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VARIATION OF *COPAEODES MINIMA* AND THE STATUS OF *COPAEODES RAYATA* (LEPIDOPTERA: HESPERIIDAE: HESPERIINAE)

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ABSTRACT

Examination of more than 600 specimens of *Copaeodes minima* (W. H. Edwards, 1870) (Hesperiidae: Hesperiinae) indicated phenotypic variation throughout its distribution. A dark form occurs in response to low temperatures during development. Its genitalia do not vary concomitantly. Both *C. minima* and its synonym, *Copaeodes rayata* Barnes & McDunnough, 1913, were described from the pale form of the species. A lectotype is designated for *Copaeodes rayata*.

Key Words: *Copaeodes minima,* forms, phenology, polyphenism, synonymy, temperature

RESUMEN

Una revisión de mas de 600 especímenes de *Copaeodes minima* (W. H. Edwards, 1870) (Hesperiidae: Hesperiinae) indicó una variación fenotípica para toda su distribución. Una forma oscura se presenta como respuesta a las temperaturas bajas durante su desarrollo. Su genitales no varían simultáneamente. Ambos *C. minima* y su sinónimo, *Copaeodes rayata* Barnes & McDunnough, 1913, fueron descritas de la forma pálida de esta especie. Se designa un lectotipo de *Copaeodes rayata*.

Butterflies with multiple annual generations that emerge over the span of several months or occur throughout the year often exhibit seasonal polyphenism (Shapiro 1976). The expression of alternate phenotypes is determined by variation in the developmental environment (Shapiro 1976; Nijhout 1999). Polyphenism usually evinces itself as differences in wing pattern, size, and/or color, but it also is less commonly seen in the shape and proportions of the wings. Only a few butterflies with seasonal forms have been investigated in depth; these are largely within the Pieridae and Nymphalidae (e.g., Hidika & Takabashi 1967; Oliver 1970, 1976; Hoffmann 1974; Riley 1980; Yata et al. 1984; Roskam & Brakefield 1999; Windig & Lammar 1999), but the phenomenon has also been documented for Papilionidae (Edwards 1871; Endo & Murakami 1985), Lycaenidae (Sakai & Masaki 1965; Endo et al. 1985), Riodinidae (McAlpine 1971; Austin 1988), and Hesperiidae (Burns 1964; Ishii & Hidaka 1979).

In North America, a few hesperiine skippers (Hesperiidae: Hesperiinae) exhibit seasonal phenisms including *Hylephila phyleus* (Drury, 1773) (Shapiro 1974; Tveten & Tveten 1996), *Atalopedes campestris* (Boisduval, 1852) (Leussler 1938; Durden 1982; Warren 2005), and *Polites sabuleti* (Boisduval 1852) (Shapiro 1974, 1975), among others (pers. obs.). *Copaeodes minima* (W. H. Edwards 1870), is another hesperiine that expresses seasonal variation with a pale phenotype through most of the year and a darker phenotype often appearing during cooler months with shorter photoperiods. Durden (1982) may have been the first to formally note this as a "genitalically distinct winter f. *rayata* Barnes & McDunnough, 1913." The nature of the genital differences between forms was not elaborated nor was there mention of any differences in superficial characters. Lewis (1985) reported that adults taken in Florida from Jan to Mar had more extensive dark scaling posteriorly on the dorsal hindwing and on the ventral hindwing than did adults from other times of the year.

The seasonal occurrence of the dark form of *C. minima* and the genital morphology of both forms are examined in this study and the status of the name *Copaeodes rayata* Barnes & McDunnough, 1913, is evaluated.

MATERIALS AND METHODS

Specimens of *Copaeodes minima* housed at the McGuire Center for Lepidoptera and Biodiversity

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and in ADW's personal collection were examined as follows: USA: Alabama (26 males, 11 females), Florida (224 males, 52 females), Georgia (58 males, 34 females), Louisiana (22 males, 8 females), Mississippi (10 males, 10 females), North Carolina (12 males, 7 females), South Carolina (2 males), Texas (36 males, 11 females); MEXICO: Chiapas (3 males, 3 females), Colima (3 males), Distrito Federal (3 males, 2 females), Durango (2 males), Guerrero (2 males), Hidalgo (1 male, 1 female), Jalisco (3 males, 1 female), Michoacán (6 males, 4 females), Morelos (3 males, 1 female), Nayarit (8 males, 2 females), Nuevo León (1 female), Sinaloa (30 males, 8 females), Sonora (3 males, 1 female), Veracruz (2 males, 4 females), Yucatan (3 males), Zacatecas (1 male), unknown state (1 female); CENTRAL AMERICA: Belize (1 female), Costa Rica (5 males), El Salvador (23 males, 8 females), Honduras (2 males), Nicaragua (16 males, 1 female). The occurrence of pale and dark phenotypes, judged by the darkness of the ventral hindwing, was tabulated by month for each state and country represented. Twenty-five males (15 pale form from Florida, Louisiana, Texas, Nicaragua; 10 dark form from Florida, Texas, North Carolina) and ten females (5 pale form from Florida, Texas; 5 dark form from Florida, Texas) were dissected to examine any differences that may exist in their genitalia.

