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BIOLOGY OF THE BLACK-ANTENNA RACE OF *PHYCIODES THAROS THAROS* (NYMPHALIDAE) IN ONTARIO

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ABSTRACT. The black-antenna race of *P. tharos tharos* (Drury) occurs north to the Canadian zone of the Ottawa valley, far beyond the Carolinian or Upper Austral range limit previously indicated for the species. It is also reported for the first time from northern New York State and Quebec. The northernmost colonies are restricted to alvars or old pastures over limestone, but hay field and old field mosaics, dune slacks and prairies on sandy soils are utilized farther south. The foodplant at the northernmost sites was *Aster ciliolatus* based oviposition in the field and subsequent rearing in the laboratory. Available evidence suggests that the black-antenna race of *P. tharos tharos* may have invaded the Ottawa valley over the past five years: it is now widespread but local in southern Ontario, having been found in 65 locations. The flight period extends from late May to late October and is essentially continuous at some locations.

Additional key words: oviposition, foodplants, *Aster ciliolatus*, habitat, flight period.

Recent books (e.g., Scott 1986a, Opler & Krizek 1984, Opler & Malikul 1992) and monographs (Scott 1986b, 1994) follow Oliver (1980) in splitting *P. tharos* into two entities: the northern *P. cocyta* (Cramer) (= *P. selenis*, *P. pascoensis*, *P. morpheus*) and the more southern *P. tharos tharos* (Drury). Unfortunately, ecological and distributional data on the two species are confused because they previously were treated as one, and it is often unclear to which species certain information applies. The purpose of the present work is to provide ecological, distributional, and behavioral data for the black-antenna race of *P. tharos tharos* (subsequently referred to here simply as *P. tharos*) in Ontario, and update the otherwise comprehensive information available in the Ontario Butterfly Atlas (Holmes et al. 1991) and the annual summaries of the Toronto Entomological Association.

MATERIALS AND METHODS

Because females of *P. tharos* are often morphologically inseparable from those of *P. cocyta* and *P. batesii*, only males were used to develop distributional data. Males of the black-antenna race of *Phyciodes tharos tharos* were distinguished from *P. cocyta* males by the following characters in order of importance: (1) unscaled portions of the tip of the antenna (nudum) being all black or mostly black (black border and lattice with brown steps) instead of uniformly brownish-yellow, yellow or orange; (2) antennal clubs mostly club-shaped rather than elongate; (3) postmedian black line on upper hindwing extending through all or most cubital and medial cells rather than lacking in two or more cells; (4) median black band crossing upper forewing mostly well developed; (5) forewing 14–16 mm from base to apex instead of 16–18 mm; and (6)

marginal crescent patch on underside of hindwing dark brown instead of tan. Although a relatively small, multi-brooded race of *Phycioides* with yellow or brownish-yellow nuda, best referred to *P. cocyta*, occurs in parts of Ontario and New York state, this differs from the evidently more western orange antenna race of *P. tharos* in having the black lines on the upper wings less well developed. Only specimens having black antenna were accepted as the black-antenna race of *P. tharos*, but some variation was permitted in the other characters. However, the suite of characters associated with black antennae held together quite well. Black antennae were generally associated with well developed black lines on the upper wings for example, the most notable exception being a specimen at LEM from Laval (discussed below).

Collections examined included those at Agriculture Canada in Ottawa (CNC), the Royal Ontario Museum in Toronto (ROM), the University of Guelph (UG), Lyman Entomological Museum at Ste. Anne de Bellevue (LEM), and the University of Western Ontario (UWO). Members of the Toronto Entomological Association reporting *P. tharos* in recent season summaries (e.g., Hanks & Hess 1992, Hanks 1993, 1994, 1995) were contacted to confirm reports; their private collections were checked for other records of *P. tharos*. The map was produced using Quikmap version 2.5 (ESL Environmental Sciences Ltd., Sidney, British Columbia). Data for male *Phyciodes tharos tharos* examined in institutional collections are as follows:

