



A new species of *Cyllopsis* R. Felder, 1869 from the highlands of Chiapas, Mexico (Lepidoptera: Nymphalidae: Satyrinae)

ANDREW D. WARREN^{1,4}, SHINICHI NAKAHARA^{1,3,4}, JORGE LLORENTE-BOUSQUETS²,
ARMANDO LUIS-MARTÍNEZ² & JACQUELINE Y. MILLER¹

¹McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, P.O. Box 112710, Gainesville, Florida 32611 USA.

²Museo de Zoología, “Alfonso L. Herrera”, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apdo. Postal 70-399, México 04510 D.F., México

³Department of Entomology and Nematology, University of Florida, P. O. Box 110620, Gainesville, Florida 32611 USA.

⁴Corresponding authors. E-mail: awhesp@gmail.com; snakahara@ufl.edu

Abstract

A new species of *Cyllopsis* R. Felder, 1869, is described and illustrated from the highlands of Chiapas, Mexico. *Cyllopsis tomemmelii* A. Warren & Nakahara, **sp. nov.**, is currently known from 13 specimens (9 males and 4 females) collected on March 26–28, 1959, southeast of San Cristóbal de Las Casas. Despite extensive studies on the butterfly fauna of this region, this species has not since been encountered. We discuss possible relationships between this new species and other species of *Cyllopsis*.

Key words: Biogeography, butterfly, coniferous forest, endemic, pine-oak forest

Resumen

Se describe e ilustra una especie nueva de *Cyllopsis* R. Felder, 1869, de Los Altos de Chiapas, México. *Cyllopsis tomemmelii* A. Warren & Nakahara, **sp. nov.**; actualmente se conocen 13 ejemplares (9 machos y 4 hembras) recolectados entre el 26 y 28 de marzo de 1959, al sudeste de San Cristóbal de Las Casas. A pesar de estudios extensivos sobre la fauna de mariposas diurnas de esta región, esta especie no se ha recolectado nuevamente. Se discuten las posibles relaciones entre esta especie y otras especies del género *Cyllopsis*.

Palabras clave: Biogeografía, mariposa, bosque de coníferas, bosque de pino-encino, endémico

Introduction

The genus *Cyllopsis* R. Felder, 1869, is comprised of 29 species, distributed from the southern United States to Panama, with most species occurring in Mexico (Warren *et al.* 2016). Miller (1974) revised the genus and named fourteen new taxa from Mexico, Guatemala, El Salvador and Nicaragua. Since then, four additional species have been described from Mexico (Beutelspacher 1982; Miller & De la Maza 1984), Belize (Miller 1978) and Costa Rica (Chacón & Nishida 2002). *Cyllopsis* occupies a basal position with the subtribe Euptychiina, in a clade together with *Paramacera* A. Butler, 1868, *Inbio* Nakahara & Espeland, 2015 and *Atlanteuptychia* Freitas, Barbosa & Mielke, 2013 (Nakahara *et al.* 2015). Little is known about the biology of *Cyllopsis* species. Habitats range from arid chaparral to humid cloud forests. Available life history data suggest that larvae feed on grasses (*e.g.*, Edwards 1868-1897; Bailowitz & Brock 1991), including *Chusquea* Kunth in cloud forest habitats (DeVries 1987). While *in situ* studies of adult *Cyllopsis* butterflies have not been conducted, the pattern of ventral hindwing markings strongly suggest that these butterflies mimic various species of jumping spiders (Salticidae), with the metallic spots and lines resembling the spider's eyes and legs (pers. obs. ADW).

While some *Cyllopsis* species are widely distributed in the United States and Mexico, various species are known from just one or a few nearby localities and apparently have highly restricted geographic distributions. These “microendemic” species include *Cyllopsis caballeroi* Beutelspacher, 1982, known only from the area around Puerto Vallarta, Jalisco and Nayarit, Mexico; *C. clinas* (Godman & Salvin, 1889), known only from the Sierra de Atoyac de Álvarez in Guerrero, Mexico; the extraordinary, whitish, *C. emilia* I. Chacón & Nishida, 2002, known from a single specimen from Cerro de la Muerte in Costa Rica; *C. jacquelineae* L. Miller, 1974, known just from the Pacific slope of Guerrero and Oaxaca, Mexico; *C. nelsoni* (Godman & Salvin, 1881), known from two volcanoes in Guatemala and Chiapas, Mexico (see De la Maza & Warren 2014); *C. wellingi* L. Miller, 1978, endemic to the Maya Mountains in Belize; and *C. whiteorum* L. Miller & J. De la Maza, 1984, known only from cloud forests in northern Oaxaca, Mexico.