Results and Discussion

Wings. *Copaeodes minima* is a very small butterfly, with mean male forewing length of pale form = 8.9 mm (range 8.3-9.6 mm, n = 10), of dark form = 8.9 mm (range 8.5-9.3 mm, n = 10); mean female forewing length of pale form = 9.5 mm (range 9.1-10.2 mm, n = 10), of dark form = 9.6 mm (range 9.2-9.9 mm, n = 10) distributed from the southeastern United States, through much of Mexico, and southward into Central America as far as Panama (MacNeill 1975; Pyle 1981; Opler & Krizek 1984). The species has multiple annual generations, flying throughout the year at some localities (Kimball 1965; Brock & Kaufman 2003). Its pale phenotype is widely illustrated (Scott 1986, Tveten & Tveten 1996; Brock & Kaufman 2003, and Figs. 1a-d, 4 herein). Among samples from the United States (n = 523), 15% are of a dark phenotype (Fig. 1e-h) that apparently has not been illustrated previously. Both sexes of this form have increased black scaling proximad on the dorsum of both the forewing and hindwing and especially in the anal cell of the hindwing (see also Lewis 1985). On the venter, the orange is a deeper shade than on the pale form, especially on the hindwing where it becomes bronzy on extreme specimens. On this wing, there is often more black scaling proximad and in much of cell 2A-3A and the anal cell. The amount of white scaling on the hindwing is reduced on this form except for the ray from the base of the discal cell to the tornus in cell M_1-M_3. This latter is much more prominent on the darker ground color of the dark form; on the pale form the ray is often inconspicuous.

In Florida, *Copaeodes minima* has been recorded in every month, although it may be decidedly uncommon from Nov through Apr (Fig. 2a), but this probably also reflects in part the abundance of collectors. During those months, the majority (53%, n = 62) of individuals are of the dark form (occurring from Oct through May). This dark phenotype is also the majority form (61%, n = 23) among samples from Nov to Apr (occurring from Sep through Apr) elsewhere in the United States. The dark form has not been seen within samples of *C. minima* from the United States during the mid-summer months of Jun, Jul, and Aug (except a probably mislabeled sample from Georgia) and represents only 9% of specimens from Apr through Oct (n = 466), but, as noted above, predominates between Nov and Mar.

Smaller samples of *C. minima* from south of the United States also include the dark phenotype (Fig 2b). In Mexico, where the sample is somewhat more equitably distributed throughout the year, 33% of specimens examined (n = 102) were of the dark phenotype occurring most abundantly (50%, n = 62) from Dec to May. Dark individuals, however, occur during much of the year in Mexico. At least some of those from "summer" may be attributed to specimens from cloud forest, a habitat that experiences low temperatures at any time. In Central America only 7% of individuals (n = 56, including 1 male from Costa Rica) are dark, these occurring from Jan to Mar. The vast majority of individuals taken during those months (82%, n = 22), however, are of the pale phenotype.

Polyphenism among butterflies results from interactions of seasonally dynamic environmental variables, including temperature, photoperiod, and perhaps humidity and precipitation acting alone, in concert, or as redundant mechanisms (Shapiro 1977, 1978b, 1984; Smith 1991; Windig et al.1994). While the seasonal occurrence of the dark form suggests it to be a "winter" form, the occurrence of the dark form at the same time of year as pale phenotypes indicates that the forms of *C. minima* are not strictly seasonal phenomena. Truly seasonal phenomena must have a photoperiodic cue for its expression. Although other environmental variations (temperature, precipitation, humidity, etc.) are highly correlated, on average, with photoperiod, these are averages; the only non-varying local component is photoperiod. Lewis (1985) determined that the dark form was induced by constant low temperature (20°C) during development. This effect was significantly different from the preponderance of pale individuals produced at a constant higher temperature (30°C). Photoperiod (10h, 16h) had

