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THE CASE FOR TAXONOMIC RECOGNITION OF THE TAXON *ENODIA ANTHEDON BOREALIS* A.H. CLARK (SATYRIDAE)

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ABSTRACT. Clark (1936) described the taxa *anthedon* and *borealis* both as new subspecies of *Enodia portlandia* (Fabricius, 1781). Clark described *borealis* as the northernmost phenotypically different taxon in this group. *Anthedon* later became recognized as a distinct species with *borealis* as a subspecies of it. Masters (1971) characterized *E. anthedon borealis* as displaying several subtle phenotypic differences from nominotypical *anthedon* and also noted significant differences in behavior and habitat and reinforced the continued recognition of *borealis* as a valid subspecies. However, a number of publications after 1971 generally failed to recognize subspecific status for *borealis*, either ignoring *borealis* entirely (but frequently describing its habits and/or habitat as for species *anthedon*) or delegating it to status of junior synonym of nominotypical *anthedon*. This literary history is reviewed. This paper then presents current research which not only indicates *borealis* is a valid subspecies, but that some degree of speciation may be evident. Thus, the subspecific status of *borealis* is maintained and additional species status research is sought.

HISTORICAL TREATMENT OF *ANTHEDON* AND *BOREALIS* IN THE LITERATURE

AUSTIN H. CLARK 1936: REVIEW OF THE GENUS *ENODIA*

Enodia portlandia anthedon A.H. Clark, 1936 (Original Description)

Diagnosis: In general similar to *E. p. portlandia* (Fabricius); wings beneath without white; ocelli of fore wings beneath in a straight line; ocelli of hind wings beneath each with a circular white pupil. From *E. creola* (Skinner) it differs in the absence of white beneath; in having the post-median line on the under side of the fore wing with a slight angle, at vein 4; in the somewhat less produced primaries, especially of the male; and in the absence of the broad furry band on the upper surfaces of the primaries of the male.

Type: U.S.N.M. no. 51137 (William Barnes collection), from Lava, Sullivan County, N. Y., taken in June.

Enodia portlandia borealis A.H. Clark, 1936 (Original Description)

Diagnosis: Closely resembling *E. p. anthedon*; upper surface darker, with the dark margin of the hind wings broader and more uniform; lower surface darker and more brownish, usually with the ground color less varied and sometimes quite uniform, with only faint indications of a narrow lighter line enclosing the rows of spots on the fore and hind wings; on the hind wings the dark band between the light line enclosing the row of spots and the fine submarginal light line is, beyond the fourth and fifth spots, broader - usually much broader - than the distance between the submarginal line and the edge of the wing.

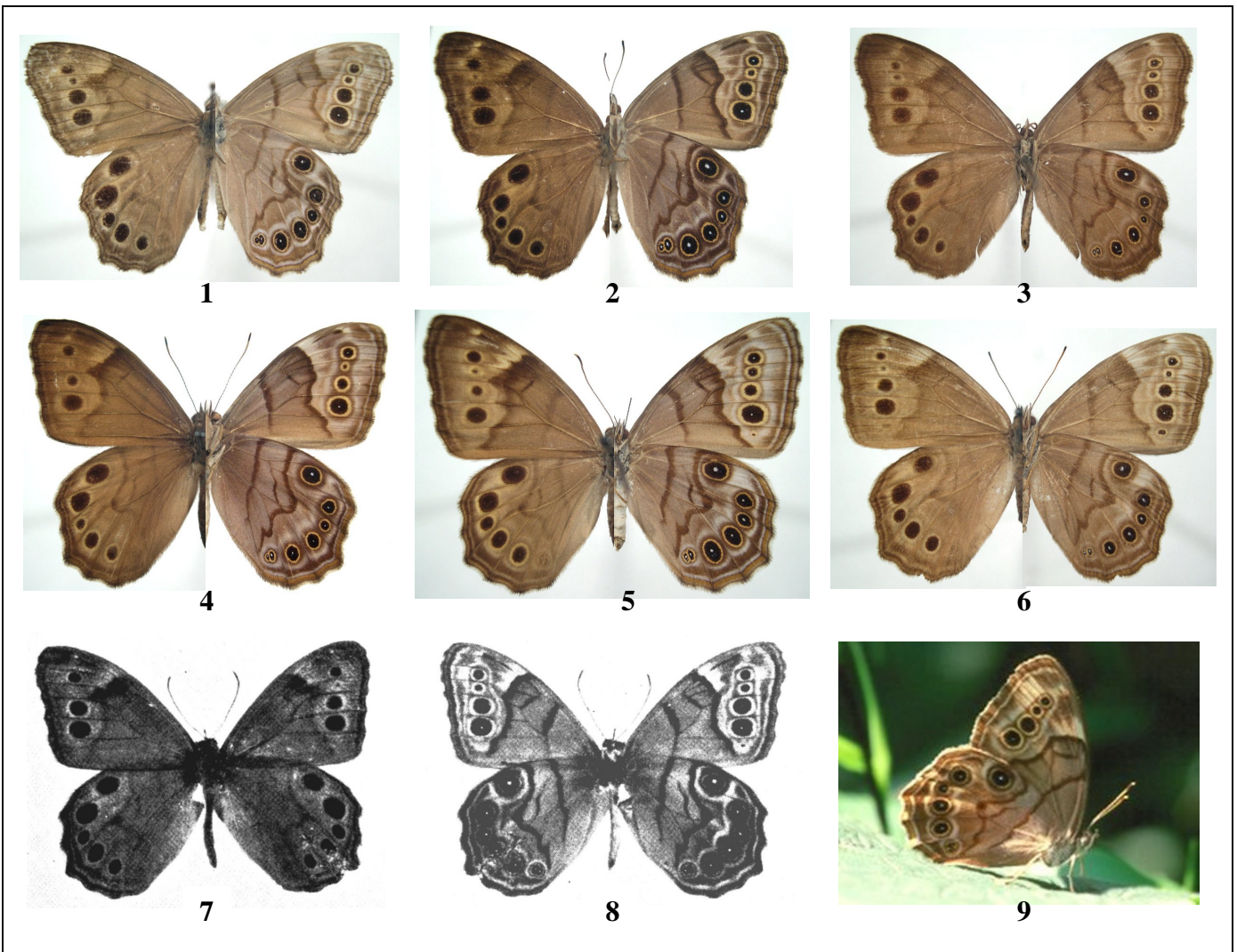
Type: U.S.N.M. no. 51138 (William Barnes collection), from Hymers, Ontario, July 1 – 7.

