Volume 9, Number 10 **31 December 2021**

The Taxonomic Report

OF THE INTERNATIONAL LEPIDOPTERA SURVEY

ISSN 2643-4776 (print) / ISSN 2643-4806 (online)

Reevaluation of the described subspecies of *Euphydryas phaeton* (Drury, 1773) with a replacement name for *Melitaea phaeton schausi* (Clark, 1927).

Harry Pavulaan
606 Hunton Place NE
Leesburg, Virginia, 20176, U.S.A.

ABSTRACT. The present paper reevaluates the subspecific standing of the nominotypical and three described subspecies of *Euphydryas phaeton* (Drury, 1773). The nominotypical subspecies *phaeton* occupies the mid-Atlantic region, with undefined zones of contact with described subspecies *borealis* (F. Chermock & R. Chermock, 1940) to the north, and subspecies *schausi* (Clark, 1927) to the south. Nominotypical *phaeton* is an intermediate phenotype between *borealis* and *schausi*, which are each noticeably different from each other but both reasonably similar to intermediate (nominotypical) *phaeton*. Both *borealis* and *schausi* were synonymized under nominotypical *phaeton* since about time of their descriptions, by authors and list makers who did not justify their reasoning for essentially ignoring the original descriptions. The common belief is that there is no phenotypic difference between the three described northeastern subspecies and all are treated as nominotypical *E. p. phaeton.* In the present analysis, recently described subspecies *ozarkae* (Masters, 1968) bears a striking resemblance to *schausi*, making delineation of the zone of contact between the two very difficult, other than by habitat and primary host preference of each. Subspecies *schausi*, having been originally described within the genus *Melitaea*, is preoccupied by the name *Melitaea schausi* (Godman & Salvin, 1901), presently considered a junior synonym of *Chlosyne definita definita.* Thus, a replacement name for *schausi* (Clark, 1927) is necessary.

INTRODUCTION

A reevaluation of the four described subspecies of *Euphydryas phaeton* is presented here. Two of the subspecies, *schausi* and *borealis,* while each described in accurate detail, were subsequently ignored by many authors and list makers, who did not justify their reasoning for essentially ignoring the original descriptions, thus giving one a clear picture of "armchair taxonomy" and how it affects future analyses of lepidoptera, and no doubt other organisms. Each is evaluated here, based first on the taxon's original description, followed by the interpretations of authors and list makers of the time. A new analysis is finally presented that shows convincing differences between southeastern subspecies *schausi* and northern subspecies *borealis.* Nominotypical *phaeton* is an intermediate phenotype between the southern and northern subspecies, making it very similar to each when only compared to either southern or northern populations individually. Only when one compares *schausi* to *borealis,* are differences very evident. An interesting issue arises when comparing *ozarkae* to *schausi.* Careful comparison of both phenotypes shows a remarkable similarity. No new taxonomic realignments are proposed here in this regard.

***Melitaea phaeton* (Drury, 1773)**

Melitaea phaeton was originally illustrated as a drawing in Illustrations of Exotic Entomology, Vol. 1 (Drury, 1773: plate 21) (**Fig. 2**) along with a description and location (New York) on pages 42-43 (**Fig. 1**). Drury opted to not apply the Linnean name system, but simply referenced "*phaeton*" in the Index, thus technically leaving the illustrated species in Vol. 1 unnamed. Apparently, an Index to the First Volume was published with Vol. 2 (Drury, 1773), but not in early prints (Calhoun, pers. corr.). That Index included the binomial names of specimens illustrated in Vol. 1, thus making the date of description 1773 per ICZN Opinion 474 (ICZN, 1957). The name *Melitaea phaeton* is found along with the text in the Westwood Edition of Illustrations of Exotic Entomology, Vol. 1 (Westwood, 1837: page 39) (**Fig. 3)**. Westwood references Plate 21 from the original Vol. 1 of Drury (1773); also appropriately numbered as Plate 21 in the Westwood Edition. The illustration fairly well matches typical specimens of *Euphydryas phaeton* from the Mid-Atlantic region centered around New York City. The precise origin of the original specimen illustrated by Drury is unknown, but was likely collected by his correspondent in the New World, Thomas James, who lived in Brooklyn, N.Y. and frequently sent specimens to Drury in England. Thus, the specimen that served for the original illustration was most likely collected in the rural western end of Long Island. See discussion in Calhoun (2010) and also Pavulaan (2020) for details and circumstances surrounding Drury's collection and personal contacts. Interestingly, the illustrated type in Drury (1773) is more aligned with the *schausi* phenotype. Assuming it was collected in New York, it represents a variant. [This paper will not attempt to refine the original TL.]

FIG. III. and IV. Expands three inches and almoſt three quarters.

Upper-ſide.—The *Antennæ*, *Head*, *Eyes*, *Back* and *Abdomen*, are black.—The *Superior Wings*, alſo are black; with nine red ſpots placed near the external edges; above which are two rows of ſpots, of a lemon colour, with ſome other ſmall ones placed near the upper edges.—The *Inferior Wings*, likewiſe, are black, having eight red ſpots placed cloſe to the external edges; the two next the abdominal corner, being almoſt united. Theſe, as alſo thoſe on the ſuperior wings, being nearly of a triangular form. Above theſe is a row of lemon coloured ſpots, ſhaped like creſcents; and above that is another row of lemon coloured ſpots, that are nearly round, all placed circularly, anſwering to the ſhape of the wing.—The *Edges* of all the wings, are even.

Under-ſide.—The *Palpi* and *Legs*, are red.—The *Superior Wings*, are black, with a red indented margin. Along the external edge, is a row of lemon coloured creſcents above it. Near the anterior edge, about the middle of each wing, are two larger red ſpots, and a leſſer one at the corner, next the ſhoulders. The remainder of the wings, is ſprinkled with lemon coloured ſpots, of different ſhapes and ſizes, in all about twenty-ſix on each.—The *Inferior Wings*, are black, having their external-edges margined with triangular red ſpots; above which, is a row of lemon coloured creſcents; and over theſe, is a row of round lemon coloured ſpots. The remaining part of the wings, is covered with lemon coloured and red ſpots; the former very ſmall, and the latter pretty large, angularly ſhaped.

I received it from New York, where my correſpondent aſſures me, he has caught them in June and September; from whence he is induced to believe there are two broods in a year.

I have not ſeen it deſcribed in any author.

Fig. 1: Original description of *Melitaea phaeton* [unnamed] in Illustrations of Exotic Entomology, Vol. 1 (Drury, 1773: pages 42 and 43)

Fig. 2: Original illustration of *Melitaea phaeton* in Illustrations of Exotic Entomology, Vol. 1 (Drury, 1773)

MELITÆA PHAETON.

Plate XXI. fig. 3. 4.

ORDER: Lepidoptera. SECTION: Diurna. FAMILY: Nymphalidæ, *Swe.*

GENUS. MELITÆA, *Fabr.* Argynnis, *Latr. et God.* Papilio (Dan. Festiv.), *Drury.*

MELITÆA PHAETON. Alis subrotundatis integerrimis, nigris, singularum extimo suprà, paginâ omni subtùs fulvo flavoque maculatis. (Expans. Alar. 3 unc. 9 lin. fere.)

SYN. Papilio (Dan. Festiv.) Phaeton, *Drury, App. v.* 2. *Fabr. Ent. Syst.* III. 1. *p.* 46. *No.* 140. *Cramer, pl.* 193. *f.* C. D. Argynnis Phaetontea, *Latr. et God. Enc. Méth.* ix. *p.* 288. *Boisdur. Hist. nat. Lep. pl.* 7. *B. f.* 3.

HABITAT: New York; taken in June and September, whence there are probably two broods in the year.

Upper Side. Body and wings black. The anterior pair of the latter with nine red spots placed near the external edges; above which are two rows of spots, of a lemon colour, with some other small ones placed near the upper edges. Posterior wings with eight red triangular spots, placed close to the external edges. Above these is a row of lemon-coloured crescents; and above that is another row of lemon-coloured round spots. The wings are entire.

Under Side. Anterior wings black, with a red indented margin; within the external edge is a row of lemon-coloured crescents. Near the costa, about the middle of each wing, are two larger red spots, and a smaller one at the corner, next the shoulders. The remainder of the wings is sprinkled with lemon-coloured spots, of different shapes and sizes, in all about twenty-six on each. Posterior wings black, having their external edges margined with triangular red spots; above which is a row of lemon-coloured crescents; and over these is a row of round lemon-coloured spots. The remaining part of the wings is covered with lemon-coloured and red spots; the former very small, and the latter rather large, and angularly shaped.