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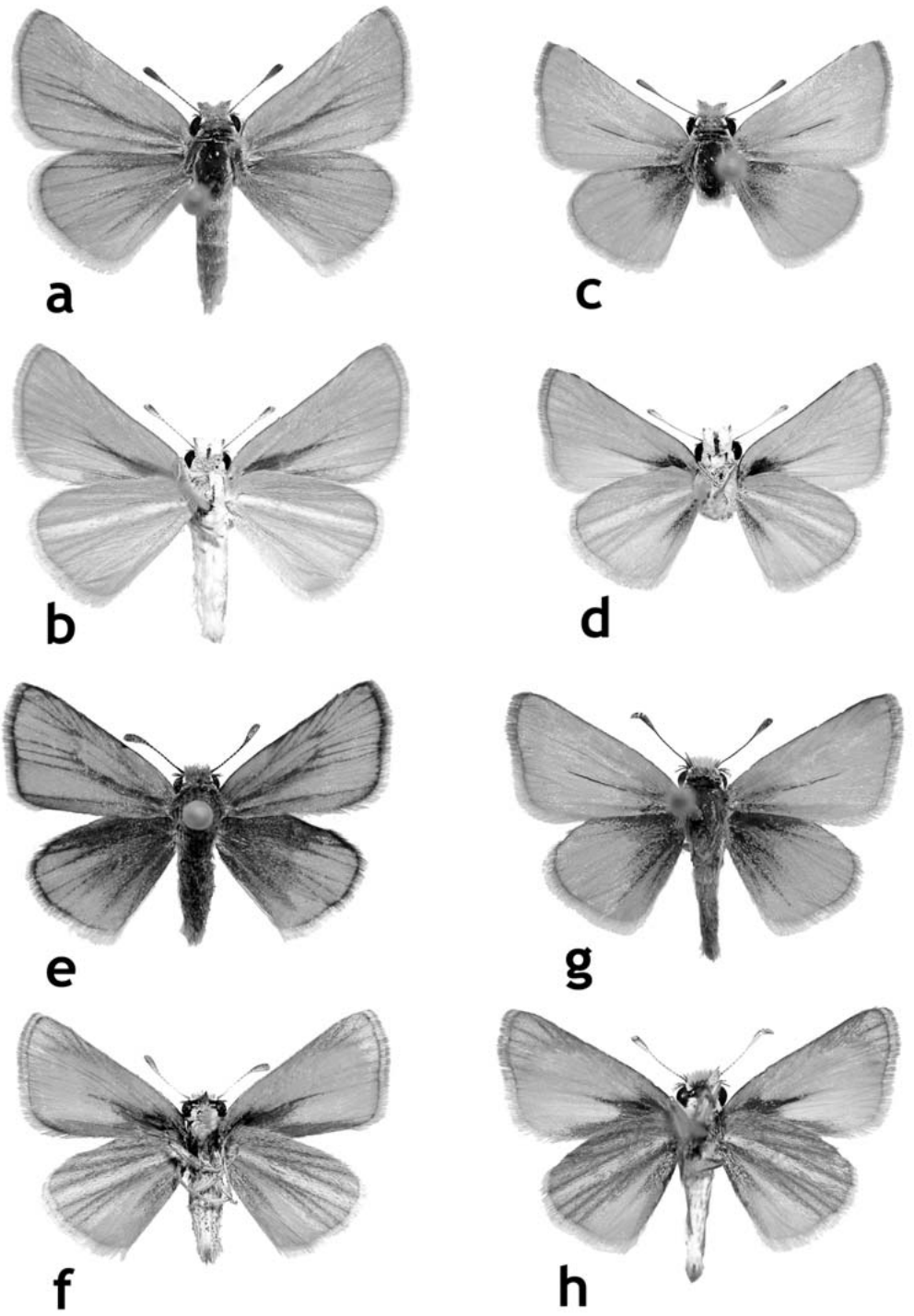
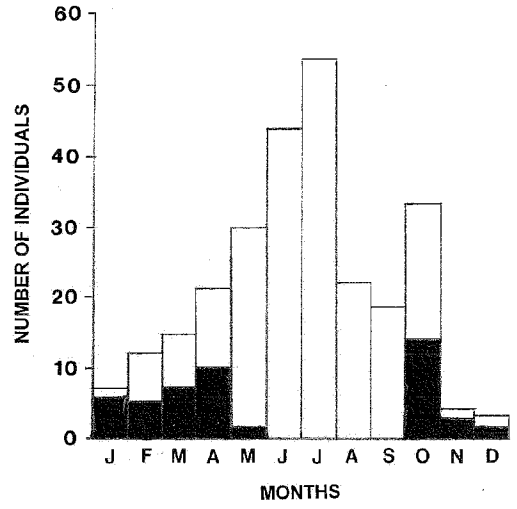
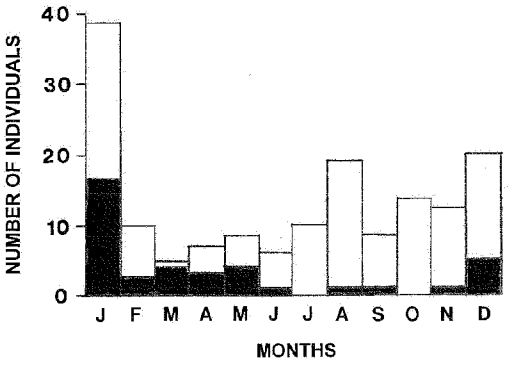


