) Above Santa Leticia, Huila, on the road to Puracé, just within the Department of Cauca (2650–3300 m);
(d) Above San José de Isnos in Huila (1900–2550 m).

Mr Hardy and I also collected at one site on the east slope of the Western Cordillera: southwest above Cali in the northern Farallones de Cali (Department of Valle)—the old gold-mining area of “Monte Socorro” (1850–3450 m).

(3) The collections made by myself in 1982 at the following sites:
(a) In the Central Cordillera
   (i) East slope—below Santa Leticia in Huila (2350–2400 m);
   (ii) East slope—above San José de Isnos in Huila (2100–2900 m);
   (iii) West slope—above Coconuco, southeast of Popayán, in Cauca (2600–3100 m).
(b) In the Eastern Cordillera (all in Cundinamarca)
   (i) West slope—above Zipaquirá (3000–3300 m);
   (ii) West slope—above Fusagasugá (2650–2850 m);
   (iii) West slope—Boquerón de Chipaque, southeast of Bogotá (3100–3200 m);
   (iv) West slope—west of Facatativa (1800–2750 m);
   (v) East slope—between Gachetá and Guasca, northeast of Bogotá (2500–3150 m).

All the specimens obtained between 1977 and 1982 by Messrs Bernard and Hardy and myself are the property of the British Museum (Natural History). They represent 102 of the 125 pronophiline species in the list; I have also seen five of the others elsewhere.

(4) Locality data on specimens in the collections of the British Museum (Natural History) in London.

Eastern Cordillera butterflies mostly bear the label, “Bogotá”, but some have more detailed data, e.g.
West slope—Pacho; La Veja (? = La Vega) (both in Cundinamarca); and Muzo (Boyacá);
East slope—Villavicencio; Llanos de Río Meta; Choachí (all southeast of Bogotá).

Detailed locality data on Central Cordillera specimens include:
Quindiu (= Quindio) Pass (presumably to the immediate south of the Nevados del Tolima and Quindio); Popayán in the south (west slope); Manizales and Pereira in the north (west slope); and Valdevia (= Valdivia) in the extreme north of the range.

Specimens labelled “Cauca Valley” may have been obtained either on the
west slope of the Central Cordillera or the east slope of the Western Cordillera.

Western Cordillera specimens bear the following labels: “Monte Socorro” (southwest of Cali); “Chocó” (west slope); and “Frontino, Antioquia” in the extreme north.

(5) The collection of Colombian butterflies made by Dr E.W. Schmidt-Mumm, lodged at his residence in Bogotá. Most of his pronophilines are from the Eastern Cordillera, the sites including San Pablo (Albán), Madrid, Subachoque and Fusagasugá on the west slope in Cundinamarca; and Guayabetal, Río Negro (Meta), Fómeque, Sumapaz and Cruz Verde on the east slope near Bogotá.

(6) Locality data in the literature, notably the following:

(a) Krüger (1924, 1925), who collected extensively in all three cordilleras. Although he was one of the few authors to give feasible and accurate altitude data, and to distinguish east and west slopes in each range, he gave no precise localities, restricting his information on distribution to degrees of latitude. His type specimens, unfortunately, have not been traced, and his descriptions lacked illustrations.

(b) Fassl (1911, 1915, 1918), who also collected in all three Cordilleras (making transects across both sides) and gave precise locality data but unreliable and vague altitude data.

(c) Thieme (1905, 1907), who made the first attempts to monograph the Andean Pronophilini (with the notable exceptions of the genera Lymanopoda, Penrosada and Manerebia). It is doubtful if he was correct in assuming that all Kalbreyer’s specimens from the “coast (= Western) Cordillera” came from there, since they include several species known otherwise only from the Eastern Cordillera.

(d) Weymer (1912), who largely drew his information from Thieme’s monographs and from Fassl’s collections.

ANNOTATED CHECKLIST OF GENERA AND SPECIES

The genera are listed in alphabetical order. Within them, the species are assembled phyletically, closely related ones being listed together and in order of increasing altitude. The criteria used for assessing degrees of relationship are discussed in the Introduction.

Abbreviations

The following abbreviations are employed:

A&B Dr M. J. Adams (M.J.A.) and Mr G. I. Bernard (G.I.B.)
A&H Dr M. J. Adams and Mr P. J. Hardy (P.J.H.)
ESM Dr Ernesto W. Schmidt-Mumm
BMNH British Museum (Natural History), London
MNHU Museum für Naturkunde der Humboldt-Universität, Berlin
EC Eastern Cordillera
CC Central Cordillera
WG Western Cordillera
(E) East slope
(W) West slope
(B) Both slopes
Department of Tolima
Department of Huila, and that part of Cauca in the Puracé area
Species referred to as occurring in the “Sierra de Perijá” are known only from
its northern region, the Serranía de Valledupar (see Adams & Bernard, 1979).

Genus *Altopedaliodes* Forster

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

*Altopedaliodes nebris* (Thieme)

*Pedaliodes nebris* (Thieme), 1905: 98, pl. 1, fig. 10. 23 syntypes, COLOMBIA
[MNHU?].

*Altopedaliodes nebris* (Thieme); Forster, 1964: 148.

Apolinar (1914: 76–78) described eight forms of this unusually variable
species: f. *albipunctata*—with a white spot anterior to the five orange spots on the
forewing upperside; f. _athymi_—lacks brown patches proximal to the orange spots
of the forewing; f. _conchae_—lacks the brown patches on forewing upperside, but
present on underside; f. _abadiae_—lacks orange spots on forewing, but has brown
patches on both wing surfaces; f. _paulia_—lacks spots and patches on both
surfaces of forewing; f. _tripunctata_—has only three of the outer row of spots on
both surfaces of forewing; f. _modesta_—completely lacks outer spots on upperside
and has yellow hindwing band reduced to two spots; f. _estanislaoi_—lacks yellow
band on hindwing and proximal brown patches on forewing.

*Distribution*: A&B: EC(E), 2800–3300 m; ESM: EC(W), Zipaquira; Fassl
(1918: 44): EC(W), c. 3000–3500 m; Krüger (1924: 28): EC, 3200–3300 m;
Thieme (1905: 98): found by Kalbreyer “doubtless in the high mountains of the
province of Antioquia” (?).

*Bionomics*: George Bernard and I found *A. nebris* flying low over the ground in
open marshy terrain.

*Altopedaliodes reissi* (Weymer)

*Pedaliodes reissi* Weymer, 1890: 110, pl. 1, fig. 4. 1♂ syntype, COLOMBIA
[MNHU?].

*Pedaliodes reissi* var. *flavomaculata* Krüger, 1924: 28. ♂, ♀ syntypes, COLOMBIA:
“südlich von Meila” (whereabouts of types unknown).

*Altopedaliodes reissi* (Weymer); Forster, 1964: 148.

Krüger’s name *flavomaculata* relates to the population from Huila, which has
larger, yellower markings than the typical population from Tolima.

*Distribution*: A&H: CC(T), 3450–3600 m; Thieme (1905: 96): Popayán,
CC(H); Krüger (1924: 28): CC(T&H).

*Bionomics*: Stübel found *A. reissi* in the snow-mountains of Popayán (Thieme,
1905); Hardy and I found it in páramo, with a fast and erratic flight.
Altopedaliodes flavopunctata (Krüger), **comb. nov., stat. nov.**
(Figs 1, 22)

Pedaliodes paeonides (Hewitson) var. flavopunctata Krüger, 1924: 28. 2♂ syatypes, COLOMBIA: Central Cordillera (east side), 2800–3000 m (whereabouts of types unknown).

Krüger's unillustrated description of *flavopunctata* tallies with a series of two males and a female obtained by A&H at similar altitudes on the same slope of the Central Cordillera, whose spot distribution and genitalia place it in the

Figures 1–6. Male genitalia of Andean Colombian pronophiline species. Fig. 1, *Altopedaliodes flavopunctata* (Krüger), **comb. nov., stat. nov.** Fig. 2, *Lymanopoda schmidtii* sp. nov. Fig. 3, *Lymanopoda siventici* (Apolinar), **comb. nov.** Fig. 4, *Lymanopoda hulana cajamarca* subsp. nov. Fig. 5, *Parapedaliodes nora* sp. nov. Fig. 6, *Parapedaliodes zipa* sp. nov.
Figures 7–12. Male genitalia of Andean Colombian pronoline species. Fig. 7, *Pedaliodes pimienta* sp. nov. Fig. 8, *Pedaliodes manis* (Felder & Felder). Fig. 9, *Pedaliodes manneja* Thieme. Fig. 10, *Pedaliodes pisonia* (Hewitson). Fig. 11, *Pedaliodes socorae* sp. nov. Fig. 12, *Pedaliodes pollonia* sp. nov.

Genus *Altopedaliodes*. It does not resemble *paeonides* at all closely and clearly merits specific status. It may fly parapatrically below the closely related *A. reissi*. **Distribution:** A&H: CC(H), 3150–3300 m.

**Bionomics:** Found flying low in bushy vegetation below páramo.

Genus *Corades* Hewitson

*Corades* Hewitson, [1849]: 115. Type-species: *Corades enyo* Hewitson, by monotypy.
Figures 13-18. Male genitalia of Andean Colombian pronophile species. Fig. 13, *Pedaliodes parranda* sp. nov. Fig. 14, *Pedaliodes palpita* sp. nov. Fig. 15, *Pedaliodes ralphi* sp. nov. Fig. 16, *Pedaliodes guicana* sp. nov. Fig. 17, *Pedaliodes fuscata paraputra* subsp. nov. Fig. 18, *Pedaliodes hardyi* sp. nov.

*Corades enyo almo* Thieme

*Corades enyo* Hewitson [1849]: 117, *annulosa* pl. 4. 2♂ syntypes, VENEZUELA: Caracas (BMNH) [examined].

*Corades enyo* Hewitson var. *almo* Thieme, 1907: 222. Syntype series, COLOMBIA: Bogotá; ECUADOR: Santa Inez; PERU: Limbani and Huancabamba [MNHU?].

Typical *C. enyo* is known only from the Venezuelan coast range; subsp. *almo* occurs between Colombia and Bolivia (BMNH and Forster, 1964: 187).

*Distribution:* A&B: EC(W), 2250 m; Krüger (1925: 12): CC, 2000 m; WC, 2200 m.

*Bionomics:* Common in the lower cloud-forests of all three Cordilleras.

**Corades chelonis chelonis** Hewitson

*Corades chelonis* Hewitson, 1863: 71, figs 1, 2. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].


The typical race occurs in Colombia, being replaced in Venezuela by subsp. *rubeta* Thiem and in Ecuador by subsp. *lactefusa* Thiem; BMNH specimens from Peru, however, are indistinguishable from typical *chelonis*.

*Distribution:* A&B: EC(B), 2400–2850 m; A&H: CC, 2400–3100 m; Fassl (1915: 11): WC, c. 3000–3650 m.

*Bionomics:* *C. chelonis* flies parapatrically above its close relative, *C. enyo*. Both species are fond of resting on foliage 2 m or more above the ground.
Corades peruviana Butler
(Fig. 23)

Corades iduna Hewitson, 'local form' from Nauta, E. Peru; Butler, 1868: 185.

Corades iduna Hewitson form peruviana Butler, 1873: 224. Lectotype ♀, PERU: Nauta (BMNH), here designated [examined] (Fig. 23).

Corades peruviana Butler; Thieme, 1907: 226.

Butler (1873) referred back to his original description (Butler 1868) and gave what he considered to be a form of C. iduna the name peruviana. Although the original specimen purportedly came from Nauta, he specified in his second paper that peruviana is from E Peru but not Nauta. The BMNH, however, in 1858 received a male peruviana labelled as from Nauta, and this I have designated as lectotype.

The only Colombian record was given by Thieme (1907: 226), from the Western Cordillera; he also gave Ecuador as a locality, but erroneously declared that it does not occur in Peru. The BMNH has specimens from Ecuador and N, NE and E Peru. C. peruviana is a close relative of C. iduna, which flies in S Peru, Bolivia and Argentina.

Corades medeba columbina Staudinger

Corades medeba Hewitson, 1850: 439, pl. 10, fig. 4. 2♂ sytypes, BOLIVIA (BMNH) [examined].

Corades medeba Hewitson var. columbina Staudinger, 1894: 77. Syntype series, VENEZUELA: Mérida [MNHU?].


Distribution: BMNH: Venezuela to Bolivia (species); A&B: EC(B), 2550–2850 m; A&H: CC, 2300–2850 m.

Bionomics: See next species.

Corades cybele Butler

Corades cybele Butler, 1866: 40, pl. 3, fig. 2. 2♂ sytypes, COLOMBIA: Bogotá (BMNH) [examined].


Distribution: BMNH: Colombia to Peru; A&B: EC(E), 2500 m; A&H: CC, 2450–2950 m; Fassl (1915: 11): WC, c. 3000–3650 m; Fassl (1918: 44): EC(W), c. 2250–2500 m.

Bionomics: C. cybele tends to extend to higher altitudes than its close relative, C. medeba. Both species rest and feed among leaf litter on the forest floor.

Corades pannonia ploas Thieme

Corades pannonia Hewitson, 1850: 438, pl. 10, figs 1, 2. Lectotype ♂, VENEZUELA [coast range] (BMNH) [examined], designated by Adams & Bernard, 1981: 351.

Corades pannonia Hewitson var. ploas Thieme, 1907: 212. Syntype series, COLOMBIA and VENEZUELA: Mérida [MNHU?].
Corades fluminalis Butler, 1870: 26; Butler, 1874: 182, pl. 62, fig. 8. 1♀ syntype, [no locality] (BMNH) [examined].

Typical pannonia comes from the Venezuelan coast range; subsp. ploas (with which fluminalis was synonymized by Thieme, 1907: 212) occurs in the Venezuelan Cordillera de Mérida and all three of the Colombian Cordilleras.


Corades cistene dymanatis Thieme

Corades cistene Hewitson, 1863: 72, figs 4, 5. Lectotype ♀, BOLIVIA (BMNH) [examined], designated by Adams & Bernard, 1981: 351.

Corades cistene Hewiston var. dymanatis Thieme, 1907: 220. Syntype series, VENEZUELA, COLOMBIA and ECUADOR [MNHU?].

Thieme (1907: 220) explained that Hewitson’s original description of cistene probably referred to a Bolivian specimen, although his figured specimen does not tally and represents the Peruvian race (var. generosa Thieme, 1907). Subsp. dymanatis is distributed between the Venezuelan Mérida range and Ecuador, including all three Colombian Cordilleras. A&H obtained, in the CC(T), an aberration in which the brown post-discal band on the underside hindwing is missing and is replaced by sandy yellow speckled with brown.

Distribution: A&B; Adams: EC(B), 2500–3150 m; A&H; Adams: CC, 2600–3100 m; Fassl (1918: 44): EC(B), c. 2750–3250 m.

Bionomics: see next species.

Corades chirone Hewitson

Corades chirone Hewitson, 1863: 71, pl. 36, fig. 3. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].

Distribution: BMNH: Colombia and Ecuador; A&B: EC(E), 2600–2700 m; A&H; Adams: CC, 2850–2950 m; Fassl (1918: 44): EC(E), c. 2500–2750 m; Fassl (1915: 11 and BMNH): WC, “3500–3600 m”.

Bionomics: C. chirone flies sympatrically with its much commoner close relative, cistene. Both can be baited to faeces; in my experience, fresh specimens come to the bait each day. Both species seem to replace the parapatrically lower species, pannonia.

Genus Daedalma Hewitson

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

Daedalma dinias Hewitson

Daedalma dinias Hewitson [1858]: [85], pl. 1[43], figs 1–3. Lectotype ♂, COLOMBIA: ‘Bogotá’ (BMNH—Type No. Rh.4063), here designated 1♂ paralectotype, ?COLOMBIA: Bogotá [PERU or BOLIVIA] (BMNH) [both examined].
**Daedalma dinias** Hewitson var. *oenotria* Weymer, 1912: 266, pl. 56, row f. Syntype series, COLOMBIA: Bogotá [MNHU?].

**Daedalma dinias** Hewitson form *parvomaculata* Krüger, 1924: 47. 3♂, 1♀ syntypes, COLOMBIA: Western Cordillera (whereabouts of types unknown).

**Daedalma dinias** Hewitson var. *boliviana* Staudinger, 1897: 139. Syntype ♂ series and 2♀, BOLIVIA and PERU: Chanchamayo [MNHU?]; illustrated by Staudinger, 1888: pl. 84.

Hewitson (1858) originally figured a Colombian female and a male whose appearance tallies with Peruvian and Bolivian populations (and whose label bears a question mark in front of the word “Bogota”). Staudinger (1888) illustrates this male, and Weymer (1912: pl. 56, row f) figures both sexes. Colombian males have a less rounded, more rectangular orange forewing patch than those from Peru and Bolivia, and in the former it does not extend distad of the discal cell, while in the latter most of it does so. Similarity of the undersides suggests that the two populations may be considered as separate subspecies, and we treat the Colombian population from which the female type came as typical.

The population from which the original male type most probably came was subsequently named var. *boliviana* by Staudinger (1897), referring to the Peruvian and Bolivian subspecies. Weymer (1912) confused this with typical male *dinias*, and erroneously considered that they should be synonymized. Staudinger’s (1897) description of *boliviana* shows that he treated Weymer’s (1912) form *oenotria* as typical *dinias*. This form, described from Bogotá, has a forewing orange patch like typical *dinias*, but it fails to show through to the underside in the male. In the female it does show through, but it differs from the typical race in having orange rather than whitish subapical markings on the underside forewing, and a single orange costal patch on the underside hindwing instead of two parallel ones.

It seems probable that *oenotria* is the subspecies in the Eastern Cordillera of Colombia, the typical subspecies flying in the Central Cordillera. Thus the lectotype ♀ of *dinias* is unlikely to have come from Bogotá, but rather from the Central Cordillera. In the Western Cordillera, Krüger (1924) reported another form with a very small orange patch, *parvomaculata*, which may be the local subspecies there.


**Bionomics:** As Krüger (1924) points out, the species is fond of *Chusquea*; both sexes sun themselves on foliage or on the ground, and males are attracted to excrement.

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**Daedalma drusilla** Hewitson

**Daedalma drusilla** Hewitson, 1858: 86, fig. 7. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].

**Daedalma dora** Staudinger, 1897: 138, pl. 5, fig. 7. 3♂, 1♀ syntypes, COLOMBIA: Páramos de Bogotá and “Rio Dagua” [MNHU?] **syn. nov.**

**Daedalma drusilla** Hewitson; Thieme, 1907: 136; Weymer, 1912: 266.

**Daedalma dora** Staudinger; Thieme, 1907: 137; Weymer, 1912: 266.
Staudinger's illustration of *dora* is of the female. His description of the male, and Weymer's (1912) figure of it, tally exactly with Hewitson's (1858) *drusilla* type, and I hereby synonymize the two. *D. drusilla* occurs in Colombia (only known from the Eastern Cordillera); in Ecuador it is replaced by the larger, longer-tailed *inconspicua* Butler, which should perhaps be treated as a subspecies of *drusilla*.


*Bionomics*: Krüger (1924) observed a specimen sitting in a low bush, with the wings open. Schmidt-Mumm (pers. comm.) noted females to be attracted to faeces bait. This species seems to be the parapatric replacement of *dinias* in the uppermost cloud-forests of the Eastern Cordillera.

**Genus Dioriste** Thieme

*Dioriste* Thieme, 1907: 171. Type-species: *Pronophila tauropolis* Westwood, by original designation.

**Dioriste leucospilos** (Staudinger)

*Oxeoschistus leucospilos* Staudinger, 1875: 108. Syntype series, PERU: Chanchamayo [MNHU?].

*Dioriste leucospilos* (Staudinger); Thieme, 1907: 173; Weymer, 1912: 270, pl. 58, row c.

*Distribution*: BMNH: Ecuador and Peru; Thieme (1907: 174): Ecuador and Peru; ESM: EC, between Pitalito and Mocoa, and Florencia, c. 1500 m (2♂).

Dr Schmidt-Mumm is the only person to have recorded this species from Colombia.

**Genus Eretris** Thieme


**Eretris calisto calisto** (Felder & Felder)

*Pronophila calisto* Felder & Felder, 1867: 472. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined].

*Eretris calisto* (Felder & Felder); Thieme, 1905: 133; Weymer, 1912: 263, pl. 56, row b; Adams & Bernard, 1977: 269.

*Distribution*: A&B: EC, Ocaña (north), 1400 m; Fassl (1918: 44): EC(W), c. 2000–2250 m; Krüger (1924: 32): EC(W), 1700 m; BMNH: Honduras, Venezuela to Peru.

*Eretris calisto oculata* (Felder & Felder), *stat. nov.*

*Pronophila oculata* Felder & Felder, 1867: 472. 2♂, 1♀ syntypes, COLOMBIA: Bogotá (BMNH) [examined].
Figures 22–31. The left half shows the upperside, the right half the underside. Fig. 22, *Altopedaliodes flavopunctata* (Krüger), *comb. nov.*, *stat. nov.*, male. Fig. 23, *Corades peruvianna* Butler, male lectotype. Fig. 24, *Eretrias centralis* Krüger, male. Fig. 25, *Lymanopoda schmidti* sp. nov., male paratype. Fig. 26, The same, female holotype. Fig. 27, *Lymanopoda lactea* Hewitson, female. Fig. 28, The same, male *coffea* form nov. Fig. 29, *Lymanopoda melendexa* sp. nov., male holotype. Fig. 30, *Lymanopoda vicentienz* (Apolinar), *comb. nov.*, male. Fig. 31, The same, female.
Eretris oculata (Felder & Felder); Thieme, 1905: 133; Weymer, 1912: 263, pl. 56, row d.

E. calisto and oculata are of the same size and shape, and their markings differ only in that oculata has no silver coloration in its post-discal band on the underside hindwing. Their geographical separation suggests that they are subspecies, but oculata appears to have a disjunct distribution, on the east slope of the Eastern Cordillera and in the Western Cordillera and Panamá; similarly, typical calisto occurs in Honduras and Venezuela, as well as the west slope of the Eastern Cordillera.

Distribution: Fassl (1918: 44): EC(E), 750–1150 m; Krüger (1924: 32): EC(E), above 800 m; WC, above 1600 m (with a lighter underside); L. Miller (photographs sent to BMNH, 1978): Panamá.

Eretris porphyria porphyria (Felder & Felder)
Pronophila porphyria Felder & Felder, 1867: 470. 1♂ syntype, VENEZUELA (BMNH) [examined].
Eretris porphyria (Felder & Felder); Thieme, 1905: 132; Weymer, 1912: 263, pl. 56, row b; Adams & Bernard, 1981: 353.

Week’s (1902) description of mariona fits typical porphyria, except that it implies that it possesses six ocelli on the underside hindwing. However, his illustration (Weeks, 1905: pl. 38) shows five ocelli, as in porphyria. The two taxa are hereby synonymized.

As in most species of Eretris, porphyria can be divided into a number of races: indeed, almost every population has its own distinguishing characteristics. The typical subspecies is known from the Mérida range in Venezuela and both sides of the Eastern Cordillera of Colombia. It has a rather straight yellowish post-discal line on the underside hindwing and five ocelli.

Distribution: A&B: Venezuelan Cordillera de Mérida, 2200–2800 m; A&B: EC(E), Cocuy; EC(W), Arcabuco, 2300–2700 m.

Eretris porphyria decorata (Felder & Felder), stat. nov.
Pronophila decorata Felder & Felder, 1867: 470, pl. 67, fig. 11. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined].
Eretris decorata (Felder & Felder); Thieme, 1905: 132; Weymer, 1912: 263, pl. 56, row b.

In this race, the yellow post-discal line curves basad in cell Cu1; the type has six underside hindwing ocelli.

Distribution: ESM: EC(W), Albán.