NEW YORK: Stony Point, 20 Jul 1995 (CNC); Chaumont, 2 Sep 1995 (CNC); Lockport, 11 km E, 14 Sep 1995 (CNC). **ONTARIO**: St. Davids, 23 Aug 1930 (UWO), 1 Aug 1932 (CNC); Brighton, 3 Aug 1932 (CNC); Fort Erie, 6 Aug 1948, 7 Aug 1948 (CNC); Marmora, 25 Jul 1952 (CNC); Ancaster, 26 May 1952 (CNC); Simcoe, 27 May 1953 (UG); Pottageville, 5 Sep 1955 (ROM); Unionville, 1956 (ROM); Don Valley, Toronto, 21 Jun 1958, 31 May 1958 (ROM); Dunn Twp., 27 Jul 1958, 1 Aug 1958, 16 Aug 1959, 18 Aug 1959, 16 Aug 1960, 29 Aug 1962 (UWO); Toronto, Don valley, 10 Jun 1959, 9 Aug 1959 (ROM); Orillia, 25 Jul 1959 (ROM); Toronto, Willowdale, 5 Jun 1960 (ROM); St. Catherines, 13 Sep 1961 (UG); Long Point, 25 May 1963 (ROM); Chaffeys Locks, 17 Jul 1963, 22 Jul 1970, 28 May 1971, 23 May 1974 (ROM); Dunnville, 22 May 1965 (ROM); Rondeau Park, 12 Jul 1965 (ROM); Wainfleet, 31 May 1969 (CNC); Oakville, 6 Jun 1976 (UG); Dundas, 21 Jul 1981 (UG); Aberfoyle, 10 Jul 1983 (UG); Vienna, 22 Aug 1987 (UG); 4 km W Dwyer Hill Siding, 22 Jul 1995 (CNC); Flood Rd., Rideau Twp., 22 Jul 1995 (CNC); 1 km W Metcalfe, 22 Jul 1995 (CNC); 2 km W Metcalfe, 22 Jul 1995 (CNC); 5 km N Metcalfe, 29 Jul 1995 (CNC); Huycks Bay, 9 Jul 1995 (CNC); Presqu'ile Park, 15 Jul 1995 (CNC); Bells Corners, 30 Jul 1995 (CNC); Batawa, 7 Aug 1995 (CNC); Kemptville, 1 Sep 1995 (CNC); Queenston, 14 Sep 1995 (CNC); Almonte, 5 km NE, 3 Sep 1995 (CNC); Dwyer Hill Siding, 5 km SE, 4 Sep 1995 (CNC); 2.5 km SW Phragmites fen near Dwyer Hill Siding, 2 Sep 1995 (CNC); Mud Pond 1 km SE, 2 Sep 1995, (CNC); 1 km N Constance Lake, 2 Sep 1995 (CNC); Dwyer Hill Siding 3 km SE, 2 Sep 1995 (CNC); Prospect, Lanark 2 Sep 1995 (CNC). **QUEBEC**: Klock Rd., Aylmer, 2 Aug 1995 (CNC).

Observations of oviposition were made in the field by following females very slowly. Samples of plants upon which eggs were laid were identified using Semple and Heard (1987), and are deposited in the herbarium of Agriculture Canada in Ottawa (DAO). Larvae were reared

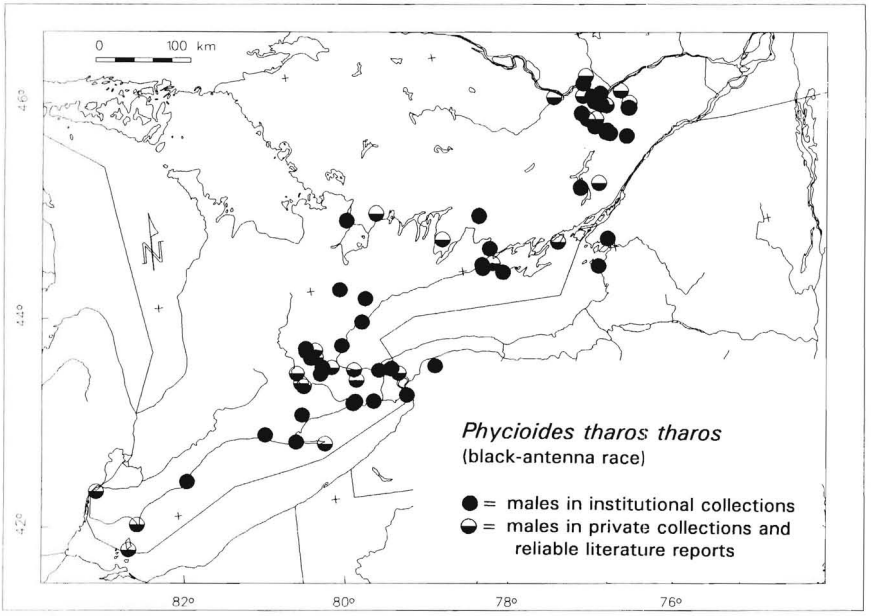

FIG. 1. Distribution of the black-antenna race of *Phyciodes tharos tharos* in Ontario and adjacent regions. Based on males examined in institutional collections (dots, see Materials and Methods) and males in private collections or reliable literature reports of males (half-dots).

to adults on the same plants upon which the eggs were laid. Representative samples of butterflies were placed in CNC. Names for vascular plants listed for habitats were taken largely from Gleason and Cronquist (1991).