Fig. 1. Forms of *Copaeodes minima*: (a) female, pale form - FLORIDA: Manatee Co.; Terra Ceia, 9 July 1981, J. C. Downey, dorsal surface; (b) same, ventral surface; (c) male, pale form - FLORIDA: Manatee Co.; Terra Ceia, 9 July 1981, J. C. Downey, dorsal surface; (d) same, ventral surface; (e) female, dark form - FLORIDA: Sarasota Co.; Sarasota, 12 January 1976, H. L. King, dorsal surface; (f) same, ventral surface; (g) male, dark form - FLORIDA: Dade Co.; (no locality), 5 January 1978, James Lewis, dorsal surface; (h) same, ventral surface.

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a



b

Fig. 2. Phenology of forms of *Copaeodes minima*. Shaded and unshaded bars are number of specimens examined of dark and pale individuals, respectively. (a) Florida (n = 265), (b) Mexico and Central America (n = 158).

no significant effect on phenotype. Although Lewis (1985) acknowledged a caveat of a constant thermal environment in his experimental protocol, these data did indicate that temperature during development may be the principal driving factor in the seasonal variation of *C. minima* with little influence of photoperiod. In contrast, Ishii & Hikaka (1979) demonstrated complex interactions of photoperiod and temperature in producing seasonal forms in another species of hesperiine in Japan.

Genitalia. Male genitalia (Fig. 3a-h) of the sample examined resemble the few published figures of those for *C. minima* (Skinner & Williams 1923; Lindsey et al. 1931; Evans 1955; Forbes 1960). These are rather simple as characteristic of many hesperiines with an unadorned tegumen and an uncus that narrows to a very thin and weakly hooked caudal end. The combined ventral arm of the tegumen and dorsal arm of the saccus is sinuate, having a prominent cephalic bend in the ventral third. The anterior arm of the saccus is long (longer than the valva) and extends straight cephalad. The valva is narrow and projects caudad as a lower process of the harpe and an upper process of similar length from the ampulla that curves slightly inward. The aedeagus is very thin and about twice the length of the valva. Female genitalia (Fig. 3i-l), not previously illustrated for *C. minima*, have a more or less square and largely membranous sterigma. The lamella antevaginalis and lamella postvaginalis are fused wherein lies the ostium bursae. The lateral portion of the lamella postvaginalis is well-sclerotized as a pair of thin and widely-spaced arms extending caudad and twisted about 1/3 the distance from their caudal end. These arms are joined by a membranous area that is very lightly sclerotized caudad with a triangular projection from the caudal margin. The well-sclerotized antrum (colliculum of de Jong 1984) opens broadly caudad, narrows cephalad, and is about twice as long as its caudal width. This joins with a short membranous portion of the ductus bursae. The latter continues cephalad as a short sclerotized tube that divides into a pair of sclerotized spikes apparently supporting the corpus bursae caudad. The corpus bursae is bulbous and enclosed in a very thin and often almost invisible membranous sac. There is no appendix bursae as shown for *Copaeodes castanea* Mielke, 1969, by Mielke (1969). A long antrum and the narrow membranous area and cephalic sclerotized bifurcation of the ductus bursae appears typical of the Thymelicini (Warren 2006; Warren et al., in press; see also figures in Mielke 1969; de Jong 1984; de Prins et al. 1992).

The extension of seasonal polyphenism to genital morphology is virtually unknown among butterflies (but see Scudder 1889; Reinhardt 1969 cited by Shapiro 1978a; Windig & Lammar 1999). Although Durden (1982) did not initially state how genitalia vary seasonally, he later (Durden 2007) indicated that the "apical process of the male valvae" was "much longer" on *Copaeodes rayata* than on *C. minima*. This process from the ampulla of examples examined from both Texas and Florida, although showing minor individual variation (Fig. 3), does not vary seasonally in *C. minima*. Other structures of the genitalia also exhibit individual variation (e.g., the saccus in Figs. 3a, 3b), but we did not observe any temporally varying differences in the genitalia of either sex.