Eretris porphyria catargyrea (Staudinger), comb. nov., stat. nov.
Pedaliodes catargyrea Staudinger, 1888: 233, pl. 83 (as phyllalia). Syntype(s), COLOMBIA: Antioquia [MNHU?].
Weymer (1912: 263) concurred with Thieme's (1905: 132) decision to synonymize *catargyrea* with *decorata*. The two taxa are closely similar, but they differ in that *catargyrea* has only five underside hindwing ocelli. The race has a disjunct distribution, being the only *porphyria* subspecies in the Central Cordillera, but occurring also on the east slope of the Eastern Cordillera.

**Distribution:** Adams: EC(E), Gachetá, 2500 m; A&H (Adams): CC (T & H), 2400–2850 m.

*Eretris porphyria perija* Adams & Bernard, **stat. nov.**

*Eretris perija* Adams & Bernard, 1979: 99, fig. 15. Holotype ♂, COLOMBIA: Serranía de Valledupar, 2300 m (BMNH) [examined].

The population described as *E. perija* by Adams & Bernard (1979), from the Colombian Sierra de Perijá, is not sufficiently distinct from typical *porphyria* to merit specific status.

**Distribution:** A&B: EC, Serranía de Valledupar, Colombian/Venezuelan border, 1900–2400 m.

**Bionomics:** This butterfly has a skipping flight and occurs around clumps of bamboo, rarely descending lower than 2 m from the ground (Adams & Bernard, 1979).

*Eretris apuleja apuleja* (Felder & Felder)

**Pronophila apuleja** Felder & Felder, 1867: 471. 1♂ syntype, [ECUADOR or COLOMBIA?] “Venezuela” (BMNH) [examined].

**Pronophila phyllalia** Hewitson, 1868: pl. 4, figs 21, 22. 1♂ syntype, ECUADOR (BMNH) [examined].

*Eretris apuleja* (Felder & Felder); Butler, 1868: 175; Thieme, 1905: 132; Weymer, 1912: 263, pl. 56, row b.

*Eretris phyllalia* (Hewitson); Thieme, 1905: 133.

*Eretris apuleja* form *phyllalia* (Hewitson); Weymer, 1912: 263; Gaede, 1931: 504 (as var.).

*Eretris ochrea* Thieme var. *bogotana* Krüger, 1924: 35. Syntype series, [No locality—?COLOMBIA: Bogotá] (whereabouts of types unknown), **syn. nov.**

Adams & Bernard (1981: 370) synonymized *phyllalia* with *apuleja*. In general, the species is characterized as follows: there is no yellowish post-discal line on the underside hindwing, but a suffusion of orange-brown, which may or may not have yellow patches in it; there is no grey coloration basad of the ocelli. Like *porphyria*, it occurs in a number of geographical races, some of which have disjunct distributions. The typical race is known only from the west slope of the Eastern Cordillera; Krüger's (1924: 35) unillustrated description of *E. ochrea* Thieme var. *bogotana* tallies with this race and is (tentatively) synonymized.

**Distribution:** Adams: EC(W), Facatativa & Fusagasugá, 2650–2850 m; ESM: EC(W), Facatativa.

**Bionomics:** In common with other *Eretris* species, *apuleja* is rarely encountered far from clumps of *Chusquea*, on the narrow leaves of which the butterflies rest and sun themselves.
Eretris apuleja ochrea Thieme, stat. nov.

Eretris ochrea Thieme, 1905: 135, pl. 3, fig. 41. 1♂ syntype, ECUADOR: Baños [MNHU?].
Eretris ochrea Thieme; Weymer, 1912: 264.

Unlike typical apuleja, which has a sizeable rust-brown patch at the anal angle of the upperside hindwing, subsp. ochrea has barely a trace; it is also smaller and the yellow patches on the underside hindwing are less distinct, especially in the populations from the Eastern and Western Cordilleras.

Distribution: Adams: EC(E), Gachetá, 3000 m; ESM: EC(E), 2700 m; A&H: Adams: CC(H), 2750–2950 m; A&H: WC, 2900 m; Fassl (1915: 11 and 2♂ in BMNH): WC, c. 3000–3650 m (as subrufescens).

Eretris apuleja subrufescens (Grose-Smith & Kirby), stat. nov.

Pedaliodes subrufescens Grose-Smith & Kirby, 1895: fig. 5. 1♂ syntype, [COLOMBIA] “Costa Rica” (BMNH) [examined].
Eretris subrufescens (Grose-Smith & Kirby); Thieme, 1905: 134; Weymer, 1912: 264, pl. 56, row c.

Grose-Smith & Kirby (1893–1895) merely figured the type male of this taxon without reference to its type-locality; the butterfly itself is labelled “Costa Rica”, but the race is unknown in that country (P. DeVries, pers. comm.). Thieme (1905) believed that the taxon occurred in Bolivia. Weymer (1912) reported it from Monte Socorro (WC), referring, as did Fassl (1915), to the dark population there of ochrea. The subspecies is distinguished by having no yellow on the underside hindwing (except in the female); the posterior half or more of the underside hindwing is suffused with rust-brown.

Distribution: A&B: EC(E), Cocuy, 2600–2700 m; A&H: CC(T), 2600–3100 m; Krüger (1924: 35): CC(T).

Eretris apuleja altamira Adams & Bernard, stat. nov.

Eretris altamira Adams & Bernard, 1979: 101, fig. 16. Holotype ♀, COLOMBIA: Serrania de Valledupar, 2600 m (BMNH) [examined].

The population first described from the Colombian Sierra de Perijá by Adams & Bernard (1979) as E. altamira has the underside like that of faded E. apuleja ochrea, and is not sufficiently distinct to merit specific status.

Distribution: A&B: EC, Serranía de Valledupar, Colombian and Venezuelan borders, 2600–3100 m.

Bionomics: Adams & Bernard (1979) comment on the typical behaviour of this Eretris, and the difficulty of obtaining specimens due to its high flight.

Eretris centralis Krüger

(Fig. 24)

Eretris centralis Krüger, 1924: 32. 3♂, 1♀ syntypes, COLOMBIA: Central Cordillera, 3000–3200 m (whereabouts of types unknown).
Krüger's (1924) detailed description of this species corresponds with males we obtained, both in one of the type localities (Huila in the Central Cordillera) and on both slopes of the Eastern Cordillera at 3150 m; the EC individuals have slightly less bright underside markings, but are otherwise indistinguishable. The species, which is characterized by its total lack of ocelli, was not reported in the Zoological Record.

**Distribution:** Krüger (1924: 32): CC(T and H), 3000–3200 m; A&H; Adams: CC(H), 2950–3100 m; Adams: EC(E), Gachetá, 3150 m; EC(W), Zipaquirá, 3150 m; ESM: EC(E), EC(W), localities as above.

**Bionomics:** The butterflies skip around the tops of clumps of chusque and commonly fly over open land from gully to gully. *E. centralis*, found only in the very uppermost cloud-forests, can be considered as the topmost member of a parapatric series of four *Eretris* species, replacing each other up the altitude gradient: *calisto*, *porphyria*, *apuleja* and *centralis*.

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*Eretris ocellifera* (Felder & Felder)

*Pronophila ocellifera* Felder & Felder, 1867: 471. 2♂️ syntypes, COLOMBIA: Bogotá (BMNH) [examined].

*Eretris ocellifera* (Felder & Felder); Thieme, 1905: 132; Weymer, 1912: 263, pl. 56, row c.

*Eretris subpunctata* (Grose-Smith & Kirby) form *umbrina* Weymer, 1912: 263, pl. 56, row c. ♀️ syntype, COLOMBIA: Monte Tolima [MNHU?], **syn. nov.**

This species is generally larger than *porphyria*; the inner edge of the post-discal band on its underside hindwing is more dentate and the ocellus in cell C1 is very much larger than any of the others; it has five or six ocelli. Weymer's (1912) description of f. *umbrina*, and his illustration, tally well with female *ocellifera*.

**Distribution:** The species is widespread in all three of the Colombian Cordilleras. A&B: EC(W), 2550–2650 m; A&H: CC(T&H), 2450–2650 m; A&H: WC, 2650/2700 m; Fassl (1918: 44): EC(W), c. 2000–2250 m; Fassl (1915: 11): WC, c. 2000–2300 m; Krüger (1924: 32): CC(T), 2600 m (as var. *umbrina*); Cauca valley, 1800–2200 m; WC, 1600–1800 m.

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**Genus Idioneurula Strand**

*Idioneurula* Strand, 1932: 146. Type-species: *Idioneura erebioides* Felder & Felder (replacement name for *Idioneura Felder & Felder nee Philippi*).

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*Idioneurula erebioides* (Felder & Felder)

*Idioneura erebioides* Felder & Felder, 1867: 474. 5♂️ syntypes, COLOMBIA: Bogotá (BMNH) [examined].

*Idioneura erebioides* Felder & Felder; Butler, 1868: 99; Gaede, 1931: 479.

*Idioneurula erebioides* (Felder & Felder); Strand, 1932: 146.

The butterflies vary in the extent to which they possess whitish streaks on the underside hindwing; the extreme form in which they are totally absent was given the name form *moderata* by Weymer (1912: 239). Apolinari (1914: 46) gave
the name form *intermedia* to individuals which have no underside streaks, but still possess two or three upperside ocelli.

**Distribution:** A&B: EC(B), 2250–2850 m; Fassl (1918: 44): EC(B), c. 2650–3500 m.

**Bionomics:** The species occurs in open marshy ground and on damp roadside verges, flying rather slowly and close to the ground.

Genus *Junea* Hemming

*Junea* Hemming, 1964: 137. Type-species: *Daedalma doraete* Hewitson (replacement name for *Polymastus* Thieme nee Claparède).

*Junea dorinda* (Felder & Felder)

*Daedalma dorinda* Felder & Felder, 1862: 427. 2♂, 1♀ syntypes, COLOMBIA ["Villeta, 3200"] and [no locality] (BMNH) [examined].

*Daedalma emilia* Butler, 1866: 40, pl. 3, fig. 3. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined]. **syn. nov.**

*Polymastus emilia* (Butler); Thieme, 1907: 145; Weymer, 1912: 267, pl. 67, row b.

*Polymastus dorinda* Felder & Felder; Thieme, 1907: 143; Weymer, 1912: 267, pl. 67, row b (as *dorinde*).

*Junea dorinda* (Felder & Felder); Hemming, 1964: 137.

The types of *dorinda* and *emilia* are indistinguishable, and I hereby synonymize the two.

**Distribution:** A&B: EC(W), 2650 m; A&H: CC, 2800 m; Thieme (1907: 143): "coast cordillera" and Ecuador; Fassl (1911: 26): CC, c. 2500–2900 m (as *emilia*); Fassl (1918: 44): EC(B), c. 2850–3350 m.

**Bionomics:** This species, rare in collections, is a canopy dweller, but can be baited to faeces.

*Junea doraete* (Hewitson)

*Daedalma doraete* Hewitson, 1858: figs 4, 5. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].

*Polymastus doraete* (Hewitson); Thieme, 1907: 141; Weymer, 1912: 267, pl. 67, row a.

*Junea doraete* (Hewitson); Hemming, 1964: 137.

**Distribution:** BMNH: Colombia to Peru; ESM: EC(W), c. 3100 m; A&H: CC, 2850 m; Fassl (1918: 44): EC(B), c. 2850–3350 m; Krüger (1925: 10): EC+CC, 3000–3300 m; Fassl (1911: 26): CC, c. 3100–4200 m.

**Bionomics:** As noted by Krüger (1925), this species is parapatric above *dorinda*; both have similar habits.

Genus *Lasiophila* Felder & Felder

Lasiophila zapatoza sombra Thieme, stat. nov.

Pronophila zapatoza Westwood, 1851: 358. 2♂, 1♀ sytypes, VENEZUELA: [coast range] and “Bolivia” (former in BMNH [examined]; latter not located).


Lasiophila sombra Thieme, 1907: 128. 6♂, 1♀ sytypes, COLOMBIA: Bogotá and Popayán [MNHU?].

L. zapatoza is divided up into a number of geographical races, whose males vary in their upperside markings and coloration, but whose females are virtually indistinguishable. Subsp. sombra has the darkest upperside coloration of the four named races (typical zapatoza from the Venezuelan coast range, meridae Adams & Bernard from the Venezuelan Cordillera de Mérida, semipartita Weymer from the Colombian Sierra Nevada de Santa Marta and manaurera Adams & Bernard from the Sierra de Perijá).


Bionomics: According to Adams & Bernard (1979: 102), L. z. manaurera flies slowly in sunny clearings, often out of reach, and settles on foliage.

Lasiophila circe Felder & Felder, 1859: 326. 1♂ sytype, [no locality] (BMNH) [examined].


Lasiophila circe Felder & Felder; Butler, 1868: 181; Thieme, 1907: 123; Weymer, 1912: 265, pl. 56, row e.

Adams & Bernard (1981) explained Thieme’s (1907) synonymy of praeneste with circe, which was stabilized by our lectotype designation of the Hewitson praeneste type which corresponds to circe. The species seems to vary in its upperside coloration: A&H collected a male at 3150 m in Huila (CC) with very much paler than usual coloration, and Thieme (1907: 123) named as var. cnephas a dark form from Tolima (CC), in which the rufous patches on the upperside are barely visible.

Distribution: A&B: Adams: EC(E), 2600–3000 m; Adams: EC(W), 2650–3150 m; A&H: CC, 2900–3150 m; Fassl (1918: 44): EC(B), c. 2850–3350 m; Fassl (1911: 26): CC, c. 3000–3500 m.

Bionomics: L. circe flies parapatrically above its close relative, zapatoza subsp. sombra, probably in all three Colombian Cordilleras. Both are fond of flapping close to the ground and feeding on leaf litter, but circe is warier and faster in flight.

Lasiophila behemoth Thieme

Lasiophila behemoth Thieme, 1907: 125. 2♂ sytypes, COLOMBIA [MNHU?].

Lasiophila behemoth Thieme; Weymer, 1912: 265; Gaede, 1931: 506 (as behemoth).
The only record of this species is given by the author (Thieme, 1907): two males from "Colombia" from the Maassen collection. It is described as having coloration and markings close to those of *circe*, but in size and shape it is different, with a more dentate hindwing outer margin but a very reduced inner 'tail'; in this respect, it is more like *zarathustra* Thieme. It is possible that Krüger (1924: 35) was correct in supposing that *behemoth* is a form of *circe*, but clarification must await further material.

*Lasiophila prosymna prosymna* (Hewitson)

*Pronophila prosymna* Hewitson, 1857: 79, pl. 1, figs 3, 4. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].

*Lasiophila prosymna* (Hewitson); Butler, 1868: 182; Thieme, 1907: 117; Weymer, 1912: 264.

The typical Colombian race is replaced in Ecuador by 'var. *dirempta* Thieme (1907). It occurs in all three Cordilleras.

**Distribution:** A&B: EC(W), 2400 m; A&H; Adams: CC, 2400–3100 m; Fassl (1918: 44): EC(W), c. 2000–2350 m; Fassl (1911: 26): CC, c. 2300–3000 m; Fassl (1915: 11): WC, c. 3000–3650 m.

**Bionomics:** As mentioned in the Introduction, this species appears to mimic Pedaliodes peucéstas (Hewitson) throughout their range in Colombia: *prosymna* is unique in *Lasiophila* in possessing a white oblique forewing band.

**Genus Lymanopoda** Westwood

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

*Sabatoga* Staudinger, 1897: 143. Type-species: *Sabatoga mirabilis* Staudinger, by monotypy. [**Zapatoca** Apolinar, 1924. Unjustified emendation of *Sabatoga* Staudinger.]

*Lymanopoda obsoleta* (Westwood)

*Sarromia obsoleta* Westwood [May 1851]: pl. 67, fig. 5. 1♂ syntype, BOLIVIA (BMNH) [examined].

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

*Lymanopoda larunda* Hopffer, 1874: 361. 3♂ syntypes, PERU: Chanchamayo, and VENEZUELA (whereabouts of types unknown). (Synonymy given by Weymer, 1912: 248.)

*Sarromia obsoleta* Westwood; Forster, 1964: 145.

*Lymanopoda larunda* Hopffer; Thieme, 1905: 70.


Females of this species are variable in their upperside markings; an extremely well-marked female form was given the name *gortynoides* by Weymer (1912: 248); it not only has two large, white-pupilled and orange-bordered ocelli and two small, indistinct ones anteriorly on the forewing, but also a series of five
black spots in orange rings on the hindwing. It was described from Bogotá, Mérida (Venezuela) and Bolivia.

**Distribution:** BMNH: Panamá and Venezuela to Bolivia; A&B; Adams: EC(B), 2400–2700 m; A&H; Adams: CC, 2400–2900 m; A&H: WC, 2250–2350 m; Fassl (1918: 44): EC(B), c. 1250–2500 m (as larunda, with ♀ form gortynoides); Fassl (1911: 26): CC, c. 2000–2850 m (as larunda); [3100–4000 m (as obsoleta—misidentification of excisa?)]; Krüger (1924: 19): EC, 2800 m; CC, 2000–3500 m (as obsoleta).

**Bionomics:** This very widespread species is common in the lower and middle cloud-forests, feeding on leaf litter and assembling at water seepages; it is sometimes found out of its normal range, flying with its higher parapatric relatives in the upper cloud-forest belt.

**Lymanopoda altis**

*Lymanopoda altis* Weymer, 1890: 41, 109, pl. 3, fig. 8. 2♂ syntypes, COLOMBIA: Páramo de Aponte, 2800 m; and ECUADOR (several specimens in Weymer Coll) [all in MNHU?].

*Cheimas? albofasciatus* Röber, 1927: 419, 430, pl.-fig. 8. Holotype ♂, COLOMBIA: “Sierra Nevada de Santa Marta, 1500 m” (BMNH) [examined].


The synonymy of *albofasciatus* with *altis* was given by Adams & Bernard (1977). Although Röber’s *albofasciatus* type is labelled as from the Sierra Nevada de Santa Marta, this is most probably an error: it has never been recorded from the Santa Marta range and in the nearby Sierra de Perijá it is replaced by *L. maletera* Adams & Bernard. *L. altis* occurs in all three of the Colombian Cordilleras; its closest allopatric relatives are *maletera* Adams & Bernard in the Sierra de Perijá, and *dietzi* Adams & Bernard in the Mérida range of Venezuela.

**Distribution:** A&B: EC, 2300–2650 m; A&H; Adams: CC, 2500–2950 m; Krüger (1924: 19): EC, 2600 m; CC(E), 2600 m; Fassl (1911: 26): CC, c. 2700–2900 m; BMNH: WC, Frontino.

**Lymanopoda panacea**

*Lymanopoda panacea* Hewitson, 1869: 35. 1♂, 1♀ syntypes, ECUADOR (BMNH) [examined].

*Lymanopoda ocellifera* Butler, 1873: 219. 1♂ syntype, PERU (BMNH) [examined], syn. nov.

*Lymanopoda gortyna* Weymer, 1912: 248, pl. 53, row a. 1♀ syntype, COLOMBIA: Guasca, 2500 m [MNHU?], syn. nov.

*Lymanopoda panacea* Hewitson; Thieme, 1905: 71; Gaede, 1931: 487; Brown, 1943: 101, pl. 2, fig. 1614 (genitalia); Weymer, 1912: 249, pl. 52, row g.

As judged by Dr Schmidt-Mumm’s collection from eastern Huila (EC), this species varies considerably in size within single populations. Butler’s (1873) *ocellifera* is merely a large example of Hewitson’s (1869) *panacea*, and I hereby
synthesize the two taxa. Weymer’s *gortyna* is larger even than *ocellifera*, but it has the same markings as females of Colombian *panacea*; its type locality (about 30 km northeast of Bogotá) occurs on the same slope of the EC as the Rio Negro locality where Krüger obtained two males, which he thought belonged to *gortyna* and therefore described the male for the first time (Krüger, 1924: 16, as *gortina*). He did not refer to *panacea* and his description fits typical *panacea*. I believe that the *gortyna* type is a large female of *panacea*, and hereby synonymize the two taxa.

Examination of the male genitalia shows that this species is a very close relative of *L. albocincta*, but it occurs at lower altitudes (as Krüger, 1924, pointed out, very low for a *Lymanopoda*). The two species may be parapatric.

**Distribution:** BMNH: Ecuador & Peru, 1♀ from Bogotá; ESM: EC(W), Huila (variable ♂ size); EC(E), Portachuelo, c. 1800 m. Krüger (1924: 16): EC(E), Rio Negro, 900–1600 m; [Fassl (1915: 11): WC. Misidentification of *L. caucana* Weymer?]

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**Lymanopoda albocincta** Hewitson

*Lymanopoda albocincta* Hewitson, 1861: 157, pl. 9, fig. 5. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].

*Lymanopoda issacha* Butler, 1870: 26. 1♂ syntype, [no locality—ECUADOR?] (BMNH) [examined]. (Synonymy given by Adams & Bernard, 1979: 107.)

*Lymanopoda albocincta* Hewitson; Weymer, 1912: 249, pl. 52, row e; Gaede, 1931: 484; Brown, 1943: 100, pl. 2, fig. 1620 (genitalia); Adams & Bernard, 1979: 107; 1981: 358.

The female has four white-pupilled, dark brown post-discal ocelli on the forewing, the two in cells M3 and Cul being much larger than those in M1 and M2; a pale band corresponding to the white band of the male underside hindwing is present (to a greater or lesser degree), bluish-white, on a ground colour which is much paler and more mottled than that of the male.


**Bionomics:** This species is predominantly ground-loving, feeding and resting on leaf litter.

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**Lymanopoda samius** Westwood

*Lymanopoda samius* Westwood, 1851: 402, pl. 67, fig. 6. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined].

*Lymanopoda samius* Westwood; Butler, 1868: 169; Weymer, 1912: 246, pl. 52, row c; Gaede, 1931: 487; Brown, 1943: 88, pl. 1, fig. 1640 (genitalia).

Apolinar (1914: 47, 48) named two forms of this species: *nigripunctata* with a black spot in the discal cell on the upperside forewing, and *confluens*, in which the black post-discal spots in cells M2 and M3 of the upperside hindwing merge with each other and with the black outer border.

**Distribution:** A&B: EC(E), Cocuy, 2800/2850 m; Adams: EC(W),
Pronophilines of Colombian Andes

2700–2750 m; EC(E), 2500 m; Krüger (1924: 19): EC, 2600–2800 m; Brown (1943: 88): EC and CC [latter in error?].

Bionomics: Almost certainly restricted to the Eastern Cordillera, *samius* is most closely related to the allopatric species *pieridina* (in the Central Cordillera), *labineta* (in the Western Cordillera and Ecuador) and *hazelana* Brown (in Ecuador); and it is the lowermost member of the parapatric series, *samius*, *ionius*, *lactealschmidti*, *vivientieni* (see Table 3).

**Lymanopoda pieridina** Röber

*Lymanopoda pieridina* Röber, 1927: 414, 430, pl.-fig. 8. Holotype ♂, COLOMBIA: “Sierra Nevada de Santa Marta” (BMNH) [examined].


Known previously only from the type, almost certainly erroneously described from the Sierra Nevada de Santa Marta, *pieridina* was rediscovered by A&H in 1979 in the Central Cordillera (Tolima). My criteria for considering this species to be closely related to *samius* and *labineta*, in spite of differences in coloration and wing shape, are similarities in the male genitalia, and in spot numbers and their distribution on the underside.

**Distribution:** A&H: CC(T), 2800–3100 m.

**Bionomics:** *L. pieridina* is parapatric below *excisa*.

**Lymanopoda labineta** Hewitson

*Lymanopoda labineta* Hewitson, 1870: 159. 1♂ syntype, ECUADOR (BMNH) [examined].

This species—brown with a broad white band across the middle of the forewing—was omitted by Weymer (1912), Gaede (1931) and Brown (1943). It is known only from the Ecuadorian type and one male obtained by Dr Schmidt-Mumm in the Western Cordillera.

