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Article



# Revision of the genus *Pyrochlora* Warren, 1895 (Lepidoptera: Geometridae: Geometrinae)

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# Abstract

The genus *Pyrochlora* Warren is revised and three new species are described: *P. motilonia*, **sp. nov**. from Costa Rica and Nicaragua, *P. kuklase*, **sp. nov.** from mountainous Ecuador, and *P. vogli*, **sp. nov.** from Northern Venezuela. Wings pattern and genitalic structures of all five species are described and illustrated.

Key words: Lepidoptera, Geometridae, *Pyrochlora, P. motilonia* sp. nov., *P. kuklase* sp. nov., *P. vogli* sp. nov., male genitalia, keys, geographical distribution.

## Introduction

Warren (1895: 90) described the genus *Pyrochlora* for *Phalaena Geometra rhanis* Cramer, based on external characters, such as the wing shape, build of antennae and hind legs, and short palpi. Dyar (1925: 7) characterized a second species, *P. majorcula*, as larger and paler in comparison to the type species, with two brown lines cutting the pale median area near the tornus of forewing. Prout (1932: 43) presented a more detailed review of the two known species. Pitkin (1996: 387) added a description of the genitalia of both known species, and made a comparison with the genitalic characters of the related genus *Tachychlora* Prout. External facies of *Pyrochlora* species is deceptively uniform (Figs. 1–11) and, seemingly, insufficient for species recognition. The three new species described here were discovered by routine checking of genitalia of different local populations from South America.

## Material and methods

Altogether 89 specimens and 19 genital slides (17  $\sigma$ , 2  $\varphi$ ) were studied from collections as follows: IZBE, Institute of Agronomy and Environmental studies at the Estonian University of Life Sciences, Tartu, Estonia; NHMT, Natural History Museum, Tallinn, Estonia; ZSM, Zoologische Staatsmuseum München, Germany; CAL, private collection of Aare Lindt, Tallinn; CAS, private collection of Allan Selin, Tallinn. Genitalic sclerites were soaked in 15% KOH solution for about 24 hours, washed with water, dehydrated in alcohol and embedded into Euparal medium. Morphological details were measured in slides and in mounted dry specimens under 40x magnification, using an ocular micrometer. When comparing wing patterns of moths from different localities, some geographical variations were found on wings below. The descaling of last abdominal sternite and measuring the antennal pectinations' length revealed further differences. Dissection of specimens from each locality confirmed the existence of five morphospecies within the genus and allopatric variation of *P. majorcula* (designated here as Form A and Form B). A further study of new material from Brazil will show how significant are the slight morphological differences between Guianan and Ecuadoran specimens of *P. majorcula*.

# Pyrochlora Warren, 1895

Pyrochlora Warren, 1895, Novit. Zool. 2: 90. Type species: Phalaena rhanis Cramer, 1777.

The genus is grouped within the tribe Nemorini according to Pitkin (1996), based on characters of male genitalia: a) the presence of central sclerotization ("midrib") of sternite A8; b) rod-like or spatulate uncus; and c) costal sclerotization of valva. Pitkin (1996) discussed the genital characters of *Pyrochlora* in comparison with those of *Tachychlora* Prout, 1912. Generic characters of *Pyrochlora* include pectinate antennae in both sexes; weakly shaped, orange or brownish fillet between antennae; orange and brown colour of frons; olive green and grey to brown pattern of wings with a distinct orange, yellow or whitish patch subtornally in forewing and subcostally in hindwing. Hind tibiae with two pairs of spurs and bearing contrasting black tufts of scales at joints; inner spurs are longer than external ones, and distance between spur pairs shorter than the longest spurs. Male hind tibia with a hair pencil concealed in a rim and distally covered by a short apical projection. *Tachychlora* species share a white head color, contrasting black and yellow markings on hindwings, much longer, filiform uncus and sidewise projecting cornuti on aedeagus.