Given the large number of phenotypically unique *Cyllopsis* species occupying highly restricted distributions, especially in Mexico, the existence of additional undescribed taxa in that region has seemed probable to us. This notion was confirmed on October 23rd, 2017, when ADW encountered a series of 9 males and 4 females of a phenotypically very unique *Cyllopsis* species, unlike any described taxon, in a drawer of unsorted *Cyllopsis* specimens at the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida. This series was collected between March 26–28, 1959, at a site southeast of San Cristóbal de Las Casas, Chiapas, Mexico, at 2383m elevation, by Thomas C. Emmel, during a three-month expedition through southern Mexico and British Honduras with ornithologist L. Irby Davis. Despite extensive lepidopterological studies in this region by various researchers since 1959, this unique species, described below, appears not to have been encountered again (De la Maza & De la Maza 1993, 2017).

Materials and methods

To examine the genitalia, abdomens were dissected using standard techniques, namely abdomens were soaked in hot 10% KOH for 5–10 minutes, dissected, stored in glycerin subsequently. Female genitalia and aedeagus were stained in diluted chlorazol black in order to further visualize characters. Dissected specimens are indicated below (in Types section). Forewing length was measured from the base to the tip of the right forewing using a digital Vernier caliper. The terminology for abdominal and genital structures follows Klots (1956) except for the terms ‘brachia’ and ‘aedeagus’ where we follow Muschamp (1915) and Peña & Lamas (2005), respectively. Nomenclature for the areas and elements of the wing pattern follows Miller (1974: 44). Terminology for wing venation follows the Comstock-Needham system described in Miller (1970: 3). Some colors in descriptions follow Ridgway (1912), namely amber brown, pale vinaceous, cream buff, and light wisteria blue.

Results

Cyllopsis tomemmelii A. Warren & Nakahara, new species

(Figs. 1–2)

Diagnosis. *Cyllopsis tomemmelii* is unique among *Cyllopsis* species in the shape of the ventral hindwing extracellular band, which generally resembles that seen in species of *Paramacera*. *Cyllopsis whiteorum* appears closest to *C. tomemmelii* in ventral wing pattern, although most pattern elements in *C. whiteorum* are rather subdued, compared to those seen in *C. tomemmelii*, and the forewings of *C. whiteorum* are considerably more falcate than those of *C. tomemmelii*. In addition, *C. tomemmelii* males lack the dense, dark forewing androconial scales seen in *C. whiteorum*. While details of all the ventral fore- and hindwing bands differ substantially, the general size, shape and coloration of *C. tomemmelii* resemble *C. suivalenoides* L. Miller, 1974, *C. suivalens suivalens* (Dyar, 1914) and *C. suivalens escalantei* L. Miller, 1974.

Description. MALE: Forewing length 18–21mm (n=5).

Head: Eyes with hair-like setae, with whitish scales at base; postgenal area and frons covered with brownish hair-like scales and whitish hair-like scales, in addition to white scales covering frons; first segment of labial palpi mainly with white long hair-like scales, second segment length almost twice as great as eye depth and covered with

brownish scales and hair-like scales laterally, with partially whitish scales and hair-like scales, dorsally with brownish long hair-like scales and whitish hair-like scales, ventrally with brownish hair-like scales and whitish hair-like scales 3–4 times as long as segment width, third segment about one-fourth of second segment in length and covered with brownish scales, with slight patch of creamy-white scales laterally; antennae approximately two-fifth of forewing length, with ca. 29–37 antennomeres ($n=2$), distal 6 or so antennomeres composing club; club rather prominent.

Thorax: Dorsally and laterally covered with whitish long hair-like scales and greyish scales; ventrally with whitish hair-like scales; foreleg brownish, with whitish long hair-like scales and brownish hair-like scales, foretarsus slightly shorter than tibia and femur, tibia and femur similar in length; midleg and hindleg pale buff, with femur ventrally with whitish long hair-like scales, tarsus and tibia with spines ventrally, pair of tibial spurs present at distal end of tibia.