Fig. 3: Revised description of *Melitaea phaeton* in Illustrations of Exotic Entomology, Vol. 1 (Westwood Edition of Illustrations of Exotic Entomology, Vol. 1 (1837).

For purposes of synonymy, the aberrant forms "**superba**" (Strecker, 1878) and "**phaethusa**" (Hulst, 1881) were each described from specimens taken on Long Island, New York, thus remaining synonyms of *E. p. phaeton.* Pelham (2008) misspelled "phaethusa" as **"phaetusa".** Aberrant form "**streckeri**" (Ellsworth, 1902) was described from a specimen taken in Broome County, N.Y., thus associated as a synonym of *E. p. phaeton.* Hübner (1816) described ***Melitaea phaëtaena***, by description apparently an aberrant form of *phaeton* [translated to read: "The wings brick red colored, cheerful yellow bands and with black lines alternately drawn"] - which was subsequently misspelled by Barnes & McDunnough (1917) as ***Euphydryas phaetana***. Godart (1819) misspelled the species as ***Melitaea phaetontea***, a synonym, which was subsequently misspelled by Barnes & McDunnough (1917) as ***Euphydryas phaetoneta***. Herrich-Schäffer, G. A. W. (1865) misspelled the species as ***Melitaea phaedon***, a synonym. Holland (1889) misspelled the species as ***Melitaea phaëtona***, a synonym.

***Euphydryas phaeton schausi* (Clark, 1928)**

In 1928, Austin Clark described new subspecies *E. phaëton schausi*. He compared nominotypical specimens of what he referred to as the "southern form" from Maryland and Virginia against specimens of what he referred to as the "northern form" from New York, Massachusetts and New Jersey. Clark makes comparisons between specimens from Cabin John, MD and Alexandria, VA (*schausi*) against samples from: Stoneham, Lincoln, Weston, and Newtonville, MA; Kendall, NY; and New Jersey (no locality). He states: "We find no difficulty in distinguishing specimens from New Jersey and northward from those from the vicinity of Washington. Typical examples of each are very distinct…" Clark's original description follows:

> "*Characters*.- Closely resembling *E. phaëton phaëton* (pl. 1, figs. 1-4) from eastern Massachusetts, but with the ground color of the upper surface of the wings deep velvety black, usually, but not always, duller and more grayish in the females, instead of blackish brown, and the light markings white instead of light straw yellow; on the fore wings the orange spots in the middle and at the tip of the cell are usually much reduced and commonly (occasionally in the northern form) entirely absent; the eight orange spots along the margin of the wing are smaller, due to the broadening of the band of black scales along the veins between them and a rounding off of their outer angles by an invasion of black scales; they are frequently very much reduced in size, especially in the females, and may be almost wholly obliterated by black scales; in the northern form the three apical spots are usually noticeably larger than the others, extending inward between the veins for a greater distance, but in the southern form these spots may be all of the same size, as is usual in the females, or they may decrease regularly from the apex posteriorly, as is usual in the males; on the hind wings there is very seldom any trace of orange except for the submarginal row of spots, which are restricted by a broadening of the narrow black border of the wings and a heavier development of black scales along the veins, especially in the females; beneath, the marginal band of orange spots is narrower than in the northern form with a more deeply crenate inner margin, and the orange markings in the basal half of the hind wings are more or less reduced by a greater development of black along the veins and an invasion of black on all sides; the light markings on the under side are also purer white than in the northern form."

Maximum wing expanse measurements (wingtip-to-wingtip of mounted specimens) of *schausi* indicated males (n=99) ranged between 45.0 to 64.0 mm, averaging 52.5 mm; females (n=61) ranged between 50.4 to 67.8 mm, averaging 60.3 mm. By comparison, males from New Jersey to Massachusetts (n=17) ranged between 49.4 to 60.0 mm, averaging 54.5 mm; females (n=8) ranged between 54.0 to 69.8 mm, averaging 59.5 mm).

The variety "**magnifica**" (Clark, 1928) was described from a specimen taken at the *schausi* TL in Maryland, thus remaining under the synonymy of *E. p. schausi.*

Literature Treatment 1929-1940

Clark (1929, 1932) oddly listed Washington D.C. area *phaeton* as subspecies *phaeton* only one year, then again four years, after he described subspecies *schausi*. It is unclear what course of events led to this taxonomic change of heart by the author of *schausi* himself. One possibility is hinted at, in the Nomenclature section of each paper. Clark indicates in each of the 1929 and 1932 papers that nomenclature is based on Barnes & Benjamin (1926), which was published prior to the description of *schausi.* It might be conjectured that Clark felt obliged to adhere to the most recent major synonymic checklist, or this adherence was insisted upon by peer reviewers William T. M. Forbes of Cornell University and William J. Holland of the Carnegie Museum. In a curious comment, Clark (1932) states: "But whatever the status of the more or less unfamiliar names may be the fact remains that radical innovations in nomenclature, whether justified or not, are wholly out of place in a local list. The object of a local list is to make clear the relation of the local fauna to the fauna of the larger area…This can be done only if in the local list a system of nomenclature is used which is in general agreement with the

nomenclature employed in similar lists…" This change, initiated by Clark himself, is likely the reason why *schausi* remained the "forgotten" subspecies and ignored by subsequent authors.

Field (1938) discussed *E. phaeton* in Kansas and Missouri and noted a phenotypic difference from northeastern nom. *phaeton*.

McDunnough (1938) lists *E. phaeton* and treats *schausi* as a junior synonym.

The following authors treated *phaeton* at species level only, for various states and regions: The Natural History Society of Maryland (1936); Saunders (1932); Wild (1939).

***Euphydryas phaeton borealis* (F. H. Chermock & R. L. Chermock, 1940)**

In 1940, brothers Frank Chermock and Ralph Chermock described new subspecies *E. phaëton borealis*. They started their description first with a conclusion:

> "In 1927, Dr. Austin H. Clark, recognized two distinct races of *E. phaeton*, the one a northern race and the other a southern race. He considered the northern race as typical and redescribed the southern race from Maryland specimens, calling it *schausi.* The southern race represents typical *phaeton,* therefore *schausi* becomes a synonym of *phaeton* leaving the northern race without a name. Dr. Clark, because of our study and extensive material on hand, has advised us to describe this unnamed northern race."

One can immediately see here a possible misinterpretation of Clark's description of "southern" (*schausi*) and "northern" (nominotypical *phaeton*) races by the Chermocks. By "southern" race, Clark described subspecies *schausi* from Maryland and Virginia, that differed from the nominotypical *phaeton* in the region of New York, New Jersey and Massachusetts, which Clark referred to as the "northern" race. Clark had correctly given ample discussion of nominotypical *phaeton* being the "northern" race. The Chermocks subsequently concluded the southern race (*schausi*) represented "typical *phaeton*" (despite the fact that nominotypical *phaeton* was described from New York) without real analysis or justification, then claimed this left the "northern" race without a name, which according to Clark, it did in fact: *E. p. phaeton*. The best interpretation I can determine is what the Chermocks might have intended to convey is that they considered *schausi* synonymous with nominotypical *phaeton* over the broad region from Virginia to Massachusetts, thus representing the "southern" race. However, Clark had not addressed populations north of Massachusetts, so the Chermocks defined a new geographic region for the "northern race". The description of ssp. *borealis* follows:

> "Upper side: the ground color of this race is a jet black, almost glossy, in contrast to the dull sooty black of typical *phaeton*; the orange marginal spots of *phaeton* are replaced by large, almost red markings which form a rather wide band intersected only by the black veins. The red spots in the cells of both wings are large and pronounced; white markings similar to *phaeton*.
>
> Lower surface: The red markings on this surface are again large and very pronounced; white markings similar to the typical form.
>
> Male wingspread averages about 42 mm.; female wingspread averages about 47 mm. Generally, this race is smaller than typical *phaeton.*"

The Chermocks list holotype and paratype locations from the following areas: Enfield, Lincoln, and Portland, ME; Hamilton, and Mer Bleue, ON; Georgeville, Knowiton, and Lanoroie QC; Baddeck, NS. This defines, in part, the range of *borealis* as determined by the Chermocks. Masters (1968) describes the range as "Maine and Quebec, into the Maritime Provinces – and interestingly, also in western Wisconsin and Minnesota…separated from the nominate subspecies by a sharp cline."