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Referring to *E. anthedon*, Clark makes the following statement:

A third form [*E. portlandia* and *E. creola* being the first two], occurring in the East from southern New Hampshire southward to the higher altitudes of North Carolina and possibly farther (pl. 22, figs. 1, 2) is lighter, less brightly marked, and usually smaller than true *portlandia*. This is the form referred to as *portlandia* by Skinner and Richards and by American authors generally. It is locally frequent in the mountains of Virginia, where its quick and active movements and its habit of keeping generally low down in the underbrush distinguish it rather sharply from the less active and commonly high flying true *portlandia* of the coastal region. Since none of the names that have been proposed for species of this genus is applicable to it, it may be known as *Enodia portlandia anthedon*.

It is interesting to note that the description of “*anthedon*” from the “mountains of Virginia” in the above paragraph is in fact quite suggestive of both the habitats and habits of *borealis*, as we discuss below. This brings into question whether *E. anthedon borealis* actually ranges far southward from its historically described range, and also whether records of “*anthedon*” from higher elevational areas of the middle and southern Appalachian Mountain regions should actually be applied to *borealis*.



Figures 1-9. *Enodia anthedon* subspecies. **Fig. 1** (D/V): ♂ *E. a. anthedon*: 4 July 2001, Merrimack, NH (leg. Grkovich). **Fig. 2** (D/V): ♂ *E. a. nr. borealis*: 15 July 2001, Rt. 112, Carroll Co., NH (leg. Grkovich). **Fig. 3** (D/V): ♂ *E. a. borealis*: 7 July 1984, Perthuis (Portneuf), Ouebec, Canada. **Fig. 4** (D/V): ♂ *E. a. anthedon*: 27 May 1994, Seneca, Montgomery Co., MD (leg. Pavulaan). **Fig. 5** (D/V): ♀ *E. a. anthedon*: 18 May 1996, Herndon, Fairfax Co., VA (leg. Pavulaan). **Fig. 6** (D/V): ♀ *E. a. borealis*: same data as Fig. 3. **Figs. 7-8** (D/V): ♂ holotype *E. anthedon* OD figures (1936). **Fig. 9** (V) ♀ *E. a. nr. borealis*: 27 July 2002, Doughton State Park, Alleghany Co., NC. Photos 1-6 by Joseph Mueller; photo 9 by Bruce Grimes.

Referring to *borealis*, Clark then writes:

Enodia portlandia borealis is very variable, but it seems always to be distinguished by the broader dark border on its hind wings above and by the relatively broad darker area between the row of spots and the submarginal light line on the hind wings below.

In his Original Description of *borealis*, Clark notes:

...twenty two specimens are at hand from the following localities:

Manitoba: Miniota, June 17, 1926, H. Gibbon (1); July 1, 1922 (1); July 10, 1920 (12). Winnipeg, July 1-7 (1); no date (1).

Ontario: Hymers, July 1-7 (2).

Quebec: Meech Lake, Ottawa County (1); somewhat intermediate between this and the previous [*antheson*] form.

Maine: Sebec Lake, July 16-23 (1); July 24-31 (2); more or less intermediate between this and the preceding form.

Clark then gives a “Key to the (...interrelationships of the...) forms included in the Genus *Enodia*”:

a 1. Male with the long fore wings more pointed than those of the female, above with a broad furry band interrupted at the veins and by long triangles in the interstices; under sides of forewings with post-medial line irregular, interrupted above vein 6, outwardly oblique between veins 6 and 4, and usually slightly indented on vein 5; on hind wings below the fourth ocellus is smaller than the fifth *creola* (pl. 22, figs. 5, 6)

a 2. Sexes practically alike; under side of fore wings with postmedial line more or less oblique from costa to vein 4, or just above it; on hind wings below the fourth ocellus is larger than the fifth *portlandia*

b 1. Wings beneath with the rows of ocelli edged with white interiorly and more or less completely exteriorly; on the fore wing a white band runs from the costa to the region of the second ocellus, and beyond this a narrower white band runs from the ocellus to the upper part of the first ocellus; row of ocelli on the under side of the fore wings curved; second and third ocelli on the under side of hind wings with elongate pupils, and fourth usually without a pupil *portlandia portlandia* (pl. 22, figs. 3, 4)

b 2. No white on wings beneath; row of ocelli on outer side of fore wings below straight; all the ocelli on hind wings below have similar circular pupils.

c 1. Dark border on hind wings above narrow and tapering anteriorly; on the hind wings below the dark band between the light line bordering the fourth and fifth spots and the submarginal light line is little, if at all, broader than the distance between the submarginal light line and the margins of the wing *portlandia antheson* (pl. 22, figs. 1, 2)

c 2. Dark border on hind wings above broader and more uniform, not narrowing appreciably anteriorly; on the hind wings the dark band between the light line bordering the fourth and fifth spots and the submarginal light line is broader, usually much broader, than the distance between the submarginal light line and the edge of the wing; ground color below browner and usually more uniform

.....*portlandia borealis*

Clark concludes his discussion of the genus *Enodia* by making the following observation:

Although when typically developed the four forms included in this genus *Enodia* are quite different, three of them are very closely related.... It appears that typical *portlandia* intergrades more or less with *antheson*, and the latter intergrades more or less with *borealis*, the relationship between the three suggesting the relations between *Cercyonis* ... *pegala*, ...*alope*, and.....*nephele* occurring in the same general region...

HISTORICAL TAXONOMIC TREATMENT OF *BOREALIS*:

Prior to 1971

We reviewed five publications from the period prior to 1971, and found that direct reference to *E. anthedon borealis* occurred in each. Macy & Shepard (1941), in their book *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*, included *Enodia portlandia borealis*, extensively citing Clark's original description outlined above, but added that "specimens from Minnesota belong to the race *anthedon*."

In *A Field Guide to the Butterflies of Eastern North America*, Klots (1951) included *Lethe portlandia borealis* with the descriptive comment: "Smaller, darker, dark border of HW above broader; dark submarginal band of HW beneath broader." The author states further: "The species as a whole represents something of a 'cline,' although there is doubtless some habitat (ecotypic) segregation due to isolation of colonies. The subspecies, not well marked, intergrade greatly, especially northward."

