# Transfer of Aulacodes eupselias Meyrick to Pyraustinae, with Notes on the Genus Marasmia Lederer and on Cataclystiform Wing Patterns in the Family Crambidae (Lepidoptera: Pyraloidea)

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# ABSTRACT

Aulacodes eupselias Meyrick, 1929, is transferred to Pyraustinae, tribe Spilomelini, near Marasmia Lederer, 1863, and Cnaphalocrocis Lederer, 1863. The characters and relationships of these 2 genera and of synonyms and segregates of Marasmia are discussed. A new genus, Marasmianympha, separated from Marasmia and Cnaphalocrocis by several character states, is described for M. eupselias, new combination. New collection records and behavioral information are given for M. eupselias and its distribution in the Marquesas is summarized. Its distinctive wing-pattern type, given the new term cataclystiform, is discussed. The occurrence of such patterns in various crambid genera is noted, and the question of their biological significance is raised.

# INTRODUCTION

Meyrick (1929) described Aulacodes eupselias from a single male from the island of Tahuata in the Marquesas Islands, French Polynesia. Later, Meyrick (1934) published on a more extensive collection made in Ua Pou and Hiva Oa, also in the Marquesas, by the Pacific Entomological Survey. Clarke (1986) recorded additional material from the Marquesas, figured the moth, and figured and described the male and female genitalia. Though the moth is quite different in appearance from the neotropical Aulacodes aechmialis Guenée, 1854, type species of the genus, it does resemble in wing pattern Indo-Australian nymphuline species placed by Hampson (1897) in Aulacodes, but now segregated under Eoophyla Swinhoe, 1900. For this reason its status as a nymphuline has never been questioned. Clarke accepted Meyrick's generic placement without comment.

Not having dissected material of the species, I was astonished upon seeing Clarke's figure to note the close resemblance of the male genitalia to those of *Marasmia trapezalis* (Guenée 1854), a widespread species of quite different maculation, also figured by Clarke (1971, fig. 63; 1986, fig. 36a, b). Supposing that some mistake had been made, I made new dissections of both male and female genitalia from specimens in the Bishop Museum. These agree with Clarke's figures of the respective sexes. It is beyond doubt that *eupselias* is a spilomeline pyraustine related to

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Marasmia, and that its resemblance to Eoophyla spp. is superficial and convergent. The placement based on genitalia is confirmed by external characters: eupselias has the bifid praecinctorium of the Pyraustinae and lacks the chaetosema present in the Nymphulinae.

Two questions arise from this change in classification: what is the exact position of *eupselias* in the *Marasmia* complex, and why is there such close similarity in wing pattern between *eupselias* and unrelated Nymphulinae?

# **SYSTEMATICS**

Klima (1939) listed 4 nominal genera in the synonymy of Marasmia, placed Cnaphalocrocis next to Marasmia in the Pyraustinae and (1937) placed 2 more nominal genera under Susumia Marumo, 1930, in the Nymphulinae. The last 2 would key to Nymphulinae on the Hampsonian diagnostic character of stalking of R2 with R3+4 in the forewing, but this is no longer considered a reliable discriminant of the subfamily (Munroe 1972). The Susumia species are closely similar in other respects to species placed in Marasmia; in fact Epimima Meyrick, 1886, listed by Klima as a synonym of Marasmia, was based on a species with R2 stalked with R3+4. The nominal genera concerned share in the following characters: frons flat or weakly rounded, oblique; labial palpus ascending, its 2nd segment with long porrect scaling anteroventrally, its 3rd short, with a short porrect tuft of scales, tending to merge with anterodorsal scaling of 2nd; maxillary palpus prominent, reaching plane of frons; proboscis well developed; eye large and globular; ocellus present; antenna filiform, with alternate dorsal scale rows obliquely raised; legs of moderate length, robust, with outer tibial spurs shorter than inner; praecinctorium short in sagittal plane, with strongly divided, transversely oriented, distal lobes; forewing with subcostal-radial field narrow, veins basally apposed or stalked; discocellulars erect, slightly curved, M2-CuA1 arising close together near posterior angle of cell, A2 weak, but forming a closed loop with A1; hind wing with cell distinctly less than ½ length of wing, SC+R1 anastomosed beyond cell to about 3/4 distance from cell to apex, discocellulars somewhat concave distad, anterior angle of cell little produced, posterior angle somewhat more so; male genitalia with uncus deeply divided into pair of lobes armed dorsally with anteriorly directed, bifid, spinelike scales, aedoeagus cylindrical, of moderate proportions, well sclerotized, vesica with 1 or 2 strong cornuti; female genitalia with short, strongly setose, anal lobes, moderately short apopohyses, simple ostium, and small, round, depressed signum.