Literature Treatment 1941-1968

Clark (1951) interestingly, dropped use of the trinomial name *schausi* in The Butterflies of Virginia and simply applied the species name *phaëton.*

Klots (1951) recognized both subspecies *phaeton* and *borealis,* but noted: "These poorly differentiated subspecies are really statistical gradations in a cline."

Tietz (1952) lists *E. phaeton* at species rank for Pennsylvania, with *schausi* as a synonym.

Furguson (1953) recognized Nova Scotia populations as *E. phaeton borealis.*

Mather & Mather (1958) list *E. phaëton phaëton* for Mississippi.

Forbes (1960) recognized both ssp. *phaëton* for New York and *borealis* as the northern race.

dos Passos (1964) listed subspecies *phaeton* and *borealis.*

The following authors also treated *phaeton* at species level only, for various states and regions: Kimball & Jones (1943); Macy & Shepard (1941); Moore (1960), Ehrlich & Ehrlich (1961); Shapiro (1966).

Euphydryas phaeton ozarkae (Masters, 1968)

Prior to the description of *ozarkae,* W. Hoffmeister (1881) described larvae in Lee County, IA (later determined to be ssp. *ozarkae*) feeding on *Aureolaria pedicularia*. Field (1938) first noted that specimens from Kansas and Missouri differed from *phaeton* in places such as Pennsylvania, New York, Maine, Wisconsin…" and suggested "Whether this material represents a new subspecies …has not yet been determined." Masters (1968) described subspecies *ozarkae* from interior North American populations that inhabit a different habitat type: dry valleys, hillsides, high well-drained hilltops, and thinly wooded ridges; and that feed primarily on *Aureolaria grandiflora*. His description follows:

"*Male* (Figs. 1, 2). – The same general appearance as nominate *E. phaeton* (Figs. 3, 4) but the red coloring is paler and of a more yellow cast. With an expanse of one forewing (base to apex) of 28 to 32 mm it is somewhat larger.

Upperside (Fig. 1): Marginal red spots are reduced in size. Black lines over veins are wider and the black marginal band invades the red band, resulting in a wider spacing of the red spots. Red spots at apex of the forewing tend to be narrow, in no case are they wider than high. Red spots in forewing cell are not well developed – 75% of specimens have only one poorly defined spot; in the remainder one spot is weakly developed and there is a faint suggestion of the second.

Underside (Fig. 2): White coloring tends to be "whiter" than on the nominate subspecies. Discal cluster of red spots are more broken and separated by black.

The genitalia (Fig. 9) do not differ from the nominate subspecies.

Female (Figs. 5, 6). – The same general appearance as nominate *phaeton* (Figs. 7, 8) but the red coloring is reduced – often wanting altogether on upper surfaces – and is of a paler, yellower cast. Very large size – expanse of one forewing (base to apex) 31 to 38 mm.

Upperside (Fig. 5): Forewing discal red is not present. Marginal red spots, if present, have a distinctly triangular shape and are reduced in size so that the space between them is as large as the spots themselves. White areas tend to be larger and "whiter" – four white bands are present on the forewing, fusing to three near the anal angle. Outer row of white spots are larger than marginal row of red spots on forewing.

Underside (Fig. 6): Discal red pattern appears to be more broken because of the wider separation of the spots. White rows tend to be wider and more regular."

At the time of the description of *ozarkae*, Masters (1968) gave the range of *ozarkae* as: Springfield, and vicinity of St. Louis, MO; Brown Co., IL; Lawrence and vic., KS; Ottawa Co., OK; and northern Arkansas. Masters commented: "While *Chelone glabra* is found throughout the Ozarks, I never found *E. phaeton* in association with it but rather with *Aureolaria*." Dole, *et al.* (2004) indicate the range of *phaeton* extending into northeast Texas, and *Plantago lanceolata* is listed as an additional host for that region. Schlicht *et al.* (2007) show *ozarkae* in extreme southeast Iowa. Interestingly, Harris (1972) writes that all Georgia specimens to his knowledge were collected on "hillsides and mountain slopes" with the host unknown and with no evidence of *Chelone glabra*. This highlights the need for more detailed fieldwork to define the eastern range of *ozarkae.* Due to phenotypic similarity to *schausi* from the present analysis, the conclusion is that *ozarkae* can be more reliably defined by habitat and primary hostplant association. Differentiating populations of *ozarkae* from *schausi* in the intervening region of the Ohio River watershed will rely heavily on host and habitat associations rather than phenotype alone.

Literature Treatment 1969-2021

Harris (1972) refers to Georgia populations as nominotypical *E. p. phaeton.* [Interestingly, all cited reports are from upland habitats, suggestive of eastward influence of *ozarkae*.]

Irwin & Downey (1973) recognized *E. p. phaeton* and *E. p. ozarkae* separately as subspecies, and indicated their separate distributions in Illinois.

Brower (1974) treats Maine populations as *E. p. borealis.*

Howe (1975) lists *E. p. phaeton* and *E. p. ozarkae* at full subspecific rank, but discusses regional variation in *E. phaeton* with great clarity: "Through the years several names have been proposed for variations among northern, central and southern populations. *E. phaeton*, described from New York, has the intermediate central coloring and pattern. The name *borealis*…was given to the northern color variation with larger, redder marginal spots and glossy jet black coloring above. The name *schausi*…is characterized as being blacker in ground color, with whiter light spots and narrower orange markings. The type locality [*phaeton*] is in a transitional area." Under the entry for subspecies *E. p. phaeton*: "If names are desired for these variations *phaeton, borealis* and *schausi* are available, but…these names do not represent separate populations, only the two extremes and middle of a cline."

Opler & Krizek (1984) simply commented: "Several subspecies of uncertain merit have been proposed. The most valid of these seem to be *E. phaeton phaeton* and *E. phaeton ozarkae* Masters. These two subspecies may be distinguished on the basis of adult coloration, habitat, and food plant."

Mather & Mather (1976, 1985) list *E. phaëton ozarkae* for Mississippi (1976), with a grammatical name correction to *phaeton* (1985).

Miller & Brown (1981) listed *E. p. phaeton* and *E. p. ozarkae* as subspecies; with *schausi* and *borealis* as junior synonyms of ssp. *phaeton.*

Hodges (1983) listed *E. p. phaeton* and *E. p. ozarkae* as subspecies; with *schausi* and *borealis* as junior synonyms of ssp. *phaeton.*

Sedman & Hess (1985) treat west central Illinois populations as subspecies *ozarkae.*

Scott (1986) recognized only *E. p. phaeton* and *E. p. ozarkae* as subspecies.

Vawter & Wright (1986) conducted a study of genetic differentiation between *E. p. phaeton* and *E. p. ozarkae* and found a lack of allozyme differentiation between New York and Missouri population samples. They concluded that populations so genetically similar are unlikely to be separate species. The authors erroneously stated that only "two subspecies have been described".

Heitzman & Heitzman (1987) treat Missouri populations as subspecies *ozarkae.*

Shull (1987) recognized *E. p. phaeton* and *E. p. ozarkae* separately as subspecies, and noted that only nominotypical *phaeton* has been found in Indiana

Klassen, *et al.* (1989) suggest that Manitoba populations are nominotypical *E. p. phaeton*, but state: "The number of Baltimore subspecies is still under investigation."

Ferris, C. D. (1989) listed *E. p. phaeton* and *E. p. ozarkae* as subspecies.

Iftner, *et al.* (1992) treat Ohio populations as nominotypical *E. p. phaeton.*

Miller (1992) recognized two subspecies, *E. p. phaeton* and *E. p. ozarkae.*

Poole & Gentili (1996) do not recognize subspecies for *E. phaeton*, and list *schausi*, *borealis* and *ozarkae* as junior synonyms.

Neck (1996) indicates the Texas records are subspecies *ozarkae.*

Allen (1997) treats West Virginia populations as nominotypical *E. p. phaeton.* However, the specimens illustrated from Elkins (plate 15, row 5) align with the *schausi* phenotype.

Layberry, *et al.* (1998) state that "only the nom nominotypical inate subspecies is found in Canada" and do not recognize *borealis.* However, the specimen illustrated from Ottawa (plate 15, no. 28) is clearly *borealis*.

Bouseman & Sternburg (2001) recognized *E. p. phaeton* and *E. p. ozarkae* separately as subspecies, and indicated their separate distributions in Illinois.