Abdomen: Eighth tergite appears as a stripe at base of eighth abdominal segment; eighth sternite appears as two sclerotized plates.

Wing venation: Like other *Cyllopsis* (e.g., Miller 1974). Most of forewing subcostal vein swollen; base of cubitus swollen; forewing recurrent vein absent; hindwing humeral vein developed; origin of M_2 closer to M_1 than M_3 .

Wing shape: Forewing subtriangular, apex rounded, costal margin convex, outer margin slightly convex, from apex to half way between M_3 and Cu_1 somewhat protruded, inner margin straight, but rounded towards thorax near base; hindwing slightly elongate towards tornus, overall appears rounded, costal margin almost straight, angled towards thorax near base, outer margin slightly undulating, inner margin slightly concave near tornus, anal lobe convex, slightly round.

Dorsal forewing: Ground color light brown, distal side and apex darker; androconial scales absent; ventral transcellular and extracellular bands visible.



FIGURE 1. *Cyllopsis tomemmelii* adult specimens, dorsal surface on the left, ventral surface on the right: a) male holotype; b) male paratype; c) female paratype (genitalic dissection number: SN-17-70); d) female paratype, with aberrant right hindwing pattern (genitalic dissection number: SN-17-71). Scale bar = 1 cm.

Dorsal hindwing: Ground color similar to forewing, black spots mirroring those ventral ocelli in cells M_2 and M_3 present, in addition to similar but faded spots in cells M_1 and Cu_1 ; rufous coloration along outer margin from M_2 towards tornus, surrounding black spots.

Ventral forewing: Ground color pale vinaceous, lighter towards distal side, area distal to extracellular band cream buff; amber brown transcellular band, extends from near costa to $2A$, almost straight, slightly traversing outwards; concolorous extracellular band extending from near costa to $2A$, parallel to transcellular band, somewhat wider; concolorous scales along discocellular vein, around origin of M_2 ; concolorous undulating submarginal band extending from apex towards tornus, curving inwards in each cell, broadens towards posterior end; marginal line, concolorous, traversing along outer margin, thinner than basal three bands; fringe greyish, slightly paler between $Sc+R_1 - M_3$.

Ventral hindwing: Ground color similar to forewing; amber brown transcellular band, jagged, extending from costa to inner margin, bent outwards soon after entering discal cell and before exiting discal cell, creamy yellow scales along distal side of transcellular band; partly concolorous extracellular band, appearing orangish around M_1 and extending down to posterior half in some specimens (variable character), mainly concolorous with previous band, strongly and irregularly jagged, strongly bent at M_1 , traverses inwards below M_1 , band somewhat terminates in discal cell (near origin of Cu_1), starts again from distal side of M_2 towards inner margin; amber brown scales present at origin of M_2 , along discocellular vein of discal cell; light wisteria blue shading present at distal side of extracellular band; submarginal band, concolorous to ventral forewing submarginal band, appears as a short band from cell Cu_1 to tornus, apparently fused to extracellular band in cell 2A; silver markings along outer margin, in cells Rs , M_1 , Cu_1 and Cu_2 (occasionally in cell $Sc+R_1$), those in cells Rs and M_1 appear as two units touching each other at distal side, whereas those in cells Cu_1 and Cu_2 appear somewhat as a continuous band; grey patch scattered with creamy white scales; ocelli in cells M_2 and M_3 , ellipse, black central area with silver band-like pupil placed distally, ringed in orange, with orange horizontal line in middle dividing ocellus into two; marginal band not discernable, outer margin appear reddish until Cu_1 , orangish below Cu_1 ; fringe greyish, slightly paler between $Sc+R_1 - M_3$.

Genitalia (Figs 2a–d): Tegumen rounded in lateral view, dorsal margin convex, ventral margin rather straight; uncus rather straight, similar to tegumen in length, basal half with hair-like setae, tapering towards posterior end, hooked at terminal point; brachia curved, half of uncus in length, tapering posteriorly and freely articulated; combination of ventral arms of tegumen and dorsal arms of saccus sinuous, broadens at middle section, but narrower towards saccus; appendices angulares present (this character was erroneously coded as “absent” for *Cyllopsis* species in Marin *et al.* (2017)), somewhat developed; saccus almost straight, similar to brachia in length; juxta present; valva sub-rectangular in lateral view, adorned with hair-like setae distally, apical process broad, terminates in hooked up angular point, middle section of valva broadens, costa developed with rounded end; aedeagus straight, similar to valva in length, slightly narrowing at posterior half, but broadens at posterior end, distal margin not discernable due to vesica, cornuti absent.