# Key to the species according to male genitalia

1	Aedeagus sack-like, oval, provided with an apical spine
-	Aedeagus simple, not sack-like, without an apical spine
2	Sternite A8 posterior margin broadly emarginated U-shaped (Fig. 23) P. rhanis
-	Sternite A8 posterior margin straight or slightly concave
3	Aedeagus long (1.75 mm) with a short (0.12 mm) apical spine directed dorsad (Figs. 27, 30). Sternite A8 broadly
	(about 1,0 mm) sclerotised and truncate at distal margin (Figs. 26, 29)
-	Aedeagus much shorter (1.6 mm) with a long (0.35 mm) apical spine hook-like (Fig. 39). Sternite A8 weakly sclero-
	tized heart-shaped at distal margin
4	Aedeagus long (2.0 mm), with long bundles of thin cornuti (Fig. 36). Sternite A8 posteriorly bilobed but not mark-
	edly sclerotized (Fig. 35) P. kuklase, sp.nov.
-	Aedeagus short (1.3 mm), flat, without any cornuti (Fig. 33). Sternite A8 delicate, not excised posteriorly

# Key to the species according to wing pattern and external facies

1	Forewing underside hindmarginal area with blackish marks fused partially, or fused into a long and broad quadran-
	gle along anal margin of wing (Fig. 21)
-	Forewing underside with three separate darkish lines (or basal and medial transverse line and larger tornal spot) sep- arate and perpendicular to anal margin (Fig. 15)
2	Hindwing above apically with a yellowish zigzag mark at costa. The basal and medial blackish marks partially fused
	along anal margin of forewing below, but palely scaled along vein CuA <sub>2</sub> (Figs. 12–14, 19) P. rhanis
-	Hindwing costal area incontrastingly paler above, without a concrete yellow mark. The basal and medial blackish marks fused into a rectangular long quadrangle or band at forewing anal margin below (Figs. 18, 21)
	P. kuklase sp.nov.
3	Wing span 23.5–26 mm in males. Three blackish marks at forewing anal margin below, equally spaced (Fig. 15).
	Hindwing below usually with one greyish blotch at apex, underside of wings greyish or yellowish grey
	P. majorcula
-	Wing span 20.5-22.5 mm in males. The basal and medial darkish mark at forewing anal margin below, close
	together; wings underside with reddish hue, hindwings with two dark blotches in terminal area
4	Forewing postmedial and medial lines fused X-shaped in anal cell, separating the yellow tornal blotch and a yellow
	line proximal to the medial line (Fig. 6); hindwing submarginal field greyish brown, ample marked yellow at costa .
-	Forewing tornal yellow blotch enlarged, covering or cutting dark lines of postmedial and medial; hindwing submar-
	ginal field brownish grey at centre, with large pale blotches at costa and tornus (Figs. 8, 9) P. vogli, sp. nov.

Figs. 2, 3, 12, 13, 14, 19, 22–24

Phalaena rhanis Cramer, 1777: 34, pl. 119, Figs. B, C. Type locality: "West Indies", according to Scoble (1999), or "Surinam" (Prout 1932).

**Measurements:** Wing span 20.0–26.0 mm in males (n=10), 30–31 mm in females (n=2). Antennae pectinate in both sexes, length of pectinations reaching 0.4–0.45 mm in males (n=15), 0.4 mm in females (n=2).

**Description:** *P. rhanis* with a well discernible costal yellow zigzag mark between the postmedial line and apex on hindwing upper side. The shape of the sternite A8 is visible without dissection when the distal end of abdomen is descaled. Series of *P. rhanis* in collections are outstanding in their relatively dark pattern of wings (see e.g. Piñas 2005, Fig. 263). Male genitalia: as in the genus description; valva without a basal costal projection. Female genitalia: antrum sclerotized, bulbous (Fig. 40; Pitkin 1996, Fig. 214).