The following segregates have been recognized in the literature:

Cnaphalocrocis Lederer, 1863:276, 384. Type species: Botys iolealis Walker, 1859:666 [cited by Lederer as jolinalis, an unjustified emendation.] Monotypy.

Maxillary palpus with loose distal scale tuft. Outer tibial spurs ½ length of inner. Forewing with R1 & R2, R3 & R4 stalked; male fovea in end of cell, overhung by tufts of hairlike scales from R and CuA at middle of cell and by an oblique tuft from costa at end of cell. Hind wing with cell about ⅓ length of wing. Valve of male genitalia with longitudinal axial sclerotized ridge arising at base, extending to terminal margin and beyond it as toothlike process.

Marasmia Lederer, 1863:277, 385. Type species: M. cicatricosa Lederer, 1863:386, pl. 2, fig. 14, pl. 12, fig. 8. Monotypy.

Dolichosticha Meyrick, 1884:293, 304. Type species: Asopia venilialis Walker, 1859:373. Monotypy.

Labial palpus ascending, with long dense scaling forming a subquadrate tuft anteroventrally; 3rd segment small, concealed. Maxillary palpus short, with expanded distal scale tuft. Outer medial and hind subterminal tibial spurs ½, terminal spurs ¾ length of inner. Forewing with

R1 & R2 separate, R3 & R4 stalked; male fovea in end of cell overhung by fringe of lead-colored scales. Hind wing with cell about 1/5 length of wing. Male genitalia with distal margin of valve deeply excavated.

Note: Meyrick evidently intended *Dolichosticha* for species without the fovea and fringe of scales in the male, but based the name on the female of a species of *Marasmia*.

Lasiacme Warren, 1896:176. Type species: Lasiacme pilosa Warren, 1896:176. Original designation.

Characters of *Marasmia*, but male with elongate abdomen and with patch of androconia on upperside of apical area of hind wing. R2 of forewing free in *L. pilosa* Warren, 1896, the type species; stalked with R3+4 in *L. mimica* Warren, 1896.

**Epimima** Meyrick, 1886:235. Type species: *Epimima stereogona* Meyrick, 1886:236. Monotypy.

Bradinomorpha Matsumura, 1920:514. Type species: Bradinomorpha nawae Matsumura, 1920:514. Monotypy.

Susumia Marumo, 1930:39, 41. Type species: Samea exigua Butler, 1879. Original designation.

Similar to *Marasmia*, but male without fan of scales overlying forewing cell and with fovea small or absent. Maxillary palpus with distal scaling tapering. R2 of forewing stalked with R3+4. Distal margin of valve of male genitalia rounded and entire.

[Unnamed] (Dolichosticha of Meyrick, in part)

Similar to *Epimima*, but R2 of forewing not stalked. Distal scaling of maxillary palpus either tapering or forming an expanded tuft. Distal margin of valve of male genitalia rounded and entire at least in *Marasmia trapezalis* (Guenée 1854) (see Clarke 1971:65, fig. 63; 1986:53, fig. 36).

Of these segregates, Cnaphalocrocis is relatively distinct. Stalking of R1 and R2 separately from R3+4 is an unusual character in Pyraustinae and is undoubtedly apomorphic. The sex scaling of the male forewing is different in configuration from that found in certain species of Marasmia and Lasiacme and is probably an independent apomorphy, though a glandular area and the tendency to form a fovea in the cell of the forewing may be a shared character of the whole Cnaphalocrocis-Marasmia complex. The sclerotized ridge on the valve of the male genitalia of Cnaphalocrocis is a 3rd important apomorphy: no homologous ridge has been recognized in the remaining species examined. It therefore appears that Cnaphalocrocis can be considered a sister group of Marasmia s.l., and that authors have been correct in separating these, as they have universally done since Lederer (1863). The genus includes the nominal species listed by Klima (1939) and also Marasmia carstenziana Rothschild 1916, which should be transferred to become Cnaphalocrocis carstenziana (Rothschild 1916), n. comb.

