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REVISION OF THE EUPTYCHIINI (SATYRIDAE)

1. Introduction and Paramacera Butler

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INTRODUCTION

At the time of my revision of the higher categories of the Satyridae (Miller, 1968) it became apparent that the Euptychiini as so defined were badly in need of a modern comprehensive treatment. The last attempt at an arrangement of all of the species within the tribe was that of Weymer (1910-1911), but his work was little more than a compilation of the species which had been described to that time and was of little more value in the understanding of the euptychiines than various papers by Butler (1866, 1867, 1868a, 1868b). Forster (1964) substantially altered taxonomic thought on the relationships of those species previously included in *Euptychia* and *Taygetis*, describing many new genera and a few species. His work, unfortunately, was by no means complete and was concerned chiefly with the Bolivian species.

This paper begins a series which will lead eventually to a monograph of the Euptychiini as defined by Miller (1968). The sheer volume of names available in the tribe (nearly a thousand species-group names have been proposed) precludes a single volume revision, if one is to make a comprehensive study. Individual papers will appear as they become available on a genus-by-genus basis, without regard to their final systematic positions within the tribe. The final paper in the series will provide a checklist for the Euptychiini and the intergeneric phylogenetic relationships, if such become apparent. For several reasons those genera that impinge on the North American fauna will be among the first considered, with the wholly Neotropical genera reserved for later treatment, generally. The primary reason for dealing with the North American species and their Neotropical congeners first is to make the results available to my colleagues in this country as soon as possible. There are a limited number of well-defined euptychiines in the United States and Canada, and with one exception these species belong to quite distinctive Mexican and Central American genera. Furthermore, enough material is available in collections in this country to do meaningful revisionary work on these genera.

By contrast, many groups of wholly Neotropical euptychiines are very poorly represented in our collections, and a great deal of material from foreign collections will have to be examined in the future. Many taxa within the tribe have been consistently misidentified and the names misapplied in the literature, based on the early work, so the types of these species, almost all in European collections, must be consulted before the chaotic nomenclature can be untangled. In other instances, hopefully fewer than I fear, the type specimens have been lost or destroyed, and neotypes will require designation, but this can be done only when the nonexistence of authentic type material has been ascertained.

The genera and their associated species will be described in detail and pertinent aspects illustrated where possible. Citations of the original descriptions, type-localities and the present location of the types will be given. Distributional data will be given for the material examined, and where possible and desirable these data will be plotted on maps. Each genus will have a key to its species, and where species are comprised of more than one subspecies, keys will be provided for the discrimination of these taxa. In the final paper in the series a key to the genera of the Euptychiini will be given.

In the future, as additional material and information become available, "Addenda and Corrigenda" sections will be appended to papers referring not to the paper at hand, but to previous papers in the series. Such sections will appear irregularly as necessary.

With the exception of the usual male (♂) and female (♀) symbols, only one set of abbreviations will appear in the text. The source of material will be abbreviated: for the present paper the following institutional and private collections have provided material examined and are abbreviated as:

- Allyn Museum of Entomology and the associated private holdings of A. C. Allyn -- (A).
- American Museum of Natural History, New York, N. Y. -- (AMNH).
- Carnegie Museum, Pittsburgh, Pa. -- (CM).
- Private collection of Eduardo C. Willing M., Merida, Yucatan, Mexico -- (ECW).
- Private collection of Kilian Roever, Phoenix, Ariz. -- (KR).
- Los Angeles County Museum, Los Angeles, Calif. -- (LACM).
- National Museum of Natural History, Washington, D. C. -- (USNM).

The genus *Paramacera*, an aberrant member of the tribe known only from Mexico and the southwestern United States, is a convenient one with which to begin the revision of the tribe. Additionally, the nomenclatorial problems associated with *Paramacera* illustrate the problems inherent in the study of the Euptychiini as a whole: too long erroneous identifications and designations have been passed uncritically from author to author.

Paramacera Butler, 1868

Paramacera Butler, 1868a: 194. Type-species: *Neonympha xicaque* Reakirt, 1867 ["1866"]: 336-337, designated by Scudder, 1875: 240.
 =*Paramecera* Butler, 1868b: 98. Type-species: *Neonympha xicaque* Reakirt, 1867 ["1866"]: 366-337, by monotypy.

As noted by both Scudder (1875: 240) and Hemming (1967: 340), Butler referred to, but did not describe, a manuscript specific name for the type of *Paramacera*. Nothing would be gained by resurrecting this name at this time, inasmuch as two specific names already have priority over it. The generic name *Paramecera* was proposed as new, not as an emendation of *Paramacera*, a few months after the latter name's proposition, hence, *Paramecera* should fall as a junior objective synonym of *Paramecera*. Various correspondents have pointed out that since *Paramecera* was compared with the genus *Amecera* Butler in the original description that perhaps *Paramacera* was the result of a typographical error. Furthermore, since the descriptions in Butler's *Catalogue* (1868b) are more detailed, it seems likely that Butler intended that paper to be the vehicle of description, rather than the brief paper in *Entomologists' Monthly Magazine* (Butler, 1868a) which actually appeared first. These correspondents may be right, but the fact remains that both generic names were proposed as new, and Butler actually designated two different, though now known to be synonymous, type-species for them. Those writers who have subsequently mentioned the genus, including

Godman and Salvin (1879-1901), Weymer (1910-1911), Holland (1931), Hoffmann (1940), dos Passos (1964) and Miller (1968), almost without exception have used "*Paramacera*", and if the spellings of the generic names in question were markedly different, Hemming's (1967: 340) validation of *Paramacera* would be open to question. Such is not the case, however; the spellings of the two names in question are similar and the pronunciations virtually the same, so there is no reason for *not* retaining the name with priority for this genus.

Superficially *Paramacera* resembles a number of Palearctic Maniolini, but structurally (especially in the form of the ♀ foreleg, the venation, etc.) members of the present genus are definitely euptychiines (Miller, 1968: 89-95). The "*Euptychia*" *paeon* (Godart) group of Euptychiini from the southern Neotropics resemble *Paramacera* superficially, but these austral insects are very different genitally and are certainly not congeneric with the northern ones. The present genus is characterized as follows:

Eyes sparsely hairy. Antennae about two-fifths length of forewing costa; club occupying distal quarter of antenna and about three times width of shaft at widest point. Palpi (Miller, 1968: fig. 207) long and more or less erect, second segment about three times length of third; hairs of palpi up to three times width of second segment.

Thorax heavily clothed with long hairs above and below. ♂ foreleg (Miller, 1968: fig. 208) reduced and slender with a monomerous, unspined tarsus. ♀ foreleg also reduced and slender than in most Euptychiini with pentamerous tarsus spined on first four subsegments (Miller, 1968: fig. 209). Mid- and hindlegs short, bearing terminal tibial spurs on both.

Wing venation (Miller, 1968: fig. 206) basically like that of most Euptychiini, but with an unusually large androconial patch outside forewing cell, beginning in anal cell, broadest in Cu_2-2A and narrowing toward M_3-Cu_1 (occasionally with small satellite patches in M_1-M_2 and M_2-M_3); forewing radius three-branched (two-branched in most Euptychiini). Forewing margin produced at apex in *P. chinanteca*, n. sp., less so in other species; hindwing margin scalloped, especially in *P. chinanteca*.

♂ genitalia with shield-like tegumen, long, slightly curved, undivided uncus and paired, tapered gnathoi which are not freely articulated. Saccus short. Valvae laterally bowed and slender, bearing teeth at distal end. Penis relatively straight and simple.

♀ genitalia relatively simple in the two species in which these structures are known and similar to one another. Ductus bursae somewhat more sclerotized than in many Euptychiini.