**Material studied:** 15 °, FRENCH GUIANA, Kaw Mts., Amazone Nature Lodge, 4°33'30"N, 52°12'25"W, 13–20.10.2006 (J. & V. Viidalepp) (gen. 7751) (IZBE); 1°, "Guyane Francaise 1986 / Exped. H. De Toulgoët /B. et J. Lalane Cassou /Ch. Gibeaux, /Cayenne Route Regina PK 32.5 / piste de Nancibo / PK 6 / 8-II-86" (ZSM e. c. Herbulot); 1°, Camp Caiman, 26.10.02 (CAS); 1°1°, ECUADOR, Napo, Puerto Misahualli, 5–9.11.2002 (CAS); 1°, Morona Santiago, Santiago, 300m, 03°02'29"S, 77°59'50"W, 26.04.2007; 1°, Morona Santiago, Santiago, 370m, 03°01'16"S, 77°56'52"W (CAL); 3°, "SO. BRASILIEN / Espirito Santo / St. Leopoldina / Umg. Dorf Tirol 650 m / 25.12.1996–10.01.97 / leg. Thöny" (gen. 7980) (ZSM); 1°, "VENEZUELA / Bolivar / Rte El Dorado à Sta Helena / au km 125 (1350m) / 20.V.1971 / C. Lemaire (gen. 7984)" (ZSM e. c. Herbulot).

Biology: confined to primary tropical rain forests on lowland and low mountains.

**Distribution:** Genitalia checked: French Guiana, SE Venezuela, Ecuador, SE Brazil (IZBE, ZSM, CAS, CAL). Literature data on *P. rhanis* from Belize and Guatemala need to be verified.

**Remarks.** The species was identified according to Cramer's good original illustrations (Prout 1932; Herbulot 1988; Pitkin 1996). Pitkin has added descriptions of genitalic structures of both sexes, including autopomorphic characters as the sternite A8 deeply and roundly emarginated (Fig. 23), the aedeagus sack-shaped with a short apical spine (Fig. 24).

## Pyrochlora majorcula Dyar, 1925

Figs. 1, 4, 5, 11, 15, 25–30

Pyrochlora majorcula Dyar, 1925: 7. Type locality: French Guiana: Cayenne.

**Measurements:** Wing span 25.0–28.0 mm in males (n=21), 33.0 mm in females (n=2). Length of antennal pectinations in males 0.51–0.52 mm (n=10) (Form A), or 0.52–0.56 mm (n=5) (Form B), 0.45 mm in female.

**Description:** The species is characterized by the sack-shaped aedeagus similar to but longer than that of *P. rhanis*, with a short apical spine; sternite A8 sclerotized and distally straight-edged, not emarginated posteriorly. There are differences between the populations from Kaw Mts. and NE Brazil (male antennae shorter pectinated; the dorsobasal appendix from valve costa pollex-like, straight, and valve ventral margin less angulate at its basal third; Fig. 25), and from Ecuador (antennal pectinations longer; the costobasal appendix of valve rounded and valve ventral margin angulate at sacculus: Fig. 28). The entire male armature is relatively more massive in moths from Ecuador and thinner in the Fr. Guyana population (Figs. 25–30). Moths from SE Brazil differ in wings shape, relatively shorter and broader, sharing genital characters of the Form A (except a slightly more slender saccus).

**Material studied:** Form A: 11♂, FRENCH GUIANA, Kaw Mts., 6.11.2002 (V. Soon), (gen. 7039, 7752, 7902) (IZBE); 2♂, Kaw Road, 04°32'N, 52°12'18"W, 07.01.2005, A. Selin & T. Armolik leg. (CAS). 2♂1♀,

"BRASILIA sept. / Amazonas / Uypiranga / V. 31 / leg. W. Hopp" (ZSM, gen. 7981). Form B: 1<sup>°</sup>, ECUADOR, Sucumbios, Panayacu riv., Jarrin Expeditiones Lodge, 0°23'S, 76°11'W, 14–19.10.1999 (gen. 6975) (CAL); 2°1<sup>°</sup>, Napo, Rio Shiripuno, 26.10.02; 1°, Napo, Sahuangal, 15.10.2002 (CAS); 1°, Morona Santiago, Santiago 370m, 03°01'16"S, 77°56'52"W, 27.04.2007 (CAL); 1°, Pichincha, Cotundo, 1080 m, 00°41'28"S, 77°43'56"W, 19.05. 2007 (gen. 7953) (NHMT).

**Biology:** Confined to tropical rain forests on lowland and low mountains.

Distribution: Fr. Guiana, N. Brazil, Ecuador (IZBE, ZSM, CAL, CAS).