FEMALE: forewing length 18mm–22mm (n=3).

Similar to male except as follows: Foreleg whitish, foretarsus divided into five distinct sub-segments; forewing appears slightly more rounded and broad, ground color of both wing surfaces paler; ventral bands appear more prominent on dorsal surface, namely by showing their actual coloration. **Female Abdomen and Genitalia (Figs 2e–g):** Intersegmental membrane of seventh and eighth abdominal segment ventrally covered with modified scales; lateral side of eighth abdominal segment sclerotized, forming a plate not fused to lamella antevaginalis; lamella antevaginalis appears as sclerotized rectangular plate, distal margin of ventral side of ostium bursae weakly sclerotized; ductus bursae membranous, ductus seminalis exits from dorsal surface, at about one-fifth distance from ostium bursae to corpus bursae, apparently slightly sclerotized at base, ductus bursae appear as groove in area posterior to origin of ductus seminalis; corpus bursae oval, similar to ductus bursae in length, together with ductus bursae extends to 5th abdominal segment, paired signa located on ventral side.

Types. Holotype male with the following labels: white, printed: 12 Km S. of Las / Casas, Chiapas / Mexico / March 26–28, 1959 / T. C. Emmel /; white, printed: FSCA / Florida State Collection / of Arthropods /; white, printed: UF / FLMNH / MGCL 1038178 /; red, printed: HOLOTYPE / *Cyllopsis tomemmelii* / A. Warren & Nakahara /. The holotype is deposited in the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida (MGCL). Paratypes (8 males, 4 females): 2 males (MGCL 1038179, MGCL 1038181), 2 females (MGCL 1038182 genitalic dissection SN-17-71, MGCL 1038183 genitalic dissection SN-14-191), same data as holotype; 1 male (MGCL 1038184), 1 female (MGCL 1038186), same locality as holotype, March 26, 1959, T. C. Emmel; 5 males (MGCL 1038187, MGCL 1038188, MGCL 1038189, MGCL 1038192 genitalic dissection SN-17-68, MGCL 1038193 genitalic dissection SN-17-69), 1 female (MGCL 1038194 genitalic dissection SN-17-70), Mexico: Chiapas: 23 Km N. of Amatenango, March 26, 1959. Paratypes are deposited in the MGCL, save 1 male and 1 female deposited in the Museo de Zoología “Alfonso L. Herrera”, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC), in Mexico City.