The characters that have been used to define the remaining segregates are less satisfactory. Since there are 30 or more species in the *Marasmia* complex, some undescribed, and I have examined the genitalia of only a few, the statements made here are preliminary. Five characters have to be considered:

- 1. R2 of forewing free vs. stalked with R3+4. The free state occurs in the large majority of Pyraustinae and may be taken as plesiomorphic. However, the stalked state has developed independently a number of times in this and related subfamilies. In the *Marasmia* complex it appears to have arisen at least twice, in *Epimima*, which has the plesiomorphic states of male forewing cell, hind-wing scaling, and distal margin of male valve, and within *Lasiacme*, which has apomorphic states of these 3 characters.
- 2. Male with fringe of leaden-colored scales overlapping fovea in cell of forewing. This is a

synapomorphy of several species, including the type species of *Marasmia*. At least some of these species have the distal margin of the male valve excavated, but I do not know whether this association is invariable. Male androconial characters are notoriously labile in Pyraustinae, and the value of this character must be viewed with reserve.

- 3. Male with patch of velvety androconia at apex of hind wing. This is a synapomorphy of a few species, all of which so far known also have the fringe of leaden-colored scales overlapping a fovea in the cell of the forewing in the male. This state defines the nominal genus *Lasiacme*. As Warren (1896) observed in his original description, R2 may be either free or stalked with R3+4 in association with this apomorphy.
- 4. Distal scale tuft of maxillary palpus expanded or tapering. This character, though extensively used by Hampson, Meyrick, and others, in defining pyraloid genera, is erratic in distribution and sometimes hard to assess. The expanded state generally seems to be associated with connecting the outline of the labial palpus with that of the frons and/or vertex when the moth is at rest. It is therefore often seen in species with porrect or dorsally truncate scaling of the labial palpus, with long maxillary palpus, and frequently also with flat and oblique frons. No doubt the expanded state is an apomorphy, but it is one that must have developed many times in the Pyraloidea. With respect to the *Marasmia* complex the expanded state is probably plesiomorphic, and it is retained in most species of the group.
- 5. Distal margin of valve of male genitalia entire or excavated. This character has been examined for only a few species. The rounded, entire margin is primitive with respect to the excavated state. The association of the excavated valve with the strongly developed fovea and leaden-colored fringe may be taxonomically significant, but, as noted above, it needs further investigation.

Evidently, while the distinction between Cnaphalocrocis and the other elements of the Marasmia complex discussed here is clear and plesiomorphic and apomorphic states within the complex seem well indicated, the classification of the complex as a whole is beset with uncertainties, and it is so far doubtful that any of the characters used, except for those that distinguish Cnaphalocrocis, are of generic value. To resolve this problem it would be necessary to examine most or all of the species and to undertake a thorough revision of the complex. As such a revision lies outside the scope of the present paper, I propose that for the present the classification should stand as follows:

Genus Cnaphalocrocis Lederer, 1863 Genus Marasmia Lederer, 1863

Synonyms: Dolichosticha Meyrick, 1884

Epimima Meyrick, 1886

Lasiacme Warren, 1896

Bradinomorpha Matsumura, 1920

Susumia Marumo, 1930

With this introduction, the systematic position of "Aulacodes" eupselias is easily resolved. As indicated in the description below, eupselias has plesiomorphic states of all the characters discussed above for both Cnaphalocrocis and Marasmia. In addition it has 2 significant plesiomorphies not seen in any of the species of Cnaphalocrocis or Marasmia I have examined. All of these have SC+RS of the hind wing anastomosed with R1 for ¾ or more of the distance from cell to apex, a state described and figured by Hampson (1898) for both genera. However, in eupselias these 2 veins are anastomosed for only about ½ the distance from cell to apex, a state found in most Pyraustinae. Also, in eupselias the discal cell of the hind wing is of normal length for Pyraustinae (i.e., about ½ as long as the wing, whereas in Cnaphalocrocis and Marasmia it is abnormally short, about ½ to ½5 the length of the wing). The following apomorphies charac-