Cech & Tudor (2005) treat *E. phaeton* at species rank and comment: "Baltimores living in dry, upland forest of the Ozark Mountains were formerly considered a separate race…but more recent investigations failed to support this distinction (Vawter & Wright, 1986). Indeed, "Ozark-like" upland populations are also now known from New England and New York." [The authors clearly do not recognize phenotypic differences for *E. phaeton* as qualifying for subspecific status, and no subsequent study has been done on purported dry-habitat *phaeton* in the northeast other than anecdotal references.]

Schlicht, *et al.* (2007) recognized *E. p. phaeton* and *E. p. ozarkae* separately as subspecies, and indicated their separate distributions in Iowa.

Scott (2008) recognizes only subspecies *E. p. phaeton* and *E. p. ozarkae,* then lists *borealis* as a synonym of *E. p. phaeton*, and does not recognize *schausi.*

Belth (2013) recognized *E. p. phaeton* and *E. p. ozarkae* separately as subspecies, and noted that only nominotypical *phaeton* has been found in Indiana, but that *ozarkae* may eventually be found in southern Indiana.

Spencer (2014) treats Arkansas populations as subspecies *ozarkae.*

Jeffords, *et al.* (2014) recognized *E. p. phaeton* and *E. p. ozarkae* separately as subspecies, and indicated their separate distributions in Illinois.

Monroe & Wright (2017) recognize Pennsylvania populations as nominotypical subspecies *E. p. phaeton.*

Pohl, *et al.* (2018) list only subspecies *E. p. phaeton* for Canada.

The following authors treat *phaeton* at species level only, for various states and regions: Acorn & Sheldon (2016); Allard (2013); Allen, *et al.* (2005); Betros (2008); Blakney (2015); Blakney & Gallagher (2020); Brock & Kaufman (2003); Carmichael & Vance (2003); Cossey (2016, 2017); Covell (1999); Daniels (2003, 2004a, 2004b, 2005); Douglas & Douglas (2005); Ebner (1970); Ely, *et al.* (1986); Feltwell & Hargreaves (1992); Glassberg (1993, 1999, 2017); Gochfeld & Burger (1997); Grehan, *et al.* (1995); Hall, *et al.* (2014); Handfield (2011); Holmes, *et al.* (1991); Howell & Charny (2010); Jones & Schaeffer (2012); Kiel (2003); Kimball & Jones (1943); Leboeuf & Le Tirant (2012); Mello & Hansen (2004); Nielsen (1999); O'Donnell, *et al.* (2007); Ogard & Bright (2010); Opler & Malikul (1998); Patterson (2011); Pyle (1981); Riotte (1992); Shapiro (1974); Shapiro & Shapiro (1973); Smith & Domingue (2019); Stichter (2015); Veilleux & Prévost (1976); Venable (2014); Wagner (2005); Weber (2002, 2006); Woodbury (1994).

COMMENTS ON DESCRIBED *E. PHAETON* SUBSPECIES

The recent traditional treatment has been to recognize either *phaeton* at species rank only (mainly for publications covering regions in the north and east), while others include *ozarkae* as distinct for its life history aspects. There is scant mention of *borealis* at subspecies rank in the literature (Klots, 1951; Ferguson, 1953; Forbes, 1960; dos Passos, 1964; Brower, 1974; Howe, 1975). What is interesting to note is that subspecies *schausi* has been nearly completely ignored by authors subsequent to its description by Clark in 1928 (with the exception of discussion in Howe, 1975) and considered simply part of the northeastern nominotypical subspecies populations. Subspecies *ozarkae*, was recognized immediately by authors after its original description by Masters in 1968, and despite habitat and primary host differences from eastern *E. phaeton* populations, appears phenotypically similar to subspecies *schausi*. Southern Appalachian Mountain records of *phaeton* are phenotypically closer to *ozarkae*. Harris (1972) describes dry upland populations in Georgia which might be considered *ozarkae*. Were it not for habitat and host differences, the two might even be considered consubspecific based on phenotype alone. An unresolved issue is the lack of published habitat, host and life history observations specific to the intervening region between the Appalachian Mountains and the Ozark Region. Presently, there is no information suggesting where *schausi* grades or transitions over to *ozarkae.* Images of *E. phaeton* photographed in Tennessee that are posted to butterfliesandmoths.org show distinct *ozarkae* phenotypes throughout much of that state, but host and habitat information are lacking. Several observations in the eastern United States indicate that isolated dry, upland populations that feed on *Aureolaria* occur near *Chelone glabra* in wet habitats in the surrounding region with no evidence of feeding on *Chelone glabra*, thus suggesting that, at least, nominotypical *phaeton* and subspecies *schausi* may be capable of adapting to habitat and host changes

that would be suggestive of *ozarkae*. These have been reported from Connecticut (Saunders, 1932) and western North Carolina.

HOSTS

E. phaeton of the northeastern U.S. and eastern Canada is historically known to dwell primarily in marshy habitats, wet meadows, brushy swamps, fens, bogs, sphagnum bogs, boggy ditches, boggy swales, mesic pastures, poorly drained pastureland, open woodland seeps, oak-pine barrens, streamsides and lake edges where the primary host *Chelone glabra* (White Turtlehead) occurs. Host use of *Chelone glabra* was first reported by W. H. Edwards (1884), in West Virginia, then by Scudder (1889), in Massachusetts. Later observations by multiple authors reported that larvae have been found on the secondary hosts *Aster* sp. (Aster), *Aureolaria flava* (Smooth Yellow False Foxglove), *Aureolaria grandiflora* (Largeflower False Foxglove), *Aureolaria pedicularia* (Fernleaf False Foxglove), *Camissonia campestris* (=*Oenothera dentata* var. *parishii*) (Mojave Suncup), *Corylus* sp. (Hazelnut), *Crataegus acrosperma* (Bigfruit Hawthorn), *Dasistoma macrophylla* (Mullein Foxglove), *Fraxinus americana* (=*biltmoreana*) (White Ash), *Fraxinus pennsylvanica* (Green Ash), *Galeopsis tetrahit* (Brittlestem Hemp Nettle), *Lonicera canadensis* (=*ciliata*) (American Fly Honeysuckle), *Lonicera japonica* (Japanese Honeysuckle), *Lonicera oblongifolia* (Swamp Fly Honeysuckle), *Lonicera tatarica* (Tatarian Honeysuckle), *Lonicera xylosteum* (Dwarf Honeysuckle), *Mimulus ringens* (Allegheny or Square-stemmed Monkey Flower), *Pedicularis canadensis* (Canadian Lousewort or Wood Betony), *Penstemon digitalis* (Foxglove Beardtongue), *Penstemon hirsutus* (Hairy Beardtongue), *Plantago lanceolata* (English or Narrowleaf Plantain), *Plantago rugelii* (Pale Plantain), *Rhinanthus minor* (=*crista-galli*) (Little Yellow Rattle), *Ribes nigrum* (European Black Currant), *Sagitaria* sp. (Arrowhead), *Salix* sp. (Willow), *Scrophularia marilandica* (Carpenter's Square), *Scrophularia nodosa* (Woodland Figwort), *Solidago* sp. (Goldenrod), *Symphoricarpos albus* (Common Snowberry), *Symphoricarpos orbiculatus* (Coralberry), *Typha latifolia* (Broadleaf Cattail), *Valeriana edulis* var. *ciliata* (Tobacco Root), *Valerianella radiata* (Beaked Corn Salad), *Verbesina alternifolia* (Wingstem), *Veronica* sp. (Speedwell), *Viburnum dentatum* (Southern Arrowwood), *Viburnum opulus* (=*trilobum*) (American Cranberry Bush), and *Viburnum recognitum* (Smooth Arrowwood). Some of the listed hosts might be in error, misidentified, or larvae were simply found on them, but not feeding. Southern New England populations have recently switched their primary host to *Plantago lanceolata*, with an associated switch to dry, open field habitats; resulting in frequent explosive population irruptions. Masters (1968) first documented populations in the U.S. interior feeding on *Aureolaria grandiflora*, which he described as subspecies *ozarkae*. Interestingly there is an account of larvae selecting *Aureolaria flava* on a "high, dry rocky ridge" in Connecticut (Saunders, 1932; O'Donnell, *et al.,* 2007) but this was never further researched. Clark (1928) indicated that captive larvae will not accept *Wisteria* (Wisteria). Saunders (1932) indicates captive larvae will not eat *Viburnum plicatum* var. *tomentosum* (Japanese Snowball).