In *The Lepidoptera of Pennsylvania*, Tietz (1952) listed *Enodia portlandia borealis* but it is not clear whether he believed it occurred in Pennsylvania, since he gave no specific locations for the state.

Forbes (1960) listed *Lethe portlandia borealis* in *Lepidoptera of New York and Neighboring States* with the following explanation: "Hardly distinct, perhaps smaller, somewhat paler and still more even in ground color", but neglected to specify distribution.

Cyril dos Passos (1964) compiled the first complete catalog of North American butterflies for the Lepidopterists' Society, published as *Society Memoir #1*, and listed subspecies *Lethe portlandia borealis*.

John H. Masters' 1971 Paper

Masters published: A Note on *Lethe anthedon borealis* (Satyridae), in the *Journal of the Lepidopterists' Society* 25(4) 1971. In this paper, he presented observations of both nominotypical *anthedon* and subspecies *borealis* in the western Great Lakes region indicating that, despite their "slight" phenotypic differences, there were some significant biological differences between them. Masters found that the most useful character for separating the two subspecies was in the ground color of the ventral hindwings. These he described as follows: "...in *borealis* it is a dull and uniform brown while in *anthedon* the background seems to be composed of several shades of brown and is much brighter." Masters also noted: "This distinction is especially evident in looking at the butterflies in series, which avoids comparing individual differences." The author plotted the distribution of both phenotypes in the western Great Lakes region and noted that the dividing line between both subspecies correlated very closely to the approximate boundary between the Canadian and Transition Zones in this region (Roberts, 1936). "Nearly every specimen examined", he wrote, "could be placed reliably into one subspecies or the other. Some degree of intergradation was noted in the character of the dark border on the dorsal hind wing, and to a lesser extent in the other characters, but in no case was more than one character involved in the intergradation."

From this narrative, it is evident that in using the word "slight" Masters meant only that there were not many differences. He was **not saying** there were **no** significant differences. He clearly related that he considered the ventral hindwing ground color a significant character to reliably and consistently distinguish these two taxa.

Masters then stated that behavioral differences, including habitat preferences, differentiated both subspecies, observing that "differences in habitat and habits are much more conspicuous." *Anthedon* males, Masters observed, "are very territorial and each male will occupy a favorite perch at some distance from the perches of his nearest neighbor". We have observed males of *anthedon* selecting in particular mid-level perches on tree trunks which overlook these woodland glades or other small openings in the forest. On the other hand, Masters stated that *borealis*: "...does not occupy a fully wooded environment, but prefers a very open wooded environment with lush undergrowth". We have found *borealis* especially near bogs or

marshes in the interface of mixed plant associations where they give way to forest. Males of *borealis* are described by Masters as exhibiting “none of the territorial characteristics that are so pronounced with *antheson*”, rather being “in fact, quite gregarious in habit”. Our observations confirm this as we have frequently found them congregating together in bushes. They often perch on low and mid-level vegetation but they also perch at higher levels on tree trunks and inside the leaf canopy – where they are well concealed. Masters also states that *borealis* “seem to be quite ‘amiable’ together and the aerial encounters of males, that are so common in nominate *antheson* and other territorial species, never appear to occur.”

Masters concluded his paper with the following statement regarding the *antheson/borealis* subspecific relationship.

One of the major criticisms leveled at the trinomial and its usage in taxonomy is that the subspecies, as currently defined and used, fails to distinguish between weakly and strongly differentiated geographical subspecies and treats them all alike. Descriptions and identifications of populations are essentially based upon morphological distinction and consequently taxonomy has been strongly oriented in this directions and populations which show strong morphological divergence have attracted the most attention. However, we have in *Lethe antheson borealis*, a very good example of very marked physiological (behavioral) differences along with weakly developed morphological differences. Differences between species, subspecies, or any taxonomic category, may be physiological, morphological, or both, and they may be phenotypic or genotypic in each case. Fortunately physiological differences, which are far more important in the long run, are usually accompanied by at least minor morphological changes which allow the taxonomist to distinguish and name the populations exhibiting them. On the other hand, as far as we know, morphological differences are usually accompanied by at least minor physiological differences; if they weren't, there would be little point in pinning a name upon them.

The North American [*Enodia*] are a good example of the problems in relying exclusively upon morphological characters for species distinctions. Ehrlich (1961) cited [*Enodia*] as one of only fourteen North American genera of butterflies that represented no problem to the taxonomist because speciation is quite distinct. Since that time field work and behavioral studies have forced us to increase the number of recognized species from three to five and we have become aware of the classification problems in the populations of *borealis* and [*Satyrodes fumosus* Leussler, both of which are still treated as infraspecific, but with reservations.

Masters thus concluded that, along with the nearly allopatric nature of their morphological [phenotypic] differences, the physiological distinctions discussed above justify the retention of *Enodia antheson borealis* as a valid, separate and distinct subspecies of *Enodia antheson*.

We state that these two may in fact be sibling species. The sinking of *borealis* into *antheson*, based on assessment via museum specimens devoid of observations of living behavior, has effectually closed the mental door of investigating the possibility of possible speciation.

After 1971

For the post-1971 period, we reviewed a rather extensive list of publications in order to evaluate the status of *Enodia antheson borealis* in those publications.

Hooper (1973), in *Butterflies of Saskatchewan* lists *Lethe portlandia borealis* and states that “[*borealis*] is found in poplar woods where it often lands on leaves about five feet from the ground and on tree trunks”.

In *Butterflies and Skippers of New York State* (Shapiro, 1974), the author lists only species entry *antheson*, but states: “Specimens from eastern New York (Clinton Co. to lower Hudson Valley and S.I. [Staten Island]) lighter and brighter than those from farther west.”

Brower (1974) makes an interesting comment in *A List of the Lepidoptera of Maine*, in which he lists *Enodia portlandia antheson*, but states: “Part of the type series of *E. p. borealis* Clark were from Maine. An attempt has been made to restrict *borealis* to Canada.” The author appears to have considered his examined material as referable to nominotypical *antheson*.

Thomas C. Emmel, in *The Butterflies of North America* (In Howe, 1975), listed subspecies *Lethe portlandia borealis* and states: “This pale northern subspecies grades southward into [subspecies] *anthesdon*.” Plate 13 in Howe illustrates a female specimen (#10) of *anthesdon* (Streator, Ill. 29 Aug. 54) appearing somewhat darker and displaying more wing contrast than the female specimen of *borealis* (#13) (Menominee Co, Mich., 1 Aug. 1950), which appears considerably more pale by comparison, while displaying less contrast in wing markings.