Four species are recognized in this genus, three of which are new. These butterflies are found from eastern Arizona to southern Mexico, but the populations are isolated and generally restricted to mesic or xeric montane habitats. The species prefer rather open coniferous grasslands; the larvae are no doubt grass feeders, though nothing is known of the life-history to my knowledge. A key to *Paramacera* follows:

KEY TO THE SPECIES OF *Paramacera* BUTLER

1. Upper surface of forewing without ocelli, or at most a small one in M_1-M_2 ; Oaxaca, Mexico *chinanteca*, n. sp.
- 1'. Upper surface of forewing with ocelli in M_1-M_2 and M_3-Cu_1 , occasionally with a subsidiary spot in M_2-M_3 2.
2. Upper surface of forewing with large, *black* androconial patch; under surface of hindwing with pale discal band terminating before costa and ocelli in hindwing spaces M_1-M_2 and M_2-M_3 silvered without black irises; Oaxaca, Mexico *copiosa*, n. sp.
- 2'. Upper surface of forewing with more nearly concolorous androconial patch; under surface of hindwing with pale discal band continuing to costa and hindwing ocelli in M_1-M_2 and M_2-M_3 below with black irises 3.
3. Upper surface of hindwing with marginal and submarginal lines reddish-brown from anal angle to at least M_3 ; Mexico *xicaque* (Reakirt)
- 3'. Upper surface of hindwing with marginal and submarginal lines fuscous (rarely reddish-brown only at anal angle); Arizona and Chihuahua, Mexico *allyni*, n. sp.

Paramacera chinanteca, new species

Figures 1, 2 (♂), 3, 4 (♀), 5 (♂ genitalia)

Male: Head, thorax and abdomen clothed with olive-brown hairs above, dark grayish ones below. Palpus black, white at tip. Antenna brown ringed narrowly with buff above, buff narrowly ringed with brown below; club brown above, buff below with tip blackish-brown. Legs clothed with long black hairs proximad, shorter buff ones on tibia and tarsus.

Forewing above olive-brown, fuscous along margin, with androconial patch only slightly darker than ground color and with no ocelli present.

Hindwing above olive-brown, slightly darker than that of forewing, with fuscous marginal and submarginal lines, minute dark brown blind ocelli from M_1 - M_2 to Cu_1 - Cu_2 , dark extradiscal zigzag band, shaded rust-brown basad, and brown patches mid-costa and marginally in $Sc+R_1+R_2$.

Forewing below as figured: warm tan, darker basally, with two straight rust-brown median bands, two dark brown marginal lines, a crenulate submarginal brown line and very small blind blackish ocelli with narrow brown rings from M_1 - M_2 to M_3 - Cu_1 .

Hindwing below as figured: base dark brown peppered with white scales, median band warm tan spotted with reddish-brown, extradiscal areas shaded purplish and marginal and submarginal lines dark brown, reddish-brown at anal angle.

Fringes of forewing above and below broadly fuscous at tends of veins, narrowly white in interspaces. Fringes of hindwing above and below white, rather broadly fuscous at ends of veins.

Length of forewing of Holotype ♂ 19.5 mm., that of the single ♂ Paratype 21.0 mm.

♂ genitalia as figured, differing from those of other members of genus particularly as regards configuration of tip of valva.

Androconial patch less well-defined than in other species because distribution of androconial scales far less dense within patch and those present scattered among regular scales. Shape of scale as in other species, but shorter than that of *P. copiosa*.

Female: Head, thorax, abdomen (what was remaining) and appendages as in ♂.

Upper surface as in ♂, but forewing extradiscal area much paler and bearing a very small blind brown ocellus in M_1 - M_2 ; hindwing ground color paler than in ♂ with markings more prominent and brown mid-costal patch only vaguely indicated.

Under surface also as in ♂, but extradiscal area of forewing much paler.

Lengths of forewings of three ♀ Paratypes 21.0, 21.0 and 22.0 mm.

The females all lacked at least distal portion of abdomen, so ♀ genitalia unknown.

Described from five specimens, two males and three females, from the high mountains of Oaxaca, Mexico.

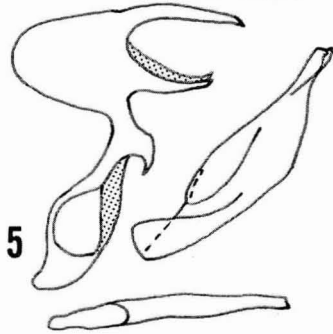
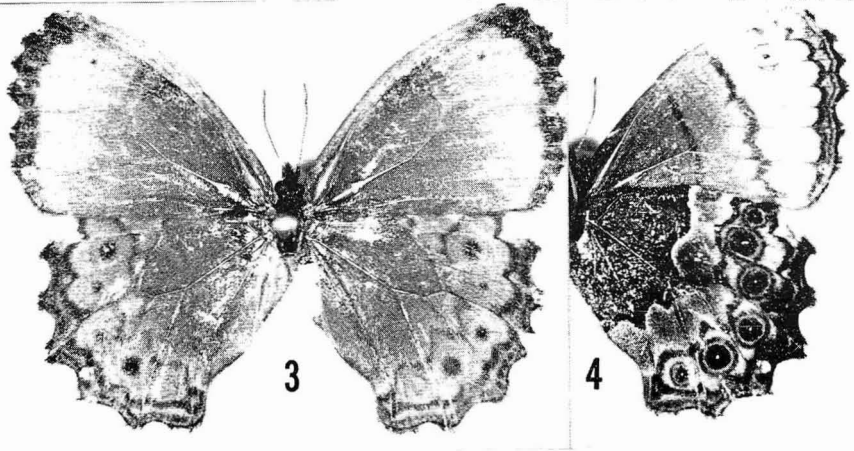
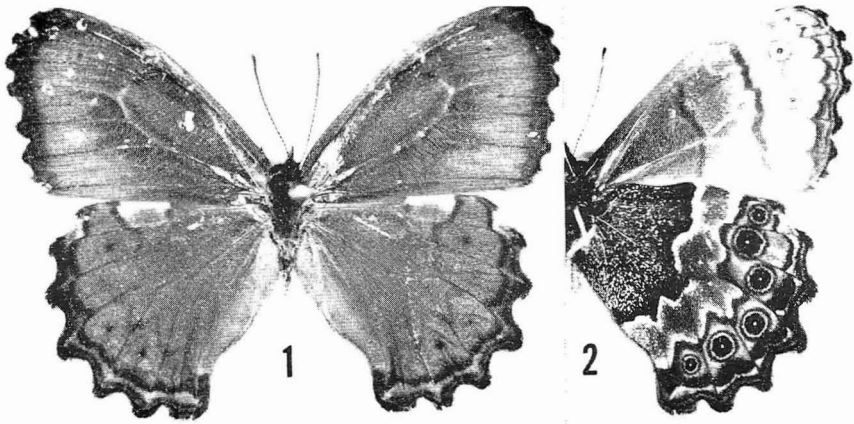
HOLOTYPE ♂: MEXICO: OAXACA: Muo Cuóu (Cerro Pelon), Mpio. Yolox, 3000 m., 17.ix.1962 (E. C. Welling).

PARATYPES: Same locality as Holotype: 1♀ 12.ix.1962, 1♀ 17.ix.1962, 1♂ (♂ genitalia slide no. M-2232, Lee D. Miller) 1♀ 18.ix.1962 (all E. C. Welling).

Disposition of type material: Holotype and ♂ Paratype (A), three ♀ Paratypes (ECW).

The specific name refers to the Chinantec tribe which inhabits the Sierra Chinantla, Oaxaca, from whence the types came.

This very striking species seems to tie *Paramacera* to more "conventional" Euptychiini through the basic lack of an upper surface pattern, especially the usual *Paramacera* large blind forewing ocelli on the upper surface. On the under side, however, *P. chinanteca* is unmistakably a member of *Paramacera*, and its genitalia are remarkably similar to those of the other three species in the genus. On the basis of the more generalized upper surface pattern and the more diffuse androconial patch I consider *P. chinanteca* to be the most primitive member of *Paramacera*. Both it and the somewhat primitive *P. copiosa* seem to be restricted to small, relict populations in the high mountains of Oaxaca, not far from populations (much larger ones, incidentally) of the widespread *P. xicaque*.