TAXONOMY

Euphydryas phaeton clarki* Pavulaan, 2021 *nomen novum

The subspecific name ***Euphydryas phaeton clarki*** is proposed to replace *Euphydryas phaeton schausi* (Clark, 1928), preoccupied by *Melitaea schausi* (Godman & Salvin, 1901) which is presently considered a subjective synonym of ***Chlosyne definita definita*** (E. Aaron, 1885). The same data (i.e., holotype, type locality) from the description of *E. p. schausi* (Clark, 1928) applies to *clarki* (I.C.Z.N. Code Article 60.3). The name *clarki* recognizes Austin H. Clark, who first described *schausi.*

Comparison of the four described subspecies

Dorsal wing characters	*borealis*	*phaeton*	*clarki* (=*schausi*)	*ozarkae*
ground color	glossy pure black	dark grayish black	sooty grayish black	dark grayish black
FW maximum length males	20-24 mm	21-26 mm	23-29 mm	24-30 mm
FW maximum length females	25-27 mm	26-29 mm	28-34 mm	30-35 mm
FW wing cell, inner orange mark	Enlarged, well-defined	Well developed, very enlarged, round, faded in some individuals	Mostly absent, variable with faded edges	Mostly absent, variable with faded edges
FW wing cell, outer orange mark	Enlarged, well-defined	Well developed, variable, enlarged irregular shape	Mostly absent, variable, with faded edges	Variable, weakly developed
FW marginal spot row alignment	Solid band, separated by black wing veins	Solid band, crenate (toothed) on inner edge, separated by black wing veins	Variable, mostly very reduced, spots separated by wide black wing veins	Very reduced, spots separated by black
FW marginal spot row color	Red	Deep orange	Deep orange	Deep orange
Shape of FW marginal spots	Distinctly square	Variable, connected U- or V-shapes	Variable, mostly rectangular, faded at edges, some with U-shape	Very reduced, appearing rounded, faded at edges
FW submarginal spot color	White with slight cream tint	White with slight cream tint	Cream	White
FW presence of submedian pattern	Only a single white dot in the wing cell	Variable, mostly weakly-developed	Absent but some have faded ghost pattern	Few white spots, but absent in most
HW wing cell, orange mark	Highly variable, mostly weakly present	Absent to mostly weakly present	Absent	Absent
HW marginal spot row alignment	Broad, forming a solid band, divided by black wing veins	Broad, forming row of connected U-shapes, divided by black wing veins	Variable, mostly very reduced, spots separated by wide black wing veins	Much reduced, divided by broad black areas
HW marginal spot row color	Red	Deep orange	Deep orange	Deep orange
Shape of HW marginal spots	Filled U-shape.	Filled U-shape.	Filled U or V-shape	Much reduced, rounded irregular shape with faded edges
HW submarginal spot row	Very thin, line-like crescents.	Broad crescents, shaped like thickened V	Broad crescents, shaped like thickened V	Broad crescents, many stretched into V-shapes
HW presence of submedian pattern	White spots absent	Variable, ghost pattern reflective of venter	Mostly absent, ghost pattern reflective of venter in some	Mostly absent, ghost pattern in some

Fig. 4. Chart comparison of the four described *E. phaeton* subspecies.

Fig. 5. Dorsal phenotypic comparison of the four described *E. phaeton* subspecies. Males on left, females on right. Subspecies from top to bottom: *borealis* (Edmundston, NB), *phaeton* (Pinelawn, NY), *clarki* (Harmans, MD), *ozarkae* (Sullivan, MO). Printed specimen images are actual size.

Conclusion

E. phaeton appears to consist of a broad cline from northeast (*borealis*) to southwest (*ozarkae*) (**Fig. 6**). The subspecies *borealis* (**Fig. 5**) is smallest, characterized by its glossy, pure black dorsal ground color and sharply-defined, deep red markings. Subspecies *ozarkae* (**Fig. 5**) is largest, characterized primarily by its very reduced deep orange markings, the marginal ones of which are rounded and display faded edges. Host and habitat presently define this subspecies. Subspecies *clarki* (**Fig. 5**) is phenotypically most similar to *ozarkae*. Where *clarki* transitions into *ozarkae* remains to be studied. The two subspecies may overlap by their habitat (dry upland vs. wetland) and primary host (*Chelone* vs. *Aureolaria*) choices. However, this may be unreliable as dry upland *Aureolaria*-associated populations tentatively identified as *ozarkae* have been documented in the east, especially in northern Georgia and Alabama.

Nominotypical subspecies *phaeton* (**Fig. 5**) is most similar to *borealis* but is clearly a transitional form between *borealis* and *clarki*. It is highly variable, characterized by well-developed interior orange markings. A small percentage of specimens could be assigned to either *borealis* or *clarki*. Thus, authors who simply compare subspecies *phaeton* to *borealis* might be tempted to dismiss *borealis* as nothing more than a variant, or synonym, of *phaeton.* Similarly, authors who simply compare subspecies *phaeton* to *clarki* might be tempted to dismiss *clarki* as nothing more than a variant, or synonym, of *phaeton.* However, when comparing subspecies *clarki* to *borealis*, the contrasting phenotypes are obvious. Despite the temptation to synonymize the names of populations within clines, especially transitional phenotypes in the middle of a cline, does this suggest dropping nominotypical *phaeton* from usage? Per rules of the I.C.Z.N., once a nominotypical taxon is described and named, that name permanently applies to that taxon, even if synonymized. But recognizing the clear differences between populations at the ends of a cline merits their recognition as named entities.

Species *E. phaeton* presents a challenge to taxonomists and evolutionary biologists. The mechanics of a cline in this species calls for further study. Relationships need to be thoroughly studied among different habitat and host-associated populations.

DISTRIBUTION

The nominotypical subspecies *phaeton* ranges from southern New England west to Illinois, primarily north of the Ohio River and into the Great Lakes region (**Fig. 6**). Subspecies *borealis* ranges throughout the Canadian Maritimes, across northern Maine, into far eastern Ontario. Some specimens from Wisconsin appear to be *borealis*, but most are *phaeton* or intermediate to *phaeton.* In eastern Ontario, male specimens appear close to *borealis*, while females appear closer to *phaeton.* Subspecies *ozarkae* ranges from Missouri and southern Illinois, east into Tennessee, Mississippi, Alabama and Georgia, and includes an isolated population in Texas. This distribution is based primarily on populations inhabiting dry, upland habitats with no association with *Chelone*. Subspecies *clarki* consists of *Chelone*-associated populations from Maryland, southward in the Appalachian Mountains. Where *clarki* and *ozarkae* meet or overlap remains problematic. Phenotypically, specimens from the Carolinas and Kentucky are difficult to assign to either subspecies, and there is virtually no life history information from this region. Though they may be differentiated by habitat and host associations, it remains to be determined what *Aureolaria*-feeding populations in this intervening region are properly referred to.

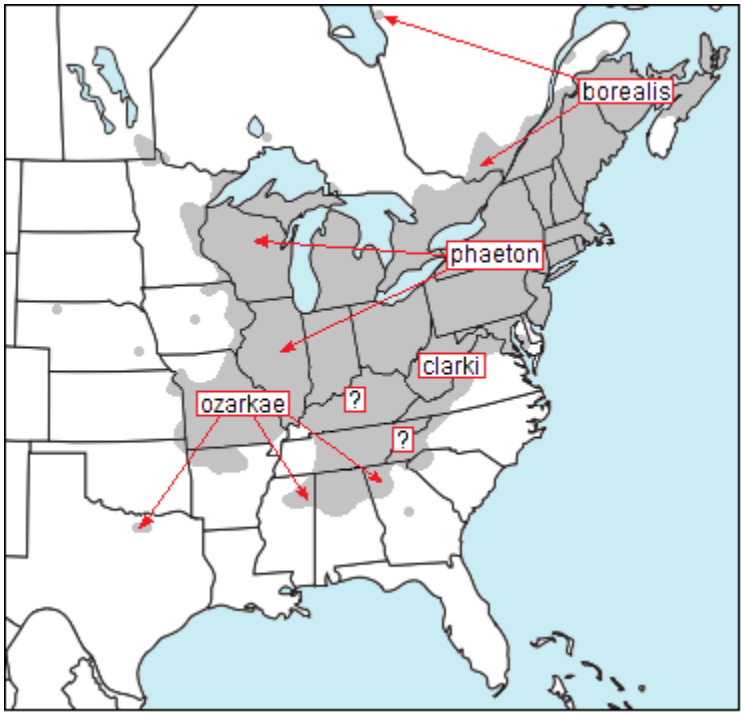

Fig. 6. Approximate ranges of *E. phaeton* subspecies. Red arrows point to range extensions. Question marks indicate region in question where *clarki* transitions into *ozarkae*.