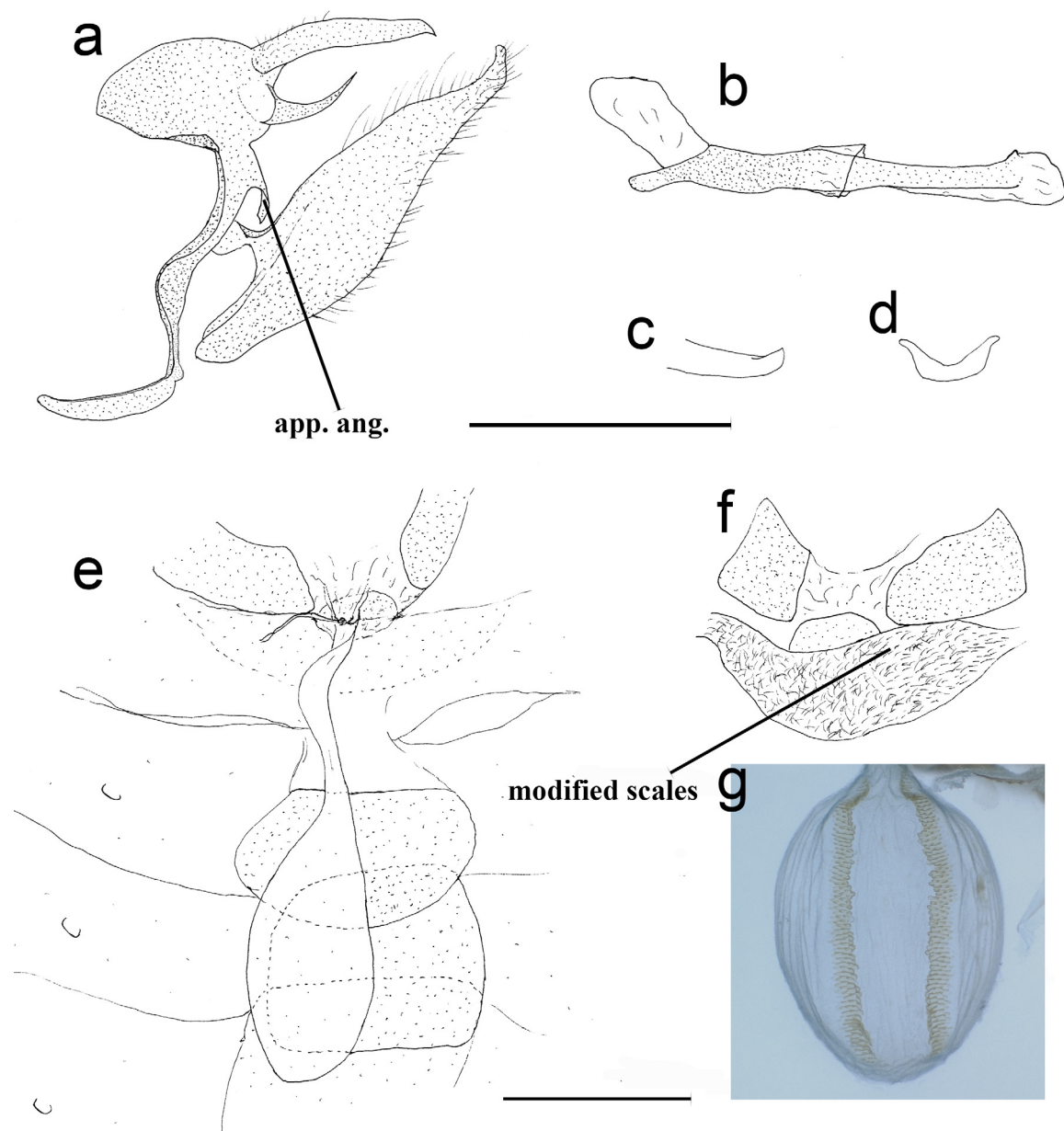


FIGURE 2. *Cyllopsis tomemmelii* genitalia: a) male genitalia in left lateral view (appendices angulares indicated as app. ang.); b) aedeagus; c) tip of valva in dorsal view; d) juxta (all drawings based on genitalic dissection SN-17-68); e) female genitalia in dorsal view; f) female genitalia in ventral view (ductus bursae and corpus bursae omitted, modified scales indicated); g) signa (all drawings and photo based on genitalic dissection SN-14-191). Upper scale bar for male genitalia, bottom scale bar for female genitalia except for (g). Both scale bars indicating 1mm.

Type locality. According to detailed field notes recorded by T. C. Emmel, all collecting on March 26–28, 1959, was conducted in the same general area; thus “12 Km S. of [San Cristóbal de] Las Casas” and “23 Km N. of Amatenango [del Valle]” refer to the same area. Thanks to a detailed map in Emmel’s field notes indicating how to reach the area from Hwy. 190, and specifically where he collected the *Cyllopsis* specimens, in addition to altimeter readings, the type locality was unambiguously identified as being in the immediate vicinity of 16°38’18.1”N 92°31’53.8”W, at 2383m elevation. At the time the type series was collected, the area was comprised of dense pine-oak forest, including many apparently old-growth pines, with a sparse understory of bunch grasses and scattered flowering plants, and various small, open, sunny areas (Fig. 3). Additional butterflies encountered by Emmel in the area, among others, included *Pterourus multicaudata grandiosus* (Austin & J. Emmel, 1998), *P.*