Pyle (1981), in the *National Audubon Society Field Guide to Butterflies*, makes no direct reference to *borealis*, but notes that “...in the much cooler northwestern portion of its range, the Northern Pearly Eye [*anthesdon*] shifts its habitat to more open woodlands with sedge marshes; the butterfly changes its behavior as well, gathering in groups and perching on bushes...”, a statement absolutely in agreement with Masters’ description of *borealis*.

Miller & Brown (1981) compiled the second complete catalog of North American butterflies for the Lepidopterists’ Society, published as *Memoir #2*. In this catalog, the authors listed *borealis* as a junior synonym of *Enodia anthesdon* (entry #711) **without explanation**. It was after this treatment that the authors of most subsequent guides of a **regional** scope decided to follow suite.

In a journal paper entitled *Butterflies of the Ottawa District* (Layberry, et. al., 1982), the authors list subspecific entry *Lethe anthesdon borealis*.

Despite the arrangement in Lep. Soc. *Memoir #2*, Hodges (1983) listed subspecies *Enodia anthesdon borealis* (as entry #4568.1(a)).

Tilden & Smith (1986) followed Miller & Brown, making no reference to *borealis* under the species entry for *Enodia anthesdon*, in *A Field Guide to Western Butterflies*.

Scott (1986), in *The Butterflies of North America*, similarly provided no mention of *borealis* under the entry of *Lethe anthesdon* (Scott dropped most North American butterfly subspecies from usage and apparently listed only those which he **personally** considered sufficiently different from other subspecies in morphology).

The authors of *The Butterflies of Manitoba* (Klassen, et. al., 1989) state: “Two subspecies are recognized. *Enodia anthesdon borealis* occurs in southern Manitoba.” Extensive life history is included. The habitat is described as “damp deciduous forest edges, clearings, glades, roads and trails, especially where the underbrush is thick.”

Ferris (1989) compiled a supplement to the Miller & Brown ‘Catalogue/Checklist’ (Lepidopterists’ Society *Memoir #3*) and retained the designation of junior synonym by making no changes to the status of *borealis* as listed in Lep. Soc. *Memoir #2*.

Opler & Malikul (1992), in the revised Peterson *Field Guide to Eastern Butterflies*, did not include *borealis* in the guide’s checklist, though the inclusion of “Damp deciduous woods, usually...near marshes” hints of *borealis* habitat.

The authors of *Alberta Butterflies* (Bird, et. al., 1995) following authors of other Provincial guides, listed *Enodia anthesdon borealis*, and describe the habitat as “poplar woods near streams and lakes”.

In *The Butterflies of Canada* (Layberry, et. al., 1998), *borealis* is, rather interestingly, not listed in the ‘Checklist of Canadian Butterflies’, nor did the authors mention it in the text under species entry *Enodia anthesdon*. The omission of *borealis* from both the checklist and the text was made despite the authors’ describing almost in detail the preferred habitat of *borealis*, stating that “...it is found only in rich deciduous or mixed wooded areas, usually where the undergrowth is thick” (this is again suggestive of the habitat for *borealis* as described by Masters), and also despite figuring a male specimen of *borealis* (pl. 18, fig. 1) from the Riding Mountains National Park, Manitoba, located 60 miles north of the town of Miniota, Manitoba (the origin of fourteen of the twenty two specimens used by Clark in his Original Description of *borealis*). The omission of *borealis* in *The Butterflies of Canada* also suggests the application of junior synonym status of *borealis* to *anthesdon* (despite the same authors’ 1982 publication *Butterflies of the Ottawa District* in which, as we state above, *borealis* was listed as a valid subspecies of *anthesdon*).

Opler & Wright (1999), in the revised Peterson 'Field Guide to Western Butterflies' likewise make no reference to *borealis*, while appearing at least in part to describe the habitat of *borealis* as "Damp deciduous woods, usually...near marshes".

In *Michigan Butterflies & Skippers* (Nielsen, 1999) lists only species *Enodia anthedon* without any reference to subspecies.

And finally, *Le Guide des Papillons du Quebec* (Handfield, 1999) describes only *Enodia anthedon*, while referencing Masters' 1971 paper on *borealis* in the Bibliography, and offering the following notes, first on habitat: "Partly shaded clearings, undergrowths and edges of humid deciduous and mixed forests, boggy or sedgy"; and then on behavior: "...it is encountered often along the edges of humid woodlands, perching high enough on vegetation or on tree trunks with its head down...with its wings closed, it is difficult to observe..." (translations from the French). It should be noted, in conclusion, that a number of these publications make indirect references to *borealis* in terms of habitat and/or behavior, while otherwise making no direct reference to *borealis*.