Figures 1-5, *Paramacera chinanteca*, new species. 1-2, Holotype ♂ upper (1) and under (2) surfaces; MEXICO: OAXACA: Muo Cuóu (A). 3-4, Paratype ♀ upper (3) and under (4) surfaces; MEXICO: OAXACA: Muo Cuóu (ECW). 5, ♂ genitalia of Paratype (slide M-2232) (A).

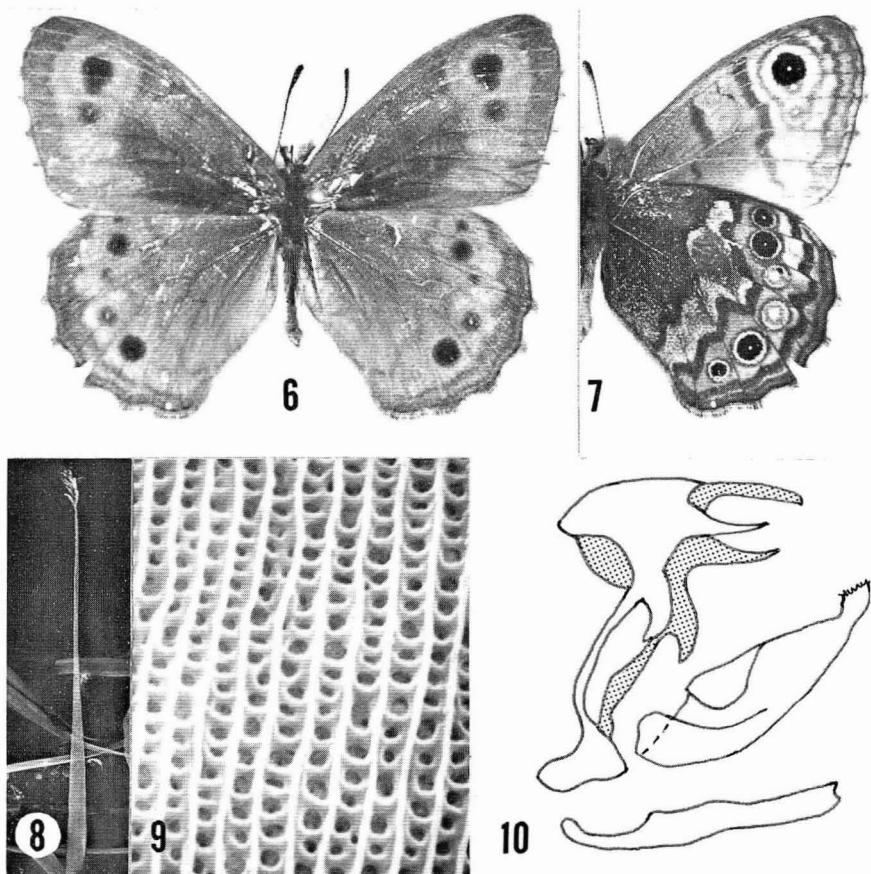
***Paramacera copiosa*, new species**

Figures 6,7 (♂), 8, 9 (androconial scales), 10 (♂ genitalia)

Male: Head, thorax and abdomen clothed with olive-brown hairs above, dark gray ones below. Antenna brown narrowly ringed with yellow above, more widely ringed with yellow below; club brown above, buff below, dark brown at tip. Palpus smoky-black, white laterally. Legs with long smoky-black hairs.

Forewing above olive-fuscous, somewhat darker in cell, with dark fuscous margin, two coalesced dull brown blind ocelli in M_1-M_2 (much the larger) and M_2-M_3 and an indistinct brown ocellus in M_3-Cu_1 ; androconial patch dark gray-black extending outside cell from anal cell to M_3-Cu_1 with a relatively straight distal margin.

Hindwing above olive-fuscous, hairs at base slightly darker, with dull brown blind extradiscal ocelli from $Sc+R_1-R_s$ to Cu_2-2A (those in $Rs-M_1$ and Cu_1-Cu_2 being the largest and most prominent, that in Cu_2-2A being very faint and that in M_3-Cu_1 bearing a small buff pupil); marginal and submarginal lines



Figures 6-10, *Paramacera copiosa*, new species. 6-7, Holotype ♂ upper (6) and under (7) surfaces; MEXICO: OAXACA: Muo Cuóu (A). 8, androconial scale, approx 165 ×. 9, interrib structure of same scale, approx. 6650 ×. 10, ♂ genitalia of Holotype (slide M-2338) (A).

dull brown anterior of Cu_1 , shading reddish-brown to anal angle.

Forewing below as figured: reddish-tan, darker basad and gray along inner margin, with two thick reddish-brown median lines, one across cell, the other relatively straight from M_1 just outside cell to 2A near anal angle; three white-pupilled black ocelli from M_1-M_2 to M_3-Cu_1 (the one in M_1-M_2 much the larger and with thick black iris) with yellow and reddish-brown rings; two marginal and a slightly dentate submarginal reddish-brown lines and a gray shade between submarginal band and rings of ocelli from R_4-R_5 to M_1-M_2 .

Hindwing below as figured: brown peppered with gray scales at base, tan central band (grayish-brown in cell) bounded on either side by reddish-brown bands and *not* continuous to costa, area enclosing ocelli grayish-violet with black, white-pupilled ocelli in $Rs-M_1$, M_1-M_2 , Cu_1-Cu_2 and Cu_2-2A and silvery-white ocelli in M_2-M_3 and M_3-Cu_1 , all with yellow and reddish-brown rings, and two marginal and one submarginal reddish-brown lines meeting at anal angle.

Fringes above pale buff, dull brown between veins (more narrowly on forewing); fringes below pales gray, brown at ends of forewing veins, dark gray at ends of hindwing veins.

Length of forewing of Holotype ♂ 21.0 mm., that of single ♂ Paratype 20.0 mm.

♂ genitalia as figured, differing from those of other species in *Paramacera* chiefly in broader valva with different terminal ornamentation and having more pronounced sacculus.

Androconial scales longer than those of other species, but with similar general appearance. Androconial mass with denser concentration of androconial scales than in *P. chinanteca* - in this more closely approximating situation in other two species.

Female: Unknown.

Described from two specimens, both males, from the high mountains of Oaxaca, Mexico.

HOLOTYPE ♂: MEXICO: OAXACA: Muo Cuóu (Cerro Pelon), Mpio. Yolox, 3000 m., 9.v.1962 (E. C. Welling); ♂ genitalia slide No. M-2338 (Lee D. Miller).

PARATYPE ♂: Same data as Holotype.

Disposition of type material: Holotype (A), ♂ Paratype (ECW).

P. copiosa is a more "conventional" *Paramacera* but can be distinguished immediately by the silvery-white ocelli without black irises in M_2-M_3 and M_3-Cu_1 on the under surface of the hindwing. The dull diffuse pattern of the upper surface gives the species its name and is characteristic when compared with the *xicaque* group. Whereas the upper surface pattern is reminiscent of the of *P. xicaque*, the heavy, rather straight extradiscal band of the forewing beneath and the general appearance of the surface on both wings suggests an affinity with *P. chinanteca*. It is curious that both *P. copiosa* and *chinanteca* have been found only at Muo Cuóu to date, but while they share a common locality, the collection dates suggest that the two species may be temporally isolated. The two species appear to be the most primitive in the genus.

Paramacera xicaque (Reakirt), 1867 ["1866"]

This species is restricted to Mexico, having its metropolis in the Valle de México, extending northward to at least northern San Luis Potosí and southward to at least Oaxaca. Our experience would indicate that this butterfly is restricted to localized populations in open woodlands, often many miles from the next population. It is therefore not surprising that some subspeciation has taken place, perhaps more than I am recognizing.

There is some question about the use of the name *xicaque* for this species, as well be discussed under the nominate subspecies, but Reakirt's name is maintained here in the interest of nomenclatorial stability.

Two subspecies are currently recognized within *P. xicaque*, but there is evidence that at least one more may be separable when more material becomes available for study. The females are more variable than are the males.