RESULTS AND DISCUSSION

Distribution. Oliver (1980) suggested that the region of sympatry of *P. tharos* and *P. cocyta* was equivalent to Remington's (1968) northeastern suture zone and he noted a northern limit of *P. tharos* extending from central New England to southern New York, southern Ontario and southern Michigan. This northern limit, approximating the northern limit of the Carolinian or Upper Austral region of southern Ontario, was drawn by Scott (1986) and Opler & Malikul (1992) as extending from western Lake Ontario to southern Lake Huron. Figure 1 documents a northern limit extending farther north into the Canadian zone in the Ottawa valley north of Ottawa to 45°36′N (Lac Philippe) and to the southern edge of the Canadian Shield north of Lake Simcoe (Kirkfield and Orillia) at 44°38′N.

With extensive abandoned pasture and rich alvar habitats on the Bruce Peninsula and Manitoulin Island, one might expect *P. tharos* to

occur there, but these areas are cooler than the rest of the Ontario range. *Phyciodes tharos* was not represented among 43 *Phyciodes* males collected throughout this region at different times by J. A. Morton. It is also shown here for the first time in northern New York (Stony Point and Chaumont).

Currently *P. tharos* is known in Quebec only from the Ottawa valley (Eardley, Lac Phillipe, Aylmer). Of 125 *P. tharos* (*sensu lato*) at LEM, of which approximately half are males, there is only one with black antennal clubs (Laval, A. C. Sheppard, 19 Aug 1972), but the median and postmedian black lines on the upper wings are poorly developed, and the crescent patch is tan instead of dark brown. This specimen is consequently not clearly referable to *P. tharos*.

Various reports from Ontario (Hanks & Hess 1992, Hanks 1993, 1994, 1995) from localities north of those shown on Figure 1 were found to be referable to *P. tharos* in the earlier broad sense, and those that could be checked proved to be *P. cocyta* (the only exception being a report from Shoal Lake Road at Hwy 17 in Kenora district (Hanks 1994) that is not supported by a specimen; A. Wormington, pers. comm). *Phyciodes tharos* occurs at similar latitudes in Manitoba (Klassen et al. 1989), Saskatchewan (Hooper 1973) and Alberta (Acorn 1993, Bird et al. 1995), and the western race with more yellow on the nudum quite possibly occurs in at least the southern Kenora and Rainy River portion of Ontario.

Status in Ontario. The relatively small number of *P. tharos* males in many institutional collections suggests the butterfly may be either rare in Ontario, or a recent arrival. The earliest collections of which I am aware are from St. Davids (43°10′N, 79°06′W) near the Niagara River in 1930 (UWO) and 1932 (CNC), and Brighton (44°02′N, 77°44′W) in Northumberland County in the eastern Lake Ontario region in 1932 (CNC). Even at this early date, Wild (1939) noted that some authorities considered the darker summer brood in the Niagara frontier region to be a distinct variety.

Although *P. tharos sensu stricto* may not be a recent arrival in the Lake Ontario region of Ontario, it was not noticed in the Ottawa valley until 1995, despite the fact that this region has received more attention from lepidopterists than any other part of Canada (Layberry et al. 1982). As soon as its habitats were understood it was found in at least 15 locations within the district (Crolla 1996); although it proved to be quite local, it is locally abundant and continuously present (the earliest collected specimen from the district was taken in 1990 at Eardley (F. Lessard, pers. comm.)). Some of the places from which it currently is known are at or near colonies of *P. batesii* which were visited a number of times by entomologists more than 65 years ago.

It seems unlikely that a few *P. tharos* would not have been taken by

the many early entomologists working in the region if it had been present, particularly in some of the habitats frequented by *P. batesii* at the time. Furthermore many of the current locations are abandoned pasturelands, which were part of a more intensively utilized agricultural landscape prior to 1960. Thus, it may have moved in over the past 30 years following abandonment of marginal pasturelands. Opler and Krizek (1984) speculated that *P. tharos* "probably expanded greatly with the cutting of eastern deciduous forests and expansion of agriculture."