**Remarks:** The specimens in the British Museum collection were identified by Prout (1932) and recently rechecked by Pitkin (1996). The type specimen no. 27500 was selected and designated as lectotype for *Pyrochlora majorcula* Dyar by L. Pitkin in the collection of Smithsonian Institution, Washington, USA. (Fig. 1).



**FIGURE 1**. Type series of *Pyrochlora majorcula*; specimen No. 27500, lower row, right. Courtesy Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, United States.

# Pyrochlora motilonia Viidalepp sp.nov.

Figs. 6, 16, 17, 31–33

**Type series:** <u>Holotype:</u> J. NICARAGUA, San Juan, Bartola at riv. San Juan, 6.06.2008 (gen. 8022) (J. Viidalepp leg.) (IZBE). <u>Paratypes:</u> 22JH: 7J, Bartola at riv. San Juan, 2–8.06.2008 (J. Viidalepp, V. Viidalepp, O. Kurina leg.)(IZBE); 1J, COSTA RICA, Bri Bri, 100m, 09°33'38"N, 82°55'00"W, 14.04.2001; 2J, Santa Cicilia, 10°56'08"N, 85°22'23"W, 28.04.2001 (gen. 6911) (CAS); 1J, Puerto Viejo, 10°20'057"N, 83°58'35,9"W, 2.05. 2001 (CAS); 3J, Limon Vesta, 12.04.2001 (CAS); 1J, Monte Verde, 10°13'16,5"N, 84°47'50,8", 30.04.2001 (CAS); 1J, Guacimal, 250m, 10°11'09"N, 84°52'23"W, 19.02.2007; 1J, Playa Hermosa, 139 m, 09°12'03"N, 83°46'24"W, 07.02.2007 (gen. 7939); 1J, Bri Bri, 100 m, 09°33'38"N, 82°55'00"W, 11.02.2007 (gen. 7956) 1J, Bri Bri, 278 m, 09°35'31"N, 82°53'45"W, 12.02.2007 (gen. 7957) (CAL); 1J, ECUADOR, Manabi, Rosa Zarte, 150m, 00°19'44"N, 79°30'28"W, 13.05.2007 (gen. 7954) (CAL). 2J, "Ecuador / 16 km E.S.E. de Santo / Domingo de los Colorados / 650 m–19 au 22.i.1975 / C. Herbulot" (gen. 7983) (ZSM). Holotype deposited in coll. IZBE, Estonian University of Life Sciences, Tartu, paratypes in NHMT, ZSM, CAS, CAL.

**Measurements:** Wing span 20.5–22.5 mm in males (n=10), length of antennal pectinations reaching 0.4–0.42 mm in Costa Rica series and 0.5–0.52 in moths from Ecuador.

**Diagnosis:** The species is characterized by smaller, delicate male genitalic armature and small, simple aedeagus (length 1.20–1.25 mm) lacking cornutus (Figs. 31–33).

**Description:** Forewing medial and postmedial lines fused X-shaped in anal area, separating the yellow tornal blotch and a yellow line proximal to the medial line (Fig. 6). Hindwing submarginal field greyish brown, ample marked yellow at costa. Hindwing below with two grey blotches in terminal area. Forewing below with two distinct lines at middle of the anal area; the tornal spot 8-shaped. Fresh specimens with wings underneath tinted reddish. Male genitalia of relatively delicate build, aedeagus not sack-shaped but short, flat and lacking apical spine. Sternite A8 not sclerotized distally.

Biology: Confined to primary rain forests on lowlands and low hills.

**Etymology.** The specific name is from the locality name Motilonia in Costa Rica. Gender feminine. **Distribution:** Nicaragua, Costa Rica; Ecuador.