KEY TO THE SUBSPECIES OF *Paramacera xicaque* (REAKIRT)

1. Hindwing extradiscal spot in M_1-M_2 elongate, tapering distad; all ocelli on upper surface very much enlarged, especially in ♀; Oaxaca, Mexico *P. xicaque rubrosuffusa*, n. ssp.
- 1'. Hindwing extradiscal spot in M_1-M_2 rounded or slightly oval, not

tapering distad; ♀ with spots normally developed

..... *P. xicaque xicaque* (Reakirt)

Paramacera xicaque xicaque (Reakirt), 1867 ["1866"]

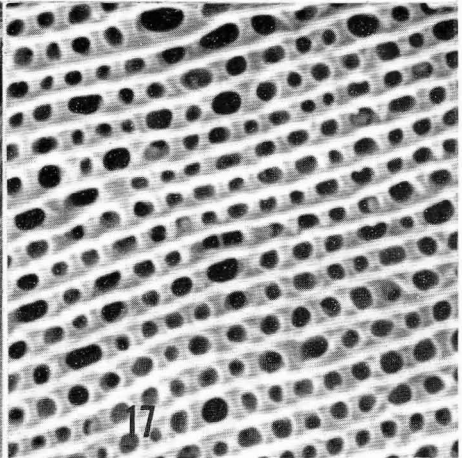
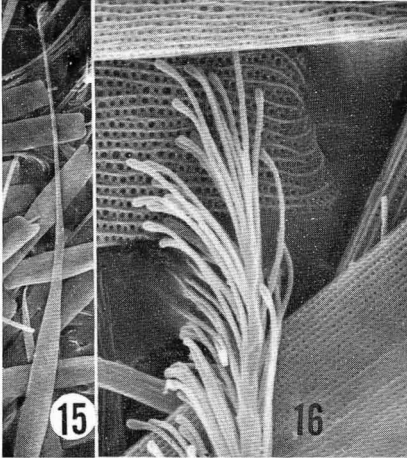
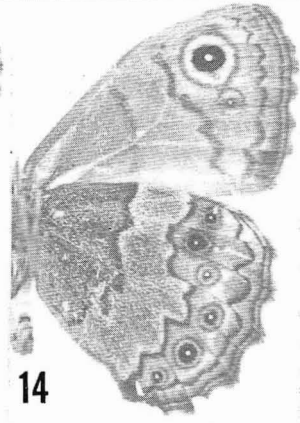
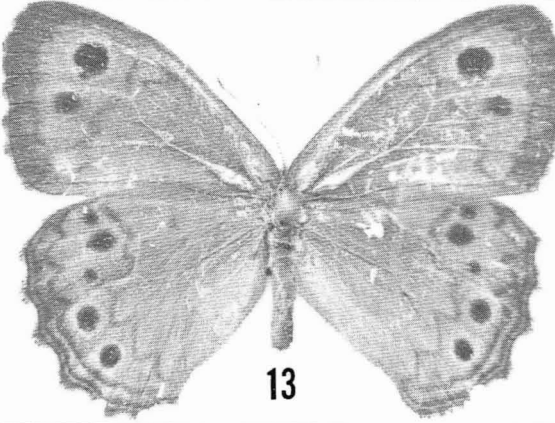
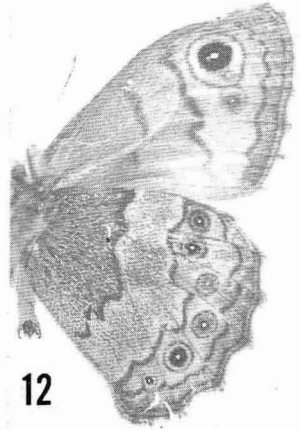
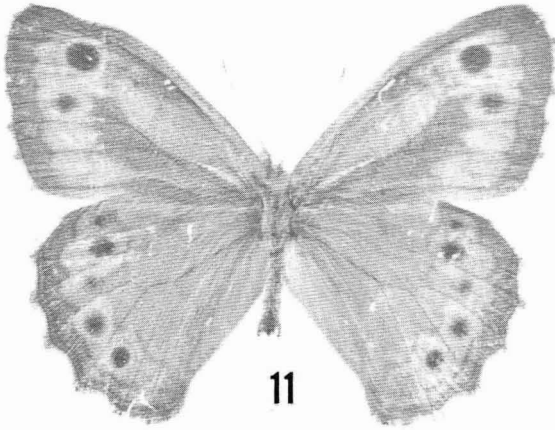
Figures 11, 12 (♂), 13, 14 (♀), 15, 16, 17 (androconial scales), 18 (♂ genitalia), 19 (♀ genitalia)

Neonympha xicaque Reakirt, 1867 ["1866"]: 336-337. Type-locality: "nr. Vera Cruz, Mexico". Type apparently lost: see notes below.
= *Neonympha epinephele* C. & R. Felder, 1867 [1864-1867]: 476. Type-locality: "Mexico". Type in British Museum (Natural History), ex Rothschild Bequest.

A certain amount of confusion surrounds the proper name to be applied to this species. The "1866" volume of *The Proceedings of the Academy of Natural Sciences of Philadelphia*, as is so often the case, was published partly during the year it represented and partly during the following one. The description of *Neonympha xicaque* Reakirt (1867 ["1866"]: 336-337) was published entirely in 1867 (A. N. S. P., 1913: xii), according to the only dates available, those of receipt of the parts by the library of the U. S. National Museum, Washington, D. C. Pages 280-336 of the *Proceedings* for "1866" were published sometime before 13 February 1867, and page 337 to the end of the volume were mailed sometime before 10 July 1867. These dates splitting Reakirt's description of *P. xicaque* are of significance since the Felder brothers described *Neonympha epinephele* in the third part of the "*Reise Novara*" which was specifically dated March, 1867, between the two parts of Reakirt's description! Articles 10-12 of the *International Code of Zoological Nomenclature* imply that the name *xicaque* could only become available after all the relevant criteria for availability were met: the major point that seems in question is whether or not the part of the description on p. 336 is sufficient to qualify the February, 1867, date as the date of publication of the name. If the description is complete enough on p. 336, then *xicaque* is legitimately the senior synonym; if the description did not provide a sufficient "indication" until July, 1867 (p. 337), then technically *xicaque* should fall to the Felders' name. The superficial character which best separates *P. xicaque* from *P. allyni* is the presence of the reddish-brown marginal and submarginal lines on the upper surface of the hindwing, and here too a problem develops. These lines are mentioned in Reakirt's original description as follows: "... [page 336] the margin presents three continuous red-brown / [page 337] lines obscured by a darker shade towards the apex ..." Therefore, the criterion of a "definition" is only partly satisfied in that part of the description published in or before February, 1867. The entire description of the under surface and the designation of the type-locality were given on p. 337. No figure was provided. The very controversial "Fifty-Year Rule" (Int. Code Zool. Nomen., 1961: Art. 23b) could be applied conveniently to suppress *epinephele*, but there is a strong possibility that this rule may be written out of the "Code" in the very near future.

There is some evidence that Reakirt may have distributed preprints of his article well before the complete publication of it in July, 1867. F. M. Brown (1964, 1965) has dealt with this phenomenon of the early distribution of preprints and accepts the date of preprint distribution as the date of publication. Ultimately the International Commission on Zoological Nomenclature must rule definitively on this subject. Recognition of a preprint date earlier than March, 1867, gives *xicaque* clear priority over *epinephele*; rejection of preprint dates gives *epinephele* priority under a strict interpretation of Articles 10 and 16 of the "Code" (Int. Code Zool. Nomen., 1961). This latter course, of course, would tend to upset the stability of nomenclature with regard to this species (such stability is an avowed aim of the "Code"): *epinephele*, when recognized as a synonym of *xicaque* has invariably been placed in the synonymy of *xicaque*. Suppression of the name *xicaque* in favor of the Felders' name would have a destabilizing effect on the nomenclature, hence, the retention of Reakirt's name in this paper.