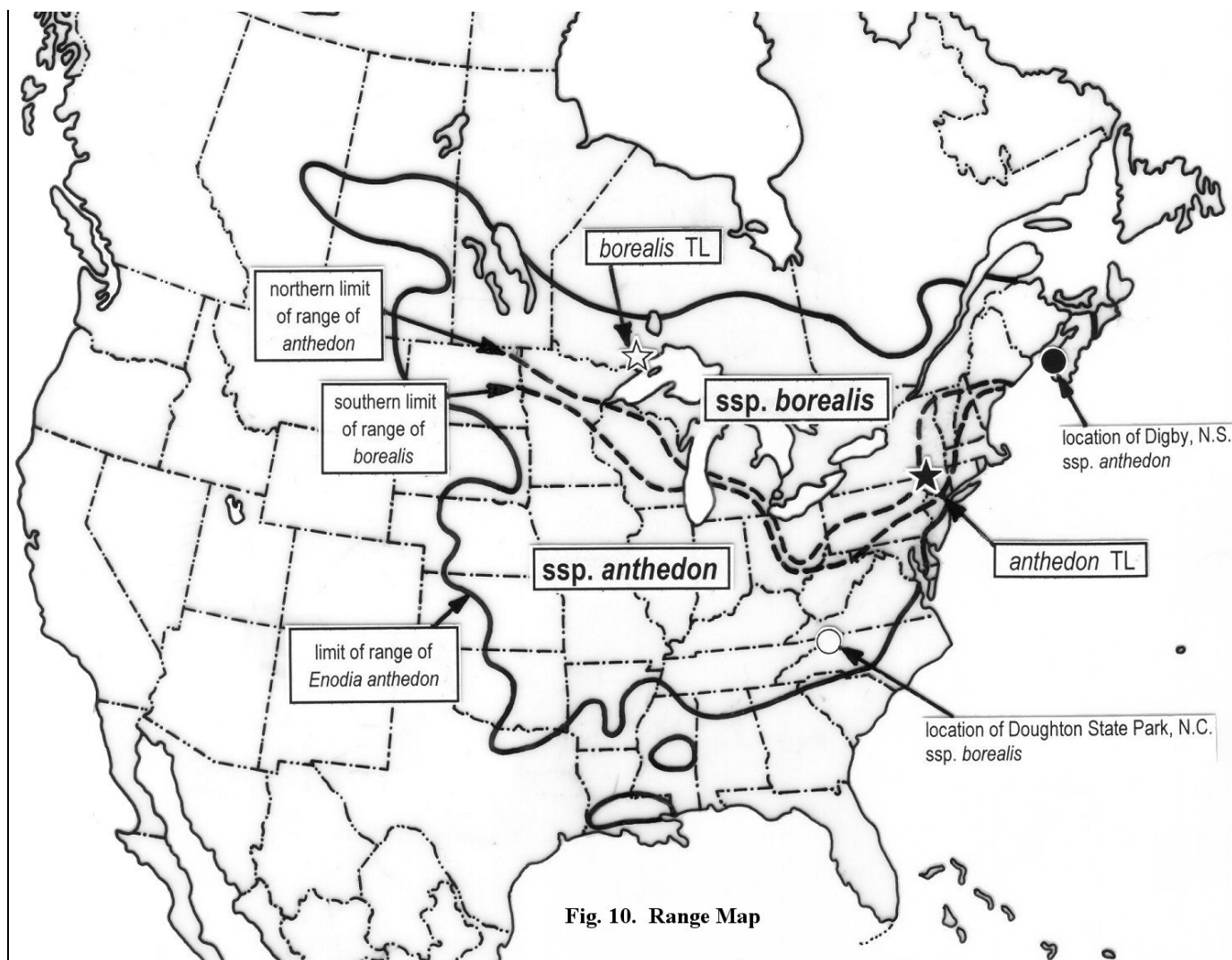
Many of the newer major regional field guides mentioned above (Opler & Malikul, 1992; Opler & Wright, 1999; also Brock & Kaufman, 2003) make minimal reference to subspecies.

FIELD OBSERVATIONS IN NEW ENGLAND AND ELSEWHERE IN THE EAST

We embarked on this study after corresponding over our personal observations of *Enodia "anthedon"* in New Hampshire. During July 2001, one of us (Grkovich) encountered two colonies of "*anthedon*" in widely different parts of the state.

The first colony, of *anthedon*, was observed on July 4, 2001, near the town of Merrimack, in the south-central part of the state, 10 miles north of the Massachusetts State line at approximate elevation of 300 feet. Here, along the Rookery Trail, behind (east of) the Fidelity Investments Inc. buildings on Constitution Road near Exit 10 of Interstate 93, specimens were observed along a gravel access road through dense Transition Zone pine-oak-birch forest, with individuals perching on birch and oak leaves in territorial fashion along the edges of the road/trail, invariably 4 to 6 feet above the surface. Perched individuals maintained distinct territorial behavior, as the average distance between two specimens was not less than approximately 30 feet. Others were observed inside the forest cover away from the trail, perching on and flying short distances between leaves and small tree trunks. No individuals were observed perching anywhere at a distance other than the previously stated 4 or 6 feet above either the surface of the trail or the ground inside the forest. Perched specimens were quite wary and were rather difficult to approach, and tended to take flight in response to any sudden human movements, sometimes relocating to another perch along the trail, but also flying into cover. Individuals (Fig. 1) were in good condition but demonstrated some wear and were no longer fresh; it was thus estimated that the flight had begun approximately one week to 10 days earlier during the fourth week of June. A second visit to the site was made on August 25, 2001 with only a very worn *anthedon* female being found.

On July 15, 2001 a second colony, this time of *borealis*, was encountered in an entirely different type of habitat in the lower Canadian Zone, along the Kancamagus Highway (Route 112) in Carroll County, near the boundary of Grafton County at elevation of approximately 1500 feet. The habitat is located 2.6 miles west along the Kancamagus Highway from the intersection of Bear Notch Road, which extends eight miles north to Highway 302 at the town of Bartlett. The colony was found approximately 1600 feet north of the highway, in a partly shaded but open woodland with very thick moist undergrowth of grasses, dense sedges and bushes, and other plants such as blackberry, black cohosh etc. The open forest lies in a low, wide flood plain of the nearby Swift River, and is dominated by firs, spruce, sugar maples, poplars, birches, willows etc.



As one hikes the distance from the highway into the habitat, one first encounters a small boggy area (however, no typical bog butterfly species have been found there), then a large open, moist field with a deep and thick grassy, sedgy area, after which the open field gives way to the open forest. The first specimens were encountered approximately 150 feet into the woodland, where numerous specimens (about two dozen) were seen occupying a rather restricted glade area which measured no more than 50 feet in width by 100 feet or so in length. The differences in behavior between these specimens and those of the colony at Merrimack were recognizable at once. These displayed a decidedly gregarious behavior quite suggestive of a colony of *Asterocampa celtis* or *clyton*, occurring in groups as numerous as a half dozen or more. They were perching on the bushes and grasses from approximately 6 feet to as low as a foot above the ground, but also on tree trunks inside the leafy canopy as high as 8 to 12 feet high where they would become well concealed.

No territorial behavior whatsoever was observed in this colony, as opposed to the individual behavior noted at Merrimack; sometimes as many as three or more specimens were observed perching on the tree trunk or plant - or even on the same large leaf. The flight of these, as observed, was quicker and more direct than the Merrimack *anthedon*. Perched specimens, particularly when sitting upon low vegetation, appeared also to be not nearly as wary and were more easily netted. Also in contrast to those at Merrimack, specimens encountered here were in fresh condition, indicating a very recent emergence of the brood. A follow-up visit to the habitat was made on August 8, 2001, with no specimens being found at that time; apparently, the flight had ended.

No specimens were seen during a visit on July 15, 2002. This likely indicated only that the flight had not yet begun due to an abnormally cold, wet and late spring in New England in 2002. On a visit to the site on August 11, 2002, a few specimens were observed. These were obviously quite past peak, and were testimonial that the flight period was ending. The site was visited again on July 15, 2003 which yielded similar observations of numerous specimens and similar behavior as made July 15, 2001.