# Pyrochlora kuklase Viidalepp sp.nov.

Figs. 7, 10, 18, 34-36

**Type series:** <u>Holotype</u>:  $\circ$ , ECUADOR, Napo, Baeza 1700 m, 00°27'09"S, 77°51'17"W, 17.05.2007 (gen. 7952) (NHMT). <u>Paratypes</u>:  $7 \circ 1 \circ$ ;  $1 \circ$ , Zamora Chinchipe, Los Equentros, 1460m, 03°48'47"S, 78°36'39"W, 21.04.2007; 2#, Zamora Chinchipe, Los Equentros, 1770m, 03°54'49"S, 78°29'58"W, 22.04.2007 (CAL);  $2 \circ 1 \circ$ , Morona Santiago, Gualaquiza, 1570m, 03°17'58"S, 78°33'28"W, 23.04.2007 (gen. 7992)(CAL); 2#, PERU, Oxapampa 2300 m (gen. 7938) (NHMT). Holotype deposited in Estonian Museum of Natural History, Tallinn, paratypes in NHMT and CAL.

**Measurements:** Wing span 22.0–25.0 mm in males, 27 mm in a female, length of antennal pectinations 0.45–0.48 mm in males, 0.25 mm in female.

**Diagnosis:** Externally the species is characterized by a large, continous, rectangular blackish marking along the anal margin of forewing underside (Figs. 18, 21). Other species have the ante- and postmedial lines marked by dark transverse lines between the discal cell and hindmargin of the forewing (if enlarged, not covering the origin of vein  $CuA_2$ ). Aedeagus with three bands of short and thin spines dorsally.

**Description:** Forewing pattern similar to that in *P. majorcula*, hindwing costal area without a concrete yellow mark. Male genitalian armature is relatively massive, aedeagus has long bundles of spiny cornuti dorsally and the sternite A8, although not strongly chitinized, is bilobed terminally (Figs. 34–36). Quite possibly, this species is pictured by Piñas (2005, Fig. 264, as a female for *P. rhanis*).

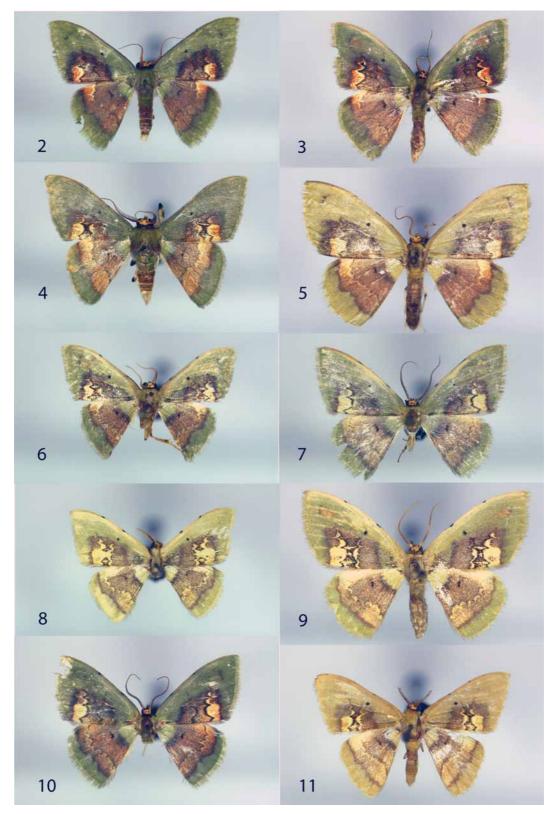
**Biology:** Confined to rich tropical mountainous forests at about 1400–2300 m above sea level.

Etymology: The specific name is from Estonian family name Kuklase. Gender masculine.

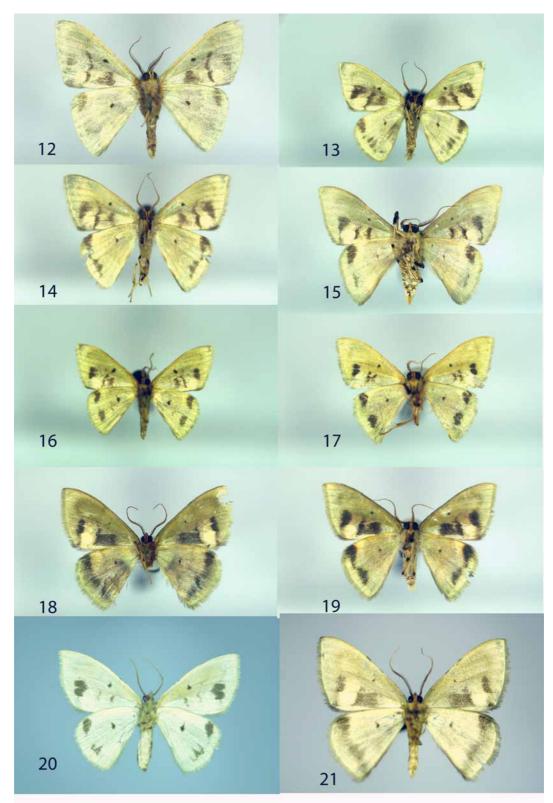
**Distribution:** Ecuador; Peru.