pilumnus (Boisduval, 1836) (Papilionidae), *Lieinix nemesis atthis* (E. Doubleday, 1842), *Colias philodice guatemalena* Röber, 1909, *Zerene c. cesonia* (Stoll, 1790), *Anteos clorinde* (Godart, [1824]), *A. maerula* (Fabricius, 1775), *Eurema mexicana mexicana* (Boisduval, 1836), *Pyrisitia proterpia* (Fabricius, 1775) (Pieridae), *Celastrina echo gozora* (Boisduval, 1870) (Lycaenidae), *Altinote ozoneme nox* (H. Bates, 1864), *Adelpha diocles creton* Godman, 1901, *A. donysa donysa* (Hewitson, 1847), *A. serpa celerio* (H. Bates, 1864), *Dione moneta poeyii* A. Butler, 1873, *Hypanartia l. lethe* (Fabricius, 1793), *Vanessa virginiensis* (Drury, 1773), *Siproeta stelenes biplagiata* (Fruhstorfer, 1907), *Anthanassa s. sitalces* (Godman & Salvin, 1882), *Phyciodes mylitta thebais* Godman & Salvin, 1878, *Consul excellens genini* (Le Cerf, 1922), *Pedaliodes napaea* (H. Bates, 1865) (Nymphalidae), and several species of Hesperiiidae (not examined, as these were sent to S. S. Nicolay) including *Zestusa staudingeri* (Mabille, 1888) and *Poanes melane poa* (Evans, 1955).

Etymology. We take great pleasure in naming this distinctive new species in honor of Dr. Thomas Chadbourne Emmel, Founding Director of the McGuire Center for Lepidoptera and Biodiversity, who collected the entire type series in 1959, and who has inspired and supported countless up-and-coming biologists. This specific epithet is regarded as a Latinized masculine noun in the genitive case.

Distribution. *Cyllopsis tomemmelii* is known to date only from the type locality. Appropriate habitats in the vicinity of the type locality should be intensively surveyed in an effort to detect the potential continued existence of the species in the region.



FIGURE 3. Pine forest habitat approximately 2 kilometers NW of the type locality of *C. tomemmelii*, about 12 kilometers SE of San Cristóbal de Las Casas, Chiapas, Mexico, March 26, 1959, photo by Thomas C. Emmel.

Discussion

The genera *Cyllopsis* and *Paramacera* are very closely associated with pine-oak, pine, and high-elevation cloud forests (Miller 1972, 1974). *Paramacera* species are endemic to the highest-elevation habitats, with *P. chinanteca* L. Miller, 1972 and *P. copiosa* L. Miller, 1972 occupying widely disjunct peaks in Guerrero and Oaxaca, Mexico (Luis *et al.* 1992, 2016). *Cyllopsis*, with *C. whiteorum* and *C. tomemmelii*, as well as various Central American species, also includes taxa endemic to habitats above 2300 m elevation. Undoubtedly, these genera have evolved in the southern Mexican and adjacent cordilleras, where various relict taxa remain in very localized areas.

While *Cyllopsis* and *Paramacera* are associated with montane forests, their populations are closely linked with

the understory of grasses in these forests, which serve as larval foodplants. Due to the disjunct distribution of these habitats in the Mesoamerican cordilleras, the flora and fauna of these habitats has evolved in allopatry. Some of these diversification events appear to be ancient, such as those in high-elevation cloud forests (Llorente-Bousquets 1984; Llorente-Bousquets & Escalante 1992; Llorente-Bousquets *et al.* 1992), while diversification events in high-elevation pine-oak and pine forests appear to have occurred more recently and in very small areas, as shown for carabid beetles in the Mexican Transvolcanic Range (Ball 1970).

The grass communities of these high-elevation montane habitats in Mexico have probably differentiated from stock that was more widely distributed during cooler and more humid periods of the Plio-Pleistocene, yet now appear relictual. This process appears to have occurred multiple times in the various cordilleras, mainly in southern Mexico, below the 19th parallel, where the majority of high-elevation montane endemics occur in the country. Similar processes in the mountains of Central America involving the genus *Chusquea* have likely led to the evolution to the microendemic taxa *Cyllopsis nelsoni* and *C. emilia*.