PROPOSED REVISION

The following revision is proposed. *Euphydryas phaeton* is divided into four previously described subspecies with a replacement name for *schausi* (Clark, 1928). Reference is made to Pelham (2008) with its original species numbers. Synonymic treatments (subjective synonyms, misspellings, variety and aberration names) are all preceded by "=" with text in grey tint.

Euphydryas phaeton (Drury, 1773) [ref. Pelham (2008), #699]

Euphydryas phaeton phaeton (Drury, 1773) [ref. Pelham (2008), #699a]

= ***phaetaena*** Hübner (1816) [ref. Pelham (2008), #699a, original description indicates an aberrant form]

= ***phaetontea*** Godart (1819) [misspelling; original description vague and general]

= ***phaedon*** Herrich-Schäffer, G. A. W. (1865) [misspelling]

= ***phaetona*** Holland (1889) [misspelling]

= ***superba*** (Strecker, 1878) [ref. Pelham (2008), #699a, described as "variety"]

= ***phaethusa*** (Hulst, 1881) [ref. Pelham (2008), #699a, described as "aberrant"]

= ***streckeri*** (Ellsworth, 1902) [ref. Pelham (2008), #699a, described as "aberration or variety"]

= ***phaetoneta*** Barnes & McDunnough (1917) [misspelling of *phaetontea* Godart (1819)]

= ***phaetana*** Barnes & McDunnough (1917) [misspelling of *phaetaena* Hübner (1816)]

= ***phaetusa*** Pelham, 2008 [misspelling of "phaethusa" (Hulst, 1881)]

Euphydryas phaeton clarki (Pavulaan, 2021) [*nomen novum*]
= ***schausi*** (Clark, 1928) [ref. Pelham (2008), #699a, subjective synonym, preoccupied]
= ***magnifica*** (Clark, 1928) [ref. Pelham (2008), #699a, described as a "variety"]
Euphydryas phaeton borealis (F. H. Chermock & R. L. Chermock, 1940) [reinstated status; ref. Pelham (2008), #699a, subjective synonym]
Euphydryas phaeton ozarkae (Masters, 1968) [ref. Pelham (2008), #699b]

ACKNOWLEDGEMENTS

Thanks go to David Wright for review; Ricky Patterson for additional review; John Calhoun for comments and guidance on the historical circumstances of *E. phaeton's* original description.

LITERATURE CITED

Acorn, J. & I. Sheldon. 2016. Butterflies of Ontario & Eastern Canada. Partners Publishing, Edmonton, Alberta: 320 pp.

Allard, S. H. 2013. Manitoba Butterflies: A Field Guide. Turnstone Press, Winnipeg, Manitoba: x + 285 pp.

Allen, T. J. 1997. The Butterflies of West Virginia and Their Caterpillars. University of Pittsburgh Press, Pittsburg, Pennsylvania: xi + 388 pp.

Allen, T. J., J. P. Brock & J. Glassberg. 2005. Caterpillars in the Field and Garden: A Field Guide to the Butterfly Caterpillars of North America. Oxford University Press, New York, New York: viii + 232 pp.

Barnes, W. & F. H. Benjamin. 1926. Check List of the Diurnal Lepidoptera of Boreal America. Bulletin of the Southern California Academy of Sciences 25(1): 3-27.

Barnes, W. & J. McDunnough. 1917. Check List of the Lepidoptera of Boreal America. Herald Press, Decatur, Illinois: viii + 392 pp.

Belth, J. E. 2013. Butterflies of Indiana: A Field Guide. Indiana University Press, Bloomington, Indiana: 323 pp.

Betros, B. 2008. A Photographic Field Guide to the Butterflies in the Kansas City Region. A Local Color Nature Series, Kansas City Star Books, Kansas City, Missouri: vi + 407 pp.

Blakney, R. R. 2015. Northern Virginia Butterflies and Skippers. Published by author, Middletown, Delaware: 69 pp.

Blakney, R. R. & J. Gallagher. 2020. Butterflies of the Mid-Atlantic. Published by authors, Middletown, Delaware: 139 pp.

Bouseman, J. K. & J. G. Sternburg. Field Guide to Butterflies of Illinois. 2001. Illinois Natural History Survey, Manual No. 9: xii + 264 pp.

Brock, J. P. & K. Kaufman. 2003. Kaufman Field Guide to Butterflies of North America. Hillstar Editions L. C. & Houghton Mifflin Company, New York, New York: 392 pp.

Brower, A. E. 1974. A List of the Lepidoptera of Maine – Part 1: The Macrolepidoptera. Life Sciences and Agriculture Experiment Station, University of Maine at Orono, Maine. Technical Bulletin 66: 136 pp. + map.

Calhoun, J. V. 2010. Affirmation of the name *Papilio hyllus* Cramer (Lycaenidae) for a Nearctic butterfly, with the designation of a neotype. Journal of the Lepidopterists' Society 64(2): 79-90.

Carmichael, I. & A. Vance. 2003. Photo Field Guide to the Butterflies of Southern Ontario. St. Thomas Field Naturalist Club Inc., St. Thomas, Ontario: 76 pp.

Cech, R. & G. Tudor. 2005. Butterflies of the East Coast: an Observer's Guide. Princeton University Press, Princeton, New Jersey: xii + 345 pp.

Chermock, F. H. & R. L. Chermock. 1940. A new race of *Euphydryas phaeton* Dru. Proceedings of the Pennsylvania Academy of Science, Vol. 14: 140.

Clark, A. H. 1928. Notes on the Melitaeid butterfly *Euphydryas phaeton* (Drury), with descriptions of a new subspecies and a new variety. Proceedings of the United States National Museum, Smithsonian Institution, Washington, D.C. Vol. 71, article 11: 1-21 + 5 pl.

Clark, A. H. 1929. Preliminary list of the butterflies of the District of Columbia. Proceedings of the Biological Society of Washington No. 42: 113-116.

Clark, A. H. 1932. The Butterflies of the District of Columbia and Vicinity. Bulletin of the Smithsonian Institution, United States National Museum No. 157: ix + 337 pp.

Clark, A. H. & L. F. Clark. 1951. The Butterflies of Virginia. Smithsonian Miscellaneous Collections 116(7): v + 239 pp.

Cossey, J. 2016. Southern Ontario Butterflies and Their Natural History. Published by author, London, Ontario: 79 pp.

Cossey, J. 2017. Familiar Butterflies of Indiana and Their Natural History. Published by author, London, Ontario: 83 pp.

Covell, C. V. Jr. 1999. The Butterflies and Moths (Lepidoptera) of Kentucky. Kentucky State Nature Preserves Commission, Scientific and Technical Series No. 6: xiv + 220 pp.

Daniels, J. C. 2003. Butterflies of the Carolinas: Field Guide. Adventure Publications Inc., Cambridge, Minnesota: 414 pp.

Daniels, J. C. 2004a. Butterflies of Georgia: Field Guide. Adventure Publications Inc., Cambridge, Minnesota: 408 pp.

Daniels, J. C. 2004b. Butterflies of Ohio: Field Guide. Adventure Publications Inc., Cambridge, Minnesota: 342 pp.

Daniels, J. C. 2005. Butterflies of Michigan: Field Guide. Adventure Publications Inc., Cambridge, Minnesota: 376 pp.

dos Passos, C. F. 1964. A Synonymic List of the Nearctic Rhopalocera. The Lepidopterists' Society, Memoir No. 1: v + 145 pp.

Douglas, M. M. & J. M. Douglas. Butterflies of the Great Lakes Region. University of Michigan Press, Ann Arbor, Michigan: 345 pp.

Drury, D. 1770. Illustrations of Natural History, Vol. 1. Printed by author, London: xxvii + 132 pp. + 51 pls, + 4 figs.

Drury, D. 1773. Illustrations of Natural History, Vol. 2. Printed by author, London: vii + 94 pp. + 50 pls. [later editions included the binomial index for Vol. 1: xiii pp.]

Ebner, J. A. 1970. Butterflies of Wisconsin. Milwaukee Public Museum, Popular Science Handbook No. 12: viii + 205 pp.

Edwards, W. H. 1884. The Butterflies of North America: Vol. 2, Second Series. Houghton, Mifflin and Company, New York, New York: 299 pp.