*Pyrochlora vogli* Viidalepp sp.nov. Figs. 8, 9, 20, 37–39

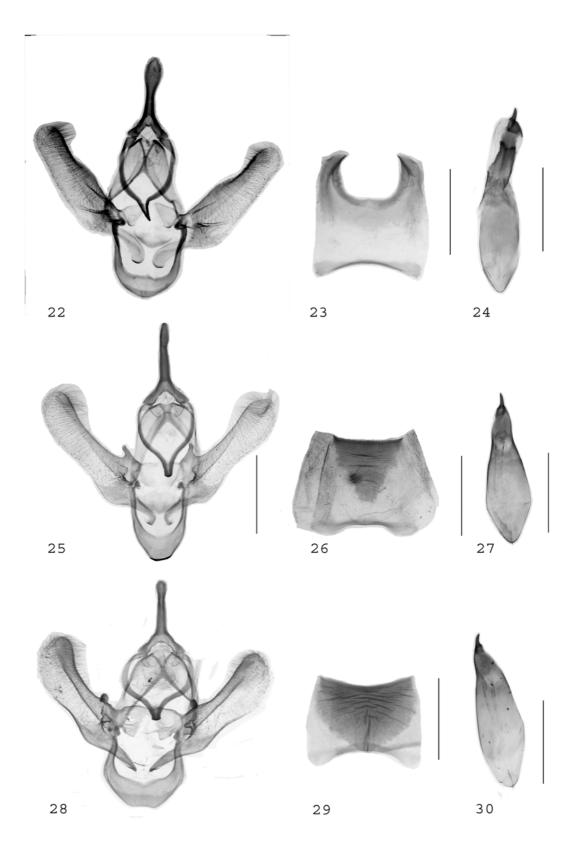
**Type series:** <u>Holotype</u>: ♂, "VENEZUELA, Maracay, ges[ammelt]. P. Vogl. / April–May 1934" (ZSM). <u>Paratypes</u>: 5♂, "VENEZUELA, Maracay, leg. P. Vogl" (ZSM). Additional labels: "Juli 1934" (1), "April–May 1934" (1), "August 1934" (1), "November 1934" (1), "Gen. prep. 7982 J. Viidalepp"); 3♀, "VENEZUELA, Maracay, leg. P. Vogl" (gen. prep. 7993) (ZSM). Additional labels: "August 1934" (1), "Staatssamml. München" (printed label with hand-written datum "17.vi" (1); "April–May 1934" and white hand-written "majorcula Dyar ?" (1). The types are deposited in the collection of Zoologisches Staatsmuseum München (ZSM).