**Distribution:** ESM: WC, Felidia, c. 2500 m.

**Lymanopoda ionius** Westwood

*Lymanopoda ionius* Westwood [1851]: 402, pl. 67, fig. 7. 1♂ syntype, COLOMBIA (BMNH) [examined].

*Lymanopoda ionius* Westwood; Butler, 1868: 169; Weymer, 1912: 247, pl. 52, row e (as *jonius*); Gaede, 1931: 485 (as *jonius*); Brown, 1943: 96, pl. 1, fig. 1636 (genitalia).

Typical *ionius* has a sandy-yellow underside ground colour; but in some populations this is considerably darker, similar to the colour of *excisa*; but the dark brown post-discal band on the underside forewing is always darker than in *excisa* and larger, incorporating the brown streak just distad of the discal cell. The second process on the valve seems to vary in length also.

**Distribution:** A&B; Adams; ESM: EC(B), 2750–3150 m; Krüger (1924: 19): EC, 2600–2800 m; CC(E), 2200–2800 m [misidentification?]; Fassl (1918: 44): EC(B), c. 2650–3500 m.
Bionomics: This species is most closely allied to *excisa*, which replaces it in the Central and Western Cordilleras, and is commoner than the other members of its parapatric series (see under *samius*).

**Lymanopoda excisa** Weymer

Lymanopoda *excisa* Weymer, 1912: 247, pl. 52, row f. Syntype series, COLOMBIA: Quindio Pass, "3500–3800 m", and Monte Socorro, "3600 m" [MNHU?].

Lymanopoda *excisa* Weymer; Gaede, 1931: 485; Brown, 1943: 96 (as a possible form of *ionius*).

Tolima (CC) specimens of this species are smaller than those found in Huila (CC) and in the Western Cordillera, and this may have led Krüger (1924: 19) into believing that the Tolima population was *ionius*. Fassl (1911: 26) listed both *larunda* (= *obsoleta*) and *obsoleta* from the Central Cordillera; it is probable that his *obsoleta*, reported as flying at the higher altitudes, referred to *excisa*, which had not been named at that time.


Bionomics: Unlike its relative, *ionius*, *L. excisa* has no parapatric replacement at the altitudes above it, and for this reason it extends right up to the tree-line.

**Lymanopoda schmidti** sp. nov.

(Figs 2, 25, 26)

Male

Forewing length 19–20 mm. Upperside forewing silvery white, with brown along costa, at apex and around outer margin; dark grey at extreme base; a series of four or five white submarginal dots in cells R5 to M3 or Cu1, those in Cu1 and/or M3 much further from the outer margin than the others. Upperside hindwing silvery white, with narrow brown outer margin, and dark grey at base and around inner margin to tornus; a general suffusion of golden-brown on one specimen.

Underside forewing orange-brown, sandy-yellow along all margins and at apex; spots as on upperside; silvery-grey submarginal patches in M3 and Cu1. Underside hindwing sandy-yellow, with patches of dull lilac forming three indistinct bands crossing the wing discally, post-discally and submarginally; a series of six post-discal black dots, some with minute white centres, in cells M1 to Cu2 (two in Cu2).

Female

Forewing length 20.5 mm. Upperside as in male, but hindwing ground colour is dusted lightly with golden-brown and the inner margin is pale yellow. Underside as in male, but paler throughout; faintly darker patches on forewing, in the basal two-thirds of the discal cell, immediately distad of the cell, and surrounding the white dots.
HoloQpe, COLOMBIA: Departamento de Cundinamarca, above Km 26 between Zipaquirá and Pacho, 3200 m, 26 viii 79 (M.J.A.).

Paratypes, locality as holotype: 1♂, 6 ii 65; 3♂, 6 i 80 (E. W. Schmidt-Mumm); 3♂, data as holotype (M.J.A. and P.J.H.); locality as holotype: 4♂, 1♀, 24 viii 82; 4♀, 3♀, 25 viii 82; 5♂, 26 viii 82 (M.J.A.).

I name this species after Dr Ernesto Schmidt-Mumm of Bogotá, who has been an invaluable friend, host and colleague, and his wife Nubia, the uncomplaining hostess. Its closest relative is *L. lactea*, which occupies the same habitat on the other (east) slope of the Eastern Cordillera; both fly parapatrically above *ionius*.

**Bionomics:** *L. schmidti* is confined to the uppermost cloud-forest on the west slope of the Eastern Cordillera, flying over clumps of chusque in wet gullies.

*Lymanopoda lactea* Hewitson
(Figs 27, 28)

*Lymanopoda lactea* Hewitson, 1861: 157, pl. 9, figs 2, 3. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].

*Lymanopoda lactea* Hewitson; Butler, 1868: 169; Weymer, 1912: 245; Gaede, 1931: 486; Brown, 1943: 90.

A series of males from three localities, collected in 1980 by Dr Schmidt-Mumm, and a female caught by myself in 1982, have been added to the solitary male syntype. This butterfly occurs above *ionius*, in the uppermost forest zone of the east slopes of the Eastern Cordillera, being replaced on the west slope by *schmidti*.

The female is larger than the male. The upperside is similar to that of a white male but with darker-brown markings and a trace of orange-brown at the tornus. The forewing underside is similar to the male, as is the hindwing underside, except that much of the wing is dusted with lilac.

In common with the similar southern Peruvian species, *umbratilis* Rosenberg & Talbot, *lactea* males exhibit a range of colour forms, the ground colour varying between white (as in the type) and sandy-brown; in the latter case, the dark markings of the underside hindwing are barely darker than the ground colour. I name this dark form *coffea* form nov. (Fig. 28).

**Distribution:** ESM: EC(E), Gachetá, Fomeque and Sumapaz (including form *coffea*); Adams: EC(E), Gachetá, 2950–3300 m.

**Bionomics:** The female I caught was on the ground among grass: it was freshly emerged and had probably come down from the bordering chusque during a brief interval of sunshine; males were seen skipping fast and high over clumps of chusque.

*Lymanopoda melendezia* sp. nov.
(Fig. 29)

**Male**

Forewing length 21 mm. Upperside ground colour brown. Forewing with four sandy-yellow post-discal streaks in cells M1 to Cu1, the longest ones (in cells M3 and Cu1) being broken in the middle by brown patches each containing a tiny whitish dot; fainter, russet-brown streaks in cells R5 and Cu2, the latter
similarly broken by a patch containing a very faint whitish dot, much more marginal than in Cu1; a sandy-yellow patch at the anterior distal end of the discal cell; three clear white submarginal dots in cells R5 to M2. Hindwing brown, with very faint russet-brown lines in cells Rs to Cu1 extending from the discal region almost to the outer margin.

Underside forewing brown, with sandy-brown apex and outer margin; markings as on upperside, with additional submarginal yellowish streaks extending distally from the three spots in cells R5 to M2. Underside hindwing russet-brown, with sandy-brown margins; long whitish streaks, along the anterior vein of the discal cell, along the posterior edge of the discal cell, and in cells M1 to Cu1, the one in Cu1 dusted with lilac and containing a tiny dark brown dot; most of cell Cu2 is dusted with lilac, as is cell Rs where it merges distally into sandy-yellow.

Female unknown.

Holotype ♂, COLOMBIA: Departamento de Boyacá, S.W. above El Arenal (south of Sierra Nevada del Cocuy), 2800/2850 m, 11 vii 77 (G.I.B.).

This species is named after Señor Julio Meléndez and his family, peasant farmers of El Arenal, in gratitude for their hospitality and companionship in 1977. As judged by its wing shape, ground colour and distribution of forewing spots, it is closely allied to altaselua Adams & Bernard, which flies at comparable altitudes in the Sierra de Perijá; its striped underside is reminiscent of the white Lymanopoda which flies immediately above it in Cocuy, viventieni: the two may be parapatric allies (and indeed, melendezia could be a brown form of a white species, as coffee is of lactea). It is probable that the species is confined to the Cocuy area of the Eastern Cordillera, being replaced to the southwest by lactea and schmidti, to which an affinity is suggested by the spot distribution on the wings.

Lymanopoda melia Weyner, stat. nov.

Lymanopoda nivea Staudinger form melia Weymer, 1912: 245, pl. 52, row c. Syntype series, COLOMBIA: Quindio Pass [MNHU?].

Lymanopoda nivea Staudinger form melia Weymer; Krüger, 1924: 10; Gaede, 1931: 487 (as var.); Brown, 1943: 92, pl. 1, fig. 1609 (genitalia) (as subspecies).

Brown's (1943) figure of the male genitalia of melia is incorrect: typical specimens from Quindio (Central Cordillera) lack the process on the valve altogether. His nivea figure is, however, correct. Their genital differences and the dissimilarities in their facies strongly suggest that they are two different species. L. nivea comes from Ecuador, but Brown (1943) also recorded melia from that country; it is possible that some individuals or populations of nivea from Ecuador are darker than the type and may lead to confusion with melia, whose distribution I believe to be restricted to the Colombian Central Cordillera.

Krüger (1924: 10) describes what he considers to be a light-coloured form of huilana—form alba—which fits melia and flies at the same altitudes (2800–3000 m); indeed, he claims that it flies together with melia. Without access to Krüger's lost material, I cannot surmise what his form alba represents, but as a forest taxon it is unlikely to belong to the páramo species huilana.
Distribution: A&H; Adams: CC(H), 2950–3150 m; Krüger (1924: 10): CC(T,W), 2600–3300 m; Fassl (1911: 26): CC, c. 3100–4000 m.

Bionomics: L. melia flies parapatrically below its near relative, huilana, skipping fast around clumps of chusque but coming to the ground in search of mineral matter or excrement.

**Lymanopoda viventieni** (Apolinar), **comb. nov.**

(Figs 3, 30, 31)

_Zapatoca viventieni_ Apolinar, 1924: 84. Holotype, COLOMBIA: Guasca (destroyed by fire).

Recognizing, correctly, that his _viventieni_ is closely allied to _Sabatoga mirabilis_ Staudinger, Apolinar (1924) suggested that the generic name be changed to _Zapatoca_, the name of the probable type-locality of _mirabilis_, which Staudinger had apparently misspelt. The genus _Sabatoga_ was synonymized with _Lymanopoda_ by Adams & Bernard (1977: 270).

**Distribution:** Apolinar (1924: 84): EC(E), Guasca; A&B: EC(E), Cocuy, 2900–3200 m; Guasca, 3250–3350 m.

**Bionomics:** _L. viventieni_ belongs in the assemblage of closely related, páramo-flying, white _Lymanopoda_ species, containing _mirabilis_ (?west slope of Eastern Cordillera), _huilana_ (Central Cordillera), _nevada_ Krüger (Sierra Nevada de Santa Marta) and _paramera_ Adams & Bernard (Sierra de Perijá). On the east slope of the Eastern Cordillera, it is the uppermost member of a series of four parapatric relatives (see under _samius_).

**Lymanopoda mirabilis** (Staudinger), **comb. nov.**

_Sabatoga mirabilis_ Staudinger, 1897: 143, pl. 5, fig. 2. Æ, Æ syntypes, COLOMBIA: “Sabatoga” [MNHU?].

_Sabatoga mirabilis_ Staudinger; Weymer, 1912: 244; Gaede, 1931: 483.

The genus _Sabatoga_, which Staudinger (1897) erected for _mirabilis_, was synonymized with _Lymanopoda_ by Adams & Bernard (1977: 270). The type-locality was stated by Apolinar (1924: 84) to be a corruption of the town of _Zapatoca_, on the west slope of the Eastern Cordillera in the Department of Santander. If, as is likely, _mirabilis_ flies in the páramo of the west slope, it is the allopatric replacement of _viventieni_, which occurs on the east slope. There are no records that I know of other than the two male types.

**Lymanopoda huilana huilana** Weymer

_Lymanopoda huilana_ Weymer, 1890: 39, 109, pl. 1, fig. 5. Syntype(s), COLOMBIA: Páramo de Huila, 4000 m [MNHU?].

**Distribution:** Weymer (1912: 245): CC(H), 4000 m; Krüger (1924: 9): CC(H), c. 3500 m.
Lymanopoda huilana tolima Weymer

Lymanopoda huilana Weymer form tolima Weymer, 1912: 245, pl. 52, row c.

Syntype(s), COLOMBIA: Páramo de Tolima, 4200 m [MNHU?].

Lymanopoda huilana Weymer var. tolima Weymer; Gaede, 1931: 485; Brown, 1943: 90, pl. 1, fig. 1638 (genitalia) (as subspecies).

This race, with its upperside forewing less dark-dusted than in typical huilana or in cajamarca subs. nov., is known only from Fassl’s specimens, probably obtained in the southern Nevado del Tolima.

Distribution: Fassl (1911: 26): CC(T), c. 4000–4500 m; Weymer (1912: 245): CC(T), 4200 m.

Lymanopoda huilana cajamarca subsp. nov.

(Figs 4, 32)

Male
Forewing length 19–22 mm. Upperside ground colour white, dusted with dark grey, and silvery-blue at the base of both wings. Forewing with dark grey markings: along costa, at apex, around outer margin, in an oblique band from the costa distal of the discal cell to the outer margin in cell M3, in streaks along veins Cu1 and Cu2 basad almost as far as the discal cell, and in lines along veins R5 and M1 across the subapical grey-white patch; a faint grey-white submarginal dot in cell M3. Hindwing with a grey-white streak in the posterior distal end of the discal cell, extending into cell M2; from this a fainter grey-white line extends post-discally to vein Rs; a series of five black submarginal spots in cells Rs to Cu1.

Underside forewing ground colour white, with costa, apex and anterior part of outer margin sandy-yellow; a patch of similar colour immediately distal of the discal cell; otherwise the dark markings of the upperside show through as pale grey; two tiny submarginal black spots in cells M1 and M2. Underside hindwing as upperside but ground colour pale grey speckled with sandy-yellow, and with brown on either side of the whitish streak in and beyond the discal cell.

Female unknown.

Holotype ♂, COLOMBIA: Departamento del Tolima, S. above Cajamarca, 3600 m, 26 vii 79 (M.J.A.).

Paratypes 3♀, data as holotype (M.J.A.).

Subsp. cajamarca differs from subsp. tolima in the following respects: it has a more pointed forewing and a more angular hindwing than tolima; it lacks the submarginal black spot on the forewing in cell Cu1; and its forewing basal grey-white area is broken by dark grey streaks on the veins. It is geographically separated, by the east–west divide in the Central Cordillera running between Ibagué and Armenia, from the populations of tolima.

Distribution: Adams: CC(T), 3600 m.

Bionomics: The butterflies fly fast and erratically low over the tussocky páramo vegetation, and also around the tops of clumps of bamboo at the very edges of the topmost cloud-forest. Like all the high-altitude white Lymanopodas, it requires longer periods of sunshine before it flies than the sympatric brown pronophilic species (in this case, Altopedaliodes reissi).
Lymanopoda lebbaea Felder & Felder, 1867: 473. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined].

Lymanopoda lebbaea Felder & Felder; Weymer, 1912: 247, pl. 52, row d (of type specimen); Gaede, 1931: 486; Brown, 1943: 96, pl. 2, fig. 1672 (genitalia).

This species appears to be restricted to the east slope of the Eastern Cordillera, being replaced on the west slope, and in the Central Cordillera, by its very close relative labda.

**Distribution:** A&B: EC(E), Cocuy, 2600/2700 m; Krüger (1924: 19): EC, 2800 m.

**Bionomics:** Although lebbaea and labda have similar wing-spot distributions to the species of the samius group (see under samius), they have brighter, more contrasting underside hindwing markings and correspondingly distinct behaviour patterns: they are most often encountered on the ground, being attracted to minerals and excrement, whereas the samius-group species come down from the chusque much more rarely.

Lymanopoda labda Hewitson

Lymanopoda labda Hewitson, 1861: 157, pl. 9, fig. 4. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].

Lymanopoda labda Hewitson; Butler, 1868: 170; Weymer, 1912: 246, pl. 52, row d; Gaede, 1931: 486; Brown, 1943: 96, pl. 2, figs 1612, 1647 (genitalia).

**Distribution:** BMNH: EC(W), Pacho; WC, Frontino; Ecuador and Peru; A&H; Adams: CC, 2400–2850 m; Fassl (1918: 44): EC(W), c. 2000–2500 m; Fassl (1911: 26): CC, c. 2000–2800 m; Krüger (1924: 19): CC(B), 2400–3000 m.

**Bionomics:** Like lebbaea, this species is attracted to mineral and organic matter on the ground, e.g. damp spots on dirt roads, and excrement.

Lymanopoda caucana Weymer

Lymanopoda panacea Hewitson form caucana Weymer, 1912: 250, pl. 52, row g. Syntypes, COLOMBIA: Cauca valley [MNHU?].

Lymanopoda panacea Hewitson var. caucana Weymer; Gaede, 1931: 487; Brown, 1943: 95 (status not indicated).

Lymanopoda caucana Weymer; Adams & Bernard, 1979: 105, figs 22, 23.

On both superficial and structural grounds, caucana clearly does not belong to the same group within Lymanopoda as panacea (e.g. panacea has two very long and thin processes on the valve, while the valve of caucana has a single, very broad, toothed process). Rather, its closest relatives are caeruleata Godman & Salvin (Santa Marta range), and the Central American species cinna Godman & Salvin (Guatemala) and euopis Godman & Salvin (Costa Rica).

**Distribution:** BMNH: CC(W), Manizales; Adams & Bernard (1979: 105): Sierra de Perija, 1800–2100 m; ?Fassl (1915: 11): WC, c. 2200–2500 m (as panacea—misidentification?).

**Bionomics:** According to Adams & Bernard (1979), this butterfly flies with a skipping action around clumps of bamboo, generally about 2 m above the ground.
Genus *Mygona* Thieme

*Mygona* Thieme, 1907: 162. Type-species: *Pronophila prochylta* Hewitson, by original designation.

*Proboscis* Thieme, 1907: 168. Type-species: *Pronophila propylea* Hewitson, by original designation. **Syn. nov.** [see *M. propylea*, below].

*Mygona irmina* (Doubleday)

*Pronophila irmina* Doubleday, [1849]: pl. 60, fig. 2. 1♂ syntype, VENEZUELA (BMNH) [examined].

*Pronophila irmina* Doubleday; Westwood, 1851: 358.

*Oxeoschistus irmina* (Doubleday); Butler, 1867: 268.


**Distribution:** BMNH: Venezuela (including coast range) to Ecuador; ESM: EC(W), 1800 m; A&H: CC, 2650 m; WC, 2700 m; Fassl (1918: 44): EC(B), c. 1750–2250 m.

**Bionomics:** This large butterfly has a slow, flapping flight, usually two or more metres above the ground, in sunny clearings deep in cloud-forest.

*Mygona propylea* (Hewitson), **comb. nov.**

(Fig. 33)

*Pronophila propylea* Hewitson, 1857: 80, pl. 1, figs 5, 6. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].

*Oxeoschistus propylea* (Hewitson); Butler, 1868: 180.

*Proboscis propylea* (Hewitson); Thieme, 1907: 168; Weymer, 1912: 269, pl. 58, row b; Gaede, 1931: 514.

The genus *Proboscis* was erected by Thieme (1907) for *propylea* because of its extended and pointed forewing apex; but the underside markings are very close to those of *M. irmina* and the male genitalia of the two species are very similar and distinct from those of *Oxeoschistus* species, which have a broader aedeagus and toothed valves. *M. propylea* and *irmina* also share a slow flight, tending to keep high above the ground. I therefore synonymize *Proboscis* with *Mygona*.

**Distribution:** BMNH: 1 from Bogotá: others from Ecuador; A&H; Adams: CC(H), 2450–2850 m; Fassl (1918: 44): EC(W), c. 2000–2350 m (according to Weymer, 1912: 269, Muzo, 2000 m); Krüger (1924: 41): CC, 2600 m.

**Bionomics:** This is the parapatric replacement, at higher altitudes, of *irmina*. The males sit high on particular leaves, frolicking among themselves high above the ground with a jerky, nonchalant flight. One male came to the ground to

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Figures 32–41. Fig. 32, *Lymanopoda huilana cajamarca* subsp. nov., male holotype. Fig. 33, *Mygona propylea* (Hewitson), **comb. nov.**, female. Fig. 34, *Mygona orsithes* (Hewitson), **comb. nov.** subsp. colombiana (Krüger), **comb. nov.**, male. Fig. 35, *Parapedaliodes nora* sp. nov., male holotype. Fig. 36, *Parapedaliodes margaretha* sp. nov., male holotype. Fig. 37, *Parapedaliodes zipa* sp. nov., male holotype. Fig. 38, *Pedaliodes pimenta* sp. nov., male holotype. Fig. 39, *Pedaliodes manneju* Thieme, male. Fig. 40, *Pedaliodes socorae* sp. nov., male holotype. Fig. 41. The same, female paratype.
feed on the sweat on my shirt; the illustrated female (Fig. 33) flew in a straight line about 2 m above the ground.

*Mygona orsedice* (Hewitson), **comb. nov.**, subsp. *columbiana* (Krüger), **comb. nov.**

(Fig. 34)

**Pronophila orsedice** Hewitson, 1878: 227. 1♂ syntype, ECUADOR (BMNH) [examined].

**Drucina orsedice** (Hewitson); Thieme, 1907: 170; Weymer, 1912: 270; Gaede, 1931: 515.

**Drucina orsedice** (Hewitson) var. *columbiana* Krüger, 1924: 41. 2♂, 1♀ syntypes, COLOMBIA: Central Cordillera (Tolima) (whereabouts of types unknown).

Although this species has ocelli on its underside in place of the orange and whitish patches in *irmina* and *propylea*, it shares an extended and pointed forewing apex with *propylea*, and a narrow aedeagus, untoothed valves, long labial palpus and basic underside hindwing pattern with both the other species. I therefore believe that *orsedice* should be transferred to the genus *Mygona*. Krüger's var. *columbiana* is the Colombian subspecies, intermediate in appearance between typical *orsedice* and Weymer's (1912) form *violacea*.

**Distribution:** BMNH: (typical subspecies, ?and others) Ecuador to Bolivia; A&H; Adams: CC(H), 2850–3200 m; Krüger (1924: 41): CC(T), east side, 2800 m, “local”.

**Bionomics:** The uppermost member of a parapatric trio of replacing congeners, flying above *propylea*, which in turn occupies an altitude band above *irmina*, *orsedice* has similar behaviour patterns to *propylea*. As Krüger (1924) noted, when at rest in cloudy periods, on broad-leaved or chusque leaves, it folds its forewings right back below the costae of its hindwings. It is rare and difficult to capture.

**Genus Oxeoschistus** Butler

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

*Oxeoschistus protogenia* (Hewitson)

**Pronophila protogenia** Hewitson, 1862: 13, pl. 6, fig. 38. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].

*Oxeoschistus protogenia* (Hewitson), Butler, 1867: 268; Thieme, 1907: 184; Gaede, 1931: 517; Forster, 1964: 182; Weymer, 1912: 272, pl. 59, row a.

**Distribution:** BMNH: EC(E), Ecuador and Peru; ESM: EC(E), c. 1000 m; Krüger (1924: 46): EC(E), 800–1000 m; Thieme (1907: 184): “coast range—Kalbreyer”.

**Bionomics:** This species flies at low elevations, in the rain-forest, being replaced higher up by *simplex*. With *simplex* it shares a similar upperside, but the light-coloured post-discal and submarginal bands on the underside hindwing are yellow and broken rather than white and continuous; its ocelli are distinctly surrounded by orange rings.
Oxeoschistus pervius Thieme, stat. nov.

Oxeoschistus submaculatus Butler & Druce var. pervius Thieme, 1907: 185. 1♂ syntype, COLOMBIA: Cauca Province [MNHU?].
Oxeoschistus puerta (Westwood) form pervius Thieme; Weymer, 1912: 271; Gaede, 1931: 517 (as var.)