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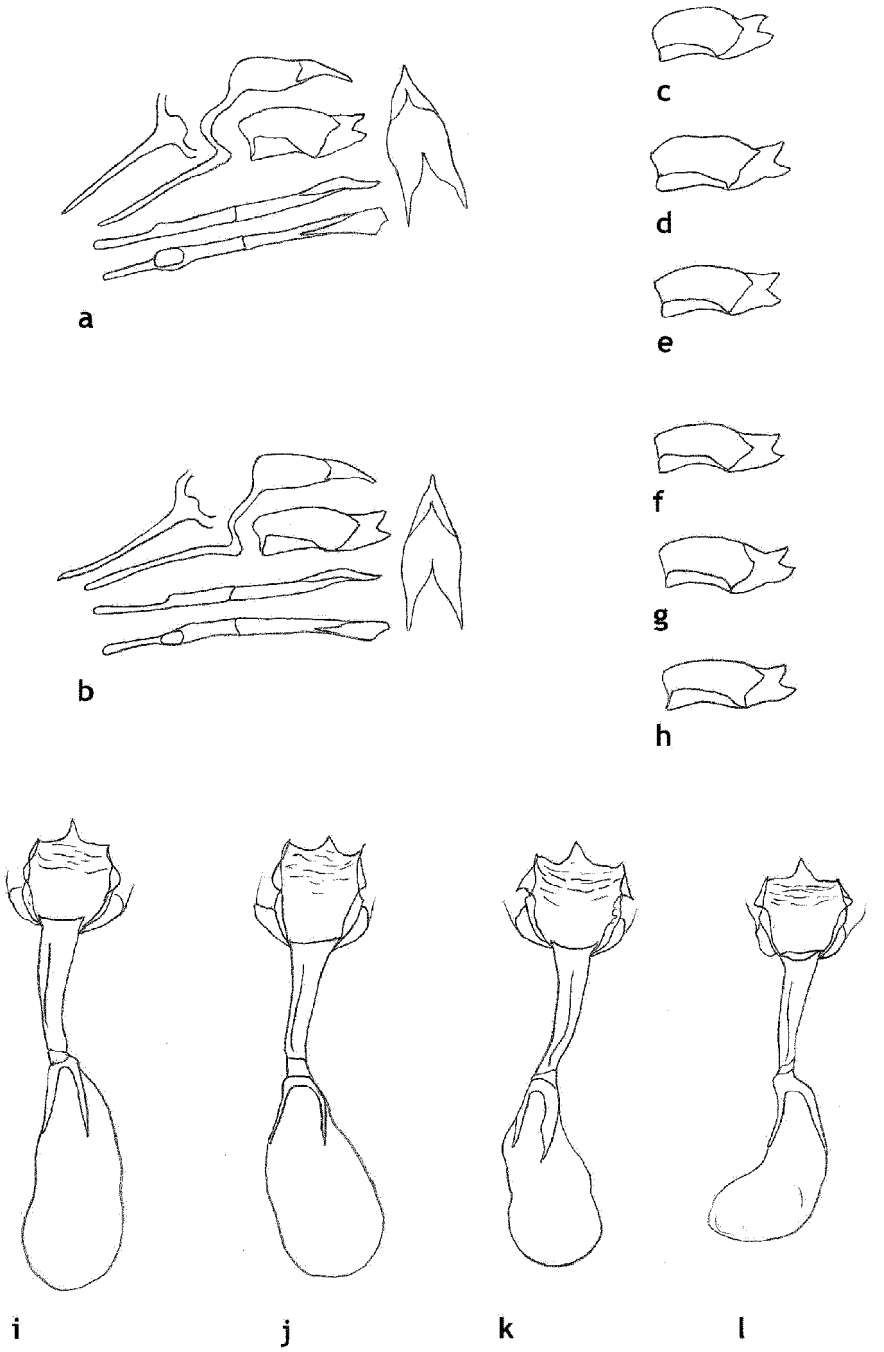


Fig. 3. Genitalia of *Copaeodes minima*: (a-h) male, lateral view of uncus, tegumen, and saccus; ventral view of saccus; dorsal view of tegumen and uncus; internal view of right valva; and lateral and dorsal views of aedeagus): (a) pale form - FLORIDA: Cass, 24 July 1953 (GTA #13858), (b) dark form - FLORIDA: Collier Co.; 30 January 1938 (GTA #13851); valvae only pale form - (c) FLORIDA: no location, 28 April 1944 (GTA #13854), (d) LOUISIANA: Sunshine, 11 September 1972 (GTA #13848), (e) FLORIDA: Cass, 29 April 1952 (GTA #13847); valvae only dark form - (f) TEXAS: Bexar Co., 9 November 1978 (GTA #13849), (g) FLORIDA: Duval Co.; Jacksonville, 30 October 1964 (GTA #13852), (h) FLORIDA: Collier Co.; Naples, 30 January 1938 (GTA #13851); (i-l) female, ventral view of sterigma, ostium, ductus bursae, and corpus bursae. (i) pale form - FLORIDA: Hendry Co.; Clewiston, 22 August 1962 (GTA #13902), (j) dark form - TEXAS: Willacy Co., 6 November 1985 (GTA #13910), (k) dark form - FLORIDA: Lake Willamasset, 22 February 1949 (GTA #13907), (l) pale form - TEXAS: Nueces Co.; Corpus Christi, August (GTA #13911).

