HEMARIS THETIS (BOISDUVAL, 1855) (SPHINGIDAE) IS A DISTINCT SPECIES

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ABSTRACT. Western North American populations previously treated as Hemaris diffinis (Boisduval) are shown to be a distinct species, Hemaris thetis (Boisduval), based on differences in habitus, genitalic morphology, mtDNA sequence variation and larval phenotype. Both species occur in strict sympathy at several localities in western Alberta without evidence of intergradation. Hemaris senta is a colour variant of H. thetis, and synonymized under the latter. Adults and diagnostic characters are illustrated, and the synonymy of H. diffinis is revised.

Additional key words: cryptic species, DNA barcoding, Hemaris senta, Hemaris diffinis.

The genus Hemaris Dalman (Sphingidae: Macroglossinae) currently contains 19 species (Kitching & Cadiou 2000), occurring primarily in temperate regions of the northern hemisphere. Four species are recognized in North America, namely thysbe (F. Abricius, 1775), gracilis (Grote & Robinson, 1865), senta (Strecker, 1878), and diffinis (Boisduval, 1836) (H odges 1971; Tuttle 2007). Hemaris diffinis and the taxa historically associated with it have long been a confusing lot, since there is little structural variation in genitalia (compared to congeners), with significant geographic and seasonal variation in phenotype. Here, I examine the morphological, ecological and molecular variation of western North American populations previously assigned to H. diffinis, with special emphasis on the contact zone between the Great Plains, Boreal and Cordilleran faunal regions in Alberta, Canada. These data show that two western species have gone under the name H. diffinis, and that H. senta is a color form of the second, unrecognized species, H. thetis.

Taxonomic history of Hemaris diffinis. The influential work of Abbot & Smith (1797) was apparently the first to illustrate H. diffinis, although referred to the European species H. fuciformis (L.) therein. Boisduval (1836) subsequently described and illustrated diffinis, and no other names for the Hemaris diffinis group were proposed until he described thetis two decades later (Boisduval 1855). As was often the case at that time, the provenance of the diffinis type material was vague, indicated only as “Amerique septentrionale”. Comparison of the illustration accompanying the description, as well as the illustration in Abbot & Smith (1797), which Boisduval (1875) considered to be diffinis, suggests that the type of diffinis represents the large, dark phenotype typical of the southeastern US populations, a conclusion also reached by Rothschild & Jordan (1903). The most likely type locality is therefore the southeastern Atlantic seaboard, possibly Georgia. Type material of diffinis is extant in the Carnegie Museum of Natural History, Pittsburgh, PA (L. Kitching, pers. comm.).

Phenotypic variation among multiple annual generations, together with geographic variation, resulted in new names being proposed for various forms of H. diffinis (sensu stricto). Through rearing a second generation from known first generation females, Smyth (1900) showed that seasonal variation in phenotypes had resulted in erroneous recognition of separate species. Rothschild & Jordan’s (1903) seminal revision reviewed the 13 diffinis-group taxa described to that point, and synonymized all but one under diffinis, based on perceived lack of diagnostic differences in male genitalia, and the phenotypic variation established to be seasonal by Smyth (1900). Rothschild & Jordan (1903) considered H. thetis (sensu novo, listed as H. brucei by these authors) distinct from diffinis, based on the fact that it occurred in sympatry with diffinis and remained distinguishable from it. These authors segregated diffinis into three subspecies, H. d. diffinis (Atlantic region), H. d. senta (Great Plains) and H. d. thetis (Rocky Mountains westward). Although various nomenclature changes were implemented by subsequent authors (discussed below), the concept of a transcontinental species and a western species was followed by subsequent authors (Barnes & McDunnough 1910; H odges 1971; Tuttle 2007).

In their checklist of the Sphingidae of North America, Barnes & McDunnough (1910) retained the species-level taxonomy of Rothschild & Jordan (1903), although revising the name senta as a senior synonym of H. brucei, and providing the name ariadne Barnes & McDunnough for the Great Plains H. diffinis senta of Rothschild & Jordan. They retained the geographic subspecific groupings of diffinis, but also recognized the taxon aethra (Strecker) in eastern North America (Ontario and Quebec) in addition to H. d. diffinis.
Subsequent faunal treatments have followed this species-level arrangement, i.e. with *H. diffinis* and *H. senta* as species, but without recognizing subspecies (Hodges 1971; Kitching & Cadiou 2000; Tuttle 2007). Bridges (1993) listed *thetis* as a subspecies of *diffinis*, but did not comment on the change in taxonomic status for *thetis*, and it was therefore again revised to synonymy under *diffinis* by Kitching & Cadiou (2000).