O. submaculatus comes from Costa Rica; puerta comes from the Venezuelan coast range. Superficial differences between Oxeoschistus populations are not large, but on the basis of whether or not the underside hindwing ocelli are orange-ringed, the genus can be divided into two groups: pervius belongs with puerta and protogenia in the orange-ringed group; since the three are widely separated geographically and protogenia is interposed between the other two, and because they have consistent differences in their upperside markings, I believe that each merits specific status.

Distribution: Thieme (1907: 185): Cauca province (CC(W) or WC?); BMNH: CC(W) and Ecuador.

Bionomics: In the absence of altitude data for this species, it can only be guessed that it may be a low-altitude allopatric relative of puerta and protogenia.

Oxeoschistus simplex Butler

Oxeoschistus simplex Butler, 1868: 180, pl. 4, fig. 2. 1♂ syntype, COLOMBIA (BMNH) [examined].
Oxeoschistus simplex Butler; Thieme, 1907: 181; Weymer, 1912: 271, pl. 58, row c; Gaede, 1931: 517.

This species, lacking orange rings around the underside hindwing ocelli, is closest to submaculatus Butler & Druce from Costa Rica.


Bionomics: O. simplex has the slow, flapping flight typical of all the Oxeoschistus species in my experience. It occurs above protogenia up the altitude gradient in the EC, and possibly above pervius in the WC and CC(W).

Genus Panyapedaliodes Forster, gen. rev.


Heimlich (1972: 184) synonymized Panyapedaliodes with Spinantenna Hayward, a decision which he based upon the supposed similarities in facies and male genital structure between S. tristis (Guérin) and form mara Thieme of P. panyasis. I cannot concur with this decision: the facies of tristis and other Spinantenna species clearly separates them from Panyapedaliodes, and the triangular valve of tristis, illustrated by Heimlich (1972), is very distinct from the more rounded tip and extra process on the valves of panyasis. Accordingly, I resurrect Panyapedaliodes.
Forster (1964) erected the genus *Muscopedaliodes* for four species, whose facies are similar (in most cases) to those of *Panyapedaliodes* species, but which are larger in wing size. His illustrations of the male genitalia of *muscosa* and *amussis* (Thieme) are very close to those of *panyasis*, *mara* and *drymaea*. Not only is the underside pattern of *muscosa* extremely similar to that of *panyasis*, but also their male genitalia are virtually indistinguishable. I therefore synonymize *Muscopedaliodes* with *Panyapedaliodes*.

I also believe that Forster's (1964: 154, fig. 187) inclusion of *granulata* Butler (1868: 173, pl. 4, fig. 8) in the *Muscopedaliodes* group was incorrect. His genitalia figure does not correspond with BMNH specimens of the species, which have heavily toothed valves, broad subunci and very long aedeagi, and are thus close to *Praepedaliodes phanias* Hewitson. I hereby transfer Butler's species to *Praepedaliodes* Forster (1964), accordingly: *Praepedaliodes granulala* (Butler), **comb. nov.** I believe that the original type-series of *granulata*, which lacks data, came from Brazil.

**Panyapedaliodes panyasis** (Hewitson)

*Pronophila panyasis* Hewitson, 1862: 7, pl. 3, fig. 22. 3♂️ syntypes, VENEZUELA and BOLIVIA (BMNH) [examined].

*Pedaliodes panyasis* (Hewitson); Butler, 1868: 179; Thieme, 1905: 81; Weymer, 1912: 254, pl. 54, row a.


**Distribution**: BMNH: Venezuela to Bolivia; A&H; Adams: CC, 2400–2550 m; Fassl (1918: 44): EC(W), c. 2000–2550 m.

**Bionomics**: The rarity of this species seems to be due to the fact that it is predominantly a canopy dweller. It is sympatric with *drymaea*, but the latter's habitat is close to the ground.

**Panyapedaliodes muscosa** (Thieme), **comb. nov.**

*Pedaliodes muscosa* Thieme, 1905: 83, pl. 2, fig. 17. 6♂️ syntypes, BOLIVIA: Yungas de la Paz [MNHU?].

*Pedaliodes muscosa* Thieme; Weymer, 1912: 255, pl. 54, row b; Gaede, 1931: 491. *Muscopedaliodes muscosa* (Thieme); Forster, 1964: 155, fig. 185 (genitalia).

**Distribution**: BMNH: WC, 2200 m (Fassl); WC, Frontino; to Bolivia; Fassl (1915: 11): WC, c. 2000–2300 m.

**Panyapedaliodes phila** (Hewitson), **comb. nov.,** subsp. *philaeenis* (Thieme), **comb. nov.**

*Pronophila phila* Hewitson, 1862: 4, pl. 1, figs 3, 4. 1♂️ syntype [no locality] (BMNH) [examined].

*Pedaliodes phila* (Hewitson); Butler, 1868: 178; Thieme, 1905: 127; Weymer, 1912: 262, pl. 55. row f; Forster, 1964: 175.

*Pedaliodes phila* (Hewitson) var. *philaeenis* Thieme, 1905: 127. 2♂️ syntypes, ECUADOR: Banos [MNHU?].
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*Pedaliodes phila* (Hewitson) form *philaenis* Thieme; Weymer, 1912: 262; Gaede, 1931: 498 (as var.).


Although *phila* possesses orange markings on the forewing and upperside hindwing, its underside hindwing is almost a carbon copy of that of *panyasis*; and although its aedeagus is broader and more contorted, its genitalia are otherwise very close to those of *panyasis*.

The type specimen of *phila* corresponds to Bolivian material in the BMNH, and the typical race extends into Peru. In Ecuador and all three Colombian Cordilleras, the butterflies are referable to subs. *philaenis*, which has less orange at the apex of the upperside hindwing than typical *phila*. Krüger’s detailed description of *combeima* tallies with *philaenis*, and I hereby synonymize the two taxa.


*Bionomics*: *P. phila* is sympatric through much of its altitude range with *Physcoapedaliodes praxithea* (Hewitson): the fact that both bear a similar orange oblique band across the forewings suggests that some benefit may accrue through mimicry.

*Panyapedaliodes drymaea* (Hewitson)

*Daedalma drymaea* Hewitson, 1858: pl. 1, fig. 6. 1♂ syntype, ECUADOR (BMNH) [examined].

*Pedaliodes angularis* Butler, 1868: 176, pl. 4, fig. 7. 1♂ syntype, PERU (BMNH) [examined]. (Synonymy given by Thieme, 1905: 81.)

*Pedaliodes drymaea* (Hewitson) Thieme, 1905: 81; Weymer, 1912: 255, pl. 54, row a; Gaede, 1931: 489.

*Panyapedaliodes drymaea* (Hewitson); Forster, 1964: 157, fig. 195 (genitalia).


*Bionomics*: *P. drymaea* is one of the very few pronophilines which can live away from forest (or natural marsh or páramo), e.g. on roadsides and in open pasture, where it is especially common, and sometimes abundant, in the Central Cordillera.

*Panyapedaliodes jephtha* (Thieme), *comb. nov.*

*Pedaliodes jephtha* Thieme, 1905: 84, pl. 2, fig. 18. 1♂, 1♀ syntypes, COLOMBIA: Antioquia [MNHU?].

*Pedaliodes jephtha* Thieme; Weymer, 1912: 255, pl. 54, row b; Gaede, 1931: 491.

*Muscopedaliodes jephtha* (Thieme); Adams & Bernard, 1981: 359.
Judged by this species' similarities to *muscosa*, it was placed in *Muscopedaliodes* by Adams & Bernard (1981). My synonymy of that genus with *Panyapedaliodes* (see under *P. muscosa*) means that *jephtha* is transferred to the latter genus. It is known from Venezuela and Colombia.

**Distribution:** A&B: EC(W), 2500/2550 m; A&H: CC, 2650/2700 m; Thieme (1905: 84): “coast cordillera, Antioquia Province—Kalbreyer”.

**Bionomics:** A rare and solitary species.

*Panyapedaliodes silpa* (Thieme), **comb. nov.**

*Pedaliodes silpa* Thieme, 1905: 80, pl. 3, fig. 29. Syntype series, BOLIVIA and PERU [MNHU?].

*Pedaliodes silpa* Thieme; Forster, 1964: 168. *Pedaliodes tomentosa* Weymer, 1912: 255, pl. 54, row b. Syntype(s), COLOMBIA: Bogotá [MNHU?], **syn. nov.**

*Pedaliodes phanias* (Hewitson) form *silpa* Thieme; Weymer, 1912: 254; Gaede, 1931: 497 (as var.).

Weymer’s (1912) illustration of his *tomentosa* is very poor, but his description tallies with *P. silpa*, which Weymer believed (incorrectly) to be a form of the Brazilian *phanias*. It is placed tentatively in the genus *Panyapedaliodes* because, although its mottled underside hindwing is consistent with the genus, it has a broad posterior tip to its aedeagus and a narrow but blunt valve tip.

**Distribution:** A&B: EC(E), 2450–2500 m; A&H; Adams: CC, 2650–2850 m; Fassl (1918: 44): EC(B), c. 2650–3150 m (as *tomentosa*).

**Bionomics:** This is another rare and solitary butterfly, with a fast flight.

**Genus** *Parapedaliodes* Forster


*Parapedaliodes nora* sp. nov.

(Figs 5, 35)

**Male**

Forewing length 25 mm. Upperside forewing rich dark brown, with an orange post-discal band from costa to 1 mm from the inner margin: the inner edge is almost parallel to the outer margin, but the outer edge is extended distally in cells M2 and Cu1, and in the anterior part of Cu2. Upperside hindwing rich dark brown with orange-brown hairs over the basal half; an orange post-discal band from the costa to the middle of cell Cu2: the inner edge forms an acute angle in cell M2; the outer edge is extended almost to the outer margin in cell M2 and the posterior part of M1.

Underside forewing colour dark brown; russet-brown in the basal two-thirds of the discal cell and sandy-brown at the apex and along the costa; the orange post-discal band is the same as on the upperside, except that it becomes sandy-yellow at the costa. Underside hindwing ground colour dark brown; sandy-brown at apex and in a narrow submarginal band in cells M3...
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and Cu1; the post-discal band, mirroring that of the upperside, is yellow, speckled slightly with brown, and its two extremities are joined by a straight yellow discal line, so forming a dark brown triangle in the middle of the wing; four white submarginal dots in cells Rs, M1, M3 and Cu1.

**Female** unknown (but see below).

*Holotype* ♂, COLOMBIA: Departamento del Tolima, S above Cajamarca, 2900 m, 23 vii 79 (M.J.A.).


This species is clearly related to *philotera* (Hewitson) (locality unknown) and *parrhaebia* (Hewitson) from Ecuador. Its upperside pattern is closest to *parrhaebia* but it is much lighter in colour and the posterior part of the hindwing band is broader; it has a darker-coloured band than *philotera*, with a more indented outer edge on the forewing, and in *philotera* the inner edge of the hindwing band forms a right angle so that the posterior part of the band and the discal line on the underside run parallel rather than converge. *P. parrhaebia* was placed in his genus *Parapedaliodes* by Forster (1964: 153) and the male genitalia of *nora* (Fig. 5) are similar to the other members of the genus, with the long pointed aedeagus, very short anterior of the 'waist', and the long saccus. *P. nora* is confined to the Central Cordillera.

Krüger (1924) found the female of what he considered to be *P. philotera*, but what was almost certainly *nora*: he described it as differing from the male only in its lighter ground colour and the lighter colour of the bands. In addition to *philotera* and *parrhaebia*, its relatives include *phintia* (Hewitson), *cyrene* (Grose-Smith & Kirby)—both from Ecuador—*zipa* sp. nov. (in the Eastern Cordillera) and *margaretha* sp. nov. (perhaps parapatric above *nora*).

**Distribution**: A&H: CC(T), 2900–3100 m; Fassl (1911: 26): CC, c. 3000–3500 m (as *philotera* [sic]—misidentification); Krüger (1924: 23): CC (T and ?H), 2600–3200 m (as *philotera*—misidentification).

**Bionomics**: see next species.

**Parapedaliodes margaretha** sp. nov.

(Fig. 36)

**Male**

Forewing length 25.5 mm. Upperside ground colour dark brown; forewing with an oblique white post-discal band from the costa to vein Cu2, its inner edge touching the discal cell; hindwing with a T-shaped white post-discal band, beginning at the costa, running distally along the anterior edge of the discal cell, bending at right-angles and continuing past the end of the discal cell as far as vein Cu2; in cell M2 the band is greatly extended distad, and posterior of vein M3 it constricts.

Underside forewing ground colour dark brown, sandy-brown at the apex and along the costa; white post-discal band as on upperside, but it is broader in cell Cu1 and continues into Cu2 as a grey extension. Underside hindwing ground colour brown, sandy-brown at apex and yellow on the costa and distally along veins Sc+R1 to M3; the white post-discal band of the upperside extends to the
inner margin as a grey extension; a narrow discal white band joins it at the costa and crosses the wing to one-third the inner margin, running parallel to the posterior part of the post-discal band; four white post-discal dots in cells Rs, M1, M3 and Cu1.

Female unknown.

Holotype ♂, COLOMBIA: Departamento del Tolima, S above Cajamarca, 3100 m, 24 vii 79 (M.J.A.).

With its white markings, the solitary known individual of this species is unlike any other named "pedaliodine", but its underside markings indicate that it belongs to the same genus as nora, philotera and parrhoebia. It is unlikely to be merely a white form of nora, with which it was found flying, since the underside patterns are distinct. The BMNH has one male of an undescribed Ecuadorian species of Parapedaliodes, which also has white instead of orange markings and a similar underside hindwing, but its forewing band is longer posteriorly; anteriorly it is more distal and its inner edge has a right-angled bend in it.

I name this species after my mother, Dr Margaretha Adams, who in 1960 made the first butterfly net that I used, and fostered the enduring enthusiasm that resulted.

Distribution: Adams: CC(T), 3100 m.

Bionomics: Since the butterfly was found at the upper limit of the altitude range of P. nora (above which the cloud-forest had unfortunately been destroyed), it is possible that the two congeners replace each other parapatrically.

Parapedaliodes zipa sp. nov.

(Figs 6, 37)

Male

Forewing length 22.5–23.5 mm. Upperside unicolorous dark brown. No scent brand visible. Faintly chequered outer margins to both wings, with a narrow inner margin of chestnut on the hindwing. Underside forewing dark brown with dark chestnut apex, bordered basally with sandy-brown; one specimen has three very faint submarginal pale dots in cells Cu1 to M2. Underside hindwing dark chestnut, with a chestnut-speckled orange patch at the tornus, extending basad up the inner margin, and a faint greyish submarginal area in cell M1, extending partially into cells M2 and Rs; 2 submarginal creamy-white spots (c. 1 mm across) in cells Cu1 and M3 (altogether absent in one specimen).

Female

Forewing length not measured. Larger than male. Underside forewing slightly paler than in male, with four tiny whitish submarginal dots in cells M1 to Cu1. Underside hindwing with the male’s markings, but the chestnut-speckled orange patch at the tornus extends in a curved band, basad of the two submarginal creamy-white spots and then up to the costa, adjacent to the distal end of the discal cell; the area between this band and the outer margin in cells M1 and M2 is of a sandy-brown colour.

Holotype ♂, COLOMBIA: Departamento de Cundinamarca, between Zipaquirá and Pacho, 3150 m, 25 viii 82 (M.J.A.).
Paratypes: 2♂, data as holotype (M.J.A.); 1♀, east above Bogotá, 22 ix 46 (Schmidt-Mumm collection).

In spite of its lack of coloured bands, the size, wing shape, very long and narrow aedeagus and lack of a male scent patch place this species in the genus Parapedaliodes, close to nora and margaretha.

**Distribution:** Adams: EC(W), 3150 m; ESM: EC(E).

**Bionomics:** The three males were all caught within a few minutes in an area of rough pasture next to a chusque-filled gully, which had been worked on several previous occasions (and by ESM). They all came from the direction of the cloud-forest further up the mountain (near the tree-line), flying close to the ground, during an unusually long sunny period.

Genus Pedaliodes Butler

Pedaliodes Butler, 1867: 267. Type-species: Pronophila poesia Hewitson, by original designation.

**Pedaliodes poesia** (Hewitson)

Pronophila poesia Hewitson, 1862: 6, pl. 3, fig. 19. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].

Pronophila phanaraea Hewitson, 1868: pl. 3, fig. 15. 1♀ syntype, ECUADOR (BMNH) [examined]. (Synonymy given by Thieme, 1905: 53.)

Pedaliodes poesia (Hewitson); Butler, 1868: 172; Thieme, 1905: 53; Weymer, 1912: 250, pl. 53, row b; Gaede, 1931: 500; Forster, 1964: 159, fig. 198 (genitalia).

This species occurs in the middle range of the cloud-forest in all three Colombian Cordilleras; there is considerable variation between different populations, in size, extent of white speckling on the underside hindwing, and the amount of white subapically on the underside forewing: the darkest specimens come from the Western Cordillera, and the largest and brightest from the west slope of the Eastern Cordillera; the latter are nearly as bright as suspiro Adams & Bernard in the Sierra de Perijá. Other members of the species-group include leucocheilus Godman & Salvin (Santa Marta range), japhleta Butler (Venezuelan Mérida range) and piletha (Hewitson) (Venezuelan coast range).

**Distribution:** BMNH: Colombia to Bolivia; A&B; Adams: EC(B), 2250–2650 m; A&H; Adams: CC, 2300–2700 m; WC, 2300–2700 m; Fassl (1918: 44): EC(W), c. 2000–2250 m; Fassl (1911: 26): CC, c. 2000–3000 m; Fassl (1915: 11): WC, c. 2000–2300 m.

**Bionomics:** It is possible that phoenissa (Hewitson) is the upper parapatric replacement of poesia.

**Pedaliodes phoenissa** (Hewitson)

Pronophila phoenissa Hewitson, 1862: 9, pl. 4, fig. 30. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined].


Pedaliodes prytanis (Hewitson) form phoenissa (Hewitson); Weymer, 1912: 257, pl. 54, row d; Gaede, 1931: 503 (as var.).
Adams & Bernard (1979), reporting this species from the Sierra de Perijá, noted that its facies and genitalia place it in a different section of the genus from *prytanis*. The only other secure records are from the Eastern Cordillera: as often, Kalbreyer’s locality data, “coast range”, reported by Thieme, are suspect.

**Distribution:** Adams: EC(W), 2700–2850 m; Fassl (1918: 44): EC(B), c. 2650–3150 m; Thieme (1905: 93): “coast range—Kalbreyer”.

**Pedaliodes proerna proerna** (Hewitson)

*Pronophila proerna* Hewitson, 1862: 9, pl. 4, fig. 29. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined].


This species may be distinguished from the other Colombian, brown, barely marked *Pedaliodes* species by its quite pointed forewing and the large continuous male scent brand which enters the discal cell; the female’s underside hindwing is close to that of *poesia*. The extent to which it has a white-speckled post-discal wedge on the underside hindwing, and the number of white submarginal dots, vary: two of our specimens (one from the CC, one from the WC) have no markings at all, whereas all our material from the west slope of the EC has a white-speckled wedge (though not as discrete as in subspp. *fumaria* Thieme from Venezuela).

**Distribution:** A&B: EC(B), 2400–2650 m; A&H; Adams: CC, 2350–2700 m; A&H: WC, 2350–2700 m; [Fassl (1911: 26): CC, c. 2000–3000 m (as *pisonia*—misidentification)]; [Fassl (1915: 11): WC, c. 2000–2300 m (as *phrasis* or *exanima* or *pisonia*—misidentification)]; [Krüger (1924: 23): Colombia, down to 700 m—misidentification, referring to *pisonia*].

**Bionomics:** Like all the dark brown and barely marked species of the genus, *proerna* is most often encountered on the ground, among leaf litter or on excrement.

**Pedaliodes obscura** Grose-Smith & Kirby

*Pedaliodes obscura* Grose-Smith & Kirby, 1894: fig. 3. 1♂ syntype, BOLIVIA (BMNH) [examined].

*Pedaliodes phrassa* Grose-Smith & Kirby, 1894: figs 7, 8. 1♂ syntype, BOLIVIA (BMNH) [examined], syn. nov.

*Pedaliodes obscura* Grose-Smith & Kirby; Thieme, 1905: 61; Forster, 1964: 162. *Pedaliodes proerna* (Hewitson) form *obscura* Grose-Smith & Kirby; Weymer, 1912: 252; Gaede, 1931: 502 (as var.).

*Pedaliodes proerna* (Hewitson) form *phrassa* Grose-Smith & Kirby; Weymer, 1912: 252; Gaede, 1931: 502 (as var.).

*Pedaliodes pronoë* Staudinger, 1897: 132, pl. 6, fig. 8. Syntype series, BOLIVIA: Cochabamba and Yungas de la Paz [MNHU?]. (Synonymy given by Thieme, 1905: 61.)

The types of *obscura* and *phrassa* differ only in size, *obscura* being slightly the smaller, having few distinguishing features other than the male scent patch and
a single white spot on the underside hindwing: I therefore synonymize *phrasa* with *obscura*. The species is very easily confused with *proerna*, with which it flies in some localities, but on its underside hindwing it lacks the faint traces of white speckling, its anal white spot is larger and tends to be oval in shape, and the ground colour is less intensely dark; its forewing is shorter and more rounded in shape and it has a distinct pale post-discal costal streak on the forewing underside.

*Distribution:* A&H; Adams: CC, 2500–2850 m; WC, 2350 m; BMNH: WC, Monte Socorro, “3800 m”; [Fassl (1915: 11): WC, c. 2000–2300 m (as *phrasis* or *exanima* or *pisonia*—misidentification?)].

**Pedaliodes pimienta** sp. nov.

(Figs 7, 38)

*Male*

Forewing length 32 mm. Upperside dark brown, paler brown at the apex and outer margin of the forewing; forewing apex and outer margin, and hindwing margin from base to cell M3 via the tornus, dusted with bluish scales. Scent patch enters discal cell; broken in cell Cu2.

Underside forewing dark brown with a clearly delimited pale area at the apex; dusted with white in this area and around outer margin; a paler brown patch occupying the basal two-thirds of the discal cell. Underside hindwing ground colour dark brown, liberally speckled with white, especially in the posterior half; a fairly distinct but narrow post-discal dark brown band between the costa and vein 2dA, running parallel to the outer margin, except in cell Cu1 where it is translated basad; a faintly darker brown outer marginal band; a submarginal white dot in cell Cu1, and another smaller one in cell Rs.

*Female unknown.*

**Holotype ♂, COLOMBIA: Departamento de Boyacá, W below Arcabuco, 2650 m, 27 vii 77 (M.J.A.).**

Although its genitalia (Fig. 7) place it in the group of *Pedaliodes* species including *proerna* and *phrasis* Grose-Smith, its large size, white-speckled underside hindwing, and large pale forewing apical patch clearly distinguish it from any other species.

*Distribution and bionomics:* Adams: EC(W), 2650 m, caught as it swooped robustly down to faeces bait on the ground.

**Pedaliodes costipunctata** Weymer, *stat. nov.*

*Pedaliodes paeonides* (Hewitson) form *costipunctata* Weymer, 1912: 256, pl. 54, row c. Syntype(s), COLOMBIA: Monte del Eden, Ibagué [MNHU?].

*Pedaliodes paeonides* (Hewitson) var. *costipunctata* Weymer; Gaede, 1931: 492.

It seems possible that this species is the Central Cordilleran sister-species of Ecuadorian *P. paeonides*, but the two are distinct enough to warrant separate specific status. *P. costipunctata* has a much shorter white costal streak on the underside hindwing (3 mm, compared to 9–10 mm in *paeonides*). Krüger (1924: 31) gave the name *obscura* to what he considered to be a dark form of *"paeonides",*
but he could well have been referring to another similar species, e.g. *proerna* or *obscura*.

**Distribution:** A&H; Adams: CC, 2500–3000 m; Krüger (1924: 31): CC and WC, 2000–3000 m (as *paeonides*); [Fassl (1911: 26): CC, c. 2500–3000 m (as *simmias*—misidentification?).]