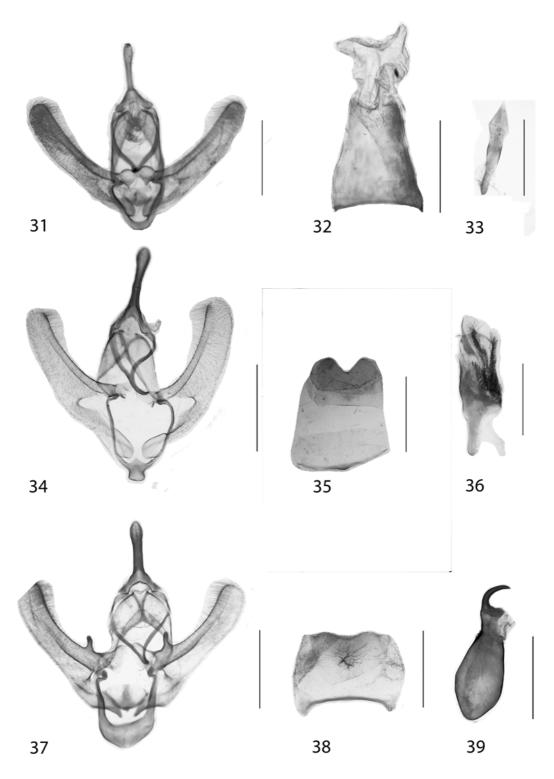
FIGURES 2–11. Adult *Pyrochlora*, uppersides of wings. 2. *P. rhanis*, male (Fr. Guiana); 3. *P. rhanis*, male (SE Brazil); 4. *P. majorcula*, male (Fr. Guiana); 5. *P. majorcula*, female (N. Brazil); 6. *P. motilonia* sp. nov., male (Costa Rica); 7. *P. kuklase* sp. nov., male (Ecuador); 8. *P. vogli* sp. nov., male (Venezuela); 9. *P. vogli* sp. nov., female (Venezuela); 10. *P. kuklase* sp. nov., male (Ecuador); 11. *P. majorcula*, male (N. Brazil).



FIGURES 12–21. Adult *Pyrochlora*, undersides of wings. 12. *P. rhanis*, male (Ecuador); 13. *P. rhanis*, male (SE Venezuela); 14. *P. rhanis*, male (Fr. Guiana); 15. *P. majorcula*, male (Fr. Guiana); 16. *P. motilonia* **sp. nov.**, male (Costa Rica); 17. *P. motilonia* **sp. nov.**, male (Ecuador); 18. *P. kuklase* **sp. nov.**, male (Ecuador); 19. *P. rhanis*, male (Fr. Guiana); 20. *P. vogli* **sp. nov.**, female (N. Venezuela); 21. *P. kuklase* **sp. nov.**, male (Ecuador).



FIGURES 22–30. Male genitalia, *Pyrochlora* spp. 22. *P. rhanis*, male armature; 23. *P. rhanis*, sternite A8; 24. *P. rhanis*, aedeagus; 25. *P. majorcula*, Form A, male armature; 26. *P. majorcula*, Form A, sternite A8; 27. *P. majorcula*, Form A, aedeagus; 28. *P. majorcula*, Form B, male armature; 29. *P. majorcula*, Form B, sternite A8; 30. *P. majorcula*, Form B, aedeagus. Scale=1.0 mm.