**METHODS AND MATERIALS**

Specimens examined. The following abbreviations are used herein for specimen depositories:

CNC: Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario
CMNH: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
CSU: C.P. Gillette Arthropod Biodiversity Museum, Colorado State University, Colorado
FMNH: Field Museum of Natural History, Chicago, Illinois
MCZ: M museum of Comparative Zoology, Cambridge, Massachusetts
MNHN: Muséum National d’Histoire Naturelle, Paris
NHML: Natural History M useum, London
UASM: University of Alberta Strickland Entomological M useum, Edmonton, Alberta

Approximately 750 specimens were examined in this study, primarily those of the CNC and UASM. Voucher specimen data for dissections and molecular analysis are given in Table 1. Data for molecular voucher specimens, including trace files and photographs, are available at http://barcodinglife.com (project: Lepidoptera: Hemaris under the “Published Projects” tab). Molecular sequences are deposited in GenBank, with accession numbers EU646618–EU646632. Distribution maps were compiled using DIVA-GIS 5.0. Geographic coordinates of collection localities were referenced using GEOLocate (Rios & Bart 2004), Placenames.com, and the Canadian Geographical Names Data Base (Natural Resources Canada 2006). Standard postal abbreviations for Canadian provinces and American states are used here.

**Morphological techniques.** Adult genitalia were prepared following the methods detailed by Lafontaine (2004). Cleaned, stained genitalia were stored and examined in 30% ethanol, and slide-mounted in Euparal before being photographed.

**Molecular techniques.** Specimens for molecular analysis were selected to maximize geographic coverage for western populations of *H. thetis* and *H. diffinis*, particularly for regions where the two taxa are sympatric. Specimens were also included from as near as practicable from the type localities of each taxon, namely north-central CA (*thetis*), central CO (*senta*) and GA (*diffinis*) (Table 1). Molecular variation was assessed based on the 658 bp ‘barcode’ region of the subunit of the cytochrome oxidase (*cox1*) gene (Hebert et al. 2003), corresponding to nucleotide positions 1490–2198 of the *Drosophila yakuba* mitochondrial genome (Clary & Wolstenholme 1985). DNA was extracted from one leg removed from a dried specimen, sent to the University of Guelph in dry Eppendorf tubes, and processed as part of the “All Leps Barcode of Life Campaign” (www.lepbarcoding.org). DNA extraction, amplification and sequencing protocols for the Barcode of Life initiative are detailed in Hebert et al. (2003). Haplotypes of all *cox1* ‘barcode’ fragments were compared with phylograms constructed using the neighbor-joining method in PAUP 4.0*b10* (Altivec) (Swofford 2002). Phyyletic distances were calculated using the Kimura-2-Parameter (K2P) distance model.
RESULTS

**Hemaris thetis** (Boisduval, 1855) Revised Status

Macroglossa thetis Boisduval, 1855: 32.

**Type material:** two syntypes [AMNH?] Type locality: not stated, implied to be “Californie”; here restricted to Kelseyville, Sonoma Co., California. Notes. Most of the types of North American sphingid species described by Boisduval (1874) were purchased by Rothschild and were subsequently deposited in the Natural History Museum (London), then later purchased by B. P. Clark and so passed to the CMNH (I. Kitching, pers. comm.). The location of types for species described by Boisduval prior to 1875 is less clear, but a thetis syntype may also be at the CMNH. The second syntype (female) may be in the AMNH based on Grote’s statement that “During our recent visit, Dr. Boisduval kindly communicated to us a specimen of S. thetis for the purpose of publishing the species...” (Grote & Robinson 1868: 325). As indicated by Boisduval (1855), the types of thetis were collected by Lorrain. Emmel et al. (1998) provide a detailed summary of Lorquin’s collecting itinerary, and conclude that he collected in (at least) Sonoma, Marin, Placer, and El Dorado counties of northern California prior to 1855. The type locality of thetis is therefore restricted to Kelseyville, Sonoma Co., California, where this species is known to occur.