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Taxonomy. *Hesperia minima* was named from at least 1 male from Waco (McLennan County), Texas (Edwards 1870). The number of specimens examined was not indicated. Edwards often stated the use of multiple specimens for a description when they were available. Brown & Miller (1977) located only 1 specimen labeled "minima" by Edwards and assumed it to be the holotype. That male, a pale phenotype, was illustrated, but with a figure caption calling it the "lectotype" (Brown & Miller 1977). Two additional names have been applied to this taxon, *Thymelicus singularis* Plötz, 1884 (*nomen nudum*, Mielke 2005) and *Copaeodes rayata* Barnes & McDunnough, 1913. The latter, described from 7 males and 3 females taken in mid-Jul in San Benito, Texas, is of the typical pale phenotype (Barnes & McDunnough 1913; see Fig. 4, note that most of the hindwings and part of the forewings on this specimen are stained and appear darker than the unstained portion, this is less noticeable on color images) and does not apply to a "winter" form (*contra* Durden 1982). To establish its unquestionable identity, clearly demonstrate that it is strictly synonymous with *C. minima*, and does not represent the dark form of *C. minima*, the specimen illustrated by Barnes & McDunnough (1913) on Plate III, Fig. 1 (also Fig. 4 herein) is here designated the lectotype of *Copaeodes rayata*. That specimen is housed at the National Museum of Natural History, Washington, DC, USA.

In conclusion, *Copaeodes minima* expresses variation in its phenotype with a dark form that most frequently occurs during the time of year with a short photoperiod, but is apparently cued by low temperature during development. This form does not have distinct genitalia and is not described by the name *Copaeodes rayata*.

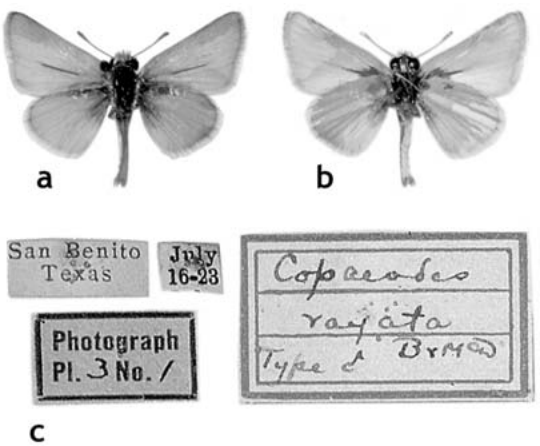


Fig. 4. Lectotype male of *Copaeodes rayata* Barnes and McDunnough, 1913. (a) dorsal surface, (b) ventral surface, (c) labels.

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LITERATURE CITED

AUSTIN, G. T. 1988. *Apodemia palmerii* (Lycaenidae: Riodininae): misapplication of names, two new subspecies and a new allied species. J. Res. Lepid. 26: 125-140.

BARNES, W., AND J. H. MCDUNNOUGH. 1913. New N. Am. Lepidoptera with notes on described species. Contrib. Nat. Hist. Lepid. North America 2: 93-162.

BROCK, J. P., AND K. KAUFMAN. 2003. Butterflies of North America. Houghton Mifflin, New York. 384 pp.

BROWN, F. M., AND L. D. MILLER. 1977. The types of the hesperiid butterflies named by William Henry Edwards. Part II, Hesperiidae: Hesperiinae: section I. Trans. American Entomol. Soc. 103: 259-302.

BURNS, J. M. 1964. Evolution in skipper butterflies of the genus *Erynnis*. Univ. California Publ. Entomol. 37: 1-214.

DE JONG, R. 1984. Notes on the genus *Thymelicus* Hübner (Lepidoptera, Hesperiidae). Nota lepid. 7: 148-163.

DE PRINS, W., D. VAN DER POORTEN, AND R. DE JONG. 1992. Rhopalocera and Grypocera of Turkey 10. Description of the female of *Thymelicus novus* (Reverdin, 1916) and additional notes on the female of some *Thymelicus* species (Lepidoptera: Hesperiidae). Phegea 20: 137-150.