terize eupselias: (1) the anterior margin of the hind wing is distinctly sinuous, whereas it is evenly convex in Cnaphalocrocis and Marasmia; (2) as already noted, in eupselias the wing pattern is strongly modified, in a way hard to derive from the usual pattern of the Marasmia complex, and involving diffusion and dislocation of the transverse bands, reduction and depigmentation of scales in circumscribed areas to form nacreous specular areas, and development of black spots and bluish white vein streaks on the subterminal area of the hind wing to give the appearance of a band of conjoined eyespots; and (3) in the female genitalia, the distal part of the ductus bursae is enlarged and has 3 prominent diverticula, not seen in any of the species of Marasmia or Cnaphalocrocis examined. One further distinctive character of eupselias is of uncertain polarity, namely, the shape of the praecinctorium, long in the sagittal plane and distally bifid into diverging longitudinal flaps, as compared with the short praecintorium with transverse, rounded, distal lobes found in Cnaphalocrocis and Marasmia. The latter condition is usually seen in Spilomelini, and I am inclined to think that the state in eupselias is apomorphic. However, there is a resemblance to probably plesiomorphic states commonly seen in Pyraustini and Evergestinae, and, until the wider relationships of the Marasmia complex are worked out in more detail, the evidence from this character must be regarded as ambiguous.

Given the sister-genus relationship already deduced for *Cnaphalocrocis* and *Marasmia*, the possession of at least 2 significant synapomorphies for these genera and of at least 3 significant autapomorphies for *eupselias* supports the erection of a new genus for the latter.

# Marasmianympha, new genus

Gender. Feminine

Type species. Aulacodes eupselias Meyrick, 1929

**Description.** External characters. Frons flat, oblique, smoothly scaled. Vertex with tufts of erect scales. Labial palpus obliquely ascending; 1st and 2nd segments with long compressed scaling, extending anteriorly from ventral surface, ending in an angle near distal end of 2nd segment; 3rd segment short, with pointed anterior tuft extending short distance along or merging with dorsal edge of anterior scaling of 2nd. Maxillary palpus long, reaching plane of vertex, distal scaling somewhat expanded. Proboscis long, coiled, with extensive basal scaling. Eye globular, narrow scaleless zone bordering it posteriorly. Ocellus large, nearly as wide as 1 antennal segment, looking dorsad, separated from eye by about its own width. Antenna filiform; dorsal scale rows slightly raised; ventral surface in male with fascicles of setae longer than antennal diameter, in female short-pilose. Chaetosema absent.

Body of moderate length and thickness. Legs robust; in both sexes outer midtibial spur about ½ length of inner, outer hind-tibial spurs nearly as long as inner. Praecinctorium prominent, long in sagittal plane, distally bifid into pair of obliquely divergent longitudinal flaps. Abdomen tapering in both sexes, slightly exceeding anal angle of wing. Seventh and 8th segments of male and 7th of female without specialized dorsal scaling.

Forewing subtriangular; costa straight to % from base, then arched to right-angled apex; termen nearly straight to M3, then evenly curved around tornus; posterior margin convex subbasally, with long scaling near base and tornus in both sexes. Underside of forewing with long fine scales in depression of discal cell and behind antemedial part of cell. Discal cell about % length of wing. SC ending on costa at % from base. R1 from cell at % from base, well separated from R2. R2 from near anterior angle of cell, basally closely apposed to R3+4. The latter a little shorter than free parts of R3 and R4. R5 from slightly behind anterior angle of cell, gently curved, not approximated to R3+4. M1 from slightly behind R5, evenly curved. Discocellular almost straight from R3+4 to M3. M2, M3, and CuA1 spaced around posterior

angle of cell, their basal parts weakly approximated. CuA2 from cell at 3/3 from base. CuP absent, represented by a fold. A1 ending at tornal angle. A2 forming a closed loop with it.

Hindwing about ¾ as wide as long; costa sinuate; apex rounded; termen evenly convex; anal angle rounded; anal margin somewhat convex. Discal cell about ½ length of wing. SC+R1 anastomosed with RS beyond cell for about 1/2 distance from cell to apex. M1 stalked for short distance with RS. Discocellular obtusely angled at middle, posterior part oblique distad to posterior angle of cell. M2, M3 and CuA1 spaced around posterior angle of cell, their basal parts not approximated. CuA2 from middle of posterior margin of cell. CuP and 2 anals present. Frenulum strong, simple in male, divided in female.