Ehrlich, P. R. & A. H. Ehrlich. 1961. How to Know the Butterflies. Wm. C. Brown Company Publishers, Dubuque, Iowa: 262 pp.

Ellsworth, A. 1902. Notes on butterflies and description of an aberration. Entomological News 13(4): 103-104.

Ely, C. A., M. D. Schwilling & M. E. Rolfs. An Annotated List of the Butterflies of Kansas. Fort Hays Studies, Third Series (Science) No. 7: 224 pp.

Feltwell, J. & B. Hargreaves. 1992. Butterflies of North America. American Nature Guides, Smithmark Publishers, Inc., New York, New York: 192 pp.

Ferguson, D. C. 1953. The Lepidoptera of Nova Scotia. Proceedings of the Nova Scotian Institute of Science, 23(3): 161-375.

Ferris, C. D. 1989. Supplement to: A Catalogue/Checklist of the Butterflies of America North of Mexico. The Lepidopterists' Society, Memoir No. 3: vii + 103 pp.

Field, W. D. 1938. A Manual of the Butterflies and Skippers of Kansas (Lepidoptera, Rhopalocera). Bulletin of the University of Kansas, Biological Series 39(10): 328 pp. + 1 map.
Forbes, W. T. M. 1960. Lepidoptera of New York and Neighboring States: Agaristidae Through Nymphalidae Including Butterflies, Part 4. Cornell University Agricultural Experiment Station, Cornell University, Memoir No. 371: 188 pp.
Glassberg, J. 1993. Butterflies Through Binoculars: A Field Guide to Butterflies in the Boston-New York-Washington Region. Oxford University Press, New York, New York: 160 pp. + 40 pl.
Glassberg, J. 1999. Butterflies Through Binoculars, The East: A Field Guide to the Butterflies of Eastern North America. Oxford University Press, New York, New York: x + 242 pp.
Glassberg, J. 2017. A Swift Guide to Butterflies of North America. Princeton University Press, Princeton, New Jersey: 420 pp.
Gochfeld, M. & J. Burger. 1997. Butterflies of New Jersey: a Guide to their Status, Distribution, Conservation, and Appreciation. Rutgers University Press, New Brunswick, New Jersey: xxii + 327 pp. + 8 pl.
Godart, J. P. 1819. *In*: Latreille, M. & M. Godart. Encyclopédie Méthodique, Histoire Naturelle, Entomologie, ou Histoire Naturelle des Crustacés, des Arachnides et des Insectes. Chez M^{me}, Veuve Agasse, Imprimeur-Libraire, Paris, France. Vol. 9(1): i-ii + 328 pp.
Grehan, J. R., B. L. Parker, G. R. Nielsen, D. H. Miller, J. D. Hedbor, M. S. Sabourin & M. S. Griggs. 1995. Moths and Butterflies of Vermont (Lepidoptera): A Faunal Checklist. Vermont Agricultural Experiment Station and State of Vermont. Miscellaneous Publication No. 116: xi + 95 pp.
Hall, P. W., C. D. Jones, A. Guidotti & B. Hubley. 2014. Butterflies of Ontario. Royal Ontario Museum, Toronto, Ontario: 487 pp.
Handfield, L. 2011. Les Papillons du Québec. Broquet, Saint-Constant, Quebec: 672 pp. + 166 pl.
Harris, L. Jr. 1972. Butterflies of Georgia. University of Oklahoma Press, Norman, Oklahoma: xvi + 326 pp. + 1 chart.
Heitzman, J. R. & J. E. Heitzman. 1987. Butterflies and Moths of Missouri. Conservation Commission of the State of Missouri, Jefferson City, Missouri: viii + 385 pp.
Herrich-Schäffer, G. A. W. 1865. Prodromus Systematis Lepidopterorum. Versuch Einer Systematischen Anordnung der Schmetterling 9(21): 1-82.
Hodges, R. W. (ed.). 1983. Check List of the Lepidoptera of America North of Mexico. E. W. Classey Limited and The Wedge Entomological Research Foundation, London, England: xxiv + 284 pp.
Hoffmeister, W. 1881. Entomological Notes. Canadian Entomologist 13(9): 196.
Holland, W. J. 1898. The Butterfly Book: A Popular Guide to a Knowledge of the Butterflies of North America. Doubleday & McClure Company, Garden City, New York: xx + 382 pp. + 48 pl.
Holland, W. J. 1931. The Butterfly Book – New and Thoroughly Revised Edition: A Popular and Scientific Manual, Describing and Depicting all the Butterflies of the United States and Canada. Doubleday & Company, Garden City, New York: xii + 424 pp. + 77 pl.
Holmes, A. M., Q. F. Hess, R. R. Tasker & A. J. Hanks. 1991. The Ontario Butterfly Atlas. Toronto Entomologists' Association, Toronto, Ontario: viii + 167 pp,
Howe, W. H. (ed.). 1975. The Butterflies of North America. Doubleday & Company, Inc., Garden City, New York: xiii + 633 pp.
Howell, W. M. & V. Charny. 2010. Butterflies of Alabama. Pearson Learning Solutions, Boston, Massachusetts: vii + 509 pp.
Hübner, J. 1816. Verzeichniss Bekannter Schmettlinge. Augsburg, Germany: 72 pp.
Hulst, G. D. 1881. Description of some New Species of North American Lepidoptera. Bulletin of the Brooklyn Entomological Society 3(9): 75-77.

I.C.Z.N. 1957. Opinion 474. Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature 16(16): 299-306. https://www.biodiversitylibrary.org/item/107766#page/358/mode/1up
Iftner, D. C., J. A. Shuey & J. V. Calhoun. 1992. Butterflies and Skippers of Ohio. Bulletin of the Ohio Biological Survey – New Series 9(1): x + 212 pp.
Irwin, R. R. & J. C. Downey. 1973. Annotated Checklist of the Butterflies of Illinois. Illinois Natural History Survey, Urbana, Illinois. Biological Notes No. 81: 60 pp.
Jeffords, M. R., S. L. Post & J. R. Wiker. 2014. Butterflies of Illinois: A Field Guide. Illinois Natural History Survey, Manual No. 14: xvii + 406 pp.
Jones, A. & E. Schaeffer. 2012. A Guide to the Butterflies of Sewanee. Self-published by authors: 108 pp.
Kiel, W. J. 2003. The Butterflies of the White Mountains of New Hampshire. The Audubon Society of New Hampshire and Global Pequot Press, Guilford, Connecticut: xxviii + 195 pp.
Kimball, C. P. & F. M. Jones. 1943. Acknowledgements, Explanations, and Annotated List of the Lepidoptera of Nantucket and Marthas Vineyard Islands, Massachusetts. Publications of the Nantucket Maria Mitchell Association, Vol. 4: 22-198.
Klassen, P., A. R. Westwood, W. B. Preston & W. B. McKillop. 1989. The Butterflies of Manitoba. Manitoba Museum of man and Nature, Winnipeg, Manitoba: vi + 290 pp.
Klots, A. B. 1951. A Field Guide to the Butterflies of Eastern North America. The Peterson Field Guide Series, Houghton Mifflin Company, Boston, Massachusetts: x + 349 pp.
Layberry, R. A., P. W. Hall & J. D. Lafontaine. 1998. The Butterflies of Canada. University of Toronto Press, Toronto, Ontario: vii + 280 pp. + 32 pl.
Leboeuf, M. & S. Le Tirant. 2012. Papillons et Chenilles du Québec et des Maritimes. Éditions Michel Quintin, Waterloo, Québec: 391 pp.
Macy, R. W. & H. H. Shepard. 1941. Butterflies. A Handbook of the Butterflies of the United States, Complete for the Region North of the Potomac and Ohio Rivers and east of the Dakotas. The University of Minnesota Press, Minneapolis, Minnesota: vii + 247 pp.
Mather, B. & K. Mather. 1958. The Butterflies of Mississippi. Tulane Studies in Zoology 6(2): 63-109.
Mather, B. & K. Mather. 1976. The Butterflies of Mississippi – supplement no. 2. Journal of the Lepidopterists' Society 30(3): 197-200.
Mather, B. & K. Mather. 1985. The Butterflies of Mississippi – supplement no. 3. Journal of the Lepidopterists' Society 39(2): 134-138.
McDunnough, J. 1938. Check List of the Lepidoptera of Canada and the United States of America: Part 1 - Macrolepidoptera. Memoirs of the Southern California Academy of Sciences, Vol. 1: 275 pp.
Mello, M. J. & T. Hansen. 2004. Butterflies Across Cape Cod: A Guide to Finding, Attracting, and Observing Butterflies on the Cape. Cape Cod Museum of Natural History and Lloyd Center for Environmental Studies, John Hay Institute, Brewster, Massachusetts. Publication No. 1: iv + 114 pp.
Miller, J. Y. 1992. The Common Names of North American Butterflies. Smithsonian Institution, Washington D. C.: ix + 177 pp.
Miller, L. D. & F. M. Brown. 1981. A Catalogue/Checklist of the Butterflies of America North of Mexico. The Lepidopterists' Society, Memoir No. 2: vii + 280 pp.
Monroe, J. L. & D. M. Wright. 2017. Butterflies of Pennsylvania, a Field Guide. University of Pittsburgh Press, Pittsburgh, Pennsylvania: xiii + 304 pp.
Moore, S. 1960. A Revised Annotated List of the Butterflies of Michigan. Occasional Papers of the Museum of Zoology, University of Michigan, Ann Arbor, Michigan: 39 pp.
Neck, R. W. 1996. A Field Guide to Butterflies of Texas. Texas Monthly Field Guide Series. Gulf Publishing Company, Houston, Texas: xvii + 323 pp. + 64 pl.