**Hemaris palpalis** Grote, 1874: 145. Revised Synonomy

**Type material:** holotype, presumably a male [MCZ]. Type locality: restricted to “Gilroy, Santa Clara County, California; about 80 miles south of San Francisco.” by Grote (1875: 224). Notes. In the original description Grote (1874) states that the type was labelled “with the ticket “Gilroy”, by the late G. R. Crotch, in British Columbia...”, subsequently corrected to Gilroy, California (Grote 1875), as also noted by Edwards (1875). Hemaris palpalis was described with “bright orange” palps, which in all likelihood was due to pollen accumulation on the palps, as noted by Rothschild & Jordan (1903).

**Hemaris rubens** H. Edwards, 1875: 88. Revised Synonomy

**Type material:** two syntypes, sex not stated [AMNH?]. Type locality: “Oregon...; Lake Tahoe, Cal.” Notes. Edwards differen-
tiated this taxon from his concept of thetis based on more red-
dish wing markings and more extensive yellow dorsal abdominal
vestiture.

Hemaris cynoglossum H. Edwards, 1875: 88. Revised Synonomy
Type material: two male and two female syntypes [AMNH?]. Type locality: "Napa County; Big Trees, Calaveras
County, Cal.; Vancouver Island." Notes. Edwards (1875) de-
scribed cynoglossum with the "thorax bright greenish olive,
without the brownish tint observed in thetis". Edwards’ concept
of thetis appears to have been of the summer-flying, more or-
ange colored thetis populations of southern California.

Macroglossa senta Strecker, 1878: 1858, pl. 2, f. 1. Revised Status
Type material: holotype [FMNH?] Type locality: Tierra
Amarilla, New Mexico. Notes. Distinguished based on entirely
yellow ventral thorax and abdomen (excluding anal tuft), and
wider ductus bursae of female genitalia (Hodges 1971). Exami-
nation of senta phenotypes from CO, UT, and CA confirms the
genitalic differences between senta and diffinis, and shows that
senta is structurally indistinguishable from thetis. Comparison of
long series of southern BC specimens shows that the extent of
ventral yellow vestiture varies somewhat, with specimens from
hotter, drier habitats tending to show more yellow on abdominal
segments 5 to 7 (some of these specimens, from Kaslo, BC were
reported as senta by Hodges (1971)). Specimens from the east
slope of the Sierra Nevada in California (Sonora Pass, Alpine
Co.; also localities cited by Tuttle [2007]) tend to be more yellow
dorsally like senta, but lack the continuous yellow ventrum. Leg
vestiture shows similar variation in extent of yellow scaling; for
example, cynoglossum was described based in part on the black
rather than yellow hind-tibiae. The consistency of the diagnostic

genitalic and larval characters discussed below, across western
populations varying from senta to thetis phenotypes, leads me to
conclude that senta and thetis represent a single species, with
thetis as the oldest name.

Hemaris brucei French, 1890: 133. Revised Synonomy
Type material: single male [destroyed?]. Type locality: "Col-
orado". Notes. Barnes & McDunnough (1910) indicated that the
type was destroyed by dermestids. However, there is a specimen
of brucei labelled "type" in the USNM, the true status of which
remains to be determined (I. Kitching, pers. comm.). French’s
material in the Illinois Natural History Survey should also be ex-
amined.

Hemaris minima Frankenbusch, 1925: 90. Revised Synonomy
Type material: described from a single specimen, sex not
stated [type depository unknown]. Type locality: implied to be
Palaearctic in original description [erroneous]. Notes. As dis-
cussed by Kitching & Cadiou (2000), the type locality is incor-
rect, since Bang-Haas (1927) examined the type of minima and
recognized it as the same taxon as "senta". Frankenbusch de-
scribed minima as having a black ventral abdomen, not yellow as
in the senta form.

Hemaris diffinis jordani Barnes & Benjamin, 1927: 51. Revised Synonomy
Type material: holotype male, allotype female, 36 male and
four female paratypes [NMNH]. Type locality: "Southern Utah".
Notes. A junior secondary homonym of Haemorrhagia fuciformis
jordani Clark, 1927; Eitschberger, Danner & Surholt (1996)
provided the replacement name heppneri.
† Haeomorrhagia diffinis thetis f. mcdunnoughi Clark, 1927: 104. **Revised Synonomy**


**Type material:** holotype male, allotype female, 36 male and four female paratypes [NMNH]. Type locality: "Southern Utah." **Notes.** Proposed as a replacement name for Hemaris diffinis Jordan & Benjamin, 1927.