Figures 11-17, *Paramacera xicaque xicaque* (Reakirt). 11, 12, ♂ upper (11) and under (12) surfaces; MEXICO: "Dept. Fed." (CM). 13-14, ♀ upper (13) and under (14) surfaces; MEXICO: HIDALGO: 5 mi. NE Zimapán (A). 15, androconial scale, approx. 230 × 16, detail at tip of same scale, approx. 2,000 ×. 17, interrib structure of same scale, approx. 6650 ×.



A redescription of nominate *P. x. xicaque* follows:

Male: Head, thorax and abdomen blackish-brown clothed with olive-brown hairs above, gray-brown ones below. Palpus dark brown above, gray-brown below. Antenna brown above, narrowly ringed with cream, cream below; club brown above, cream below, blackish at tip. Legs clothed with grayish-brown hairs, tan ones distally.

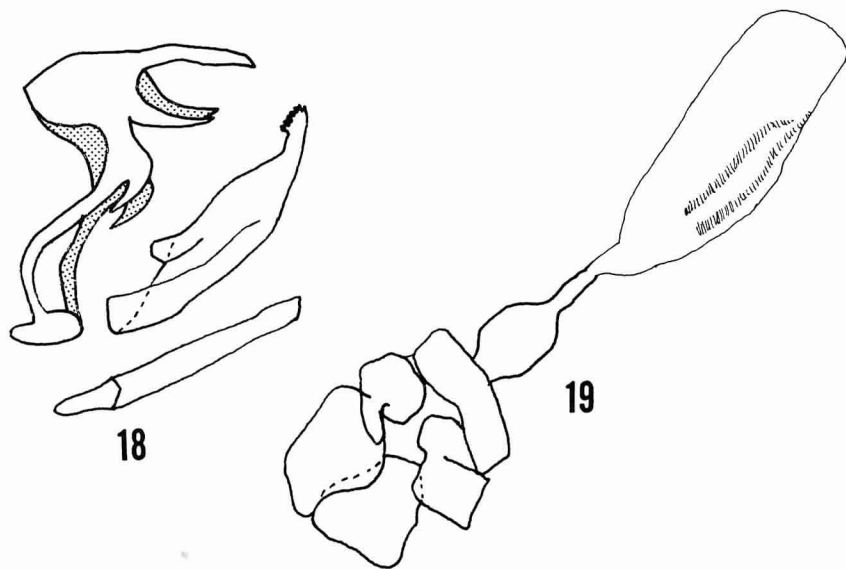
Forewing above olive-brown with costa and margin brown, a dull, slightly darker androconial patch continuous outside cell from anal cell to M_3-Cu_1 , thence broken to vein M_1 , and at least a dark brown ocellus in M_1-M_2 (usually one in M_3-Cu_1 , occasionally a small one in M_2-M_3).

Hindwing above olive-brown, darker basally and often slightly red-tinged in extradiscal areas, with at most six extradiscal brown spots from $Sc+R_1-Rs$ to M_3-Cu_1 (those in $Sc+R_1-Rs$ and M_1-M_2 often wanting) and with marginal fuscous area resolving basad into three distinct red-brown lines from at least M_2-M_3 to anal angle.

Forewing below reddish-tan, darker costad and grayish apically, with two prominent red-brown lines, one across middle of cell, the other arising near origin of Rs and proceeding posteriad toward anal angle, two straight marginal and one crenulate submarginal brown lines, grading to red-brown near anal angle (submarginal line sometimes joining outer extradiscal band near anal angle), and bearing a well-developed black ocellus with white pupil in M_1-M_2 and smaller ones in M_2-M_3 and M_3-Cu_1 surrounded by tan patch delimited by red-brown ring (occasionally with separate ring around ocellus in M_3-Cu_1).

Hindwing below basally dark brown grizzled with gray, then two zigzag red-brown bands from costa to inner margin across and outside cell enclosing a buff central area broadly overscaled with gray, then a grayish-tan distal area with a slight violet sheen enclosing six black ocelli with white pupils and tan then red-brown rings from $Sc+R_1-Rs$ to Cu_1-Cu_2 (those in $Rs-M_1$ and M_3-Cu_1 the largest), with a heavy irregular dentate red-brown submarginal line connecting at anal angle with extradiscal band and two wavy red-brown marginal lines.

Fringes white above, checkered with brown at ends of veins, tan below with brown checkering at ends of veins.



Figures 18-19, genitalia of *Paramacera xicaque xicaque* (Reakirt). 18, ♂ genitalia (slide M-2102); MEXICO: HIDALGO: vic. El Encarnación (A). 19, ♀ genitalia (slide M-1981); MEXICO: "Dept. Fed." (CM).

Lengths of forewings of ♂ specimens at hand range from 19 to 22 mm., and most specimens have forewing lengths between 20 and 21 mm.

♂ genitalia as figured and distinguished from those of the relatively close *P. allyni* particularly by the relatively shorter uncus (less than half combined length of uncus + tegemen) and the distally broader valva.

Androconia in a compact patch with dense concentration of androconial scales. Scales not so long as those of *P. copiosa* and not easily separable from those of *P. chinanteca* or *P. allyni*, although the interribs of *P. allyni* are broader and those of *P. chinanteca* not so broad as in *P. xicaque*.

Female: Upper surface similar to that of ♂, but with no androconial patch; ground color somewhat paler and extradiscal spots larger than in ♂. Females from Hidalgo are extensively laved with reddish both without and within forewing cell and extradiscally on hindwing; this color only faintly indicated in females from other *P. x. xicaque* populations examined.

Under surface similar to that of ♂.

Lengths of forewings of specimens examined range from 17 to 23 mm., most being between 20.5 and 22 mm.

♀ genitalia as figured and differing from the very similar *P. allyni* genitalia by the broader ductus bursae.

64 male and 35 female specimens have been examined representing this subspecies from the following localities, all in Mexico:

SAN LUIS POTOSÍ: El Salto, viii, 1♂ (A).

HIDALGO: 5 m. NE Zimapán, 1980-2140 m., i, ii, 11♂ 10♀ (A); vic. El Encarnación, 2400-2500 m., i, ii, 12♂ 16♀ (A).

MICHOACAN: Tancitaro, 660', vii, 1♂ (A).

DISTRITO FEDERAL: Desierto des Laones, mr. La Venta, 7800-8000', vi, 1♂ (AMNH); Desierto, iii, 3♂ 1♀ (AMNH); Popocatepetl Park, 9500-11,500', vi, 4♂ (USNM); "Dept. Fed.", v, x, xii, 14♂ 3♀ (CM)

MORELOS: Barranca des Lobos, ix, 1♀ (A).

PUEBLA: Manzanilla, ix, 3♂ 1♀ (AMNH).

VERACRUZ: Jalapa, 8♂ 3♀ (AMNH, USNM); Misantla, 1♂ (USNM).

"MEXICO": ix, 2♂ (A).

no locality: 3♂ (USNM).

The type specimen of *P. x. xicaque* appears to be lost. I have checked the collections in which it might be expected to be housed and have found no specimen that might qualify as the type. The stated type-locality -- "near Vera Cruz" -- is a most unlikely one, unless one interprets "near Vera Cruz" very broadly; the town of Veracruz (present spelling) is situated on the Gulf of Mexico at sea level, and *P. x. xicaque* is a montane, or at least foothill, insect throughout its range. Harry Clench (*in litt.*) informs me that he has been able to trace the sources of some of the material that Reakirt used in his "1866" paper, and at least some of these specimens were sent to William Henry Edwards (and ultimately to Reakirt) by a collector who resided at Orizaba, Veracruz. In all likelihood the type of *xicaque* came from this lot of specimens, and the collector might well have labelled the specimens from the state in which he lived, Veracruz. The type of this species, and several others named in the same paper, probably came from the area of a triangle bounded by Jalapa and Orizaba, Veracruz, and Puebla, Puebla, quite probably from the flanks of Mt. Orizaba. There are no recent specimens from the Veracruz side of the Veracruz-Puebla border with adequate data that have come to my attention: if such specimens are extant, they are fine candidates for designation as the neotype of this species. Until such specimens are located and a definitive type-locality can be designated, it seems inadvisable to create a neotype of *xicaque*.