*Pedaliodes manis* (Felder & Felder)
(Fig. 8)

**Pronophila manis** Felder & Felder, 1867: 469. 2♂️♀️ syntypes, COLOMBIA: Bogotá (BMNH) [examined].


*Pedaliodes pisonia* (Hewitson) form *manis* (Felder & Felder); Weymer, 1912: 254, pl. 53, row e; Gaede, 1931: 499 (as var.).

Thieme (1905: 73) considered *manis* to be synonymous with *pisonia*, and Weymer (1912) rated it as a form of *pisonia*, but the male genitalia of the two taxa are highly distinct (see Adams & Bernard, 1979: 109). *P. manis* is a sibling species with *manneja* Thieme, with which it flies, in the upper range of *manis*: the two are extremely difficult to separate on external facies, but their male genitalia are very distinct: *manis* (Fig. 8) has a long, narrow, toothed second process on the valves, almost as long as the main process; *manneja* (Fig. 9) has a short, broad and rounded second process. Forster’s (1964: fig. 221) figure clearly refers to *manneja*. *P. manis* has a more rounded forewing apex and a less dark underside hindwing ground colour, but its markings are closely similar. It flies at lower altitudes, but a considerable amount of overlap occurs with *manneja*.

**Distribution:** BMNH: Guyana, Venezuela, Costa Rica to Peru; A&B: EC(W), 2250 m; A&H; Adams: CC, 1750–2400 m; WC, 1950–2200 m; Fassl (1918: 44): EC(W), c. 1000–1650 m; Fassl (1911: 26): CC, c. 1000–2450 m; Fassl (1915: 11): WC, c. 1500–2000 m.

**Bionomics:** This species is parapatric below *manneja*, but being common and with a broad ecological niche it extends up in the lower altitudes occupied by the other species. It occurs in disturbed forest, along roadsides and in pasture land, flying close to the ground.

*Pedaliodes manneja* Thieme
(Figs 9, 39)

**Pronophila pisonia** Hewitson var.; Hewitson, 1862: 7, pl. 3, fig. 20. [Specimen lost.]

*[Pedaliodes manis* (Felder & Felder); Kirby, 1871: 104; Forster, 1964: fig. 221 (genitalia). Misidentifications.]

*Pedaliodes manneja* Thieme, 1905: 76. 6♂️♀️ syntypes, VENEZUELA [:coast range] (3 in BMNH) [examined].

*Pedaliodes manneja* Thieme; Weymer, 1912: 254; Gaede, 1931: 491; Adams & Bernard, 1979: 110.
For the differences between this species and its sibling, *manis*, see under *P. manis*. It is most closely related to *montagna* Adams & Bernard from the Venezuelan Mérida range. Typical *manneja* from the Venezuelan coast range has a very distinct whitish costal patch on the underside hindwing; westward from the coast range this becomes progressively less distinct: populations from all three Colombian Cordilleras are darker than butterflies from the type locality and from the Sierra de Perijá. It is these dark individuals that are particularly difficult to distinguish from *manis*.

**Distribution:** BMNH: Venezuela to Bolivia; A&B: Adams: EC(B), 2300–2850 m; A&H: Adams: CC, 2350–2600 m; Fassl (1911: 26): CC, c. 2500–3000 m.

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**Pedaliodes pisonia** (Hewitson)

(Fig. 10)

*Pronophila pisonia* Hewitson, 1862: 6, pl. 3, fig. 21. 1♂, 1♀ syntypes, VENEZUELA (BMNH) [examined].

**Pedaliodes pisonia** (Hewitson); Butler, 1868: 173; Thieme, 1905: 73; Weymer, 1912: 254, pl. 53, row f; Gaede, 1931: 499; Forster, 1964: 165.

Compounded by the fact that this rare species—to different degrees—has a chestnut suffusion at the inner margin of the underside hindwing, it has been confused with both *manis* and *manneja*; *pisonia* is larger than either; the outer one-third of its upperside forewing is distinctly paler; the white submarginal dot in cell Cu1 on the underside hindwing is ringed with dark brown; and the valve has a narrow, pointed process just below the rounded tip (Fig. 10). It is closely related, judged by facies and genital structure, to *dejecta* (Bates) from Costa Rica and Panamá, *ereiba* (Felder & Felder) from the Colombian Eastern Cordillera, and *pomponia* (Hewitson) from Ecuador.

**Distribution:** A&B: EC(W), 2600 m, 1 male; ESM: EC(E), lowlands, Rio Negro; [Fassl (1911: 26): CC—misidentification of *proerna*?]; [Fassl (1915: 11): WC—misidentification of *proerna*?]; [Krüger (1924: 23): Colombia, down to 700 m—misidentification of *proerna*?].

**Bionomics:** That this lowland-forest butterfly has migratory tendencies is suggested by the fact that I found a female on the Portachuelo Pass (at 1100 m in the Venezuelan coast range), well-known for its migratory butterflies, and this may explain my capture of a single male at 2600 m in the Eastern Cordillera.

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**Pedaliodes ereiba** (Felder & Felder)

*Pronophila ereiba* Felder & Felder, 1867: 469. 1♂ sytype, COLOMBIA: Bogotá (BMNH) [examined].

*Pronophila pasicrates* Hewitson, 1874: pl. 8, figs 51, 59. 1♂ sytype, COLOMBIA (BMNH) [examined]. (Synonymy given by Weymer, 1912: 262.)

**Pedaliodes ereiba** (Felder & Felder); Butler, 1868: 174; Thieme, 1905: 75; Weymer, 1912: 262, pl. 55, row f; Gaede, 1931: 490.

**Distribution:** BMNH: EC, Bogotá; Krüger (1924: 27): EC(W), Muzo, 1700 m.

**Bionomics:** This rare species, closely allied to *pomponia* (Hewitson) from Ecuador
and *pisonia*, is known only from the Eastern Cordillera, where it probably flies in the lower cloud-forests.

**Pedaliodes antigua** Adams & Bernard

*Pedaliodes antigua* Adams & Bernard, 1981: 362, figs 9 (genitalia), 22, 23. 3♂, 1♀ syntypes, VENEZUELA: Cordillera de Mérida (BMNH) [examined].

This species, originally described from old BMNH specimens from Venezuela, is found in all three of the Colombian Cordilleras, but there is some inter-population variation: the EC population has a broader white costal streak on the underside hindwing (2.5–3.0 mm in cell Rs) than typical *antigua*; the underside forewing costal streak is broader too; the Ecuadorian specimen referred to below is closest to this population. In the CC, the butterflies have a darker underside ground colour with less speckling; the hindwing costal streak is about 1.5 mm broad in cell Rs; this is similar to Weymer’s (1912: pl. 54, row c) illustration of *patizathes* (Hewitson), but the figure does not represent the BMNH type of that species, which has a more speckled underside and lacks both the costal white streak on the underside forewing and the chestnut coloration at the outer margin.

This species flies, in the CC, together with *costipunctata*, with which it is easily confused; but its white costal streak on the underside hindwing is always broader (and whiter) in cell Rs, and the submarginal white dot on the same wing is much nearer to the outer margin.

**Distribution:** A&B: EC(E), 2450 m; EC(W), 2650 m; A&H: Adams: CC(H), 2500–2700 m; [Fassl (1918: 44): EC(E), c. 2350–2750 m (as *phthiotis*-misidentification?)]; [Krüger (1924: 31): CC and WC, 2000–3000 m (as *patizathes*-misidentification?)]; Hadfield (coll. 1983): Ecuador, Las Cajas, 2400 m.

**Pedaliodes phrasicla** (Hewitson)

*Pronophila perperna* Felder & Felder, 1867: 468. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined]. [Name preoccupied by *Pronophila perperna* Hewitson, 1861.]

*Pronophila phrasicla* Hewitson, 1874: pl. 8, fig. 52. 1♂ syntype, ECUADOR (BMNH) [examined].

*Pedaliodes labulla* Thieme, 1905: 65. (Synonymy given by Weymer, 1912: 251.)

*Pedaliodes phrasicla* (Hewitson); Thieme, 1905: 56; Weymer, 1912: 251, pl. 53, row c; Gaede, 1931: 498; Forster, 1964: 161.

Thieme (1905) proposed the name *labulla* to replace the Felders’ *perperna*, but failed to note that Hewitson (1874) had already described the species under the name *phrasicla*.


**Bionomics:** This widespread species is quite common in the lower cloud-forests, preferring to fly 1–3 m above the ground. It is the lowermost of parapatric series of three species in each of the Colombian Cordilleras, always occurring below *peucetias*; the uppermost member is different in each cordillera.
**Pedaliodes peucestas** (Hewitson)

*Pronophila peucestas* Hewitson, 1862: 4, pl. 2, figs 13, 14. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].

*Pedaliodes peucestas* (Hewitson); Butler, 1868: 177; Thieme, 1905: 112; Weymer, 1912: 260, pl. 55, row c; Gaede, 1931: 496.

*P. peucestas* occurs quite commonly in all three cordilleras of Colombia. The lighter post-discal band on the underside hindwing varies in its distinctness: the darkest specimens live in the Western Cordillera.

**Distribution:** BMNH: Colombia and Ecuador; Weymer (1912: 260): EC, CC, Ecuador and Peru; A&B: EC(W), 2400–2550 m; A&H; Adams: CC, 2350–2900 m; WC, 2850/2900 m; Fassl (1911: 26): CC, c. 2000–3000 m; Fassl (1915: 11): WC, c. 2200–2500 m.

**Bionomics:** This white-banded species, occupying a band of altitudes above its relative *phrasicla*, is replaced at the highest elevations in the cloud-forest by *pallantis* (Hewitson) in the EC, *phaedra* (Hewitson) in the CC and *socorrae* sp. nov. in the WC.

**Pedaliodes pallantis** (Hewitson)

*Pronophila pallantis* Hewitson, 1862: 5, pl. 2, figs 15, 16. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].

*Pedaliodes pallantis* (Hewitson); Butler, 1868: 177; Thieme, 1905: 114; Weymer, 1912: 260, pl. 55, row c; Gaede, 1931: 493.

**Distribution:** Thieme (1905: 114): Colombia; and “Huancabamba, N Peru” (?); A&B; Adams: EC(W), 2650–3200 m; Fassl (1918: 44): EC(W), c. “2250–2500 m” (?).

**Bionomics:** This species, almost certainly confined to the Eastern Cordillera, flies—usually close to the ground—in the uppermost cloud-forests. Its closest relatives are *phaedra* in the CC and *socorrae* in the WC.

**Pedaliodes phaedra** (Hewitson)

*Pronophila phaedra* Hewitson, 1870: 158; 1871: pl. 5, figs 34, 35. 1♂ syntype, [no locality —?ECUADOR] (BMNH) [examined].

*Pedaliodes phaedra* (Hewitson); Thieme, 1905: 115; Weymer, 1912: 260; Gaede, 1931: 496.

**Pronophila palades** Hewitson, 1878: 227. 1♂ syntype, ECUADOR (BMNH) [examined]. [Name preoccupied by *Pronophila palades* Hewitson, 1872.]

**Pedaliodes phaedra** (Hewitson) var. *melaleuca* Weymer, 1890: 41; Weymer, 1912: pl. 55, row d.

**Pedaliodes phaedra** (Hewitson) ab. *palades* (Hewitson); Thieme, 1905: 115.

**Pedaliodes niphoessa** Thieme, 1905: 116, pl. 1, fig. 1. Syntype(s), COLOMBIA: Quindio Pass [MNHU?].

**Pedaliodes phaedra** (Hewitson) form *niphoessa* Thieme; Weymer, 1912: 260.

**Pedaliodes phaedra** (Hewitson) form *melaleuca* Weymer, 1912: 260. [Replacement name for *Pronophila palades* Hewitson, 1878, née Hewitson, 1872.]

Hewitson’s (1878) *P. palades* was recognized by Weymer (1912) as a form of *phaedra* in which the bands are not yellow but milky-white; since *palades* was preoccupied by another species of the same name, described by Hewitson in
1872, Weymer gave it the name _melaleuca_. Thieme's (1905) _niphoessa_ was classed as another form of _phaedra_ by Weymer. Evidence that both _melaleuca_ and _niphoessa_ (which has a whiter and broader band, entering the discal cell on the forewing) are indeed forms of _phaedra_ comes from the fact that all three were found flying together by A&H in the CC (Huila): this represents a rare case of polymorphism in the Pronophilini. The Tolima populations, however, appear to consist only of form _niphoessa_. In Ecuador, typical _phaedra_ and form _melaleuca_ fly together, along with intermediate forms, according to Weymer (1912).

**Distribution:** A&H; Adams: CC(H), 2750–3150 m (all three forms); A&H: CC(T), 2850–3100 m (_niphoessa_ only); Krüger (1924: 32): CC(H), 2600–3000 m (all three forms); CC(T), 2800–3400 m (_niphoessa_ only); Fassl (1911: 26): CC(T), c. 3000–3500 m (as _niphoessa_).

**Pedaliodes soccorae** _sp. nov._
(Figs 11, 40, 41)

**Male**

Forewing length 27–28 mm. Upperside forewing dark brown with an oblique white band from vein Sc at the costa to vein 2A near the tornus; the band cuts through the distal end of the discal cell. Upperside hindwing unicolorous dark brown, except for a dusting of whitish scales at the apex and white sections of the outer margin fringe at each indentation of the margin.

Underside forewing chocolate-brown, russet-brown at apex and a dusting of golden scales along the costa; the white oblique band as on the upperside, but slightly broader; four submarginal white dots in cells R4 to M2 (a fifth in M3 visible in some specimens), the anterior dot set in a suffusion of silver scales. Underside hindwing ground colour chocolate-brown, speckled with light brown and silver; a narrow, dark chestnut-brown post-discal strip basad of the broad, lighter-coloured post-discal band; the latter band is broadest in cells M3 and Cu1 and narrowest on vein M2; a series of five white spots in the post-discal band, in cells Rs to Cu1, the anterior one set in a silvery suffusion; a faint silvery costal streak basad of the post-discal strip.

**Female**

Forewing length 30 mm. Upperside as in male, but with more extensive whitish dusting at the hindwing apex. Underside as in male, but of a lighter colour throughout and with less contrast between the colours; fewer white spots: only two, very faint, in forewing cells R4 and R5, and the hindwing spot in cell Rs is absent.

**Holotype** ♂, COLOMBIA: Departamento del Valle, SW above Pichindé ('Monte Socorro'), 3300 m, 20 viii 79 (M.J.A.).

**Paratypes,** locality as holotype: 4♀♀, 2♂♂, 2900–3300 m, 19 viii 79; 4♀♀, 1♀, 3200–3350 m, 20 viii 79; 2♀♀, 3250–3450 m, 21 viii 79 (M.J.A. and P.J.H.); 2♂♂, 3500 and 3600 m, vii 09, BMNH (Fassl).

The underside hindwing markings and male genital structure place _sccorae_ together with _phaedra_ and _pallantis_ in the same assemblage of very closely related species; they also all occupy the cloud-forests at the tree-line. Lacking the hindwing white patch of _phaedra_, it most closely resembles _pallantis_, but _sccorae_ is larger and has a narrower forewing band. It replaces it parapatric ally, _peucesias_, above 2900 m and is restricted to the Western Cordillera.
**Distribution:** A&H: WC, 2900–3450 m; Fässl (1915: 11): WC, c. 3000–3650 m (as pallantis—misidentification).

*Pedaliodes ferratilis* Butler

*Pedaliodes ferratilis* Butler, 1873: 221. 2♂ syntypes, PERU (BMNH) [examined].


Thieme's (1905: 101) synonymy of *P. morenoi* Dognin with *ferratilis* was rejected by Adams & Bernard (1981). There is considerable variation in this species within populations, but examination of the male genitalia of a number of specimens suggests that only one species is involved. Individuals differ in wing size, the extent of the chestnut-brown suffusion on the underside hindwing distad from the inner margin, and the distinctness of the orange-speckled anal patch on the same wing.

*Distribution:* BMNH: Venezuela to Peru; A&B: EC(B), 2400–2700 m; A&H: Adams: CC, 2500–3150 m; WC, 3450 m; [Fässl (1911: 26): CC, c. 3000–3900 m (as polla—misidentification?)]; [Fässl (1915: 11): WC, c. 3500–4000 m (as polla—misidentification?)].

*Bionomics:* This is a ground-loving, fast-flying butterfly.

*Pedaliodes polusca* var. *polla* Thieme

*Pronophila polusca* Hewitson var.; Hewitson, 1862: 10, pl. 4, fig. 32. Colombia [specimen lost].

*Pedaliodes polusca* var. *polla* Thieme, 1905: 103. Syntypes, COLOMBIA (MNHU) [not examined] (BMNH—specimen lost, as above). *Pedaliodes polusca* var. *polla* Thieme; Gaede, 1931: 501; Weymer, 1912: 258 (as form).


This species, found in the Venezuelan Cordillera de Mérida and the Colombian Eastern Cordillera, is a close relative of *tyrheus* Godman & Salvin (in the Santa Marta range), *tyrheoides* Adams & Bernard (in the Sierra de Perijá) and *pollonia* sp. nov. (in the Central and Western Cordilleras). As pointed out by Krüger (1924) and Adams & Bernard (1981), *polla* flies parapatrically below *polusca*: it is smaller than *polusca*, with a yellower, more distinct underside hindwing wedge, and a more rounded forewing apex.

*Distribution:* A&B; Adams: EC(E), 2500–2850 m; EC(W), 2650–2850 m (+3200 m); Krüger (1924: 31): “all three cordilleras”, 2000–3000 m (pointing out differences between the EC and CC/WC populations).

*Pedaliodes pollonia* sp. nov.

(Figs 12, 42)

**Male**

Forewing length 25–27.5 mm. Upperside unicolorous dark brown. Scent patch unbroken except (in some specimens) in cell Cu2, c. 6 mm broad, and entering discal cell.
Underside forewing dark brown, russet-brown at apex speckled with dark brown and (in some specimens) sandy-brown; a faint pale costal streak distad of the cell; usually a faint whitish submarginal dot in cell M1. Underside hindwing russet-brown, speckled with dark brown especially in the anterior half; posterior of an almost straight line between veins 2A and M2, and in cells Cu2, 2A and 3A almost to the base, russet-brown more or less speckled with orange-brown, in some cases forming an indistinct triangular wedge; a clear whitish submarginal spot in cell Cu1, highlighted basally and distally by dark brown; a tiny whitish submarginal dot in cell Rs, and sometimes up to three similar dots in cells M1 to M3.

**Female**

Forewing length 28.5 mm. Upperside unicolorous dark brown, with a chestnut-brown anal patch on the hindwing. Underside forewing as in male but with sandy-brown coloration at the apex and a more distinct pale costal streak. Underside hindwing ground colour and markings as in male, but the submarginal band is paler at the apex and there is a narrow sandy-brown band merging into the anal orange-brown-speckled area and extending, narrowing anteriorly, to vein M2.

**Holotype** ♂, COLOMBIA: Departamento del Tolima, S above Cajamarca, 2950 m, 24 vii 79 (M.J.A.).

**Paratypes**, locality as holotype: 2♂, 2800 m, 23 vii 79; 2♂, 2900 m, 24 vii 79; 1♂, 2800–2900 m, 26 vii 79; 2♂, 2800 m, 27 vii 79; COLOMBIA: Departamento del Huila, above San José de Isnos: 1♂, 2500–2550 m, 3 viii 79; 2♂, 2500–2550 m, 4 viii 79; 1♂, 2600–2700 m, 6 viii 82; 1♂, COLOMBIA: Departamento del Cauca, between Santa Leticia and Puracé, 2650 m, 10 viii 79; 7♂, COLOMBIA: Departamento del Tolima, NW above Ibagué, 2650–2950 m, 29 viii 79; COLOMBIA: Departamento del Huila, below Santa Leticia: 3♂, 2400 m, 2 viii 82; 1♀, 2400 m, 3 viii 82; 2♂, 2350–2400 m, 4 viii 82 (M.J.A. and P.J.H.).

Compared with its closest relative, *polla*, *pollonia* has a more russet-coloured underside hindwing, with a far less distinct and darker wedge and only one distinct submarginal spot. It may also be confused with *ferratilis*, from which it is distinguished by its lighter underside ground colour, its underside hindwing wedge rather than patch at the inner margin and its white submarginal spot on the underside hindwing. This not uncommon species is replaced parapatrically at higher altitudes in the cloud-forest by *polusca*. I have not seen any specimens from the Western Cordillera, which may or may not be referable to *pollonia*. Fassl’s (1911, 1915) records of “*polla*” in the CC and WC, as judged by the high altitudes reported, were probably of *ferratilis*.

**Distribution**: A&H; Adams: CC(T&H), 2350–2950 m; Krüger (1924: 31): (CC & WC), 2000–3000 m (as *polla*).

**Pedaliodes polusca** (Hewitson)

*Pronophila polusca* Hewitson, 1862: 10, pl. 4, fig. 31. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined].

*Pedaliodes polusca* (Hewitson); Butler, 1868: 176; Thieme, 1905: 103; Weymer, 1912: 258, pl. 54, row f; Gaede, 1931: 500; Forster, 1964: 169.
This species is found in the Eastern and Central Cordilleras, but is replaced in the Western Cordillera by its near relative *parranda* sp. nov. Specimens from the CC tend to be slightly more orange-speckled underneath than those from the EC.

**Distribution:** A&B; Adams: EC(E), 2650–3150 m; EC(W), 3100–3300 m; [Fassl (1918: 44): EC(B), c. 2650–3150 m (as *paneis*—misidentification?)]; A&H; Adams: CC, 2850–3150 m; [Fassl (1911: 26): CC, c. 3000–3900 m (as *paneis*—misidentification?)]; Krüger (1924: 31): “all three cordilleras”, 2800–3500 m (WC population confused with *parranda*?).

**Bionomics:** In both the EC and the CC, *polusca* is parapatric above its smaller relative, *polla*, with the transition altitude on the west slope of the EC apparently higher than elsewhere. In the CC, there is a third parapatric member in the very topmost forest: *palpita* sp. nov. Like *polla* and *pollonia*, *polusca* is a species which tends to remain close to the ground. I have two males with distinct birds’ beak-marks on their wings.

**Pedaliodes parranda sp. nov.**

*(Figs 13, 43, 44)*

**Male**

Forewing length 33–34 mm. Upperside unicolorous dark brown, paler brown only at the costa of the hindwing. Underside forewing dark brown; chestnut-brown, speckled with dark brown, at the apex; very faint tiny white submarginal dot in cell M1. Underside hindwing russet-brown, speckled with dark brown and suffused with dark orange in cells Cu1 to 3dA, except at their bases; a series of five submarginal yellowish dots in cells Rs to Cul, largest in Cu1 and sometimes extremely faint (or absent) in Rs to M2.

**Female**

Forewing length 33 mm. Upperside dark brown. Forewing with a row of five faint paler-brown submarginal dots in cells R5 to Cu1, and an indistinct paler-brown post-discal costal streak. Hindwing with a marginal suffusion of chestnut-brown from halfway along the inner margin to cell M3.

Underside forewing dark brown; sandy-brown and russet-brown at the apex; a sandy-brown post-discal costal streak; an area of chestnut-brown in the distal half of the discal cell and extending into cell Cu1. Underside hindwing as in male, but with a slightly paler ground colour; the orange suffusion is more clearly defined, making up a post-discal band between the inner margin and vein Rs, wedge-shaped as far as vein M2, and a costal streak; post-discal dots as in male, but larger.

**Holotype** ♂, COLOMBIA: Departamento del Valle, SW above Pichindé (Monte Socorro), 3300 m, 20 viii 79 (*M.J.A.*).

**Paratypes** locality as holotype: 3♂, 2900/3100 m, 19 vii 79; 5♂, 3200–3450 m, 20 vii 79; 5♂, 1♀, 3200–3450 m, 21 vii 79 (*M.J.A. and P.J.H.*); 2♂, 3600 and 3800 m, vii 09, BMNH (*Fassl*).