**Diagnosis.** Habitus. Although there is some geographic variation in the extent of yellow vestiture on the thorax and abdomen, thetis can be reliably separated from diffinis where the two are sympatric or parapatric based on the following traits (Figure 1): The central anal tuft is black or black with some dorsal yellowish hairs (senta phenotypes, Fig. 1b), never solid yellow as in diffinis (Fig. 1c). The dorsal thorax and basal abdominal segments are evenly olive-coloured, not orange-yellow with pale yellow subdorsal hairs (giving a striped appearance) as in diffinis; subdorsal yellow stripe not extending through 4th abdominal segment (yellow subdorsal stripe extending through 4th segment in diffinis). These traits remained constant in all material examined from geographic areas where thetis and diffinis occurred together (central and southwestern AB; central CO), and specimens could be easily assigned to one of the two species based on color pattern. As discussed above under Senta, ventral color is variable in thetis and is not a reliable diagnostic trait. The specimen illustrated as H. Senta in Tuttle (2007: Plate 5 Fig. 18) is actually H. diffinis.

**Genitalia.** The most pronounced structural differences are in the female genitalia. The lamella postvaginalis forms a broader band, and the ridges forming the origins of the anterior apophyses are more strongly tapered caudally in thetis; the lamella postvaginalis also has a pronounced median lobe on the proximal margin, absent in diffinis (Fig. 2). The dorsal sclerotized plate of the ductus bursae is on average wider in thetis compared to diffinis, the width being about 1–1.2X that of the plate length, compared to 0.5–0.7X in diffinis (Fig. 2). The male genitalia are more variable, but the following subtle differences are evident: overall, the saccular region has a smoother (more finely scobinate) more elongate appearance in thetis than diffinis, with the scobinate, inner base flattened or convex, not curved and ridge-like as in diffinis (Fig. 3); the left saccular extension is on average shorter, more triangular, and broader-based (Fig. 3).

**Larva and pupa.** Tuttle (2007) provides an excellent summary of the larval differences between thetis (as western diffinis and senta) and diffinis, and the following is based largely on the description given therein: caudal horn short and stout, purplish in color and lacking a yellow base, curving caudal; spiracles orange. In diffinis, the horn is longer, black with a bright yellow base, and straight or curved cephalad, and the spiracles are black. Based on the few examples of pupal cases available to me (two thetis and three diffinis), the cremaster of thetis has a slightly broader base with a rounded taper towards the apex, compared to a straight taper in diffinis, giving the overall appearance of a more robust cremaster in thetis. More pupae should be examined to assess the variability of this trait.

**Molecular variation.** Nine H. thetis specimens were sequenced from southern British Columbia, southwestern and central Alberta, California, and Colorado, and compared to ten diffinis sequences from southeastern Alberta, southwestern Saskatchewan, Oklahoma, and Georgia (Table 1). Hemaris thetis samples consisted of three haplotypes, with six haplotypes for the diffinis samples (Fig. 4). Specimens from areas of sympatry identified as H. thetis based on color pattern exhibited "thetis" haplotypes (voucher numbers CnCnctoctolidae13841, CnCnctoctolidae13842, Uasm58223, Uasm58404; Table 1, Figure 1), as did the nominate thetis specimen from CA and senta from CO (Table 1; Figure 1). Although diffinis specimens from the immediate areas of sympathy (dissection numbers CnC13736, CnC13744, CnC13745; Table 1) were too old for molecular analysis, those from nearby sites expressed "diffinis" haplotypes (e.g. Uasm99164, Uasm99165; Table 1).

**Divergence rates between thetis and diffinis ranged from 2.0% to 3.3% averaging 2.8%. A single sequence of H. gracilis was included for comparison, which differed from thetis and diffinis by averages of 7.9% and 8.4%, respectively. Divergence rates between thetis and diffinis are slightly higher than those observed in other Macroglossinae, i.e. members of the Hyles euphorbiaceae (L.) complex where Hundsdoerfer et al. (2005) observed interspecific divergence rates of 0.1–2.1% (uncorrected pairwise distances, cox1-2 genes). Additional geographic and molecular sampling of the Hemaris diffinis group should be carried out to confirm if the variation of the cox1 gene is fully congruent with the non-molecular characters that distinguish Hemaris thetis.

**Biology.** Typical of the genus, H. thetis is diurnal and hovers at flowers to take nectar. I have found yellow spring-blooming flowers to be especially productive for finding thetis, such as dandelion (Taraxacum officinale Wigg.) (Asteraceae), early yellow locoweed (Oxypetes
sericea Nutt.) (Fabaceae) and also stickseed (Hackelia sp.) and ornamental sour cherry (Prunus cerasus L.) (Rosaceae). Larval hosts consist of members of the Caprifoliaceae, but specific host species for \textit{thetis} should be re-assessed in light of the confusion with \textit{diffinis}.