We have taken this butterfly in wooded montane habitats, both very dry as northeast of Zimapán and mesic as near El Encarnación, in Hidalgo. These two localities are discussed in some detail by Miller and Miller (1970) and Clench (1971).

The flight of these insects is erratic and near the ground, usually in or near the underbrush. They are rather nervous and difficult to approach, but their flight is weak enough to make capture on the wing easy. The butterflies will "sun" themselves, especially in the early morning, by alighting on the ground with the wings held upright and oriented so that sunlight gets maximum intensity on one side or the other; the insects will walk around on the ground, turning about until they achieve the optimum position with regard to the sun.

The ruddy upper surface and very dark under surface of the Hidalgo specimens suggest that these insects might represent another subspecies, but the material from other localities in the Valle de México is generally somewhat faded, and at least some of the differences noted may be those of fresh *vs.* worn specimens. Material from either side of the Hidalgo populations, from El Salto, San Luis Potosí, to the northeast and from Distrito Federal to the southwest, are almost indistinguishable. The presence in Hidalgo of a subspecies surrounded on all sides by the nominate one, while not impossible, is somewhat less than likely.

The present species is distinguished from the more northern *P. allyni*, described below, by the very prominent red-brown marginal and submarginal lines on the hindwing above extending from at least M_1-Cu_1 to the tornus in even worn specimens; these lines are either totally fuscous or only faintly reddened in the tornal area in *P. allyni*. There are also genitalic differences which may be seen in comparison of the figures of the terminalia of both species (Fig. 18 - *xicaque*; Fig. 28 - *allyni*). Additionally, the northern insect is superficially larger and duller than is *P. xicaque*.

Specimens from the most southerly population thus far examined, from the mountains of eastern Oaxaca, are distinct and are described below.

***Paramacera xicaque rubrosuffusa*, new subspecies**

Figures 20, 21 (♂), 22, 23 (♀)

Male: Upper surface differs from that of nominate *xicaque* in the less olive ground color, the extradiscal area of the forewing and most of the hindwing strongly reddened and by the hindwing extradiscal spot in M_1-M_2 elongated distad. Beneath the ground color of the hindwing is paler and the hindwing extradiscal spots larger than in the nominate subspecies.

♂ genitalia as in *P. x. xicaque*, but the uncus is straighter; androconia as in the nominate subspecies.

Length of forewing of Holotype ♂ 21.0 mm., those of the 134 ♂ Paratypes ranging from 18.0 to 22.5 mm., most having forewing lengths between 21.0 and 21.5 mm.

Female: Redder above than any nominate ♀ *xicaque* with a better defined, broader chocolate-brown forewing margin and much larger extradiscal spots on both wings with one in hindwing space M_1-M_2 elongated distad. Forewing beneath redder than in nominate subspecies, hindwing paler and all extradiscal ocelli larger in present subspecies.

♀ genitalia indistinguishable from those of *P. x. xicaque*.

Lengths of forewings of the 52 ♀ Paratypes ranging from 21.0 to 24.5, most being between 22 and 23 mm.

Described from 187 specimens, 135 males and 52 females, from the mountains of Oaxaca, Mexico.

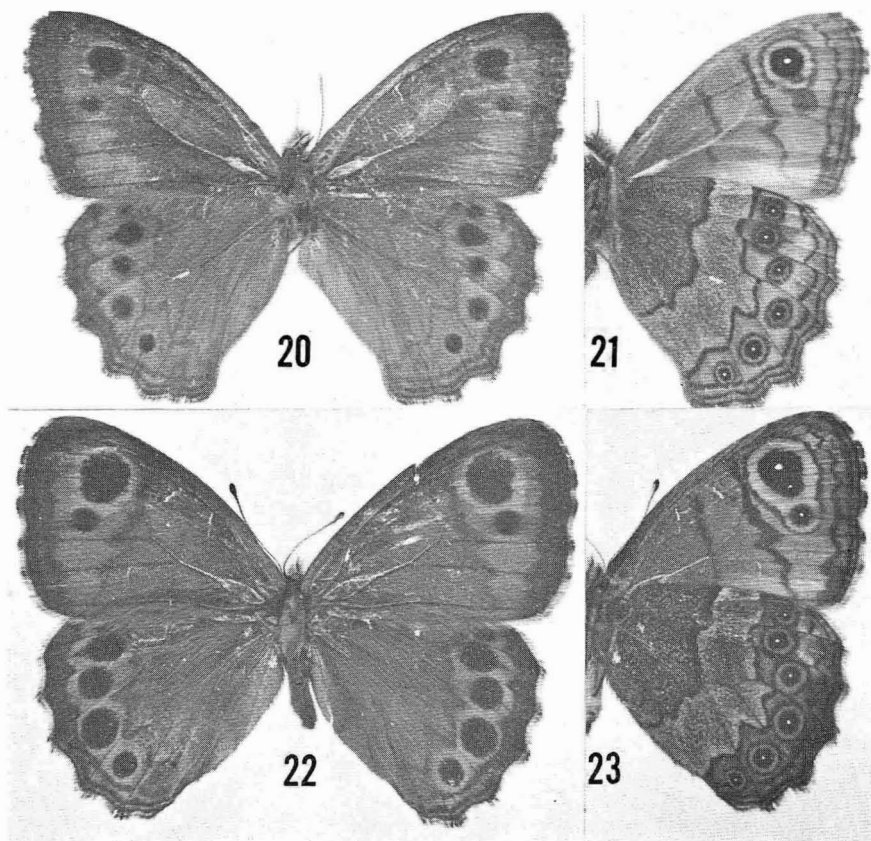
HOLOTYPE ♂: MEXICO: OAXACA: San José Pacífico, Mpio. Río Hondo, 2400 m., 9.x.1967 (E. C. Welling); ♂ genitalia slide No. M-2101 (Lee D. Miller).

PARATYPES: Same locality as Holotype: 132♂ 51♀, x-xi; OAXACA: Cerro Machín, Mpio. Comaltepec, 2800 m., 1♂ 1♀, xi; Agua Azul, Mpio. S. Andrés Paxtlán, 2300 m., 1♂ x (all E. C. Welling).

Disposition of type material: The entire type-series is now in collection (A), but Paratypes will be distributed to various museums and to Mr. Welling at a later date.

This subspecies is somewhat larger than is typical *xicaque* but is particularly characterized by the reddish upper surface and the elongate hindwing discal spot in M_1-M_2 . The straighter uncus in the present species is also characteristic, but certainly not at the specific level.

I am unable to determine to which subspecies the Oaxaca specimens mentioned by Godman and Salvin (1879-1901: 101) belong, though from the description given by those authors, they seem to be the nominate one. I also expected that *P. xicaque* in some form would have been found in the montane areas of Chiapas and possibly even Guatemala, but extensive collections from Chiapas by Mr. Robert Wind and others have not located the species in that state: perhaps Oaxaca is the southernmost limit for it.



Figures 20-23, *Paramacera xicaque rubrosuffusa*, new subspecies. 20-21, Holotype ♂ upper (20) and under (21) surfaces; MEXICO: OAXACA: San José Pacífico (A). 22-23, Paratype ♀ upper (22) and under (23) surfaces; MEXICO: OAXACA: San José Pacífico (A).