DURDEN, C. J. 1982. The butterfly fauna of Barton Creek Canyon at the Balcones Fault Zone, Austin, Texas, and a regional list. J. Lepid. Soc. 36: 1-17.

DURDEN, C. J. 2007. DesertLeps Message 2905 (14 Nov. 2007). http://pets.groups.yahoo.com/group/DesertLeps/message/2905 (acc. 26 Nov. 2007).

EDWARDS, W. H. 1870. Descriptions of new North American diurnal Lepidoptera. Trans. American Entomol. Soc. 3: 189-196.

EDWARDS, W. H. 1871. The Butterflies of North America, Vol. 1. American Entomol. Soc., New York. 163 pp.

ENDO, K., AND Y. MURAKAMI. 1985. Photoperiodic control of the determination of three different seasonal phenomena in the swallowtail butterfly, *Papilio xuthus* L. Zool. Sci. 3: 755-760.

ENDO, K., Y. MARUYAMA, AND K. SASAKI. 1985. Environmental factors controlling seasonal morph determination in the small copper butterfly, *Lycaena phlaea daimio* Seitz. J. Insect Physiol. 31: 525-532.

EVANS, W. H. 1955. A Catalogue of the American Hesperiidae in the British Museum. Part IV. Hesperiinae and Megathyminae. British Museum (Natural History), London. 499 pp.

FORBES, W. T. M. 1960. Lepidoptera of New York and Neighboring States. Part IV. Agaristidae through Nymphalidae including Butterflies. Mem. Cornell Univ. Agric. Exp. Sta. 371: 1-188.

HIDAKA, T., AND H. TAKABASHI. 1967. Temperature conditions and maternal effect as modifying factors in

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the photoperiodic control of the seasonal forms in *Polygonia c-aureum* (Lepidoptera, Nymphalidae). Annot. Zool. Jap. 40: 200-204.

HOFFMANN, R. J. 1974. Environmental control of seasonal variation in the butterfly *Colias eurytheme*: effects of photoperiod and temperature on the pteridine pigmentation. J. Insect Physiol. 20: 1913-1924.

ISHII, M., AND T. HIDAKA. 1979. Seasonal polymorphism of the adult rice-plant skipper, *Parnara guttata guttata* (Lepidoptera: Hesperiidae) and its control. Appl. Entomol. Zool. 14: 173-184.

KIMBALL, C. P. 1965. The Lepidoptera of Florida. An Annotated Checklist. Division of Plant Industry, State of Florida Department of Agriculture, Gainesville, FL. 363 pp.

LEUSSLER, R. A. 1938. An annotated list of the butterflies of Nebraska, with the description of a new species (Lepid.: Rhopalocera). Entomol. News 49: 3-9, 76-80, 213-218, 275-280.

LEWIS, J. E. 1985. Temperature induced seasonal melanism in the wings of *Copaeodes minima* (Lepidoptera: Hesperiidae). Florida Entomol. 68: 667-671.

LINDSEY, A. W., E. L. BELL, AND R. C. WILLIAMS, JR. 1931. The Hesperioidea of North America. Denison Univ. Bull. Jour. Sci. Lab. 26: 1-142.

MCALPINE, W. S. 1971. A revision of the butterfly genus *Calephelis* (Riodinidae). J. Res. Lepid. 10: 1-125.

MACNEILL, C. D. 1975. Subfamily Hesperiinae, pp. 425-508 *In* W. H. Howe [ed.], The Butterflies of North America. Doubleday, Garden City, NY. 633 pp.

MIELKE, O. H. H. 1969. Novos Hesperiinae brasileiros (Lepidoptera, Hesperiidae). Revta bras. Biol. 29: 1-12.

MIELKE, O. H. H. 2005. Catalogue of the American Hesperioidea: Hesperiidae (Lepidoptera). Vol. 4. Hesperiinae: 1: *Adlerodea - Lychnuchus*. Sociedade Brasileira de Zoologia, Curitiba. pp. 775-1058.

NIJHOUT, H. F. 1999. Control mechanisms of polyphenic control in insects. BioSci. 49: 181-192.

OLIVER, C. G. 1970. The environmental regulation of seasonal dimorphism in *Pieris napi oleracea* (Pieridae). J. Lepid. Soc. 24: 77-81.

OLIVER, C. G. 1976. Photoperiodic regulation of seasonal polyphenism in *Phyciodes tharos* (Nymphalidae). J. Lepid. Soc. 30: 260-263.

OPLER, P. A., AND G. O. KRIZEK. 1984. Butterflies East of the Great Plains, an Illustrated Natural History. John Hopkins Univ. Press, Baltimore. 294 pp.

PYLE, R. M. 1981. The Audubon Society Field Guide to North American Butterflies. A. A. Knopf, New York. 925 pp.