On the other hand, *P. tharos* is quite local in the Ottawa valley and was previously lumped with *P. cocyta*, which is more conspicuous, widespread, and abundant early in the season. Consequently *P. tharos* may not have been collected "accidentally." Appropriate species-rich habitats undoubtedly existed within regional alvar landscapes (see Catling & Brownell 1995) in pre-settlement times due to fires, and it was collected as far north as Marmora in 1952.

Although *P. tharos* is clearly widespread in Ontario and occurs in both restricted natural habitats (alvars, dune slacks, prairies) and anthropogenic habitats (abandoned pastures and hay-old field complexes), the species does appear to be local and absent over vast areas. In contrast, its close relative *P. cocyta* is ubiquitous over much of the province in June and early July. *Phyciodes tharos* has been found in 65 locations and is currently known from at least 27 locations (where a location is defined as an area of occurrence at least 3 km from another area of occurrence). Consequently, its provincial ranking should be S3-S4, possibly uncommon but with sufficient occurrences to be secure, according to the Nature Conservancy of Canada system.

Oviposition and foodplants. In southern Quebec at Aylmer (45°14′N, 75°31′W) and in southern Ontario at Metcalfe (45°24′N, 53°75′W) and Dwyer Hill Siding (45°02′N, 75°49′W), females were observed ovipositing between 1300–1430 h. They flew short distances of 1–2 m, usually alighting and resting for 2–5 minutes, then crawled through the grasses and herbs 2–5 cm above the soil apparantly searching for a foodplant. The crawls involved distances of 0.1–0.5 m and the crawling period lasted for 2–30 minutes with or without resting periods of up to 10 minutes (characterized by slow closing and opening of the wings to a horizontal position). During a crawl leading to oviposition a female moved over the same leaves 2–6 times with or without resting periods, and finally settled on the edge of a leaf with wings slowly closing and opening to an angle of 45°. The abdomen was curled under the leaf and pale green eggs were deposited adjacent to, or on top of others, on the lower leaf surface. The egg clusters included 52, 58 and 64 for the three locations listed above (respectively). Oviposition lasted approximately 20 minutes. The plant upon which eggs were laid at each of the three sites

was *Aster ciliolatus* Lindl. (Asteraceae), a species with elongate rhizomes that forms loose to dense patches. In all cases the females used relatively small, non-flowering rosette plants and placed eggs on leaves approximately 3 cm above the soil surface. The patches utilized were sparse rather than dense and lacked flowering plants, but the leaves upon which the eggs were laid were young and succulent. Larvae from the Aylmer site were reared on *Aster ciliolatus* from eggs to adult butterflies over 68–71 days (indoors).

Aster ciliolatus has not previously been reported as a foodplant of *P. tharos* (in either the broad or restricted sense). The range of this aster includes the boreal and mixed forest regions of eastern and central North America south to northern New England and the Great Lakes west across the northern edge of the prairie region (Semple & Heard 1987). Thus, this larval foodplant is only available at the northern range limit of *P. tharos*. It was present at all sites north of Lake Ontario and there was a clear correlation between the amount of it and the abundance of *P. tharos*. Further south in Ontario *Aster oolentangiensis* and *A. pilosus* are suspected larval hosts.

Habitats. The major habitat of the most northerly sites is dry, abandoned pasture with short grasses and rosette-forming herbs (e.g. *Danthonia spicata* and *Solidago nemoralis*), especially where these drier areas are interspersed with or adjacent to more moist open habitats. This habitat is prevalent in some alvar landscapes (i.e. areas supporting natural limestone barrens, see Catling and Brownell 1995) north of Lake Ontario. Here the abandoned pastures take a long time to develop complete tree and shrub cover because of the combined effects of moisture extremes, periodic drought and thin soil. Abundance of *Aster ciliolatus* and overall plant diversity is lower in the sites that have experienced the least past disturbance. Natural alvar complexes where tree and shrub cover is limited by fire or cutting, as well as drought, tend to have large populations of both *Aster ciliolatus* and *P. tharos* as well as a high diversity of both native and introduced plant species in a mosaic of wet and dry habitats. Landscapes where drought is the only factor have fewer plant associations, many of the potential open associations having developed tree or shrub cover.