***Paramacera allyni*, new species**

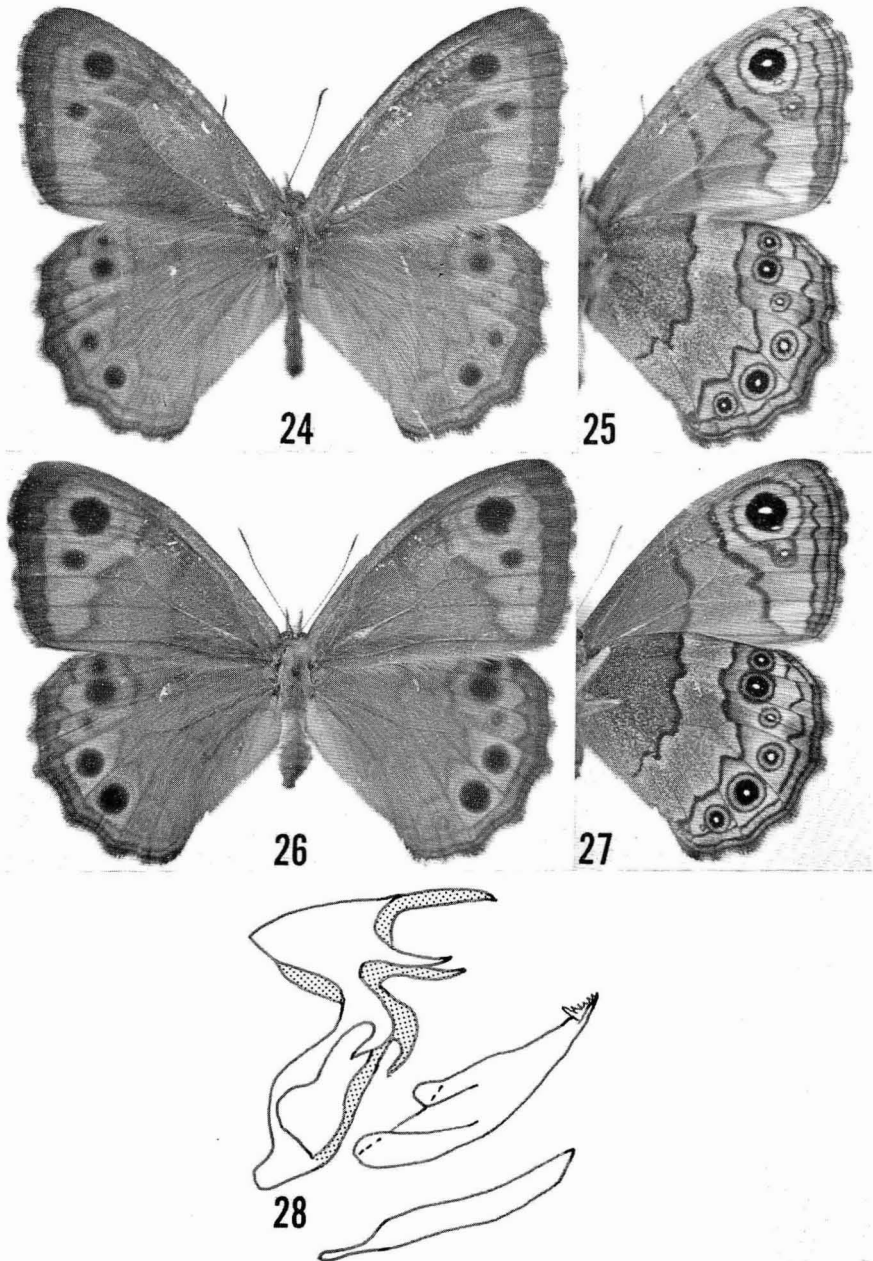
Figures 24, 25 (♂), 26, 27 (♀), 28 (♂ genitalia)

Paramacera [sic.] *xicaque* of authors, not Reakirt (1867 ["1866"]: 336-337).

Male: Differs from that of *xicaque* above by the more uniform olive-brown ground color, the duller fuscous extradiscal spots, the marginal lines of the hindwing being uniformly fuscous or only slightly tinged with reddish at anal angle (never bright red-brown from M_2 - M_3 to tornus as in Mexican *xicaque*) and in the androconial patch being better developed in forewing spaces M_1 - M_2 and M_2 - M_3 outside cell. Below differing from *xicaque* in the paler ground color, especially outside hindwing cell where the area enclosing the ocelli is silvery-gray.

♂ genitalia similar to those of *xicaque*, but uncus longer (greater than half length of uncus + tegumen) and valvae more gently tapered distad to narrower process.

Androconia similar to those of *P. xicaque*, but the rib spacing is greater



Figures 24-28, *Paramacera allyni*, new species. 24-25, Holotype ♂ upper (24) and under (25) surfaces; ARIZONA: Cochise Co.: Barfoot Park, Chiricahua Mtns. (A). 26-27, Paratype ♀ upper (26) and under (27) surfaces; ARIZONA: Cochise Co.: Barfoot Park, Chiricahua Mtns. (A). 28, ♂ genitalia of Holotype (M-2199) (A).

in the present species.

Length of forewing of Holotype ♂ 22.0 mm., those of 93 ♂ Paratypes range from 21.0 to 23.0 mm., averaging 22.1 mm.

Female: Differs from ♀ of *P. xicaque* in same general characteristics as does ♂, but without androconial spot, of course. Reddish tinge above, where present, only faintly indicated and mostly on forewing.

♀ genitalia similar to those of *P. xicaque*, but distal part of ductus bursae not so bulbous as in that species.

Lengths of forewings of 31 ♀ Paratypes range from 21.5 to 24.5 mm., averaging 22.9 mm.

Described from 124 specimens, 93 males and 31 females, from the Chiricahua Mountains, Arizona.

HOLOTYPE ♂: U. S. A. : ARIZONA: Cochise Co.: Barfoot Park, 8000', Chiricahua Mtns., 12.vii.1970 (K. Roever); ♂ genitalia slide No. M-2199 (Lee D. Miller).

PARATYPES: Same locality as Holotype: 15♂ 4♀, vii; same locality as Holotype, but 8600', 2♂ 1♀, vii; same locality (as "Barefoot" Park), no elevation, 2♀, vii; upper camp, Pinery Canyon, Chiricahua Mtns., 1♂, vi; Pinery Canyon, 3♂, vi; Rustler Park, Chiricahua Mtns., 5♂ 18♀, vii, viii; above Rustler Park, 8200', 4♂, vi, vii; "Chiricahua Mtns.", 63♂ 6♀, vi, vii.

Disposition of type material: Holotype ♂, 15♂ and three ♀ Paratypes (A); nine ♂ and 21 ♀ Paratypes (AMNH); 25♂ Paratypes (LACM); 15♂ and three ♀ Paratypes (CM); 21♂ and three ♀ Paratypes (USNM); five ♂ and one ♀ Paratypes (KR).

I take great pleasure in naming this species for Mr. A. C. Allyn in recognition of his contributions to lepidopterology.

In restricting the type-locality of *P. allyni* to the Chiricahua Mountains, I have excluded additional material from the type series which has, nevertheless, been examined. These specimens, 89 in all, 75 males and 14 females, refer to this species and bear locality labels as follows:

U. S. A.: ARIZONA: Apache (?) Co.: "White Mtns.", 8500', 2♂, vi (AMNH). Cochise Co.: Miller Canyon, 6 mi. SW Rt. 92, Huachuca Mtns., 7500', 1♂, vii (KR); "Huachuca Mtns.", 35♂ 6♀, vi-ix (AMNH, CM, LACM, USNM); "H. Ariz." [Huachucas?], 1♂, vi (AMNH); Ft. Huachuca, 1♂ 1♀ (LACM); Paradis, 13♂ 2♀, vi, vii (AMNH, USNM). Santa Cruz Co.: Nogales, 2♂ vi (CM, USNM). "So. Arizona", 2♂ vi (AMNH, LACM). "Ariz.", 2♂ 1♀, vi (AMNH, USNM).

MEXICO: CHIHUAHUA: "Chihuahua" (Harry K. Clench has determined a more precise locality for these specimens from the notes that the collector Townsend made, which notes are now in the archives of Carnegie Museum: Upper Rio Piedras Verdes [30° 15' N, 108° 15' W], 7100-7300'), 3♂ 1♀, viii, ix (CM).

This species, long confused with *P. x. xicaque*, can be separated from that species by its larger size, by the lack (or virtual lack) of red-brown tornal shading on the hindwing above, by the generally duller upper surface coloration, the silvery extradiscal part of the hindwing below and by the genitalic characteristics cited in the description.

The Chihuahua specimens are more "washed out" than are those from Arizona and could represent a different subspecies, but the material at hand is not sufficient to confirm such a judgment with certainty.