*P. parranda* differs from its nearest relative, *polusca*, in its larger size (particularly of the hindwing) and the absence of an orange-brown wedge on the male underside hindwing. It is restricted to the uppermost forests of the Western Cordillera.
**Pedaliodes palpita sp. nov.**  
(Figs 14, 45, 46)

**Male**

Forewing length 27–29 mm. Upperside forewing dark brown, with a row of four sandy-brown or orange submarginal dots in cells M1 to Cu1. Upperside hindwing dark brown, suffused post-discally with russet-brown; costa sandy-brown; outer and inner margins orange-brown; two submarginal orange-brown spots in cells M3 and Cu1, in some specimens joined to the costa by indistinct stripes of the same colour.

Underside forewing dark brown with silver-grey and russet-brown at apex, and a whitish post-discal costal streak; a suffusion of brick-red in the basal half of the discal cell, extending into cell Cu2; four whitish or sandy-brown spots as on the upperside. Underside hindwing golden-brown, speckled with dark brown and yellow; a curved wedge of yellow or orange-yellow from the inner margin and tornus to vein M2; marginal and submarginal area of the same colour in cells M3 and Cu1; a costal streak and a patch in the discal cell contiguous with the median vein; two yellowish submarginal spots in cells M3 and Cu1 (sometimes three very faint additional ones in Rs to M2).

**Female**

Forewing length 28 mm. Upperside as in male, but slightly paler ground colour. Underside forewing as in male, but with apex and outer margin sandy-brown, and brick-red area filling the whole discal cell, extending into cells M3 and Cu1 as well as Cu2; a post-discal russet-brown band extending from the costal streak to cell Cu2. Underside hind-wing sandy-brown, speckled with dark brown, and with grey at the base; wedge, costal streak and cell patch much less distinct than in male, and larger, of the ground colour with less speckling than over the rest of the wing.

**Holotype** ♂, COLOMBIA: Departamento del Tolima, S above Cajamarca, 3600 m, 26 vii 79 (M.J.A.).

**Paratypes**, locality as holotype: 3♂, 1♀, 25 vii 79; 8♂, 2♀, data as holotype (M.J.A.).

Of similar wing size to its nearest relative polusca, palpita has pale spots on the upperside of both wings, a paler underside hindwing and the inner edge of the post-discal band on its underside hindwing projects towards the base.

**Distribution**: Adams: CC(T), 3600 m.
Bionomics: All the specimens were netted at one site in a very sheltered area of páramo, with tall grass and very tall ‘trees’ of *Espeletia*, at the edge of the uppermost cloud-forest. The butterflies flew at the very edge of the forest, usually close to the ground, sometimes straying into the páramo.

**Pedaliodes empusa** (Felder & Felder)

*Pronophila empusa* Felder & Felder, 1867: 468. 3♂ syntypes, COLOMBIA: Muzo, and [no locality] (BMNH) [examined].

*Pedaliodes empusa* (Felder & Felder); Butler, 1868: 173; Thieme, 1905: 62; Weymer, 1912: 252, pl. 53, row d; Gaede, 1931: 490; Forster, 1964: 164.

**Distribution:** A&B: EC(B), 2800–3300 m (east slope, only at Cocuy); Fassl (1918: 44): EC(B), c. 2650–3150 m (east slope population confused with *ralphi* sp. nov.?); Weymer (1912: 252): EC, Bogotá and Muzo; (? Peru, Cuzco).

Bionomics: Almost certainly restricted to the Eastern Cordillera (the west slope and the northern part of the east slope) and replaced east of Bogotá by *ralphi*, this species flies in moist páramo and open, marshy subpáramo.

**Pedaliodes ralphi** sp. nov.

(Figs 15, 47, 48)

Male

Forewing length 27–28 mm. Upperside unicolorous dark brown with fringes of forewing faintly chequered with white. Forewing scent patch uniformly 5 mm wide, extending from vein R5 to the inner margin and entering the discal cell.

Underside forewing dark brown with a russet-brown area at the apex and a few bluish-white scales at the costa basad of this; a clear, 1 mm broad white costal streak between costa and vein M2. Underside hindwing dark brown, faintly dusted with whitish scales and with a russet hue at the costa; a jagged, distinct, white post-discal band, 1–2 mm wide, extending from the costa to vein M3, its inner edge beginning at right-angles to vein M1, extending distad in cell M1, and bending back to cross cell M2 almost at right-angles to veins M2 and M3; its distal edge is less clear-cut; a submarginal white dot in cell Cu1 (and an additional smaller one in M3 in three specimens).

Female

Forewing length 25–27 mm. Upperside unicolorous dark brown, a little paler than in the male; fringes of both wings faintly white-chequered; a faint pale-brown costal streak on the forewing ‘showing through’ from the underside.

Underside forewing paler than in male, with a submarginal triangle of bluish scales at the costa and a broader white costal streak. Underside hindwing as in male, but with a sandy-brown post-discal band distad of the white band and a paler ground colour. In one specimen, the portion of the white band in cell Rs is extended basad. Both submarginal white dots are present, and one specimen has a third one in cell Cu2.

Holotype ♀, COLOMBIA: Departamento de Cundinamarca, NE of Bogotá, between Guasca and Gachetá, 3150 m, 21 vii 82 (M.J.A.).

Paratypes, locality as holotype: 1♂, data as holotype; 1♀, 3150 m, 22 vii 82
I name this species after my father, Ralph Adams, in gratitude for his continued tacit support over the 14 years of my entomological life. It is undoubtedly the local replacement of *empusa* on the east slope of the Eastern Cordillera near Bogotá: it has a darker underside ground colour and a longer white costal streak on the underside hindwing than *empusa*. It more closely resembles *paeonides* (Hewitson) from Ecuador and *albutia* Thieme from Peru: in *paeonides*, the white band on the underside hindwing runs straight between the costa and vein M2; in *albutia*, the band is broader (twice as broad in cell Rs) and less angular, crossing cell M2 at about 45°.

**Distribution:** ESM: EC, “Bogotá”; Adams: EC(E), Gachetá, 3100–3150 m.

**Bionomics:** Both sexes came down from the trees to an area of rough pasture above the tree-line during brief sunny intervals. The males flew robustly.

**Pedaliodes guicana sp. nov.**
(Figs 16, 49, 50)

**Male**

Forewing length 27–28 mm. Upperside unicolorous dark brown, with very distinct dark brown and white chequered fringes to both wings; scent patch barely entering the distal end of the discal cell.

Underside forewing dark brown with a dusting of silvery scales along the costa and at apex; whitish costal streak at two-thirds costa; a series of very faint, tiny, white submarginal dots in cells R5 to Cu1, almost parallel to the outer margin; chequered dark brown and white fringe. Underside hindwing ground colour very dark chocolate-brown, speckled faintly with grey and silvery scales; a faint but quite broad whitish costal streak, extending into a very faint grey-speckled post-discal band continuing to the inner margin; a series of small white submarginal dots, almost parallel to the outer margin, in cells Rs to Cu1, the largest in Cu1.

**Female**

Forewing length 27 mm. Upperside as in male, but paler brown, with a distinctly darker post-discal band on the forewing contiguous with the discal cell, and a narrower lighter-brown band immediately distad of it. Underside markings as in male, but hindwing submarginal dots only visible in cells M3 and Cu1. Forewing ground colour russet-brown except in a post-discal band, contiguous with the discal cell, where it is dark brown. Hindwing ground colour slightly paler than in male, but much more suffused with paler brown and silver.

**Holotype** ♂, COLOMBIA: Departamento de Boyacá, SW above El Arenal, 3400 m, 12 vii 77 (M.J.A.).

**Paratypes**, 3♀♀, 1♀, data as holotype (M.J.A.).

This dark butterfly is named after Guicán, the Indian name for the Sierra Nevada de Cocuy, on whose southern slopes it was found. Although it closely resembles *empusa*, which flies in the same locality, there is a clear separation between the two in their preferred altitudes and habitat: *guicana* replaces *empusa* above 3400 m, where the páramo becomes drier. *P. guicana* is larger, with
proportionately much longer hindwings; its underside hindwing is darker and the costal streak is less distinct.

**Distribution:** Adams: EC(E), Cocuy, 3400 m.

**Bionomics:** It flew on dry, open slopes of the páramo, studded with low-growing *Espeletia.*

*Pedaliodes plotina plotina* (Hewitson)

*Pronophila plotina* Hewitson, 1862: 4, pl. 2, figs 9, 10. 1♂ syntype, VENEZUELA [:coast range?] (BMNH) [examined].


Subspecies *rapha* Butler, with which *pharnaspes* (Hewitson) and *plotinella* Grose-Smith have been synonymized, flies in the Venezuelan Cordillera de Mérida. The typical race comes, most probably, from the Venezuelan coast range. Populations in the Sierra de Perijá and the Colombian Eastern Cordillera correspond to the typical race. Its nearest allies are *phazania* Grose-Smith (in the Santa Marta massif) and *pausia* (Central and Western Cordilleras, southwards to Bolivia).

**Distribution:** A&B: EC(W), 2250 m; ESM: EC(W), 1800 m.

**Bionomics:** It flies close to the ground.

*Pedaliodes pausia lucipara* Weymer

*Pronophila pausia* Hewitson, 1862: 8, pl. 4, fig. 25. 1♂ syntype, BOLIVIA (BMNH) [examined].

*Pedaliodes loca* Staudinger, 1894: 74, 75. (Synonymy given by Thieme, 1905: 104.)

*Pedaliodes lora* Grose-Smith & Kirby, 1895: fig. 6. 1♂ syntype, BOLIVIA (BMNH) [examined]. (Synonymy given by Thieme, 1905: 104.)

*Pedaliodes pausia* (Hewitson); Butler, 1868: 176; Thieme, 1905: 104; Weymer, 1912: 258; Gaede, 1931: 494; Forster, 1964: 171.

*Pedaliodes pausia* (Hewitson) form *lucipara* Weymer, 1912: 258, pl. 55, row a. 1♂ syntype, COLOMBIA: “Bogotá” (BMNH) [examined].

*Pedaliodes pausia* (Hewitson) form *baccara* Thieme, 1905: 105, pl. 3, fig. 35. 4♂ syntypes, COLOMBIA: Antioquia [MNHU?].

*Pedaliodes pausia* (Hewitson) var. *baccara* Thieme; Gaede, 1931: 495.

Although some individuals have three white dots on the underside hindwing, the population from the Central Cordillera is referable to *lucipara,* which, in view of its geographical separation from the typical population in Bolivia, should probably be considered as a subspecies. I have insufficient evidence to establish whether *baccara,* from Antioquia (west slope of CC or east slope of WC), is another subspecies or merely a brightly-coloured form of *lucipara.* The species is closely allied with *plotina.*

**Distribution:** A&H: CC(T), 2650 m; Fassl (1911: 26): CC(T), c. 2000–3000 m (as *baccara*).
**Pedaliodes fuscata fuscata** (Felder & Felder), sp. rev.

[**Pronophila ochrotaenia** Felder & Felder, 1867: 467, in part. Misidentification.]

**Pronophila ochrotaenia** Felder & Felder var. *fuscata* Felder & Felder, 1867: 468. 1♀ syntype, COLOMBIA: Bogotá (BMNH) [examined].

**Pedaliodes fuscata** (Felder & Felder); Butler, 1868: 178; Thieme, 1905: 121, pl. 1, fig. 6.

**Pedaliodes phaea** (Hewitson) form *fuscata* (Felder & Felder); Weymer, 1912: 261, pl. 55, row e (poor illustration); Krüger, 1924: 24; Gaede, 1931: 496 (as var.).

That *fuscata*, with its orange-brown upperside bands, is a distinct species from *ochrotaenia* and *phaea* is shown by the fact that it exists separately from (parapatrically below) *phaea* subsp. *ochrotaenia* on the east slope of the Eastern Cordillera, near Bogotá.

**Distribution:** Adams: EC(E), Gachetá, 2500 m; Krüger (1924: 24): EC(E), 2600–2900 m; Fassl (1918: 44): EC(E), c. 2350–2750 m.

**Pedaliodes fuscata parapatra** subsp. nov.

(Figs 17, 51, 52)

**Male**

Forewing length 24–29 mm. Upperside dark brown, with a distinct lightening in the distal one-third of both wings, caused by a dusting of golden-brown scales; dark brown and whitish chequered fringes.

Underside forewing dark brown in its basal two-thirds, russet-brown at the outer margin (particularly anteriorly), with a band of paler brown in between; three submarginal white dots in cells R5, M1 and M2. Underside hindwing ground colour dark brown, faintly speckled with russet- and golden-brown in the basal half; a yellow wedge-shaped post-discal band, speckled with brown and orange at its posterior end, extending from the inner margin to vein M2, and continuing as a wavy (sometimes broken) line to the costa; distad of this band are four or five white dots, surrounded by dark brown, in cells Rs or M1 to Cu1, set in an area of grey-brown or russet-brown and yellow; the outer marginal area is chestnut-brown, with indentations into the post-discal area of lighter colour. (In most specimens, the inner edge of the wedge is straight, but in some it is wavy.)

**Female**

Forewing length 27–29 mm. Upperside dark brown, with the distal suffusion of lighter scales extending further basad than in the male, occupying nearly one-half of the wings. Underside as in male, but paler throughout and a post-discal area of brick-red from cell M2 to vein Cu2 (sometimes to cell Cu2); anterior of this is a narrow but distinct whitish costal streak.

**Holotype ♀, COLOMBIA: Departamento de Boyacá, NE below El Arenal, 2300 m, 14 vii 77 (M.J.A.).**

**Paratypes,** locality as holotype (neighbourhood of El Arenal): 1♂, 2500 m, 13 vii 77; 4♂, 1♀, 2400–2450 m, 15 vii 77; 6♂, 1♀, 2400–2500 m, 13 vii 77; 18♂, 1♀, 2300–2500 m, 14 vii 77; 4♂, 1♀, 2550–2700 m, 16 vii 77; 7♂, 2300–2700 m, 17 vii 77; COLOMBIA: Departamento de Boyacá, 11 km below Arcabuco: 15♂, 2♀, 2400–2650 m, 25 vii 77; 7♂, 2650 m, 26 vii 77; 8♂, 1♀, 2400–2650 m, 27 vii 77; 1♂, 2650 m, 28 vii 77 (M.J.A. and G.I.B.).
Figures 51–59. Fig. 51, *Pedaliodes fuscata parapatra subsp. nov.*, male holotype. Fig. 52, The same, female paratype. Fig. 53, *Pedaliodes bernardi sp. nov.*, male holotype. Fig. 54, *Pedaliodes hardyi sp. nov.*, male holotype. Fig. 55, The same, female paratype. Fig. 56, *Pedaliodes armotti sp. nov.*, male holotype. Fig. 57, *Penrosada inderena sp. nov.*, male holotype. Fig. 58. The same, female paratype. Fig. 59, *Steremnia selva sp. nov.*, male holotype.
This butterfly, lacking orange-brown bands, replaces the typical race of \textit{fuscata} on the west slope of the Eastern Cordillera and in the Cocuy area on the east slope, where it flies parapatrically below \textit{phaea}. It most closely resembles \textit{vallenata} Adams & Bernard from the Sierra de Perijá, which lacks the lighter outer part on the upperside and underside and has a more pronounced yellow-brown costal streak on the underside hindwing. Interestingly, while \textit{vallenata} is the uppermost member of the three parapatric species in the group in Perijá, \textit{fuscata} subsp. \textit{parapatra} is the lowermost where it flies.

\textit{Distribution:} A&B: EC(E), Cocuy; EC(W), Arcabuco; 2300–2700 m.

\textit{Pedaliodes phaea phaea} (Hewitson)

\textit{Pronophila phaea} Hewitson, 1862: 3, pl. 1, figs 5, 6. 1♂ syntype, COLOMBIA: New Granada (BMNH) [examined].

\textit{Pedaliodes phaea} (Hewitson); Butler, 1868: 178; Thieme, 1905: 121; Weymer, 1912: 261; Gaede, 1931: 496.

The typical race of \textit{phaea} is restricted to the west slope of the Eastern Cordillera. It is the middle member of a parapatric series of three close allies: \textit{fuscata} subsp. \textit{parapatra} flies below it, and \textit{phaeina} above it.

\textit{Distribution:} BMNH: EC(W), Pacho; Adams: EC(W), 2700–2850 m; Fassl (1918: 44): EC(W), c. 2700–3000 m (as ochrotaenia).

\textit{Bionomics:} see next subspecies.

\textit{Pedaliodes phaea ochrotaenia} (Felder & Felder)

\textit{Pronophila ochrotaenia} Felder & Felder, 1867: 467. 4♂, COLOMBIA (BMNH), here designated Lectotype and Paralectotypes [examined].

\textit{Pedaliodes ochrotaenia} (Felder & Felder); Butler, 1868: 178; Thieme, 1905: 121.

\textit{Pedaliodes phaea} (Hewitson) form \textit{ochrotaenia} (Felder & Felder); Weymer, 1912: 261, pl. 55, row e; Krüger, 1924: 24; Gaede, 1931: 496 (as var.).

The specimen labelled as the type (in the Felders' handwriting) in the BMNH was mounted upside-down and placed below a series of specimens, three of them from the Felders' collection which fit the original description of \textit{ochrotaenia}; the labelled specimen, however, represents \textit{fuscata}. One of the other three Felder specimens has therefore been designated Lectotype, and the remaining three specimens as Paralectotypes. Subsp. \textit{ochrotaenia} differs from typical \textit{phaea} in the following respects: the upperside forewing band is ochreous yellow rather than orange; the upperside hindwing band is broader and less well-defined distally; the underside forewing band is paler orange; and the underside hindwing band is brighter, especially distally. The race is confined to the east slope of the Eastern Cordillera, being replaced by the typical subspecies on the west slope.

\textit{Distribution:} A&B; Adams: EC(E), Cocuy, 2600–2900 m; Gacheta, 3000 m; Krüger (1924: 24): EC (side-valleys of the Bogotá savanna), 2600–2900 m.

\textit{Bionomics:} \textit{P. phaea}, in both races, tends to fly higher off the ground than \textit{fuscata}, around clumps of chusque; it is much less common in my experience. Subsp. \textit{ochrotaenia} flies parapatrically above typical \textit{fuscata} and below \textit{bernardi} sp. nov.
Pedaliodes phaeina Staudinger

Pedaliodes phaeina Staudinger, 1897: 124. 3♂, 1♀ syntypes, COLOMBIA: Bogotá (1♂ BMNH [examined]; the rest MNHU?).
Pronophila phaea Hewitson, var. 2, 1862: 3.
Pedaliodes phaea (Hewitson) var. phaeina Staudinger; Krüger, 1924: 24.
Pedaliodes phaeina Staudinger; Thieme, 1905: 125; Weymer, 1912: 261, pl. 51, row b; Gaede, 1931: 497.

This species, with orange bands restricted to the hindwings, is the uppermost member of three parapatric species on the west slope of the Eastern Cordillera, flying above typical phaea, which in turn flies above fusca para patra.

Distribution: A&H; Adams: EC(W), 2750–3300 m; BMNH specimens: EC(W), Pacho; Fassl (1918: 44): EC(W), c. 2250–2500 m (?) (as phaeina [sic]); Krüger (1924: 24): EC(W), to over “300 m” [misprint for 3000 m?]; Thieme (1905: 125): “Centralcordillere” [error?].

Bionomics: This species comes down from clumps of chusque to rest and feed on the ground.

Pedaliodes bernardi sp. nov.
(Fig. 53)

Male

Forewing length 27.5 mm. Upperside ground colour dark brown. Forewing with slightly paler post-discal band, caused by a faint dusting of orange scales, particularly along its basal edge. Hindwing with an orange post-discal band from costa to vein Cu2, continuing faintly to the inner margin in chestnut-brown; at its narrowest, on vein M2, the band is 1.5 mm across; at its broadest, between veins M3 and Cu1, it measures 5 mm; both edges, especially the distal, are indented.

Underside forewing ground colour dark brown, with a russet-brown streak across the discal cell, and chestnut-brown from apex to half outer margin; paler brown post-discal band, with yellow and orange in its posterior half and basally at its anterior end; four submarginal white dots in cells R4 to M2. Underside hindwing chestnut-brown, speckled with orange scales; a yellowish costal streak and two yellowish patches anterior and posterior in the discal cell; yellow post-discal band, speckled with orange and brown, mirroring the upperside band, but yellow in cells Cu2 and 2dA; 3 white dots, surrounded by dark brown, in the band in cells Rs to M2; a dark brown dot in the band in cell Cu1.

Female unknown.

Holotype 3, COLOMBIA: Departamento de Boyacá, SW of El Arenal, 2650/2750 m, 17 vii 77 (G.I.B.).

This species most strongly resembles its nearest relative phaeina, which flies on the other (west) slope of the Eastern Cordillera, but it has a much narrower hindwing orange band; in phaeina, not only does the band extend distad almost as far as the outer margin, but also the outer margin itself is dusted with orange scales on both sides of the wing. P. bernardi is given specific status on the basis of the high altitudes at which it presumably flies (see Introduction). I name it after my friend and colleague of 20 years, George Bernard, who has been my
collecting companion on four trips to Colombia and Venezuela and who discovered the only specimen known.

**Distribution:** Bernard: EC(E), Cocuy, 2650/2750 m.

**Pedaliodes pylas pylas** (Hewitson)

*Pronophila pylas* Hewitson, 1862: 4, pl. 2, figs 11, 12. 1♂ sytype, COLOMBIA: New Granada (BMNH) [examined].

**Pedaliodes pylas** (Hewitson); Butler, 1868: 177; Thieme, 1905: 114; Weymer, 1912: 260, pl. 55, row c; Gaede, 1931: 503.

The underside hindwing of the species is closely similar to that of *P. fuscata*. Typical *pylas* seems to be restricted to the Eastern Cordillera and is known only from the west slope. Occasional specimens lacking the smaller of the two white patches on the upperside forewing (e.g. one male collected by ESM at Fusagasugá, EC(W)) are referable to Thieme's (1905) ab. *uniplaga* (see below).

**Distribution:** BMNH: EC(W), Pacho; ESM: EC(W), Barro Blanco; Thieme (1905: 115): EC(W), La Vega; Krüger (1924: 32): EC.

**Pedaliodes pylas unilacuna subsp. nov.**

**Pedaliodes pylas** (Hewitson) ab. *uniplaga* Thieme, 1905: 114. 2♂ sytypes, COLOMBIA [MNHU?].

**Pedaliodes pylas** (Hewitson) form *uniplaga* Thieme; Weymer, 1912: 260; Gaede, 1931: 503 (as ab.).

This race differs from the typical subspecies in lacking (in both sexes) the extra, smaller white post-discal patch near the costa of the upperside forewing.

**Holotype ♂,** COLOMBIA: Departamento del Huila, above San José de Isnos, 2550 m, 3 viii 79 (M.J.A.).

**Paratypes**, locality as holotype: 1♂, 2550 m, 2 vii 79; 6♂, 1♀, 2500–2550 m, 3 viii 79; 3♂, 2450–2550 m, 4 vii 79; COLOMBIA: Departamento del Cauca, between Santa Leticia and Puracé: 3♂, 2650 m, 10 viii 79; 3♂, 2550–2700 m, 11 viii 79; Departamento del Huila, between Santa Leticia and La Plata, 2400 m: 1♂, 2 vii 82; 1♀, 4 vii 82 (M.J.A. and P.J.H.).

All the individuals found in the Central Cordillera by A&H are referable to Thieme's (1905) ab. *uniplaga*, but are geographically separated from the typical populations where this aberration does indeed occur. I suggest that the population in the southern Central Cordillera should receive subspecific rank and, whether or not his specimens came from that cordillera, Thieme's infrasubspecific name should not be used for it.