Snowberry (Symphoricarpos species, Caprifoliaceae) is undoubtedly referable to \textit{thetis} (host records for \textit{senta}, (Tuttle 2007); also reared CNC specimens). A female \textit{thetis} (voucher # CNC_13759, Table 1) collected in boreal forest habitat was displaying oviposition flight behavior around Lonicera involucrata Rich., another probable host. Jones (1951) indicated “creeping snowberry” as a host in BC, which is unusual since this is not a true snowberry but a species of Ericaceae, Gaultheria hispidula (L.). This could be dismissed as an erroneous record, yet a reared BC \textit{thetis} specimen from a larval collection on “Chiogenes sp.” (1956; CNC) points to the same host, since \textit{G. hispidula} is the only native BC species that was previously placed in Chiogenes. This plant inhabits wet, boggy areas - perhaps boreal populations of \textit{thetis} utilize ericaceous hosts (which are also used by \textit{H. gracilis} (Tuttle 2007)).

Another odd host record requires comment: Abbot & Smith (1797) describe (and illustrate) the larvae feeding on Amsonia tabernaemontana Walt. (Apocynaceae), and Rothschild & Jordan (1903) indicate \textit{Apocynum} (Apocynaceae) as a host. Plants of the Apocynaceae are well-known for their latex production and toxic properties, and use of these plants by \textit{diffinis} should be investigated.

\textbf{Hemaris thetis} has a single annual flight throughout most of the northern parts of its range, with a second flight in the south Okanagan valley of BC (and likely southwards), as indicated by late May/early June and early to mid-July collection dates. Late June records are from higher elevations or latitudes, suggesting an extended or later spring flight, not a second brood. \textbf{Hemaris diffinis} is generally found in warmer, drier
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habitats, and is at least occasionally bivoltine (flying in May to early June and again in late July to August) as far north as the Peace River grasslands at the northwestern periphery of its range.

**Distribution.** Localities for examined specimens of *Hemaris* diffinis from the west-central BC coast to southern CA and AZ, west to central AB and CO (Fig. 5). Alaskan populations (Tuttle 2007) are likely referable to *Hemaris* diffinis as well, but this requires confirmation. By comparison, *H. thetis* is largely a Great Plains species, occurring northward in the western boreal region in more xeric habitats, such as the Peace River grasslands in northwestern AB (Fig. 5). *Hemaris diffinis* appears to be absent west of the continental divide. Both species occur together in the boreal region of central AB, and along the Rocky M Mountains foothills. In the southern portion of the AB Rocky M mountains, where prairie and foothills habitats are juxtaposed at low elevations, the two can occur in strict sympatry; both species are represented in series of specimens from Waterton Lakes and Pine Creek (west of Calgary), AB (CNC), without evidence of intermediate phenotypes.

**Discussion.**

The degree of seasonal variation exhibited by *H. thetis* appears to vary geographically. Summer-generation specimens from southern BC are not distinguishable from those of the spring generation, although July specimens from southern CA and AZ are larger and more yellow in color than the typical olive-yellow northern *H. thetis*. Structurally, these southern, summer specimens are identical to northern populations (and AZ *H. thetis* larvae are like those of the Pacific Northwest [Tuttle 2007]), so there is currently no reason to suspect that more than one species is involved. Documenting seasonal variation and voltinism throughout the range of *Hemaris* would shed additional light on these variation patterns. In a pattern parallel to that in *H. thetis*, summer generation *Hemaris diffinis* from the northwestern parts of the range vary only slightly from the spring phenotype, while summer phenotypes are slightly more orange-yellowish overall. This contrasts sharply with the substantial seasonal variation in vestiture color and width/shape of the forewing marginal band seen in eastern *Hemaris diffinis* populations (Smyth 1900). The eastern ‘subspecies’ of *Hemaris diffinis* recognized long ago by Rothschild & Jordan (1903) and Barnes & McDunnough (1910), may warrant another closer look.

**Acknowledgements.**

I thank Jocelyn Gill for providing technical assistance, and Gary Anweiler, Don Bowman, Boris Kondratieff, Doug Macaulay and Paul Opfer for providing additional data and/or specimens. I am grateful to two anonymous reviewers and Ian Kitching who kindly provided a careful critique of this manuscript, and also provided valuable information on *Hemaris* type specimens.

**Literature Cited.**


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