Male genitalia. Uncus short, deeply divided into pair of parallel-sided, distally rounded lobes, each about 4× as long as wide and dorsally densely clothed with short, strong, anteriorly directed, bifid setae. Tegumen short; dorsal element bridgelike, bearing pair of tufts of long posteriorly directed setae. Juxta subtrapezoidal, narrower dorsally, higher than wide. Vinculum V-shaped, produced into short acute saccus. From dorsolateral part of vinculum on each side a long slender corema, distally bearing dense brush of dark hairlike scales. Valve about 5× as high as ventral length; costal and ventral margins straight, parallel; distal margin evenly convex; costa narrowly and sacculus little more widely inflated; margins and mesal surface with dense vestiture of fine setae, but without special processes. Aedoeagus cylindrical, about 8× as long as wide; vesica bearing 2 strongly sclerotized cornuti, one ½, the other ½ length of aedoeagus.

Female genitalia. Ovipositor lobes high, narrow, densely setose, dorsally fused. Posterior apophysis T-shaped; shaft about as long as vertical crossbar. Eighth tergite short, wide, extending low on pleuron, its lateral margin evenly rounded, bearing radiating group of short setae near margin. Anterior apophysis about 2× as long as posterior. Ostium narrow, unarmed, ventral margin emarginate, V-shaped. Ostial chamber small, flask-shaped, sclerotized. Ductus bursae sclerotized, basally about same diameter as ostial chamber, distally expanded, spinulose, with 3 hornlike diverticula. Ductus seminalis arising dorsolaterally from expanded distal part of ductus bursae. Corpus bursae oval, finely scobinate; signum small, depressed, cup-shaped, with nipplelike central cone.

Early stages. Unknown.

Distribution. Marquesas Islands.

**Remarks.** Presumably this genus ranks among the older colonists of the islands, but there is no internal evidence of its geographical origin. Only 1 species is known.

# Marasmianympha eupselias (Meyrick, 1929), new combination

Aulacodes eupselias Meyrick, 1929:161. Aulacodes eupselias; Meyrick, 1934:336. Aulacodes eupselias; Klima, 1937:143.

Aulacodes eupselias; Clarke, 1986:81; 82, fig. 54a-c; 431, fig. 280b.

The moth and its male and female genitalia were figured well by Clarke (1986). Meyrick (1929) described the moth and Clarke the genitalia. Additional details are given in the generic description, above. The species was originally described from a single male from Tahuata Island taken at 850 ft (259 m). Meyrick (1934) gave additional records from Hiva Oa Island at altitudes from 1,350 ft (411 m) to 3,970 ft (1210 m), and from Ua Pou Island at 1,250 ft (381 m). Clarke added records from Fatu Hiva Island, from sea level to 2,025 ft (617 m). I have seen the material on which all these records were based. On the Bishop Museum Fatu Hiva Biological Expedition of 1988, additional specimens were collected as follows: Ua Pou I: Hakahau, Tehutu Rd, 1,312 ft (400 m), 9 August 1988, S. L. Montgomery & B. H. Gagné, at m/v light, 1 female; same

locality and collectors, 2,297 ft (700 m), on *Bidens* flowers at 1300 hrs (1 male) and 1400 hrs (1 female), also at Coleman lamp at night (5 females). Fatu Hiva I: Puna'ita'i Ridge above Omoa, 1,214 ft (370 m), 21 July 1988, S. L. Montgomery & D. L. Bishop, at m/v light, 1 male, 1 female; same locality and collectors, 2,789 ft (850 m), 23 July 1988, at Coleman lamp, 1 male. Hiva Oa I: Hanaiapa Rd, Teavaitapu, 1,903 ft (580 m), 15 August 1988, S. L. Montgomery & B. H. Gagné, at m/v light, 1 male. The records thus embrace 4 islands and an altitudinal range from sea level nearly to the highest summits. Though these 4 islands span a distance of about 120 statute miles, with gaps of up to 60 miles, they are the 4 most southerly of the 7 largest islands. Perhaps this is an accident of sampling, as moths of the northern islands Eiao and Ua Huka have been poorly collected; however, the 3rd largest northern island, Nuku Hiva, is one of the best collected of the archipelago and absence of *M. eupselias* from these collections may be significant. Examination of material in the Bishop Museum and comparison with a color photograph of the holotype did not show any appreciable differences in specimens from different islands or different elevations.