The discovery of a taxon as distinctive as *Cyllopsis tomemmelii*, in an area that has been relatively well studied for diurnal Lepidoptera since 1959 (*e.g.*, De la Maza & De la Maza 1993, 2017), is remarkable. Thanks to the extremely detailed field notes recorded *in situ* by Emmel, there is no doubt about exactly where these specimens were collected. Emmel described the only two species of satyrine butterflies collected in the vicinity of their March 25–28 campsite; “#1: large, very dark with reddish band on hind wings” [this has proven to be *Pedaliodes napaea*]; #2: medium-sized, velvety brown, with row of odd-shaped blue ocelli on hind wings, underside very colorful with bands.” Emmel’s satyr #2 is undoubtedly *C. tomemmelii*, as this description matches the general pattern of the taxon, and it is the only other satyrine butterfly encountered in the MGCL collections labeled from this locality and date. It should also be noted that the hand-drawn map of the area in Emmel’s field notes, drawn on March 26th, clearly indicates the area where the satyrs were common, not far from their campsite at 2335m. Emmel collected *C. tomemmelii* on March 26 and 28, but among satyrs only indicated finding *P. napaea* on March 27. During the afternoon of March 26, Emmel wrote, “The satyres were almost entirely collected in the woods on the south side of the valley. Here the oaks and pines provide shade, while bunch grass grows extensively in places.” On March 28th, Emmel continued, “Satyr spp.: Both species are rather abundant. Almost always found beneath the oak trees in open situations within the forest. The medium-sized brown species [*C. tomemmelii*] has a typical jerky satyr flight. The larger dark-brown, red-banded species [*P. napaea*] has a stronger, more rapid, jerky flight, and occasionally ventures out into the open areas to fly briefly around the flowering oak trees.”

The description of *C. tomemmelii* brings the known number of *Cyllopsis* species to 30. Given that so many *Cyllopsis* species are narrowly endemic to specific biogeographic regions in Mexico and Central America, we expect additional undescribed species to be discovered as remote cloud forest and pine-oak habitats are surveyed for diurnal Lepidoptera. We hope that a future study combining morphological and molecular characters of all *Cyllopsis* species will help resolve relationships between taxa and elucidate the phylogenetic position of *C. tomemmelii*.

Acknowledgments

We thank Thomas C. Emmel for collecting the type series of *C. tomemmelii* and for recording and sharing incredibly detailed field notes which enabled us to unambiguously identify the collecting site from 1959; we also thank Emmel for discussions, comments on this manuscript, and support. Thanks to Kathryn Daly for discussions on *Cyllopsis* and satyrine butterflies in general. We thank Jim Schlachta for scanning Emmel’s transparencies from 1959. We also thank Eduardo P. Barbosa, Keith R. Willmott, and an anonymous reviewer for thoughtful comments that improved this manuscript. SN acknowledges the National Science Foundation (Grant No. DEB-1256742), and JLB and ALM acknowledge CONACYT project 284866 and PAPIIT 212418, for support.

Literature cited

Bailowitz, R.A. & Brock, J.P. (1991) *Butterflies of Southeastern Arizona*. Sonoran Arthropod Studies, Inc., Tucson. ix + 342pp.
Ball, G.E. (1970) Barriers and southward dispersal of the Holarctic boreo-montane element of the family Carabidae in the