**Distribution:** A&H; Adams: CC(H), 2400–2700 m; Krüger (1924: 32): CC and WC.

**Bionomics:** Most commonly found, together with *P. peucestas* which also has a white band on the forewing, close to the ground in marshy cloud-forest.

**Pedaliodes pylas** f. *parma* Thieme

**Pedaliodes parma** Thieme, 1905: 115, pl. 1, fig. 2. 1♂ sytype, COLOMBIA:

"Coast cordillera (Cordillera von Ocana)" [MNHU?].

**Pedaliodes pylas** (Hewitson) form *parma* Thieme; Weymer, 1912: 260.
The single known butterfly of this taxon, found by Kalbreyer, has a larger white forewing patch, which enters the discal cell and does not extend so near to the inner margin. I do not know of a “Cordillera de Ocaña” in the Western Cordillera, and it may have been obtained near Ocaña in the north of the Eastern Cordillera. Without adequate data, it is impossible to know whether *parma* is merely an aberration of *pylas*, or represents a geographical race. It is interesting to note that Krüger (1924) found *pylas* in the WC and made no mention of *parma*.

**Pedaliodes thiemei** Staudinger

*Pedaliodes thiemei* Staudinger, 1897: 126. Syntype series, COLOMBIA: Quindio Pass, c. 4000 m [MNHU?].

*Pedaliodes thiemei* Staudinger; Thieme, 1905: 124, pl. 1, fig. 3; Weymer, 1912: 261, pl. 55, row f; Gaede, 1931: 504.

Judged by its genitalia and inconspicuous underside pattern, *thiemei* is most closely allied to *pelinna* (Hewitson) from Ecuador and north Peru, and *alusana* (Hewitson) from Ecuador.

**Distribution:** A&H: CC(H), 3050 m; Krüger (1924: 23): CC(T&H).

**Bionomics:** The single male found by A&H was flying in open, bushy, marshy land below the tree-line. Krüger (1924) pointed out that the specimens from Tolima have less bright orange bands on both sides of the wings.

**Pedaliodes porcia** (Hewitson)

*Pronophila porcia* Hewitson, 1869: 34; 1874: pl. 8, fig. 57 (as *paonides*). 1♂ syntype, ECUADOR (BMNH) [examined].

*Pedaliodes porcia* (Hewitson); Thieme, 1905: 89; Weymer, 1912: 256, pl. 54, row c; Gaede, 1931: 501.

The only difference between the syntype males of *porcia* and *pallantias* (Hewitson, 1874), both of which are Buckley specimens from Ecuador, lies in the width of the yellow costal patch on the underside hindwing. The individuals caught by A&H in the Central Cordillera have the patch somewhat intermediate in width between the two. There seems to be a strong case for synonymizing *pallantias* with *porcia*, but there is insufficient information as to whether or not they fly together in the same Ecuadorian populations. The female of *porcia* was described by Hewitson (1874), and I obtained one individual in the CC; its underside hindwing patch is white. Dr Schmidt-Mumm obtained one male in the EC with a much reduced yellow costal patch, which only extends into cell M1.

**Distribution:** ESM: EC(E), c. 3000 m; A&H; Adams: CC, 2850–3100 m; [Krüger (1924: 28): CC(E), 2800–3000 m (as *pallantias*)]; Fassl (1911: 26; 1915: 11): CC and WC; BMNH: WC, “3600” and “3800 m” (Fassl); Weymer (1912: 256): CC, Quindio, 3500 m; WC, Monte Socorro.

**Bionomics:** A very colonial butterfly, it feeds on the ground and has a robust flight.

**Pedaliodes phanoclea** (Hewitson)

*Pronophila phanoclea* Hewitson, 1877: 90. 1♂ syntype, ECUADOR (BMNH) [examined].
Pedaliodes phanoclea (Hewitson); Grose-Smith & Kirby, 1893: figs 7, 8; Thieme, 1905: 89; Weymer, 1912: 256; Gaede, 1931: 497.

To my knowledge there is only one record of this species from Colombia: one male caught by myself in the uppermost cloud-forests of the Central Cordillera (Huila).

Distribution: BMNH: Ecuador; Adams: CC(H), 3100 m.

Pedaliodes hardyi sp. nov.
(Figs 18, 54, 55)

Male
Forewing length 23–24 mm. Upperside dark brown. Hindwing with a trace of yellowish scales at the apex, and a suffusion of orange and russet-brown at the tornus, extending halfway up the inner margin. Underside forewing dark brown with a faint dusting of grey at the apex. Underside hindwing dark brown, speckled very faintly and sparingly with orange scales and dusted with grey at the outer margin; a white costal streak extending to vein M1; an almost rectangular orange-yellow patch basad of the tornus, speckled with brown, between the inner margin and vein Cu2, with a small triangular extension in the middle of cell Cu1 (and, in one specimen, a tiny yellowish dot post-discally in cell M3); chestnut-brown at tornus and at inner margin basad of the orange-yellow patch; two tiny post-discal white dots in cells Rs and Cu1.

Female
Forewing length 24 mm. Upperside forewing unicolorous dark brown, with faintly chequered outer margin. Upperside hindwing dark brown, with a narrow orange patch along the distal two-thirds of the inner margin, distally becoming chestnut-brown, and pale at the apex. Underside similar in pattern to the male, but slightly paler throughout, and the forewing has a russet hue post-discally.

Holotype ♂, COLOMBIA: Departamento de Cundinamarca, above Km 26 between Zipaquirá and Pacho, 3300 m, 26 viii 79 (P.J.H.).
Paratypes: 1♀, COLOMBIA: “Bogotá”, 1948 (Schmidt-Mumm coll.); locality as holotype: 2♂, 6 ii 65; 1♀, 19 ii 67 (E.S.M.); 1♀, 3150 m, 25 viii 82 (M.J.A.).

I name this species after my staunch companion in our Colombian visit of 1979, Peter Hardy. It most closely resembles pheretias (Hewitson) from Galgalán in Ecuador: the orange-yellow underside hindwing patch in pheretias is more triangular than in hardyi, and the upperside orange and brown suffusion on the hindwing is absent. Its other close relatives are fassli Weymer and arnotti sp. nov., both of which have their underside hindwing patch greatly extended such that it is connected to the costal streak; fassli flies in the Western Cordillera and arnotti on the east slope of the Eastern Cordillera. P. hardyi is confined to the west slope of the Eastern Cordillera.

Distribution: ESM & A&H: EC(W), Zipaquirá, 3150–3300 m.

Bionomics: The behaviour of hardyi is reminiscent of that of Altopedaliodes albarregas Adams & Bernard in the Mérida range of Venezuela: it flies robustly around the tops of chusque clumps and flowering trees in the very uppermost zone of the cloud-forest, coming down to the ground occasionally.
Pedaliodes arnotti sp. nov.  
(Figs 19, 56)

Male

Forewing length 24–25 mm. Upperside unicolorous dark brown, with white-chequered fringes, fainter on the hindwing. Scent patch narrow (2.5 mm), continuous and entering the discal cell.

Underside forewing uniform dark brown, with a white post-discal costal streak as far as vein M2. Underside hindwing uniform dark brown, with a narrow pale-yellow band crossing from the costa to the inner margin, becoming orange posteriorly, broadest at the inner margin (3.5–4.0 mm) and narrowest (less than 1 mm) in cell M1, where it is almost at right-angles to the posterior part of the band; basad of the band, at the inner margin, there is a suffusion of dark chestnut-brown; two faint white submarginal dots in cells Cu1 and Rs.

Female unknown.

Holotype ♂, COLOMBIA: Departamento de Cundinamarca, NE of Bogotá, between Guasca and Gachetá, 3150 m, 22 viii 82 (M.J.A.).

Paratypes: 1♂, data as holotype (M.J.A.); 1♂, SE of Bogotá, páramo de Fómeque, 16 iii 69 (E.S.M.).

I name this species after the Arnott family of Tortola, British Virgin Islands: Bob and Pat, their daughter Valerie and their son Stephen at Bryanston School, my association with whom has been a pleasure. The butterfly has as its closest relatives hardyi, from the other (western) slopes of the Eastern Cordillera, fassli from the Western Cordillera and pheretias from Ecuador; it most closely resembles fassli, but it is smaller, and its underside hindwing band is narrower posteriorly and yellow rather than white at the costal end.

Distribution: Adams: EC(E), 3150 m; ESM: EC(E), c. 3000 m.

Bionomics: One of the two 1982 males was caught on faeces bait and the other in rough pasture enclosed by uppermost, very moist cloud-forest containing good stands of chusque; others were seen flying sturdily and erratically around certain trees at the forest edge.

Pedaliodes fassli Weymer, stat. nov.

Pedaliodes chrysotaenia (Hopffer) form fassli Weymer, 1912: 259, pl. 55, row b.

Syntype(s), COLOMBIA: Monte Socorro, 3400 m [MNHU?].

Pedaliodes chrysotaenia (Hopffer) var. fassli Weymer; Gaede, 1931: 489.

The shapes and positions of the underside hindwing bands of fassli and chrysotaenia are sufficiently dissimilar to rule out the possibility that they are conspecific (the latter species is from Ecuador and Peru); indeed fassli is much more closely related to pheretias, hardyi and arnotti than to chrysotaenia. It is restricted to the topmost forest belt in the Western Cordillera.

Distribution: A&H: WC, 3450 m; Weymer (1912: 259): WC, Monte Socorro, 3400 m; Fassl (1915: 11): WC, Monte Socorro, c. 3500–4000 m.

Pedaliodes spina Weymer, stat. nov.

Pedaliodes pactyes (Hewitson) form spina Weymer, 1912: 259, pl. 55, row b.

Syntype series, COLOMBIA: Quindio Pass, 3800 m [MNHU?].

Pedaliodes pactyes (Hewitson) var. spina Weymer; Gaede, 1931: 492.
P. spina differs from the Bolivian type male of pactyes in the BMNH (but not illustrated by Weymer, 1912) in the colour of its underside hindwing band, which in both species crosses the wing from costa to inner margin: in pactyes it is completely yellow, whereas in spina the anterior half to two-thirds is white. The positions of the underside hindwing submarginal white dots—further distad of the band than in pactyes—place spina closer to chrysotaeniua, which was not illustrated with Hopffer's (1874) original description but of which Weymer’s (1912) figure has an underside band similar to that of pactyes. It is possible that all three are closely related species. P. spina is represented at the BMNH by a series from E Ecuador; the only Colombian records are Fassl’s from the Quindio Pass.

Distribution: BMNH: E Ecuador; Fassl (1911: 26): CC(T), c. 3000–3900 m (as pactyes); Weymer (1912: 259): CC(T), 3800 m (Fassl).

Genus Penrosada Brown

Penrosada Brown, 1944: 255. Type-species: Lymanopoda leaena Hewitson, by original designation.

Penrosada lanassa (Felder & Felder)

Pronophila leaena Hewitson var. lanassa Felder & Felder, 1867: 474. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined].
Lymanopoda leaena (Hewitson) form lanassa (Felder & Felder); Weymer, 1912: 249, pl. 52, row f; Gaede, 1931: 486 (as var.).
Penrosada lanassa (Felder & Felder); Brown, 1944: 258; Forster, 1964: 147.

Satisfactory classification of the taxa within this genus of strongly colonial and seasonal butterflies, most of which have a straight yellow band across their underside hindwings, is not made easy by Brown’s (1944) confused treatment and the mistakes in his figures of their genitalia. Typical lanassa comes from the Eastern Cordillera; Ecuadorian material in the BMNH is similar but distinct and the genitalia are similar to those figured (as lanassa) by Brown (1944: fig. 1616). The genitalia of typical lanassa look most like Brown’s (1944: fig. 1613) figure of “leaena”. It seems likely that lanassa is confined to the Colombian Eastern Cordillera, not extending into Ecuador, and this is corroborated by the fact that in the mountains between the Eastern Cordillera and Ecuador—the Central Cordillera—it is replaced by inderena sp. nov.

Distribution: A&B; Adams: EC(B), 2250–2650 m; ESM: EC, up to 2700 m.

Penrosada inderena sp. nov.
(Figs 20, 57, 58)

Male
Forewing length 18–19 mm. Upperside unicolorous dark brown; two small submarginal ocelli, black with white pupils and bordered by chestnut-brown, on the hindwing in cells Cu1 and Cu2.

Underside forewing dark brown, with a dark chestnut-brown sheen; two faint darker-brown lines, a straight post-discal one and a wavy submarginal one.
Underside hindwing dark brown, with a straight pale-yellow band crossing the wing, 1 mm broad, its inner edge contiguous with the distal end of the discal cell; a wavy submarginal darker-brown line; three white-pupilled, chestnut-bordered, black ocelli between the line and the band in cells Cu1 and Cu2 (two in Cu2); in some individuals, the faintest trace of submarginal whitish spots in one or more of cells M1 to M3.

**Female**

Forewing length 19 mm. Upperside unicolorous dark brown. Forewing with the two lines showing faintly through from the underside, and a faint black-pupilled, russet-brown submarginal ocellus in cell Cu1. Hindwing dusted with sandy-yellow along outer margin; the band and the line showing through faintly; ocelli as in male.

Underside ground colour brown. Forewing as in male, but with a well-formed submarginal black ocellus, white-pupilled and russet-brown-bordered, in cell Cu1, and three tiny white submarginal dots in cells M1 to M3. Hindwing as in male, but the band is whitish.

**Holotype 3**, COLOMBIA: Departamento del Tolima, S above Cajamarca, 2900 m, 23 vii 79 (M.J.A.).

**Paratypes**, locality as holotype: 4♂, 1♀, 2800/2900 m, 23 vii 79; 1♀, 2900 m, 24 vii 79; 4♂, 2800–2900 m, 26 vii 79; 1♂, 2800 m, 27 vii 79; 4♂, COLOMBIA: Departamento del Tolima, NW above Ibagué, 2450–2500 m, 31 vii 79 (M.J.A. and P.J.H.); 1♀, COLOMBIA: de Bogotá a Buenaventura, 1877–8, ex Oberthür Coll., BM 1927–3 (Thieme); 1♂, Torne, Cauca, i 07 (Paine and Brinkley); 5♀, Monte Tolima, 2500 m, ii 10 (Fassl); 2♀, Cañon del Tolima, 2500 m, xi–xii 09, Rothschild Bequest, BM 1939–1 (Fassl).

This species—named after “Inderena”, the Colombian Instituto del Desarrollo de los Recursos Naturales y Renovables, whose efforts at conservation have at least ensured the continued existence in some places of cloud-forest along either side of streams—appears to replace *lanassa* from the Eastern Cordillera and *franciscae* Adams & Bernard from the Venezuelan Andes. It is smaller than *franciscae*, with a narrower, paler band and fewer ocelli on the underside hindwing; its band is slightly broader than that of *lanassa*, which has no ocelli in either sex. It is also a close relative of *satura* (Weymer) from Ecuador, whose ocelli lie closer to the band.

**Distribution:** A&H: CC(T), 2450–3100 m; [Fassl (1911: 26): CC(T), c. 2000–4000 m (as *leaena*—misidentification, at least in part?)].

**Bionomics:** Like all Penrosada species in my experience, *inderena* is a delicate butterfly, skipping around clumps of chusque and resting on the foliage, sometimes coming to the ground to feed on excrement.

**Penrosada leaena** (Hewitson)

*Lymanopoda leaena* Hewitson, 1861: 156, pl. 9, fig. 1. 1♀ syntype, ECUADOR: Quito (BMNH) [examined].


Unlike the *lanassa* group of species, *leaena* has a wide distribution, extending with little morphological change between the Eastern Cordillera and Peru. It
also seems to have a particularly wide altitude tolerance, though Fassl’s records of the species may at least in part have been confused with *inderena*. Its underside hindwing yellow band is twice as broad as that of *lanassa*. Brown’s (1944: fig. 1613) figure of the genitalia of “*leaena*” differs from my own preparation of a Peruvian specimen in having the teeth at the tip of the valves, rather than at the side just below the tip.

**Distribution:** BMNH: EC(E), Choachi; Ecuador and Peru; Adams: EC(E), Gachetá, 2500 m; ESM: EC(E), Cruz Verde above Bogotá, above 2700 m; Fassl (1918: 44): EC(E), c. 1250–1750 m; EC(W), c. 2000–2500 m; Weymer (1912: 248): EC(E), 2000–2500 m; CC (south), Páramo de Aponte, 2800 m; CC(T), Quindío Pass, 3800 m (?); Fassl (1911: 26): CC(T), c. 2000–4000 m (part confused with *inderena*).

*Penrosada levana* (Godman), *comb. nov.*

*Lymanopoda levana* Godman, 1905: 188, pl. 10, fig. 10. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined].

*Lymanopoda levana* Godman; Weymer, 1912: 248, pl. 51, row b; Gaede, 1931: 486.

*P. levana*’s wing shape, yellow legs and male genitalia clearly place it in Brown’s (1944) genus *Penrosada*, even though its underside hindwing is distinctive, lacking a clear yellow band. It is found in Panamá and at the tree-line in the Colombian Eastern Cordillera.

**Distribution:** BMNH: Panamá, Chiriquí; Colombia; A&B; Adams: EC(B), 3150–3300 m; ESM: EC(W), Subachoque, c. 2700 m.

**Bionomics:** A&B found this species in rough grassland between chusque-filled gullies at the tree-line, and skipping around clumps of the bamboo.

*Penrosada apiculata* (Felder & Felder)

*Pronophila apiculata* Felder & Felder, 1867: 474. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined].

*Lymanopoda apiculata* (Felder & Felder); Weymer, 1912: 248, pl. 53, row a (misprinted as “*apiciculata*”); Gaede, 1931: 484.

*Penrosada apiculata* (Felder & Felder); Brown, 1944: 257, pl. 1, fig. 1622 (genitalia).

Weymer (1912: 248) gave the name *curvilinea* to the form of this species with a curved, whitish post-discal line across the underside hindwing; it flies with typical *apiculata*, which merely has a row of indistinct chestnut-brown post-discal patches. Known in Colombia only from the Eastern Cordillera, the species extends as far as Peru.

**Distribution:** BMNH: Colombia to Peru; A&H; Adams: EC(W), 3150–3300 m; Weymer (1912: 248): EC(E), Chiquipa; Fassl (1918: 44): EC(B), c. 2650–3500 m.

**Bionomics:** This species not only flies with *levana* in the EC(W), but also seems to share its habitat and behaviour.

**Genus Physcopedaliodes** Forster

**Physcopedaliodes porina** (Hewitson), **comb. nov.**

*Pronophila poruna* Hewitson, 1862: 9, pl. 4, fig. 28. 1♂ syntype, [no locality—BOLIVIA?] (BMNH) [examined].

* Pedaliodes porina* (Hewitson); Butler, 1868: 177; Thieme, 1905: 112; Weymer, 1912: 260, pl. 55, row c; Gaede, 1931: 501.

* Pedaliodes corderoi* Dognin, 1893: 367. 2♂ syntypes, ECUADOR (BMNH) [examined], **syn. nov.**

* Pedaliodes porina* (Hewitson) from *corderoi* Dognin; Weymer, 1912: 260, pl. 55, row c; Gaede, 1931: 502 (as var.).

* Corderopedaliodes corderoi* (Dognin); Forster, 1964: 155, fig. 194 (genitalia).

Although one of the two *corderoi* types does have a broader white band than the other, they are from the same locality and the other is identical to the *porina* type. For this reason, I synonymize *corderoi* with *porina*. The genus *Corderopedaliodes* (Forster, 1964) was synonymized with *Physcopedaliodes* by Adams & Bernard (1977: 277): the species share similar wing shapes and speckled underside markings, as well as male genital structure. The widespread species is known only from one record in Colombia, a male caught by Dr Schmidt-Mumm.

**Distribution:** BMNH: Ecuador to Bolivia (?Argentina); ESM: EC(W), Belleza, Santander, c. 1800 m.

**Physcopedaliodes praxithea** (Hewitson), **comb. nov.**

*Pronophila praxithea* Hewitson, 1870: 157; 1871: pl. 5, figs 28, 29. 1♂ syntype [no locality—BOLIVIA?] (BMNH) [examined].

* Pedaliodes praxithea* (Hewitson); Thieme, 1905: 127; Weymer, 1912: 262, pl. 56, row a; Gaede, 1931: 502; Forster, 1964: 175.

Although *praxithea* is larger than the other members of this genus, its underside hindwing markings and pattern are very closely similar, especially to *symmachus* (Godman & Salvin); its genitalia are close to those of *pandates* (Hewitson). It has the same propensity for staying close to the ground as *symmachus* in the Santa Marta massif and *porina* (as I observed at Machu Picchu in Peru in 1983 and in Bolivia in 1985). Bolivian specimens in the BMNH most closely resemble the type, which bears no locality label; individuals from Colombia, Ecuador and Peru have a shorter orange patch on the hindwing; Hewitson described it, however, as from Ecuador.

**Distribution:** BMNH: Colombia to Bolivia; A&B: EC(W), 2550 m; A&H; Adams: CC(H), 2450–2800 m.

**Bionomics:** Although we found only one male in the EC, it flew quite commonly above San José de Isnos in the CC(H). It has a sturdy flight, quickly returning to the trees in the cloud-forest when disturbed at its normal resting place on the ground.

**Genus Praepronophila** Forster

**Praepronophila perperna** (Hewitson), **comb. nov.**

*Pronophila perperna* Hewitson, 1862: 16. 2♂, 1♀ syntypes, ‘SOUTH AMERICA’ [VENEZUELA, coast range?] (BMNH) [examined].

*Pronophila satyroides* Felder & Felder, 1867: 469. 2♂ syntypes, VENEZUELA: Caracas (BMNH) [examined]. (Synonymy given by Thieme, 1905: 68).

*Pedaliodes perperna* (Hewitson); Butler, 1868: 173; Thieme, 1905: 68; Weymer, 1912: 253, pl. 53, row e; Gaede, 1931: 495.

The underside markings and pattern of *perperna* are almost identical to those of *petronius* Grose-Smith, even though the former butterfly is considerably smaller. The aedeagus of *perperna* seems to vary: that of a Venezuelan coast range specimen is slightly contorted as in *Pedaliodes sensu stricto*, but it is narrow, with a short anterior end, in a male from the Eastern Cordillera of Colombia; the latter is close to *petronius*, including the valves. *P. petronius* is clearly closely related to the Bolivian species *emma* (Staudinger), for which Forster (1964: 183, genitalia fig. 263) erected the genus *Praepronophila*: their undersides are very similar indeed, except that *emma* has four white patches on the forewing showing through from the upperside. (Forster (1964: 165), in the same paper, also included *emma* under *Pedaliodes*!) *P. perperna* and *petronius* both occur in Costa Rica, but apparently allopatrically (P. DeVries, pers. comm.). For these reasons, I believe that both species should be included in the genus *Praepronophila*.

**Distribution:** BMNH: Costa Rica to Venezuela; A&B: EC(north), Ocaña, 1400 m; Thieme (1905: 69): CC(W), Cauca; Fassl (1915: 11): WC, c. 1500–2000 m (2♂ in BMNH).

**Praepronophila petronius** (Grose-Smith), **comb. nov., sp. rev.**

*Pedaliodes petronius* Grose-Smith, 1900: figs 4, 5. 1♂ syntype, COLOMBIA: Valdevia (BMNH) [examined].

*Pedaliodes petronius* Grose-Smith; Thieme, 1905: 69.

*Pedaliodes perperna* (Hewitson) form *petronius* Grose-Smith; Weymer, 1912: 253; Gaede, 1931: 495 (as var.).

The reasons for including *petronius* in Forster’s (1964) genus *Praepronophila* are given above, under *perperna*; in addition, the male genitalia of the two species are closely similar. The much larger size of *petronius*, and its subapical whitish markings on the forewing, make it very unlikely that it is merely a subspecies of *perperna*, and the two species’ allopatry within Costa Rica (and perhaps also in the Colombian Western Cordillera) rules out the possibility of its being a form of *perperna*.