These behavior, habitat, and flight period observations of the *borealis* colony at the Kancamagus Highway are quite in contrast with those of the more southern *antheodon* colony at Merrimack. Similar observations of colonies of *borealis* have since been made during early July 2003 at Pinkham Notch, Coos Co., NH at about 2,000 ft. elevation and also in a lush Upper Transition Zone / lower Canadian Zone habitat near Green River, Guilford Center, Windham Co., VT in mid to late July 2003.

Our conversations revealed that Pavulaan had encountered and collected a small series of *antheodon* along the same highway (the Kancamagus) at the Jigger Johnson Campground of the White Mountain National Forest near a rocky area adjacent the Swift River. The specimens taken at this location matched specimens of non-typical *antheodon* from Rhode Island, Maryland and Virginia. This location is only 2 miles east of the *borealis* colony described above. The habitat (dense, mixed deciduous streamside forest dominated by firs and sugar maples, but generally with a rather sparse undergrowth consisting primarily of ferns) and behavior (widely-dispersed individuals perching chiefly on tree trunks in territorial fashion rather than on ground vegetation) is rather similar to those of the colony at Merrimack, and is also typical for *antheodon* in areas farther to the south. These observations would suggest that the area along the Kancamagus Highway lies within a tension or contact zone between two populations of *antheodon* having differing origins. It is also remarkable that two such differing colonies of *E. antheodon*, one displaying characteristics and habits of non-typical *antheodon*, and another displaying characteristics of *borealis*, have been found in such close proximity to one another.

It is interesting to note that Grkovich also visited the site of the *antheodon* colony at Jigger Johnson Campground on August 11, 2002 and failed to observe any adult specimens of *antheodon*, despite favorable weather and the presence of specimens of *borealis* at the nearby habitat for that subspecies earlier that same afternoon.

We have closely observed and documented the behavior of various populations of *antheodon* at several widely distributed, more southerly locations. These locations of *antheodon* include: In Rhode Island, along the Blackstone River near Quinville, and the Arcadia Management Area near Escoheag; in Maryland, Cedarville State Forest near Cedarville, McKee-Beshers Wildlife Management Area near Seneca, and Great Falls National Park near Potomac; in Virginia, Great Falls National Park near McLean, Runnymede Town Park in Herndon, Hemlock Overlook Regional Park near Clifton, private lands near Waterford, and in Shenandoah National Park near Front Royal; and finally, one location in Missouri, August A. Busch Memorial Wildlife Area near Weldon Spring.

At each of these locations, habitat and adult behavior was remarkably similar, with adults displaying a preference for dense deciduous woodland with a sparse understory consisting primarily of non-woody plants and grasses (similar to the habitat of the colony of *antheodon* observed at Merrimack, NH). Some of these locations have an almost savannah-like appearance, were it not for the dense tree canopy which provides total shade, and are generally surrounded by denser woodland. This habitat type provides a relatively unobstructed view and flight area for the adults. The adults (generally the males) have been observed perching on bare earth or on tree trunks and were extremely wary of approaching humans. Their habit of frequently flying from one tree to another and keeping several meters' distance from nearby adults gives the impression of territorial behavior. Colonies were generally very small (fewer than five individuals being seen during each visit) and were confined to a small area (generally less than 30 meters in diameter).

Some colonies seemed to persist in a particular location for only one or two years, subsequently relocating a year later by a distance of several hundred meters, or being replaced by other colonies in the general vicinity. But the colony at Quinville, Rhode Island persisted at the same location throughout the

study period. Despite these observations, questions remain over divergent behavioral patterns and habitat selection in different regions and between some colonies in relatively close proximity to one another, such as those in northern New Hampshire.

In consideration of the statement of Clark (1936) referred to above, regarding the “*antheson*” from the “mountains of Virginia”, one wonders how far to the south (or also to the north) the two taxa may, unbeknownst and undocumented, occur in such proximity to each other while at the same time remaining distinct. The question of how far south *borealis* might range in the Appalachians has been responded to in part by the discovery of an unusual colony of *antheson* in the southern Appalachian Mountains on July 27, 2002 by Bruce Grimes and Clyde Kessler. They observed and photographed several “*antheson*” (Fig. 9) at Doughton State Park along the Blue Ridge in Alleghany Co., North Carolina. These displayed considerably more brownish ground coloration on the undersides than is normally seen in *antheson* from that region. This noticeable difference prompted them to report this finding to us.

Grimes also informed us that individuals were observed displaying what could only be described as “communal” behavior on a wooded hillside above a boggy area. This behavioral pattern is similar to that described by Masters (1971) for *borealis* and to the behavior we have observed for *borealis* in northern New Hampshire. (Interestingly, *Satyroides appalachia* had previously been observed in this exact same area. There is no waterway present in the area, and the forest can be described as having some understory growth, but not dense.) These observations were made at approximately 3500 feet elevation within generally Transition Zone forest of the southern Appalachians. Our conclusion is that this represents a mid-high altitudinal colony of *borealis* far to the south into the range of nominotypical *antheson* and thus has significant implications relative to the taxonomic relationship between *borealis* and *antheson*.

Of similarly great interest to us was the documentation by Grimes and Kessler of nominotypical *antheson* approximately 125 miles to the northeast along the Blue Ridge, at approximately 4000 feet elevation on Apple Orchard Mountain in Botetourt Co., Virginia. Grimes and Kessler provided photographic evidence showing the grayish brown ventral surface with the presence of a faint violet tinge characteristic of nominotypical *antheson*.

DISCUSSIONS OF COMPARATIVE PHENOTYPIC CHARACTERISTICS

According to the Original Descriptions (Clark, 1936) for both subspecies as cited above, *borealis* differs phenotypically from *antheson* as follows:

1. Upper surface darker, with the dark margin of the hind wings broader and more uniform.
2. Lower surface darker and more brownish, usually with the ground color less varied and sometimes quite uniform, with only faint indications of a narrow lighter line enclosing the rows of spots on the fore and hind wings.
3. On the hind wings beneath, the dark band between the light line is, beyond the fourth and fifth spots, broader – usually much broader – than the distance between submarginal line and edges of the wing.