P. allyni is found in the high pine woodlands in the mountains of southeastern Arizona, and its habits are comparable with those of *P. xicaque*. I have no idea what the habitat is like in Chihuahua where Townsend took the short series in Carnegie Museum, but I assume it is similar to that in the Arizona mountains based on the other species taken there, including the type-series of *Speyeria nokomis coerulescens* (Holland). The White Mountains, Apache (?) Co., Arizona seem a bit strange, since *P. allyni* has not been recorded from intervening and equally logical areas, such as Mt. Graham or the Santa Catalina Mountains, but suitable-looking habitat is not uncommon in at least the southern Whites, so the record may be correct. If it is, I can see no reason why *P. allyni* shouldn't be found in the mountains of southern New Mexico and perhaps on Guadalupe Peak, Texas.

PHYLOGENETIC AND ZOOGEOGRAPHIC CONSIDERATIONS

It is rather difficult to postulate which of the euptychiine stocks gave rise to *Paramacera*, but this really will be the province of the final paper in this

series. Some inferences, however, may be drawn within the genus.

Despite the close similarity in the genitalia of all four species, *P. chinanteca* has a highly aberrant pattern for a *Paramacera*, but a more "conventional" one within the tribe. Unfortunately, the pattern represented by *P. chinanteca* is not duplicated elsewhere in Central America by any euptychiine group, but it is represented in South America by members of the "*Euptychia*" paeon complex. These latter insects are genitally very remote from *Paramacera*. This factor suggests that the basic stock from which *Paramacera* rose is a rather ancient one in the tribe and that the genus may have been isolated from its nearest relatives over a considerable period of time. *Paramacera* is not the only member of this ancient Mesoamerican fauna: the primitive danaid genus *Anelia* Hübner (= *Clothilda* Blanchard) and the satyrid genera *Cyllopsis* and *Pindis* have their metropolis in Mexico and/or Central America, for example. One can only assume that the progenitor of *Paramacera* arrived or arose in Mexico (possibly Central America) during the Tertiary when this area was isolated from South America, or possibly the "proto-*Paramacera*" represents one of the original invading stocks of Euptychiini from the Old World and never made it into South America. In either event, *Paramacera* is an old euptychiine genus, far older than most of the South American genera and more distinct.

With the exception of *P. copiosa*, which seems to be of an earlier vintage, the remaining *Paramacera* are closely related and seem to represent a much more recent radiation of the genus. The bifurcation of *P. xicaque* and *P. allyni* is likely to be of post-Pleistocene age and coincident with the drying of the entire area from Arizona through the Valle de México which effectively separated the ancestral stocks into a northern (*allyni*) and southern (*xicaque*) populations.

Three of the four species of *Paramacera* are found in the mountains of Oaxaca, and this area appears to be a likely site of the basic evolution within the group. The fourth species, and certainly the youngest in the genus, is found far to the north of the other three and is an offshoot of one of the Mexican species. Two species, *P. chinanteca* and *copiosa*, are known only from very small relict populations high in the mountains of Oaxaca, and both species appear to be "on the way out", a common fate for primitive, less well-adapted species. The other species were derived from a single widespread species during glacial maximum, at which time the pine woods environment was much more widespread and continuous than is the case today. The contraction of these woodlands during recent times probably caused the present-day fragmentation of the populations and their subsequent evolution.

The distribution of the species of *Paramacera* is shown on the map in Fig. 29.

ACKNOWLEDGMENTS

Many people have aided in the analysis of this genus and in the final preparation of the manuscript. Mr. William D. Field (USNM), Mr. Julian P. Donahue (LACM) and Dr. Frederick H. Rindge (AMNH) lent material for the study and were patient with me when the entire manuscript was rewritten after discovery of the two species from Oaxaca, *P. chinanteca* and *P. copiosa*; I am most grateful for their generosity and forbearance. Mr. Harry K. Clench (CM) made the collections of that institution available to me and gave helpful advice and information relative to several vexing points in the study. Dr. F. Martin Brown, Colorado Springs, Colorado, was a great help in resolving some of the problems of authorship and in the dating of relevant publications. Mr. Kilian Roever, Phoenix, Arizona, collected the basic type-series of *P. allyni* at my request and was generally most cooperative. Sr. Eduardo C. Welling M. of Mérida, Yucatán, Mexico, collected the type-series of *P. xicaque rubrosuffusa* at my request, then generously made available two species hitherto unsuspected by me for description in this paper: to him, of course, I owe a great debt of thanks. The photographs which illustrate this paper and the electron micrography of the androgonial scales were done by Mr. A. C. Allyn of this institution. Mr. Allyn and my wife and colleague, Jacqueline, read and commented upon the manuscript.

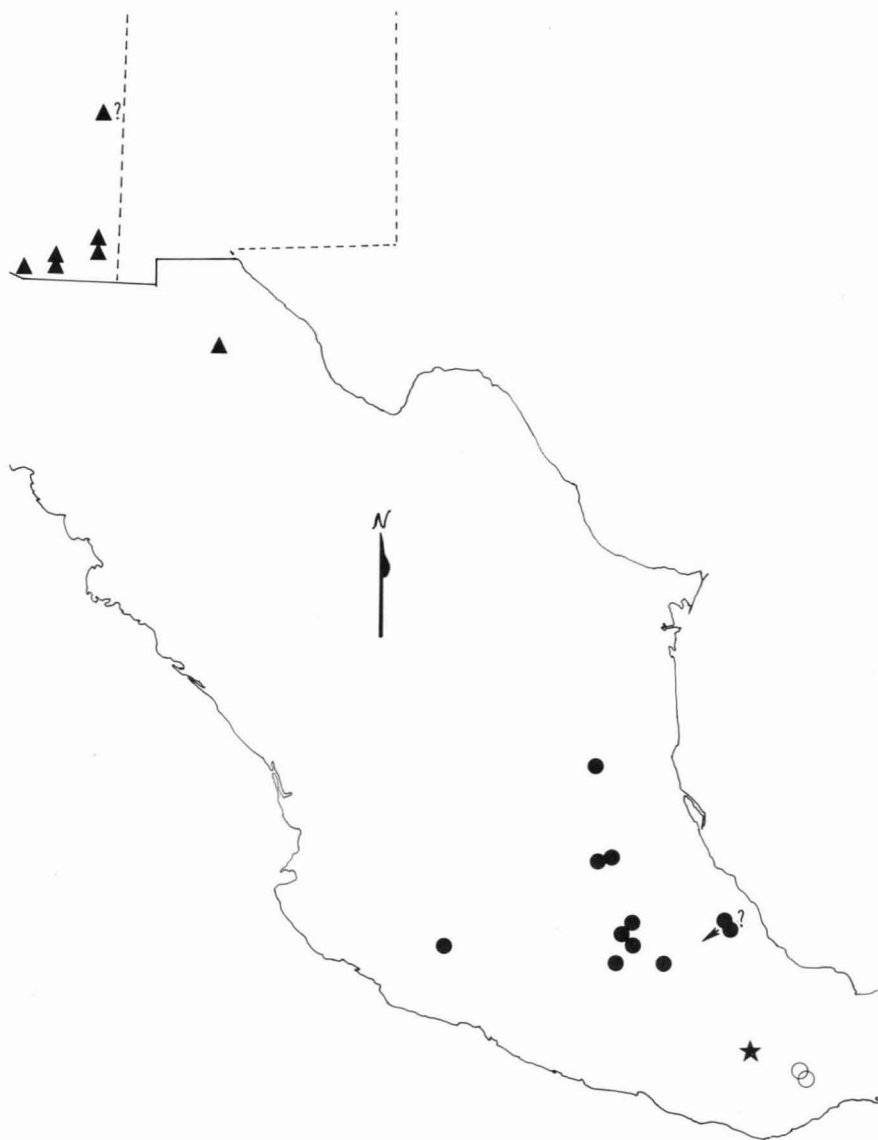


Figure 29, distribution of *Paramacera*. Closed circles, *P. x. xicaque*; open circles, *P. xicaque rubrosuffusa*; closed triangles, *P. allyni*; star, only spot from whence *P. chinanteca* and *P. copiosa* are known.

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