Reduction in overall plant diversity due to reduction in kinds of open habitat in the less disturbed sites reduces nectar resources for adults: the less extreme site conditions associated with past or present reduction in woody cover allow flowering herbs to survive dry periods thus providing continuous resources for *P. tharos* adults. The continuity of nectar resources may be important to adult *P. tharos* since presence of the insect appears to be a consequence of continuous emergence (although there are definite peaks in some locations).

In the Burnt Lands alvar complex near Almonte, Ontario, fire was historically a factor in maintaining open conditions; but with a landscape broken by roads and quarries and with increasing development from housing, fires are no longer a significant environmental factor. In one extensive area, however, tree cover has been eliminated and shrub cover greatly reduced to improve the operation of radio towers, and this area contains a high plant diversity and *P. tharos* is locally abundant. The dominant plants in one of the major plant associations at this site include the grasses *Agrostis stolonifera*, *Carex pennsylvanica*, *Carex umbellata*, *Danthonia spicata* and *Poa pratensis*, and the herbs *Aster ciliolatus*, *Comandra umbellata*, *Fragaria virginiana*, *Prunella vulgaris*, *Senecio pauperculus*, *Solidago juncea*, *S. nemoralis*, and *S. ptarmicoides*.

The abandoned, rugged pastures on shallow, calcareous soil over limestone where *P. tharos* occurs are dominated by the grasses *Agrostis stolonifera*, *Danthonia spicata*, *Dactylis glomerata*, *Festuca* spp., *Poa compressa*, *Panicum philadelphicum*, *Sporobolus vaginiflorus*, and the herbs *Aster ciliolatus*, *Daucus carota*, *Echium vulgare*, *Fragaria virginiana*, *Hieracium pilloselloides*, *Leucanthemum vulgare*, *Melilotus alba*, *Origamum vulgare*, *Prunella vulgaris*, *Rudbeckia hirta*, *Senecio pauperculus*, *Solidago canadensis*, *S. nemoralis*, *Trifolium* spp. and *Vicia cracca*. The continuity of blossoms from spring through summer to fall in these habitats is to a large extent a result of the presence of introduced species. The nearly complete restriction of *P. tharos* to the dry alvar and abandoned limestone pasture habitats at its northern range limit could relate to the relatively warmer microclimate of these dry, open sites as well as to both adult and larval foodplant availability.

Farther south of the alvar landscapes and particularly in the Carolinian region of Ontario and northern New York, the main species of *Aster* associated with *P. tharos* at several sites is the white *A. pilosus*. Adult *P. tharos* occur in association with this species in natural habitats such as dune slacks dominated by the graminoids (grasses and sedges) *Cladium mariscoides*, *Poa compressa*, and *Schizachyrium scoparium*, and in old fields dominated by the grasses *Agrostis* spp., *Dactylis glomerata*, *Phleum pratense*, *Poa compressa*, *Poa pratensis*, and the herbs *Daucus carota*, *Solidago canadensis*, and *S. nemoralis*. Occupied habitats are primarily in areas of sandy soils subject to moisture extremes and where encroachment of shrubs such as *Cornus racemosa* is relatively prolonged. It also occupies hayfields that are cut once, but in these habitats there is probably an enforced displacement after cutting to adjacent uncut or abandoned fields. Cutting of hay results in a second or late blooming of *Daucus carota*, *Trifolium* spp., and other species, thus improving the local continuity of adult food resources. The hayfields often have *Trifolium* spp., *Lotus corniculatus*, *Dipsacus sylvestris*, *Ambrosia*

artemisiifolia among the dominants, the only prominent aster being *Aster pilosus* var. *pilosus*. In the dune slacks the prominent aster is usually *Aster pilosus* var. *pringlei*, but *A. dumosus* is also present.

In one prairie situation in southern Ontario (Brant County), *P. tharos* occurred in a hilly area dominated by *Schizachyrium scoparium*, *Sorghastrum nutans* and *Aster oolentangiensis* with no other *Aster* species evident. This site had been impacted previously by grazing and had many alien species. Other southern Ontario prairies surveyed were without populations of *P. tharos*.

In many cases *P. tharos* was found to be absent from areas within the general region of occurrence indicated in Figure 1. Some of the sand barrens and granite rock barrens searched had large populations of *Aster ciliolatus*, but there were periods of 4 weeks or more during the summer when nectar resources were essentially adsent. In contrast, the closely related, and more or less univoltine, *P. cocyta* was present in most if not all of these sites. All sites where *P. tharos* was found including abandoned pastures, disturbed alvar, dune complexes, and hayfield-old field landscapes, had in common a high floristic diversity and a continuous supply of adult food resources, as a result of a mosaic of different habitats lacking woody cover.