An examination of the series of *E. antheson* housed in the U.S. National Museum of Natural History (Smithsonian) collection in Washington D.C. intended to confirm whether the phenotypic differences cited by Clark (1936) were indicative of true geographic variation (as opposed to mere individual variation). Careful examination revealed that regional variation does exist (Map: Fig. 10), but is, by most accounts slight and is initially suggestive of a cline (by evidence of phenotypic characters only). However, the cline is not continuous, and has some inconsistencies suggestive of post-glacial movements from several directions. It might be theorized that populations of nominotypical *antheson* and *borealis* came into secondary post-glacial contact and reintegrated phenotypically at different points in their range. Yet, in some regions reintegration appears to be incomplete, as evidenced by behavioral and slight phenotypic differences between nearby colonies, which may also be indicative of early stages of speciation.

To supplement Clark's descriptions, we note the following additional characters that distinguish *borealis* from *anthesdon*:

1. Upper surface not necessarily darker but with a paler brown cast than *anthesdon*; *anthesdon* having a more grayish brown cast. Wing markings more washed in appearance, having less contrast than in *anthesdon*. Specimens of *borealis* from Manitoba are generally lighter than *anthesdon*, while specimens of *borealis* from eastern Canada and northern New England are at least as dark as *anthesdon*, but with a more brownish cast. [One factor in the appearance of northern *borealis* being lighter than *anthesdon* may be in the age of specimens. Fresh specimens from central Canada were not available to us.]
2. Lower surface of the forewings displaying considerably more whitish wash exterior to the jagged postmedian brown band and between the row of eyespots and the wing margin. This character is subject to great individual variation in both subspecies, but the degree of whitish wash is generally greater in *borealis* and lesser in *anthesdon* when comparison is made between series.
3. Lower surface of the hindwings lacks the peculiar violet tinge frequently found in *anthesdon* populations, especially from those in the southern portion of the species' range. This violet tinge is most pronounced in the interspace between the straight postbasal band and the jagged median brown band. In *anthesdon*, the violet tinge is frequently expressed in the white outer "halo" which encases the row of hindwing eyespots.
4. *Borealis* appears to be slightly smaller (by 2 mm) than nominotypical *anthesdon*, on average. A moderate sample (10 specimens of Canadian *borealis* and 20 specimens of "true" *anthesdon*) showed the forewing of *anthesdon* to be roughly 28 mm. in length, while only 26 mm. in *borealis*.

Based on all of the distinguishing features, examination of the limited series available at the U.S.N.M. revealed that the nominotypical *anthesdon* phenotype mainly inhabits the southern portion of the species' range, primarily the central and southern U.S., southern Appalachian Mountains (with the exception of the North Carolina colony) and adjacent Piedmont and a narrow area along the coast into southern New England. A single specimen from Digby, Nova Scotia was of the nominotypical type. *Borealis*, in the "true" sense (displaying little tendency toward intermediate characters), ranges throughout the northern portion of the species' range, primarily in the Great Lakes region, westward to Alberta, and north to the limits of the species' range in south-central Canada. Norbert Kondla provided a photograph of a typical *borealis* from Elk Island, Alberta (leg. Bob Carrol, July 6, 2001). This specimen appears to be a darker (more "typical"?) variant of *borealis*. Specimens assignable to *borealis* range to the south end of a broad "tension" zone stretching from northern Minnesota, through Wisconsin, Michigan, eastern Ohio, through central Pennsylvania, eastern New York and northern New England. Within this tension zone, *borealis*, *anthesdon*, and intermediate forms occur.

Masters (1971) concluded that there was a dividing line between both subspecies in the region immediately west of the Great Lakes that correlated very closely to the approximate boundary between the Canadian and Transition Zones in that region. This could not be verified from the U.S.N.M. series. Ironically, the distribution of specimens in the U.S.N.M. series indicated a broad band across Wisconsin where both *borealis* and *anthesdon* types occurred, including intermediates. However a reasonably distinct line of demarcation appears to exist to the east of that region, mainly through Michigan. Interestingly, this line corresponds to the division between sibling species pairs *Pterourus glaucus* and *P. canadensis*, *Phyciodes tharos* and *P. cocyta* "selenis" [sensu Nielsen, 1999] and also between *Celastrina ladon* and *C. lucia* in Michigan (Nielsen, 1999). While the term "blend zone" might seem tempting, we prefer to refer to this as a "tension" zone or zone of contact. Interestingly, populations in the southern Great Lakes region (Michigan and Ohio) and southern Ontario contain a high degree of intermediates which retain the basic pale brown coloration of *borealis* but the sharpness and contrast of wing markings that characterize nominotypical *anthesdon*.

On the other hand, specimens from northern New England and eastern Ontario appear to be slightly darker and grayer brown like *anthesdon* but with wing markings more washed-out in appearance, as in "true" *borealis*. What is more interesting is that no intermediates were examined that occurred south of

the tension zone. In other words, intermediates are evident only from areas where *borealis* occurs. South of the tension zone, only “true” *anthedon* types are evident with the exception of the North Carolina colony. However, north of the tension zone (that is, north of areas where “true” *anthedon* has been recorded), intermediates range broadly into the southern and eastern portions of the range of *borealis*. We suspect that phenotypic review of such limited series such as those of the U.S.N.M. masks what is truly happening in nature. Documentation of the field biology of the intermediate specimens is critical to further study, and is currently unknown to us other than our New Hampshire observations and those of Grimes and Kessler in North Carolina. Additional and expanded field observations would likely reveal much more to us about their nature.