Nielsen, M. C. 1999. Michigan Butterflies and Skippers: A Field Guide and Reference. Michigan State University Extension, East Lansing, Michigan: 248 pp.
O'Donnell, J. E., L. F. Gall & D. L. Wagner. 2007. The Connecticut Butterfly Atlas. State Geological and Natural History Survey, Bulletin No. 118: 376 pp.
Ogard, P. H. & S. Bright. 2010. Butterflies of Alabama: Glimpses into Their Lives. University of Alabama Press, Tuscaloosa, Alabama: xvii + 486 pp.
Opler, P. A. & G. O. Krizek. 1984. Butterflies East of the Great Plains: an Illustrated Natural History. The Johns Hopkins University Press, Baltimore, Maryland: xvii + 294 pp. + 54 pl.
Opler, P. A. & V. Malikul. 1998. Eastern Butterflies. Peterson Field Guides, Houghton Mifflin Company, New York, New York: xvii + 486 pp.
Patterson, J. 2011. The Butterflies of Minnesota: A 'Flier's Manual. Trafford Publishing, U.S.A.: 410 pp.
Pavulaan, H. 2020. Designation of neotype of *Hemileuca maia* (Drury, 1773) and refinement of its type locality (Bombycoidea, Saturniidae, Hemileucinae). The Taxonomic Report 8(4): 1-12.
Pelham, P. J. 2008. A Catalogue of the Butterflies of the United States and Canada, with a Complete Bibliography of the Descriptive and Systematic Literature. The Journal of Research on the Lepidoptera 40: xiv + 658 pp.
Pohl, G. R., J-F. Landry, B. C. Schmidt, J. D. Lafontaine, J. T. Troubridge, A. D. Macaulay, E. J. van Nieukerken, J. R. DeWaard, J. J. Dombroskie, J. Klymko, V. Nazari & K. Stead. 2018. Annotated Checklist of the Moths and Butterflies (Lepidoptera) of Canada and Alaska. Pensoft Publishers, Sofia, Bulgaria: 580 pp.
Poole, R.W. & P. Gentili. 1996. Nomina Insecta Nearctica: A Check List of the Insects of North America. Volume 3. Diptera, Lepidoptera, Siphonaptera. Entomological Information Services, Rockville, Maryland: 793 pp.
Pyle, R. M. 1981. National Audubon Society Field Guide to North American Butterflies. Alfred A. Knopf, Inc. & Chanticleer Press, Inc., New York, New York: 924 pp.
Riotte, J. C. E. 1992. Annotated List of Ontario Lepidoptera. Royal Ontario Museum, Publications in Life Sciences, Toronto, Ontario: viii + 208 pp.
Saunders, A. A. 1932. Butterflies of Allegheny State Park. New York State Museum Handbook No. 13: 270 pp.
Schlicht, D. W., J. C. Downey & J. C. Nekola. 2007. The Butterflies of Iowa. University of Iowa Press, Iowa City, Iowa: xii + 233 pp.
Scott, J. A. 1986. The Butterflies of North America: A Natural History and Field Guide Stanford University Press, Stanford, California: xiii + 583 pp.
Scott, J. A. 2008. Biological Catalogue of North American Butterflies. Papilio (New Series) No. 20: 1-51.
Scudder, S. H. 1889. The Butterflies of the Eastern United States and Canada, with Special Reference to New England. Vol. 1. Published by author, Cambridge, Massachusetts: xii + 766 pp.
Sedman, Y. & D. F. Hess. 1985. The Butterflies of West Central Illinois. Western Illinois University Series in the Biological Sciences, No. 11: 118 pp.
Shapiro, A. M. 1966. Butterflies of the Delaware Valley. Cushing – Malloy, Inc., Ann Arbor, Michigan. Special Publication of the American Entomological Society: vi + 79 pp.
Shapiro, A. M. 1974. Butterflies and Skippers of New York State. Search (Agriculture) 4(3): 1-60.
Shapiro, A. M. & A. R. Shapiro. 1973. The ecological associations of the butterflies of Staten Island. Journal of Research on the Lepidoptera 12(2): 65-128.
Shull, E. M. 1987. The Butterflies of Indiana. Indiana Academy of Science and Indiana University Press, Indianapolis, Indiana: viii + 262 pp.
Smith, C. R. & E. A. Domingue. 2019. Butterflies and Moths of the Smokies. Great Smoky Mountains Association, Gatlinburg, Tennessee: 301 pp.

Spencer, L. A. 2014. Arkansas Butterflies and Moths. Ozark Society Foundation, Little Rock, Arkansas: xiv + 314 pp.
Stichter, S. 2015. The Butterflies of Massachusetts. Published by author: 488 pp.
Strecker, H. 1878. Butterflies and Moths of North America, a Complete Synonymical Catalogue of Macrolepidoptera, with a Full Bibliography. B. F. Owen, Reading, Pennsylvania: ii + 283 pp. + 2 pl.
The Natural History Society. 1936. Familiar Butterflies of Maryland. The Natural History Society of Maryland & Enoch Pratt Free Library, Baltimore, Maryland: 30 pp.
Thomas, A. W. 1996. A Preliminary Atlas of the Butterflies of New Brunswick. New Brunswick Museum, Publications in Natural Science, No. 11: 41 pp.
Tietz, H. M. 1952. The Lepidoptera of Pennsylvania: a Manual. Pennsylvania State College, School of Agriculture, Agricultural Experiment Station, State College, Pennsylvania: xii + 194 pp.
Vawter, A. T. & J. Wright. 1986. Genetic differentiation between subspecies of *Euphydryas phaeton* (Nymphalidae: Nymphalinae). Journal of Research on the Lepidoptera 25(1): 25-29.
Veilleux, C. & B. Prevost. 1976. Les Papillons du Québec. Les Éditions de L'Homme, Montreal, Quebec: 142 pp. + 4 pl.
Venable, R. 2014. Butterflies of Tennessee. Maywood Publishing, Franklin, Tennessee: 391 pp.
Wagner, D. L. 2005. Caterpillars of Eastern North America. Princeton Field Guides, Princeton University Press, Princeton, New Jersey: 512 pp.
Weber, L. 2002. Butterflies of New England. Kollath-Stensaas Publishing, Duluth, Minnesota: x + 172 pp.
Weber, L. 2006. Butterflies of the North Woods: Minnesota, Wisconsin & Michigan. Kollath-Stensaas Publishing, Duluth, Minnesota: viii + 280 pp.
Westwood, J. O. 1837. Illustrations of Exotic Entomology, Containing Upwards of Six Hundred and Fifty Figures and Descriptions of Foreign Insects, Interspersed with Remarks and Reflections on Their Nature and Properties. By Dru Drury-A New Edition, Brought Down to the Present State of the Science, with the Systematic Characters of Each Species, Synonyms, Indexes and Other Additional Matter. Henry G. Bohn, London. Vol. 1: xxvi + 123 pp. + 20 pl.
Wild, W. 1939. The Butterflies of the Niagara Frontier Region and Beginner's Guide for Collecting, Rearing and Preserving Them. Bulletin of the Buffalo Society of Natural Sciences 19(1): 3-55.
Woodbury, E. N. 1994. Butterflies of Delmarva. Delaware Nature Society & Tidewater Publishers, Centreville, Maryland: xxii + 138 pp.