Flight period. The earliest adult flight dates for Ontario are 22–26 May (Dunnville to the Ottawa district, respectively). The latest dates range from 13 October at Ottawa (pers. obs.) to 23 October on Point Pelee (Hanks & Hess 1992, reported by A. Wormington). Adult emergence appears to be almost continuous, with worn and fresh specimens of both males and females being found in most samples. At locations where there are large populations, adults were encountered from early June to early October. Appearance of the butterflies seems to depend as much on the weather as on a regular schedule of consecutive broods, but there were three clear peaks of abundance in 1995 (early June, mid-July to early August, and late August to early September).

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LITERATURE CITED

ACORN, J. 1993. Butterflies of Alberta. Lone Pine Publishing, Edmonton, Alberta. 141 pp.

BIRD, C. D., G. J. HILCHIE, N. G. KONDLA, E. M. PIKE & F. A. H. SPERLING. 1995. Alberta butterflies. Provincial Museum of Alberta, Edmonton. 347 pp.

CATLING, P. M. & V. R. BROWNELL. 1995. A review of the alvars of the Great Lakes region: distribution, floristic composition, biogeography and protection. Can. Field Nat. 109(2):143–172.

CROLLA, J. 1996. The Pearl Crescent (*Phyciodes tharos*) in the Ottawa District. Trail & Landscape 30(2):51–57.

GLEASON, H.A. & A. CRONQUIST. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. Second Edition. The New York Botanical Garden, Bronx, New York. 910 pp.

HANKS, A. J. 1993. Butterflies of Ontario and summaries of Lepidoptera encountered in Ontario in 1992. Toronto Entomol. Assoc. Occ. Publ. 25–93. 102 pp.

———. 1994. Butterflies of Ontario and summaries of Lepidoptera encountered in Ontario in 1993. Toronto Entomol. Assoc. Occ. Publ. 26–94. 100 pp.

———. 1995. Butterflies of Ontario and summaries of Lepidoptera encountered in Ontario in 1994. Toronto Entomol. Assoc. Occ. Publ. 27–95. 92 pp.

HANKS, A. J. & Q. F. HESS. 1992. Butterflies of Ontario and summaries of Lepidoptera encountered in Ontario in 1991. Toronto Entomol. Assoc. Occ. Publ. 24–92. 94 pp.

HOLMES, A. M., Q. F. HESS, R. R. TASKER AND A. J. HANKS. 1991. The Ontario Butterfly Atlas. Toronto Entomol. Assoc. 167 pp.

HOOPER, R. R. 1973. The butterflies of Saskatchewan. Museum of Natural History, Regina. 216 pp.

KLASSEN, P., A. R. WESTWOOD, W. B. PRESTON & W. B. MCKILLOP. 1989. The butterflies of Manitoba. Manitoba Museum of Man and Nature, Winnipeg. 290 pp.

LAYBERRY, R. A., J. D. LAFONTAINE & P. W. HALL. 1982. Butterflies of the Ottawa district. Trail and Landscape 16(1):3–59.

OLIVER, C. G. 1980. Phenotypic differentiation and hybrid breakdown within *Phyciodes "tharos"* (Lepidoptera: Nymphalidae) in the northeastern United States. Ann. Entomol. Soc. Am. 73:715–721.

OPLER, P. A. & G. O. KRIZEK. 1984. Butterflies east of the Great Plains. Johns Hopkins Univ. Press, Baltimore. 294 pp.

OPLER, P. A. AND V. MALIKUL. 1992. A field guide to the butterflies. Houghton Mifflin Co., New York. 396 pp.

SCOTT, J. A. 1986a. The butterflies of North America, a natural history and field guide. Stanford University Press, Stanford, California. 583 pp.

———. 1986b. The courtship of *Phyciodes*, and the relationship between *Phyciodes tharos tharos* and *Phyciodes tharos morpheus* (=*pascoensis*) in Colorado. Papilio, new series, 5:1–8.

———. 1994. Biology and systematics of *Phyciodes*. Papilio, new series, 7:1–120.

SEMPLE, J. C. & S. B. HEARD. 1987. The asters of Ontario: *Aster* L. and *Virgulus* Raf. (Compsitae: Astereae). Univ. Waterloo (Waterloo, Ontario), Biol. Ser. No. 30. 88 pp.

WILD, W. 1939. The butterflies of the Niagara frontier region. Buffalo Soc. Natural Sci. Bull. 19(1):1–55.

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