Of special interest to us was the zone of contact in New Hampshire. We examined short series of specimens of *E. anthedon anthedon* and *E. anthedon borealis* from the two New Hampshire colonies described above, in order to develop and compare the relative phenotypical characteristics of both. Reference is made to Figure 1 (Merrimack, N.H., 4 July 2001) and Figure 2 (Swift River, Rt. 112W, Carroll Co, N.H., 15 July 2001). While slight, we note the following phenotypic differences between specimens from the two colonies:

1. Overall ground color of both the upper and undersides of the wings are lighter in *anthedon* than in *borealis*.
2. Position of the second, small ocellus in Cell M₂/M₃ of the forewing is positioned more inwardly toward the discal cell in *anthedon* than in *borealis*.
3. While the general lighter area between the postmedian dark line and the row of ocelli of the forewing is more extensive and is (perhaps) somewhat more whitish-brown in *borealis* than *anthedon*, the narrow lighter line enclosing the rows of ocelli on both forewing and hindwing is noticeably narrower in *borealis* than in *anthedon*. This is especially noticeable on the hindwing; and there the line is particularly narrow and faint on the marginal side of the ocelli.
4. The lower ocelli of the hindwing in cells M₁/M₂, M₂/M₃, M₃/CU₁, and CU₁/CU₂, average slightly smaller and somewhat less elongate in *borealis* than in *anthedon*.
5. The dark lines on the underside are somewhat more extensive and are thicker in *borealis* than in *anthedon*. This is particularly true in the innermost, submedian line extending toward the anal angle of the hindwing; in some *anthedon* the line is incomplete and disappears only a short distance beyond the cell, while in *borealis* the line is more complete and often is fully connected to the postmedian dark line above the sixth ocellus.
6. The dark band enclosing the ocelli of the hindwing beneath is broader in *borealis*, as noted in the Original Description. However, in our New Hampshire specimens of *borealis*, the dark band is also broader at each ocellus and thus across the entire submarginal area of the hindwing, not only at the fourth and fifth ocelli. The corresponding dark band enclosing the four ocelli of the forewing appears to us to be somewhat wider in *borealis* as well.
7. Finally, the ground coloration on the underside of *borealis* has only a tendency toward a tinge of violet, in both the lighter and darker areas of the wings. This violet tinge is stronger in *anthedon* and becomes more pronounced and “pearly” the farther south it ranges into the southern Appalachian region.

While we anticipate that future examinations of longer series of specimens from these two colonies will reveal as expected that specimens intermediate in appearance to *anthedon* and *borealis* occur within both, the phenotypic differences between specimens examined from the two colonies described above, while slight, appear to be rather consistent and are also consistent with the characters described for *anthedon* and *borealis* in their Original Descriptions. These differences are initially less conspicuous than the well-documented differences between the two in terms behavior and preferences of habitat. We can perhaps also conclude that had the latter two differences not been noted between individuals of the two colonies, then the slight differences in phenotypic characters along with the agreement of these color and pattern characters with the Original Descriptions, might have remained uncovered and thus may have as a result continued unnoticed.

CONCLUSIONS

Based upon our research and observations documented in part herein, we theorize that populations of an ancestral *Enodia* were separated during the final glacial maxima (or perhaps during a previous one), and as a result these now separated populations embarked onto and progressed along the path toward speciation. These populations eventually developed on the one hand slight phenotypic differences, but on the other hand more importantly they also developed significant behavioral differences as well. Full speciation between the two, however, did not become fully evolved during this period of separation. After the passing of the most recent Ice Age and the subsequent warming of the climate, the ranges of these separated populations were extended once again and as a result the two came once again into contact along a broad front within the Transition Zone (which is in itself a zone of contact or tension, between the northern Canadian Zone and the southern Austral Zones). This broad front stretches from the Dakotas to Ohio, and thence eastward into Maine. It is entirely possible that an undocumented second and narrower tension zone or front between the two extends southward along the higher and cooler Transition Zone regions of the southern Appalachians as well. The conclusion of the Ice Age would have also interrupted the process toward full speciation, with the two taxa thus overlapping in what we today observe as the current tension zone between them.

Under the scenario theorized above, reintegration of the taxa appears to be occurring at this time. However, secondary contact appears to not have occurred uniformly throughout the broad tension zone, as evidenced by the differing degrees of intermediacy observed in specimens from the Great Lakes region on the one hand, and through eastern Ontario and Quebec and into northern New England on the other. As described above, intermediates occur in Ohio and Michigan, which retain the basic pale brown ground color or hue of *borealis* but display the greater contrast in wing markings of *anthesdon*. In eastern Canada and in northern New England, intermediates occur which possess the darker gray-brown ground color or hue of *anthesdon*; yet the wing features in these are less contrasty and are more washed-out, as in *borealis*. These intermediate forms in general appear to occur well to the north of the northern limit of "true" nominotypical *anthesdon* phenotypes, where they gradually blend into "true" *borealis* populations, which occur in the northern and western portions of the species' overall range. While these have been documented as occurring north of the northern range of "true" *anthesdon* populations, we have however found no *borealis* or intermediate types south of the tension zone, with the exception of the single high-altitude colony in western North Carolina discussed above.

While full speciation between the two is not complete, full reintegration is also apparently either incomplete or inconsistent, as evidenced by known colonies of the two occurring in close proximity to one another. These colonies, as documented from New Hampshire and North Carolina, occur in differing habitat and display differing behavioral traits. The fact that a colony referable to *borealis* persists in North Carolina appears to us to be evidence of the likelihood that speciation did in fact occur there in its earliest stages. One might well be left to wonder about the fact that such a unique colony would persist so far south and yet remain distinct following the most recent glaciation. It is also possible that such isolated colonies may be eventually doomed to extinction due either to a hypothetical further climate change or by ultimate reintegration into nominotypical *anthesdon* at some point in the future.

COMMENTS ON TAXONOMIC CONCLUSIONS

A review of subsequent literature following the description of *borealis* by Clark in 1936 clearly demonstrates individual author preferences over whether to accept the taxon *borealis* as either a subspecies or as a junior synonym of *anthesdon*. This likely reflects either: (1) an individual author's personal interpretation of what delineates or defines a subspecies; (2) an author's personal bias for or against the naming of phenotypically differentiated populations as subspecies; (3) an author's personal

experience (or lack of) with the taxon in question; or (4) a blind following of, or a reluctance to deviate from, prevailing or popular taxonomic usage or the prescribed arrangements of popular authors.

We acknowledge that, while the taxon *borealis* differs only slightly in phenotypic characters from its sister subspecies, nominotypical *anthon*, and that many authors may consider this too minimal to differentiate subspecies, Masters pointed out that there were physiological differences as well. We believe that our observations confirm Masters' conclusions. Some authors might have either overlooked these physiological differences or simply considered them too minimal also. In the absence of a more thorough study that examines this issue in much greater depth, we encourage future authors and listmakers to thoroughly research outstanding issues such as the current one, prior to revising taxonomy without providing detailed justification. Thus, we retain usage of the original description of *borealis* by Clark (1936) as valid, and consider the paper by Masters (1971) as reinforcing the status of *borealis* at subspecific rank. The present paper in addition poses the question as to whether primitive speciation between *anthon* and *borealis* should be further considered. Such issues will require DNA analysis to fully resolve.

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