REINHARDT, R. 1969. Über den Einfluss der Temperatur auf den Saisondimorphismus von *Araschnia levana* L. (Lepidopt. Nymphalidae) nach photoperiodischer Diapause-Induktion. Zool. Jabrb. Physiol. 75: 41-75.

RILEY, T. J. 1980. Effects of long and short day photoperiods in the seasonal dimorphism of *Anaea andria* (Nymphalidae) from central Missouri. J. Lepid. Soc. 34: 330-337.

ROSKAM, J. C., AND P. M. BRAKEFIELD. 1999. Seasonal polyphenism in *Bicyclus* (Lepidoptera: Satyridae) butterflies: different climates need different clues. Biol. J. Linn. Soc. 66: 345-356.

SAKAI. T., AND S. MASAKI. 1965. Photoperiod as a factor causing seasonal forms in *Lycaena phlaeas daimio* Seitz (Lepidoptera: Lycaenidae). Kontyû 33: 275-283.

SCOTT, J. A. 1986. The Butterflies of North America, a Natural History and Field Guide. Stanford Univ. Press, Stanford, CA. 583 pp.

SCUDDER, S. H. 1889. The butterflies of the Eastern United States and Canada with Special Reference to New England. Publ. by author, Cambridge, MA. 1958 pp.

SHAPIRO, A. M. 1974. The butterfly fauna of the Sacramento Valley, California. J. Res. Lepid. 13: 73-82, 115-122, 137-148.

SHAPIRO, A. M. 1975. Genetics, environment, and subspecies differences: the case of *Polites sabuleti* (Lepidoptera: Hesperiidae). Great Basin Nat. 35: 33-38.

SHAPIRO, A. M. 1976. Seasonal polyphenism. Evol. Biol. 9: 259-333.

SHAPIRO, A. M. 1977. Photoperiod and temperature in phenotype determination of Pacific slope Pierini: biosystematic implications. J. Res. Lepid. 16: 193-200.

SHAPIRO, A. M. 1978a. The assumption of adaptivity in genital morphology. J. Res. Lepid. 17: 68-72.

SHAPIRO, A. M. 1978b. The evolutionary significance of redundancy and variability in phenotypic-induction mechanisms of pierid butterflies (Lepidoptera). Psyche 85: 275-283.

SHAPIRO, A. M. 1984. Polyphenism, phyletic evolution, and the structure of the pierid genome. J. Res. Lepid. 23: 177-195.

SKINNER, H., AND R. C. WILLIAMS. 1923. On the male genitalia of the Hesperiidae of North America. Paper III. Trans. American Entomol. Soc. 49: 129-153.

SMITH, K. C. 1991. The effects of temperature and daylength on the *rosa* polyphenism in the buckeye butterfly, *Precis coenia* (Lepidoptera: Nymphalidae). J. Res. Lepid. 30: 225-236.

TVETEN, J. V., AND G. TVETEN. 1996. Butterflies of Houston and Southeast Texas. Univ. Texas Press, Austin. 304 pp.

WARREN, A. D. 2005. Lepidoptera of North America 6. Butterflies of Oregon. Their Taxonomy, Distribution, and Biology. Proc. C. P. Gillette Museum of Arthropod Diversity. Colorado State Univ., Fort Collins, CO. 408 pp.

WARREN, A. D. 2006. The Higher Classification of Hesperiidae (Lepidoptera: Hesperioidea). PhD Dissertation, Oregon State Univ. 458 pp.

WARREN, A. D., J. R. OGAWA, AND A. V. Z. BROWER. *in press*. Phylogenetic relationships of subfamilies and circumscription of tribes in the family Hesperiidae (Lepidoptera: Hesperioidea). Cladistics 24.

WINDIG, J. J., P. M. BRAKEFIELD, N. REITSMA, AND J. M. G. WILSON. 1994. Seasonal polyphenism in the wild: survey of wing patterns in five species of *Bicyclus* butterflies in Malawi. Ecol. Entomol. 19: 285-298.

WINDIG, J. J., AND P. LAMMAR. 1999. Evolutionary genetics of seasonal polyphenism in the map butterfly *Araschnia levana* (Nymphalidae: Lepidoptera). Evol. Ecol. Res. 1: 875-894.

YATA, O., T. SAIGUSA, A. NAKANISER, H. SHIMA, Y. SUZUKI, AND A. YOSHIDA. 1984. Seasonal polyphenism in four Japanese *Pieris* (*Artogeia*) species, pp. 317-320 *In* R. I. Vane-Wright and P. R. Ackery [eds.], The Biology of Butterflies. Academic Press, New York. 429 pp.

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