Though the new material collected by the Fatu Hiva Biological Expedition does not significantly extend the geographical or altitudinal range of the species, it does shed interesting light on the habits of the moths. By good fortune I had been able to call the attention of Dr. Montgomery and the late Dr. Wayne Gagné to the anomalous pattern and misunderstood taxonomic position of *M. eupselias* in the spring of 1988, just before the embarkation of the expedition. As a result, Dr. Montgomery and Mrs. Betsy Gagné were on the lookout for the moth and were able to report on its activity and resting patterns. As will be seen from the above records, adults were active not only at night, when they were taken at ultraviolet and ordinary light as had been reported in previous publications, but also in the daytime, when they were found sucking nectar from *Bidens* flowers. The resting position was also observed, and the moths are described as holding the wings flat or slightly sloping in a half-extended position, like that of *Omiodes* (*Hedylepta*) spp., or for that matter of many species of Pyraustinae. The biological significance of this will be discussed in the next section.

## CATACLYSTIFORM PATTERNS IN THE CRAMBIDAE

I coin the term cataclystiform to denote wing patterns similar to that of the well-known European nymphuline Cataclysta lemnata (Linnaeus 1758), characterized by a row of black spots with contrasting white, blue, or metallic pupils or interspaces on or near and parallel to the terminal margin of the hind wing. Frequently, but not always there is an array of wedge-shaped stripes radiating from the tornus to the distal part of the costa of the forewing. In the Nymphulinae such patterns are found in the tribe Nymphulini in such genera as Neocataclysta Lange, 1956, and Chrysendeton Grote, 1881, probably evolved independently of each other and of Cataclysta. They occur also in the Argyractini in numerous species of Petrophila Guilding, 1830, and related genera, in ecologically similar but probably taxonomically removed Old World genera such as Eoophyla and Margarosticha Lederer, 1863, and in more bizarre Nymphulinae such as Cryptocosma Lederer, 1863. These and other Nymphulinae must represent at least several parallel origins of cataclystiform patterns, building on similar fundamental elements.

It is well known that similar patterns occur in other subfamilies. In the Glaphyriinae the genera Dicymolomia Zeller, 1872, and the related Chalcoela Zeller, 1872, are examples, to which can be added Cosmopterosis Amsel, 1956; Aureopteryx Amsel, 1956; and Heptalitha Munroe, 1964, among others. In the Pyraustinae, certain species of Talanga Moore, 1885, were placed in Nymphulinae near Eoophyla, until Janse (1935) showed their relationship to species of Glyphodes Guenée, 1854, and allied genera. Marasmianympha eupselias provides another example in the Pyraustinae, and more can probably be added in this and other subfamilies.

So widespread and distinctive a pattern can be expected to have a biological meaning, but

we can only speculate as to what it is. There seems no doubt that the contrasting and often shining marginal spots have the function of attracting visual attention. In Nymphulinae and Glaphyriinae at least, the termen of the hind wing is often held in a somewhat elevated position, so that the spots show to advantage. I had supposed that *M. eupselias* might raise its hind wings in the same way; however, Montgomery and Gagné specifically looked for this behavior but did not observe it. The forewing stripes converging on the tornus make one think of the well-known "backward" or "false head" patterns of many butterflies and some moths, which direct the aim of predators to nonvital parts of the insect. The moths seem too small to be flashing alarming eyelike patterns to discourage predators, but Dr. L. Orsak (pers. comm.) suggests that *Eoophyla* and *Talanga* spp. may be mimics of jumping spiders, a possibility he is investigating in the field in Papua New Guinea.

It should be noted that there are no other good examples of the cataclystiform pattern in the Marquesas, or indeed in any other islands closer than Samoa and Fiji, where several species of Nymphulinae have it. I except a recently introduced species of *Usingeriessa* Lange, 1956, a nymphuline genus related to *Petrophila*, in Hawai'i. There is a species of *Talanga* in the Marquesas, but it is not closely related to the cataclystiform species and it has only rudiments of such a pattern, though it could well be interpreted as having a "backward" pattern. We can therefore exclude at least interpyraloid mimicry in trying to explain the cataclystiform pattern of *Marasmianympha*. However, the pervasive occurrence of cataclystiform patterns, not only in the tropical continents and continental islands, but also in the more humid parts of the temperate zones, suggests a phenomenon of wide biological interest, and one that deserves attention from ethologists and evolutionary biologists.

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