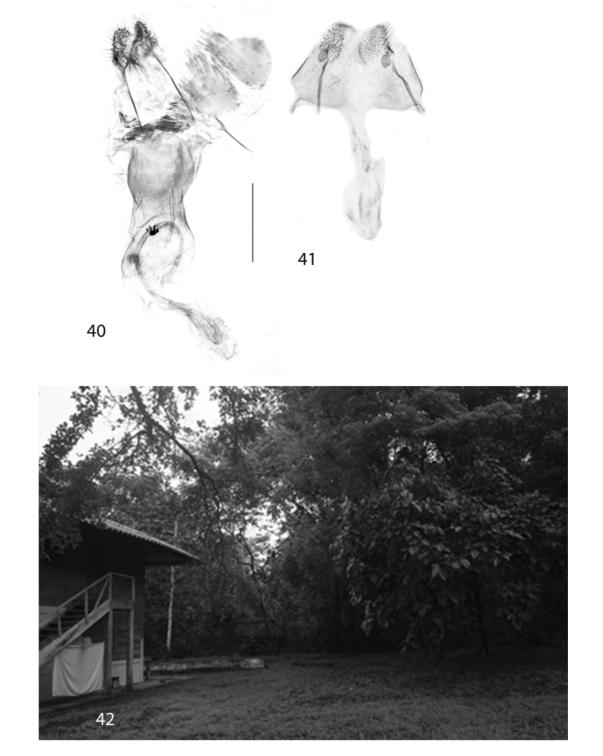


FIGURES 31–39. Male genitalia, *Pyrochlora* spp. 31. *P. motilonia* sp. nov., male armature; 32. *P. motilonia* sp. nov., sternite A8; 33. *P. motilonia* sp. nov., aedeagus; 34. *P. kuklase* sp. nov., male armature; 35. *P. kuklase* sp. nov., sternite A8; 36. *P. kuklase* sp. nov., aedeagus; 37. *P. vogli* sp. nov., male armature; 38. *P. vogli* sp. nov., sternite A8; 39. *P. vogli* sp. nov., aedeagus; 37. *P. vogli* sp. nov., male armature; 38. *P. vogli* sp. nov., sternite A8; 39. *P. vogli* sp. nov., aedeagus; 37. *P. vogli* sp. nov., male armature; 38. *P. vogli* sp. nov., sternite A8; 39. *P. vogli* sp. nov., aedeagus. Scale=1.0 mm.

**Measurements:** Wing span 21.0–24.0 mm in male, 26.0–29.0 mm in female. Length of antennal pectinations in male 0.45–0.48 mm, 0.3 mm in female.

**Diagnosis:** Forewing tornal blotch enlarged, underside with dark markings separated. Hindwing with large yellow blotches at costa and tornus. Aedeagus short sack-shaped with longer apical hook.

**Description:** Externally similar to pale *P. majorcula*, but with medial and postmedial lines fused X-shaped in anal area of forewing and broken by yellow connection of light blotches distal and proximal to it, i.e the yellow tornal blotch enlarged and fused with, or connected to yellow shading proximal to the medial line. Hindwing above with postmedial line supported distally by a dull yellow line, costal yellow blotch at postmedial area large and expanded along costa towards wing base. The postmedial field at hindwing tornus with a distinct yellowish blotch, while this area is not paler in other species.



**FIGURES 40–42.** 40. *Pyrochlora rhanis*, female genitalia; 41. *P. vogli* **sp. nov.**, female genitalia; 42. Collecting site of *P. motilonia* in wet tropics of Bartola, Nicaragua. Scale=1.0 mm.

Male genitalia with aedeagus similar to that in *P. rhanis* and *P. majorcula*, sack-like with an apical spine, but aedeagus shorter (1.6 mm) and the apical spine long (0.35 mm) (Fig. 39). Valva with basal costal projection finger-shaped as in *P. majorcula*. Sternite A8 distal sclerotization weakly heart-shaped, 0.8 mm broad and incised 0.4 mm deep. Female genitalia: antrum slenderer than in *P. rhanis*, not bulbous (Fig. 41).

**Etymology:** The specific name is from the family name of the collector, P. Vogl. Gender masculine. **Distribution:** N. Venezuela.

### Conclusions

The genus *Pyrochlora* is deceptively coloured—the type species *P. rhanis* is relatively dark in wing pattern, whereas paler specimens hitherto were supposed as *P. majorcula* in collections. A detailed study revealed three new, partially allopatric species from Ecuador, North Venezuela, Nicaragua and Costa Rica, while *P. rhanis* occurs widely distributed from Guianas to Ecuador and SE Brazil, and *P. majorcula* from Guianas to North Brazil and East Venezuela. The discovery of an endemic species from Maracay, Venezuela is interesting from a biogeographical point of view. The distribution of the species is concentrated to Guianan and Brasilian shields and Andean mountains, whereas records are lacking from vast inland areas.

The complex splits into two clades according to the male genitalia. *P. rhanis*, *P. majorcula* and *P. vogli* share a heavier build of the ring of tegumen + vinculum, and a sack-shaped aedeagus with an apical spine or hook. The two new species, *P. motilonia* and *P. kuklase* share a more delicate armature of genitalia and differ in build of aedeagus.

#### Acknowledgments

A. Hausmann provided study material from the ZSM collection. Patricia Gentili-Poole kindly put photographic documentation of the Dyar's types at the author's disposal. Harry Mannil kindly supported A. Selin during his collecting trip and allowed collecting in his farm "Motilonia" in Costa Rica. O. Kuklase has backed A. Lindt in various ways. Frédéric Le Corre provided facilities and support for some Estonian lepidopterists during their trips in French Guiana, and J.-M. Maes organized entomological trip in Nicaragua. I. Renge kindly revised and commented the first version of the manuscript, and comments and suggestions by three anonymous referees were helpful in improving the final version.

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