- mountains of Mexico. *Anales Escuela Nacional de Ciencias Biológicas*, 17, 91–112.
- Beutelspacher, C.R. (1982) Lepidópteros de Chamela, Jalisco, Mexico I. Rhopalocera. *Anales del Instituto de Biología. Universidad nacional autónoma de México* (Zoología), 52 (1), 371–388.
- Chacón, I. & Nishida, K. (2002) A new species of *Cyllopsis* (Lepidoptera: Nymphalidae: Satyrinae) from Costa Rica. *Revista de Biología Tropical*, 50 (2), 679–683.
- De la Maza, R.G. & De la Maza, J. (1993) *Mariposas de Chiapas*. Gobierno del Estado de Chiapas, Mexico. 223 pp.
- De la Maza, R.G. & De la Maza, J. (2017) Las mariposas diurnas (Papilionoidea y Hesperioidea) de Los Altos de Chiapas, Mexico, distribución, composición, origen y evolución. *Revista de la Sociedad mexicana de Lepidopterología* (Nueva serie), 5 (1), 9–40.
- De la Maza, R.G. & Warren, A. (2014) *Cyllopsis nelsoni* (Godman & Salvin 1881) (Nymphalidae-Satyrinae) nuevo registro para Chiapas y México. *Revista de la Sociedad mexicana de Lepidopterología* (Nueva serie), 1 (2), 2–4.
- DeVries, P.J. (1987) *The Butterflies of Costa Rica and their Natural History. Papilionidae, Pieridae, Nymphalidae*. Princeton University Press, Princeton. xxii + 327pp.
- Edwards, W.H. (1868–1897) *The Butterflies of North America*. Houghton Mifflin & Co, Boston. 1: [i], ii, [163], v, 52 pp., 50 pls. (1868–1872); 2: [i], [358] pp., 51 pls. (1874–1884); 3: [viii], [432] pp., 51 pls. (1887–1897).
- Klots, A.B. (1956) Lepidoptera. In: Tuxen, S. L. (Ed.), *Taxonomist's Glossary of Genitalia in Insects*. Copenhagen, Munksgaard, pp. 97–111.
- Llorente-Bousquets, J. (1984) Sinopsis Sistemática y biogeográfica de los Dismorphiinae de México con especial referencia al género *Enantia* Huebner (Lepidoptera: Pieridae). *Folia Entomologica Mexicana*, 58, 1–206.
- Llorente-Bousquets, J. & Escalante, P. (1992) Insular biogeography of submontane humid forests in Mexico. *Tulane Studies in Zoology and Botany*, 1, 139–146.
- Llorente-Bousquets, J., Luis-Martínez, A. & González, L.L. (1992) Diferenciación de *Prepona deiphile* en Mesoamérica y descripción de dos subespecies nuevas (Lepidoptera: Nymphalidae). *Tropical Lepidoptera*, 3, 109–114.
- Luis-Martínez, A., Llorente-Bousquets, J. & Vargas-Fernández, I. (1992) Redescubrimiento de *Paramacera copiosa* en la Sierra Madre del Sur, Guerrero, México (Lepidoptera: Nymphalidae: Satyrinae). *Tropical Lepidoptera* 3, 115–117.
- Luis-Martínez, A., Hernández-Mejía, B., Trujano-Ortega, M., Warren, A., Salinas-Gutiérrez, J., Ávalos-Hernández, O., Vargas-Fernández, I. & Llorente-Bousquets, J. (2016) Avances faunísticos en los Papilionoidea (Lepidoptera) *sensu lato* de Oaxaca, México. *Southwestern Entomologist*, 41 (1), 171–224.
<https://doi.org/10.3958/059.041.0119>
- Marín, M.A., Peña, C., Uribe, S.I. & Freitas, A.V.L. (2017) Morphology agrees with molecular data: phylogenetic affinities of Euptychiina butterflies (Nymphalidae: Satyrinae). *Systematic Entomology*, 42, 768–785.
<https://doi.org/10.1111/syen.12245>
- Miller, L.D. (1970) Nomenclature of wing veins and cells. *Journal of Research on the Lepidoptera*, 8 (2), 37–48.
- Miller, L.D. (1972) Revision of the Euptychiini (Satyridae). 1. Introduction and *Paramacera* Butler. *Bulletin of the Allyn Museum*, 8, 1–18.
- Miller, L.D. (1974) Revision of the Euptychiini (Satyridae). 2. *Cyllopsis* R. Felder. *Bulletin of the Allyn Museum*, 20, 1–98.
- Miller, L.D. (1978) Notes and descriptions of Euptychiini (Lepidoptera, Satyridae) from the Mexican region. *Journal of the Lepidopterists' Society*, 32 (5), 75–85.
- Miller, L.D. & De la Maza, J. (1984) Notes on *Cyllopsis*, especially from Mexico, with description of a new species (Lepidoptera: Satyridae). *Bulletin of the Allyn Museum*, 88, 1–7.
- Muschamp, P.A.H. (1915) The Ci-deviant genus *Epinephele*. *The Entomologist's Record and Journal of Variation*, 27, 152–156.
- Nakahara, S., Janzen, D.H., Hallwachs, W. & Espeland, M. (2015) Description of a new genus for *Euptychia hilara* (Lepidoptera, Nymphalidae, Satyrinae). *Zootaxa*, 4012 (3), 525–541.
<https://doi.org/10.11646/zootaxa.4012.3.7>
- Peña, C. & Lamas, G. (2005) Revision of the butterfly genus *Forsterinaria* Gray, 1973 (Lepidoptera: Nymphalidae, Satyrinae). *Revista Peruana de Biología*, 12, 5–48.
- Ridgway, R. (1912) Color Standards and Color Nomenclature. Washington, D. C., published by the author, 43pp. + 53 color plates.
<https://doi.org/10.5962/bhl.title.62375>
- Warren, A.D., Davis, K.J., Stangeland, E.M., Pelham, J.P. & Grishin, N.V. (2016) Illustrated Lists of American Butterflies [15-IX-2016]. Available from: <http://www.butterfliesofamerica.com/> (Accessed 15 Mar. 2018)