**Distribution:** BMNH: Costa Rica; CC(north), Valdevia (type male and four other males); L. Miller (pers. comm.): Panamá, Chiriquí.

**Genus Pronophila** Doubleday

*Pronophila* Doubleday, [1849]: pl. 60, figs 1–3. Type-species: *Pronophila thelebe* Doubleday, by subsequent designation (Butler, 1867: 266).
Pronophila bogotensis Jurriaanse


As pointed out by Adams & Bernard (1977, 1979, 1981), this species has been confused by most authors with thelebe Westwood, which occurs in the Venezuelan coast range (and perhaps in the southern Venezuelan Pantepui mountains); it is larger than thelebe, with a much darker underside; the white post-median patch in cell M2 of the forewing is smaller and does not appear continuous with the main patch in M1 as in thelebe. It is confined to Colombia and the Mérida range of Venezuela; closely related populations in Peru and Bolivia have extra subapical white patches on the forewing in cells R4 and R5. The species has also been confused with thelebina Thieme; for example, the BMNH specimens of bogotensis are labelled as such. Weymer's (1912: pl. 59, row b) illustration of "thelebe" is of bogotensis.

Distribution: BMNH: Colombia (as thelebina); ESM: EC, c. 2000 m; [Thieme (1907: 197); Weymer (1912: 272, pl. 59, row b): Venezuela to Bolivia (as thelebe)]; [Fassl (1918: 44): EC(W), c. 2000–2250 m; EC(E), c. 1750–2250 m (as thelebina—confused with either bogotensis or orchewitsoni?)]; [Fassl (1911: 29): CC(T), c. 1300–2000 m (as thelebe)]; [Krüger (1925: 11): East Andes, Magdalena valley, 800–1500 m (as thelebe)].

Bionomics: This species flies quite high above the ground in the trees of the upper rain-forests and lower cloud-forests.

Pronophila brennus Thieme

Pronophila brennus Thieme, 1907: 199. Syntype series, Western COLOMBIA [MNHU?].
Pronophila brennus Thieme; Weymer, 1912: 272, pl. 59, row c; Gaede, 1931: 518.
Pronophila thelebe Westwood form brennus Thieme; Krüger, 1925: 11.

This species, which is similar in appearance to bogotensis but with pale brown subapical markings on the upperside forewing, also flies at the same altitudes, and it may therefore be its allopatric replacement on the west slope of the Central Cordillera and in the Western Cordillera.

Distribution: BMNH; Thieme (1907: 199); Weymer (1912: 272): CC(W) and WC, 1400 and 1600 m; ESM: WC, c. 2000 m; Fassl (1915: 11): WC, c. 1500–2000 m; Krüger (1925: 11): Cauca valley; and WC(E), 1500 m [with "thelebe form thelebina", which is "probably only a light form of brennus"].

Pronophila orchewitsoni Adams & Bernard

[Pronophila orchus (Latreille); Hewitson, 1862: 10. Misidentification and misspelling.]

Pronophila orchewitsoni Adams & Bernard, 1979: 115, figs 35, 36. Holotype ♂, COLOMBIA (BMNH) [examined].
As pointed out by Adams & Bernard (1979), Hewitson (1862), in meaning to refer to Latreille's (1799-1804) *Satyrus orcus*, described another species; later authors have mistakenly treated his misspelled *orchus* as the valid name for this, which we subsequently named *orchewitsoni*. It flies in all three of the Colombian Cordilleras, as well as Ecuador, and is replaced in the Santa Marta range by *juliani* Adams & Bernard and in the Venezuelan Andes by *epidipnis* Thieme. It is parapatric above *bogotensis* in the Eastern and Central Cordilleras (and perhaps above *brennus* on either side of the Cauca valley). The whitish subapical markings on the upperside forewing vary, even within the same populations.

**Distribution:** BMNH: Colombia and Ecuador (as *orcus*); A&B: EC(B), 2400–2650 m; A&H: CC, 2500–2700 m; WC, 2350 m; Krüger (1925: 11): CC(T), west side, 2600–3000 m (as *orcus*).

**Bionomics:** Although this species is most often seen flying high around trees at the cloud-forest edge, it can be baited to faeces on the ground.

*Pronophila orcus orcus* (Latreille)

*Satyrus orcus* Latreille, 1799–1804: 72, pl. 35, figs 1, 2. Syntype(s), [COLOMBIA] (depository unknown).

*Satyrus orchamus* Godart, 1823: 486. (Synonymy given by Thieme, 1907: 202).

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

*Pronophila porsenna* Hewitson, 1862: 12, pl. 5, fig. 34. 1♂ syntype, COLOMBIA (BMNH) [examined]. (Synonymy given by Thieme, 1907: 202.)


Typical *orcus* is almost certainly from Colombia; the species is distributed between Venezuela and Bolivia, existing in a number of geographical races.

**Distribution:** BMNH: Colombia to Bolivia (form *obscura* Butler (= var. *parallela* Thieme) in the Venezuelan coast range may represent a subspecies of *orcus*); A&H; Adams: CC, 2300/2350 m; WC, 2100–2350 m; Fassl (1918: 44): EC(W), c. 2250–2500 m; Fassl (1911: 29): CC(T), c. 2500–3000 m [+2200 m according to Weymer, 1912: 273]; Fassl (1915: 11): WC, c. 2000–2300 m; Krüger (1925: 11): WC(B), south, 1600–2200 m.

**Bionomics:** This species, unlike *bogotensis* and *orchewitsoni*, is fond of resting on the ground and flying low over leaf litter and at roadsides; it is strongly attracted to faeces.

**Genus Pseudomaniola Röber**

*Pseudomaniola* Röber, [1889]: 222. Type species: *Daedalma phlooe* Staudinger, by subsequent designation (Hemming, 1943: 23–24).

*Pseudomaniola phaselis* (Hewitson), **comb. nov.**

*Pronophila phaselis* Hewitson, 1862: 14, pl. 6, fig. 7. 1♂ syntype, [VENEZUELA] (BMNH) [examined].

Cowan (1968) explained why Hayward (1950) was correct in reinstating Pseudomaniola Röber, in spite of the fact that Hemming (1967) had upheld the view that Catargynnis Röber is the valid name: Röber (1889) erroneously believed that his Pseudomaniola had been predated by Weymer’s (1890) different genus of the same name, and so he replaced it by Catargynnis. Thus Pseudomaniola Röber is valid, and Weymer’s genus is a junior homonym which Hayward (1950) replaced by Neomaniola.

Like all Pseudomaniola species in my experience, phaselis is very rare and solitary. It is very widespread, occurring between the Venezuelan coast range and Bolivia. Thieme (1907) reported it from the EC(W) at La Vega and from Kalbreyer’s often dubious locality, the “coast cordillera”. There are no recent records from the main Colombian Andes; Krüger (1924: 41) did not find it and Fassl made no mention of it in any of his three papers. Adams & Bernard (1977: 267) refer to its presence in the Santa Marta range.

Pseudomaniola pholoe (Staudinger), **comb. nov.**

*Daedalma pholoe* Staudinger, 1888: 234, pl. 84. Syntype(s), COLOMBIA: Cauca Province [MNHU?].

*Oxeoschistus phalsi* Grose-Smith, 1900: pl. 1, figs 1, 2. [Type specimens lost?] (Synonymy given by Thieme, 1907: 153).

*Catargynnis pholoe* (Staudinger); Thieme, 1907: 153; Weymer, 1912: 268, pl. 57, row d; Gaede, 1931: 513.

This species is known only from the slopes on either side of the Cauca Valley (CC(W) and WC(E)), and it may be the allopatric replacement there of phaselis. *Distribution: BMNH: CC(W), Pereira; Cauca Valley; Krüger (1924: 41): WC(E), 1500 m.*

Pseudomaniola loxo (Dognin), **comb. nov.**

*Oxeoschistus loxo* Dognin, 1891: 132. 2♂ syntypes, COLOMBIA (BMNH) [examined].

*Pronophila sagartia* Grose-Smith, 1900: pl. 1, fig. 2. 2♂ syntypes, COLOMBIA (BMNH) [examined]. (Synonymy given by Thieme, 1907: 155.)

*Daedalma bronza* Weeks, 1901: 355; 1905: pl. 35. 9♂ syntypes, COLOMBIA: Bogotá district (MCZ, Harvard?). (Synonymy given by Thieme, 1907: 155.)

*Catargynnis loxo* (Dognin); Thieme, 1907: 155; Weymer, 1912: 268, pl. 57, row d; Gaede, 1931: 512.

Since this rare species seems to prefer higher elevations than phaselis, it may be parapatric above it. It is known only from the Eastern Cordillera and the east slope of the Central Cordillera.

*Distribution: A&H: CC(H), San José de Isnos, 2550 m, flying over dirt road; Thieme (1907: 155): EC(W), La Vega; “coast cordillera—Kalbreyer”; Fassl (1911: 26): CC(T), east slope, c. 2600–2900 m; Fassl (1918: 44): EC(W), c. 2000–2350 m.*

Pseudomaniola ilsa (Thieme), **comb. nov.**

*Catargynnis ilsa* Thieme, 1907: 155, pl. 1, fig. 6. 1♂, 1♀ syntypes, COLOMBIA: Cauca Province [MNHU?].

*Catargynnis ilsa* Thieme; Weymer, 1912: 268, pl. 57, row c; Gaede, 1931: 512.
Mirroring the case of *pholoe* and *phaselis*, this species seems to replace its close ally *loxo* on the west slope of the Central Cordillera and in the Western Cordillera.

**Distribution:** BMNH: WC, 2400 m; Fassl (1915: 11): WC, c. 2000–2300 m; Krüger (1924: 41): CC(W), 2600 m.

**Genus *Punapedaliodes* Forster**


*Punapedaliodes cocytia* (Felder & Felder), **comb. nov.**

*Pronophila cocytia* Felder & Felder, 1867: 468. 1♂ syntype, COLOMBIA: Cordillera de Bogotá (BMNH) [examined].

*Pronophila phaesana* Hewitson, 1868: pl. 4, fig. 23. [Type-specimen(s) lost?] (Synonymy given by Thieme, 1905: 118.)

*Pedaliodes cocytia* (Felder & Felder); Butler, 1868: 178; Thieme, 1905: 118; Weymer, 1912: 260, pl. 55, row d; Gaede, 1931: 489.

This species is placed in Forster’s (1964) genus *Punapedaliodes* on the basis of similarities in facies, altitude preferences and the short and very broad aedeagus. It appears to be confined to the Eastern Cordillera of Colombia.

**Distribution:** A&B; Adams: EC(B), 2700–3300 m; Weymer (1912: 260): EC, Bogotá plateau, 2600–3200 m; Fassl (1918: 44): EC(B), c. 2650–3150 m.

**Bionomics:** Found by A&B both in open, cultivated land at the tree-line and in dry gallery forest rich in chusque.

**Genus *Steremnia* Thieme**

*Steremnia* Thieme, 1905: 137. Type-species: *Pedaliodes (?) polyxo* Godman & Salvin, by subsequent designation (Hemming, 1943: 25).

*Steremnia pronophila* (Felder & Felder)

*Sterona pronophila* Felder & Felder, 1867: 475. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined].

*Pseudosteroma pronophila* (Felder & Felder); Weymer, 1912: 241, pl. 51, row g; Gaede, 1931: 481; Forster, 1964: 143.

*Steremnia pronophila* (Felder & Felder); Brown, 1941: 434, pl. 1, fig. 1602 (genitalia).

Brown (1941) was correct in asserting that there are no consistent differences between the species placed in *Steremnia* by Thieme (1905) and those in Weymer’s (1912) *Pseudosteroma*, in morphology or genital structure. But he was incorrect in identifying Ecuadorian butterflies as belonging to *pronophila*: that species is confined to the Colombian Eastern Cordillera, and specimens that resemble it from Ecuador and Peru are all referable to *selva* sp. nov. (see below); the genitalia figured by Brown as of *pronophila* tally with those of *selva*, whose valve ‘shoulder’ is less rectangular than that of *pronophila*. 
Distribution: A&B; Adams: EC(B), 2450–3200 m; Weymer (1912: 241): EC, 2800/3000 m; “CC, Quindio, 3800 m” (confused with selva or monachella?); Fassl (1918: 44): EC(B), c. 2650–3500 m; Fassl (1911: 26): CC, c. 2750–4250 m (confused with selva and/or monachella?); Fassl (1915: 11): WC, c. 3000–3500 m (confused with selva and/or monachella?).

Bionomics: This species is found in open places within the cloud-forest, e.g. on wet patches on wide dirt tracks. The same habitat in the CC and WC is occupied by monachella (Weymer), which is clearly very closely related: female pronophila is similar in appearance to male monachella.

Steremnia monachella (Weymer)

Pseudosteroma monachella Weymer, 1912: 241, pl. 52, row a. Syntype(s), north PERU: Huancabamba, 3000 m [MNHU?].
Pseudosteroma monachella Weymer; Gaede, 1931: 481; Forster, 1964: 143.
Steremnia monachella (Weymer); Brown, 1941: 434, pl. 1, fig. 1603 (genitalia).

This species, more brightly marked on the underside than pronophila, seems to be its allopatric replacement in the Colombian Central and Western Cordilleras, and its distribution extends to Bolivia. Some Ecuadorian and all Colombian specimens have a slightly darker underside than the typical Peruvian butterflies. It may be distinguished from pronophila by the following: it has an oval sandy-brown patch at the tornus of the underside hindwing; the scent patch is narrower; the forewing is more indented in cell M3; and the ‘shoulder’ on the valves is more rounded. Weymer’s (1912) and Fassl’s (1911; 1915) references to “pronophila” in the CC and WC may have been to monachella or selva (see above, under pronophila).

Distribution: A&H; Adams: CC(T&H), 2750–3600 m; A&H: WC, 3400/3450 m.

Bionomics: Like S. pronophila, monachella has a similar fondness for open places; it also occurs in the páramo just above the trees.

Steremnia selva sp. nov.
(Figs 21, 59)

Male

Forewing length 22–24.5 mm. Upperside unicolorous dark brown, with yellow-chequered fringes on the forewing and anteriorly on the hindwing; a faint dusting of lilac at tornus of hindwing. Large compact scent patch entering discal cell and occupying the distal one-third of it.

Underside forewing dark brown, paler in the distal half; lilac dusting in the apical region; a series of five submarginal dots in cells R5 to Cu1, whitish and clearest in R5, yellowish and faint in the others. Underside hindwing mottled chocolate-brown and paler brown, and dusted with blue scales; a series of five submarginal dots, parallel to the outer margin, in cells Rs to Cu1, those in Rs and Cu1 whitish, the other three yellowish and less discrete (in some individuals, the dot in M1 is also whitish); a white costal streak, dusted with brown, to vein M1 and continuing faintly to the discal cell.
Female unknown.

Holotype ♀, COLOMBIA: Departamento del Cauca, W above Santa Leticia, 2800 m, 9 viii 79 (M. J. A.).

Paratypes, locality as holotype: 4♂, 2850–2950 m, 9 viii 79; 6♂, 2900–3150 m, 10 viii 79; 5♀, 2850–2950 m, 11 vii 79 (M. J. A. and P. J. H.); 1♀, ECUADOR: Cuenca, Las Cajas, 2200 m, 2 ix 83 (R. Hadfield).

This species, whose name is Spanish for "forest", is best distinguished from the very closely similar pronophila by its geographical distribution (found in Ecuador and the Colombian Central Cordillera) and its habitat: unlike pronophila and monachella, it is a denizen of deep cloud-forest; at its CC locality, it is replaced at the forest edges and open places nearby by monachella. It also differs from pronophila in the following respects: it is larger (male pronophila has a forewing length of 19–21 mm) and paler on the underside; it has a broader male scent patch; on the underside hindwing the costal streak is less bright; and the 'shoulder' on its valves is less rectangular (but less rounded than in monachella). This is most probably the species referred to by Brown (1941: 434) as Ecuadorian pronophila.

Distribution: A&H: CC(H), 2800–3150 m; R. Hadfield: Ecuador, Las Cajas, 2200 m.

Bionomics: The butterflies were found by A&H on the ground, in small sunny patches along the banks of a stream deep inside very moist cloud-forest.

Genus Steroma Westwood

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

Steroma bega bega Westwood

Steroma bega Westwood [1850]: pl. 66, fig. 6; [1851]: 400. 1♂ syntype, VENEZUELA [:coast range?] (BMNH) [examined].

Steroma zibia Butler, 1870: 23. 1♀ syntype, VENEZUELA (BMNH) [examined].

(Synonymy given by Adams & Bernard, 1979: 117.)


The typical race of this species, with its almost complete, rhomboid-shaped, silvery-white costal patch on the underside hindwing, is found in Venezuela (coast range and Cordillera de Mérida), in the Sierra de Perijá and on the east slope of the Colombian Eastern Cordillera. It is replaced on the west slope, in the Central Cordillera and southwards to Bolivia by subsp. andensis Felder & Felder. Forster's (1964) reason for reinstating andensis as a species separate from bega was the supposed concurrence of the two in Bolivia, bega preferring the higher elevations in the upper cloud-forests; but I believe that it is unlikely that the upper species is indeed bega, since it is unknown from anywhere between Colombia and Bolivia and because he refers to it as having a larger male scent patch than andensis, which is not the case in Venezuelan or Colombian bega. More probably it is a new, unnamed species, similar in appearance to bega. (This view was corroborated during my 1985 visit to Bolivia.)
Distribution: BMNH: Venezuela; A&B; Adams: EC(E), 2400/2500 m; [A&B: Venezuelan coast range, 1800–2700 m; Venezuelan Mérida range, 2300–2800 m; Sierra de Perijá, 1800–2300 m].

Steroma bega andensis Felder & Felder, stat. rev.

Steroma andensis Felder & Felder, 1867: 475. 1♂ syntype, COLOMBIA: Bogotá (BMNH) [examined].
Steroma bega Westwood form andensis Felder & Felder; Weymer, 1912: 241, pl. 51, row g; Gaede, 1931: 480 (as var.); Brown, 1941: 433 (as subsp.).
Steroma andensis Felder & Felder; Forster, 1964: 142.

The only consistent difference between bega and andensis lies in the extent of silvery-white in the underside hindwing costal patch: in andensis it is confined to narrow, sometimes broken, lines along its distal and basal edges.

Distribution: BMNH: Colombia to Bolivia (Bristow coll.: Ecuador, 2065–2660 m); A&B: EC(W), 2550–2650 m; A&H; Adams: CC, 2350–2900 m; Fassl (1911: 26): CC, c. 2000–3000 m (as bega); [Adams, 1985: Bolivia, 1650–2800 m].

Genus Thiemeia Weymer


Thiemeia phoronea (Doubleday)

Pronophila phoronea Doubleday, 1851: 358, pl. 60, fig. 1. 1♂ syntype, VENEZUELA (BMNH) [examined].
Daedalma phoronea (Doubleday); Butler, 1868: 183.
Catargynnis phoronea (Doubleday); Thieme, 1907: 150.
Thiemeia phoronea (Doubleday); Weymer, 1912: 267; Gaede, 1931: 511 (as Thimeia).
Thiemeia ortruda (Thieme) var. obscurata Krüger, 1924: 38. 1♂, 1♀ syntypes, COLOMBIA: Western Cordillera, west slope, south (depository unknown).

Typical ortruda is from Peru and Bolivia; Krüger’s male, from his unillustrated description, seems to be indistinguishable from typical phoronea, which is represented at the BMNH from Venezuela and Ecuador; his female is like neither ortruda nor phoronea, but the insufficiency of material makes it impossible to know whether this is a subspecies or a female variety. However, given the distributions of the two species, Krüger’s specimens almost certainly belong to phoronea. They are the only Colombian records that I know of.

Colombian species of doubtful classification

Pedaliodes pheretias (Hewitson)

Pronopliha pheretias Hewitson, 1872: pl. 7, fig. 46. 1♂ syntype, ECUADOR (BMNH) [examined].
Pedaliodes pheretias (Hewitson); Thieme, 1905: 101; Weymer, 1912: 258, pl. 54, row f; Gaede, 1931: 497.
Fassl (1911: 26) obtained a species in the Central Cordillera which he referred to as *pheretias*. Since the species has close relatives at similar very high altitudes in the Eastern Cordillera (*hardyi* and *arnotti*) and in the Western Cordillera (*fassli*), it is likely that Fassl’s belongs to this group. But it is not certain that it is indeed *pheretias*, the type material of which is from Ecuador, especially since Weymer (1912), referring to Fassl’s specimens only, describes the species as having a white “elongate costal spot” on the underside hindwing (yellow in type *pheretias*) and a “rather small red-yellow anal spot” (large in *pheretias*).

**Pedaliodes pacifica** Krüger


Krüger (1924) believed that this species was close to *praxithea*, but his unillustrated description is reminiscent of the Ecuadorian *phoenicusa* (Hewitson), with similar submarginal ocelli on the underside, but without the orange patches on the upperside forewing. Neither *praxithea* nor *phoenicusa* belongs in the genus *Pedaliodes*: the former is combined with *Physcopedaliodes* in this paper, and the latter may be in that genus or in *Parapedaliodes*, but its wing shape and markings make it an anomalous species. (This species was rediscovered by Dr Schmidt-Mumm in 1985 in Chocó on the west slope of the Western Cordillera, at 2200 m; preliminary studies of its facies and genitalia suggest a relationship, not with *phoenicusa*, but with the group of Ecuadorian *Pedaliodes* species including *pelinna* (Hewitson).)

**Pedaliodes puracana** Krüger

*Pedaliodes puracana* Krüger, 1924: 28. 5♂ syntypes, COLOMBIA: Central Cordillera, east side, Huila, N of Volcán de Puracé, c. 3200 m (depository unknown).

Extremely large (forewing length 35–37 mm) and with a unique pattern of markings on the upper- and underside, this species is very unlikely to belong in *Pedaliodes*. If it is a pronophiline at all, it would appear to be a representative of a new genus. (Krüger’s description was unillustrated.)

Species of doubtful Colombian status

*Cheimas opalinus* (Staudinger)

*Oxeoschistus opalinus* Staudinger, 1897: 145, pl. 5, fig. 10. 6♂ syntypes, VENEZUELA: Sierra Nevada bei Merida (MNHU).

*Cheimas opalinus* (Staudinger); Thieme, 1907: 176; Weymer, 1912: 271, pl. 58, row d; Gaede, 1931: 516.

This species, common in the uppermost cloud-forests of the Venezuelan Cordillera de Mérida, has not to my knowledge been recorded in the literature as coming from anywhere else but Venezuela. However, in the BMNH main collection there are specimens labelled “Colombia” and “Ecuador”. I would consider these as mislabellings, were it not for the fact that I believe I saw an individual *opalinus* sunning itself high up on chusque foliage at 2950 m in the Central Cordillera (Huila), above the altitudes at which the only species with which it could be confounded, *Mygona irmina*, normally flies.
Steremnia rugilas Thieme

Steremnia rugilas Thieme, 1905: 137, pl. 3, fig. 42. Holotype ♀, PERU (BMNH) [examined].
Steremnia rugilas Thieme; Weymer, 1912: 242, pl. 52, row a; Gaede, 1931: 481; Brown, 1941: 436, pl. 1, fig. 1605 (genitalia); Forster, 1964: 144.

Thieme’s (1905) description of this species referred to a single male in the Rothschild collection at Tring (now at the BMNH) with no locality label; but the type now bears the label “Peru”, which is one of the countries in which it flies (Dr G. Lamas’s collection at the Museum of Natural History in Lima has it from between 2800 and 3300 m east above Lima). It is also reported by Brown (1941) as being common throughout the Ecuadorian páramos. Weymer (1912) claimed that the species was known only from Fassl’s material obtained at 3000 m on the Quindío Pass (CC(T)), but Fassl (1911: 26–27) makes no reference to it. The evidence that rugilas extends into Colombia is insufficient.

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