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

B. CHRISTIAN SCHMIDT

Canadian Food Inspection Agency, Canadian National Collection of Insects, Arachnids and Nematodes, K.W. Neatby Bldg., 960 Carling Ave., Ottawa, ON CANADA K1A 0C6; email: schmidtcb@inspection.gc.ca

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 sympatry at several localities in western Alberta without evidence of intergradation. *Hemaris senta* is a colour variant of *H. thetis*, and synonomized under the latter. Adults and diagnostic characters are illustrated, and the synonomy 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* (Fabricius, 1775), *gracilis* (Grote & Robinson, 1865), *senta* (Strecker, 1878), and *diffinis* (Boisduval, 1836) (Hodges 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 (I. 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* French 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; Hodges 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*.

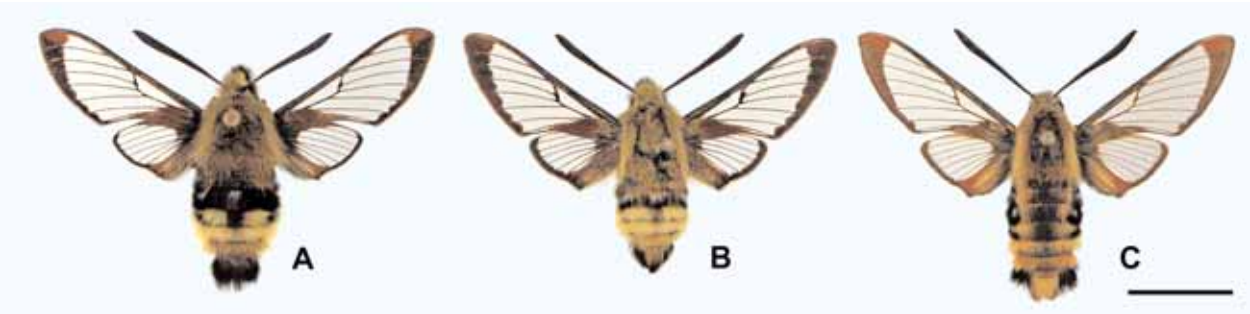

FIG. 1. Habitus of adult *H. thetis* (**A, B**) and western North American *H. diffinis* (**C**). The typical *thetis* phenotype is shown in (**A**) (AB: 15 km SW Beaver Mines, 23-v-99, B.C. Schmidt coll.), the "*senta*" phenotype in (**B**) (CO: 4 mi NW Boulder, 6900', 8-vi-61, W.R.M. Mason coll.), and typical Western *diffinis* (**C**) (SK: 13 KM NNE Eastend, 29-v-03, B.C. Schmidt coll.).

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

DEB: Private collection of Don. E. Bowman, Pueblo West, Colorado.

FMNH: Field Museum of Natural History, Chicago, Illinois

MCZ: Museum of Comparative Zoology, Cambridge, Massachusetts

MNHN: Muséum National d'Histoire Naturelle, Paris

NHML: Natural History Museum, London

NMNH: National Museum of Natural History (formerly United States National Museum), Washington, DC

UASM: University of Alberta Strickland Entomological Museum, 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 co-ordinates 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 first 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). Phyletic distances were calculated using the Kimura-2-Parameter (K2P) distance model.

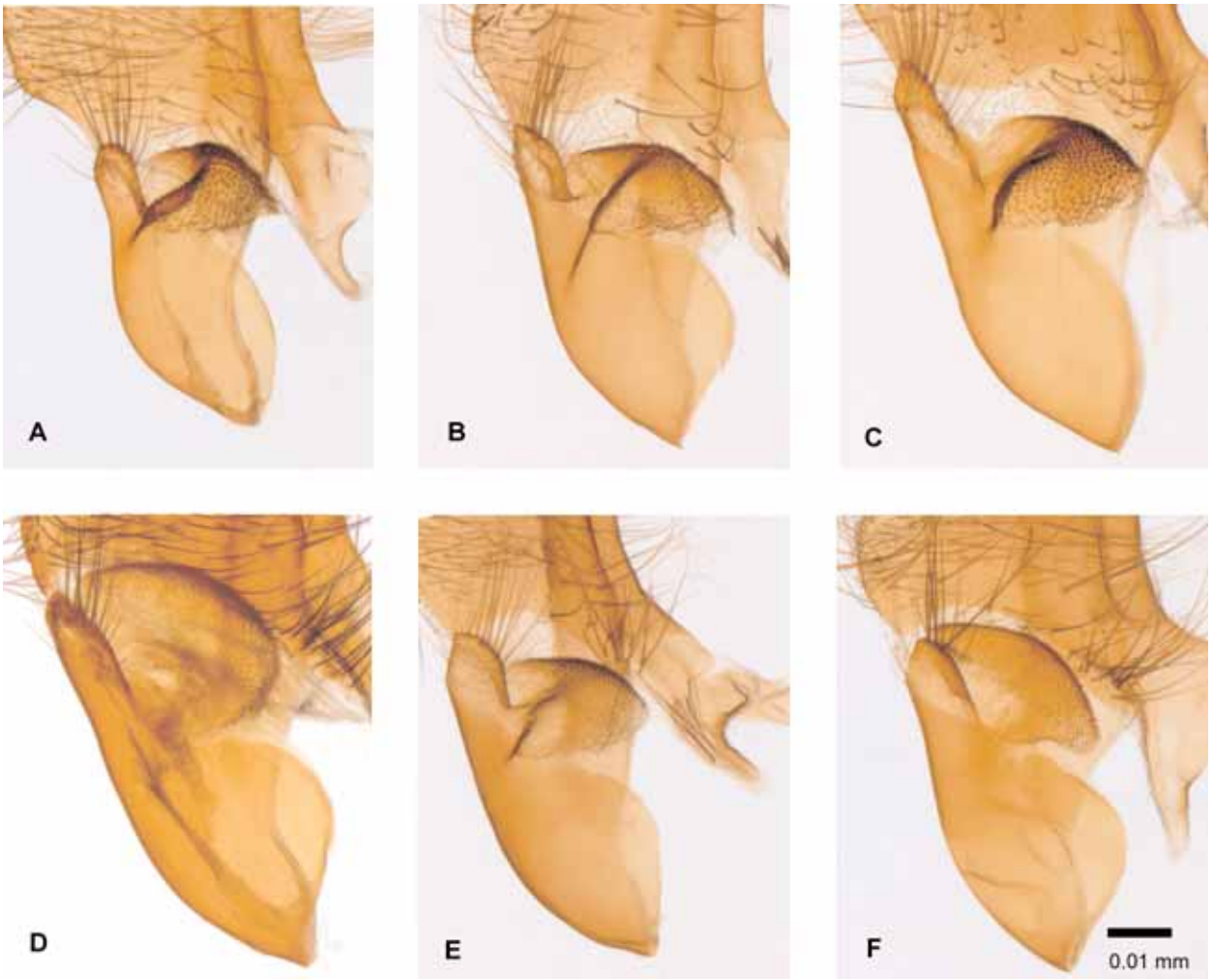

FIG. 2. Variation in structure of the left sacculus in *H. thetis* (top row) and *H. diffinis* (bottom row). Specimen data is given in Table 1 with corresponding dissection numbers: A) CNC13740, B) CNC12738, C) CNC13746, D) CNC13755, E) CNC13747, F) CNC13741.

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 CMN*H*. 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 Lorquin. 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-

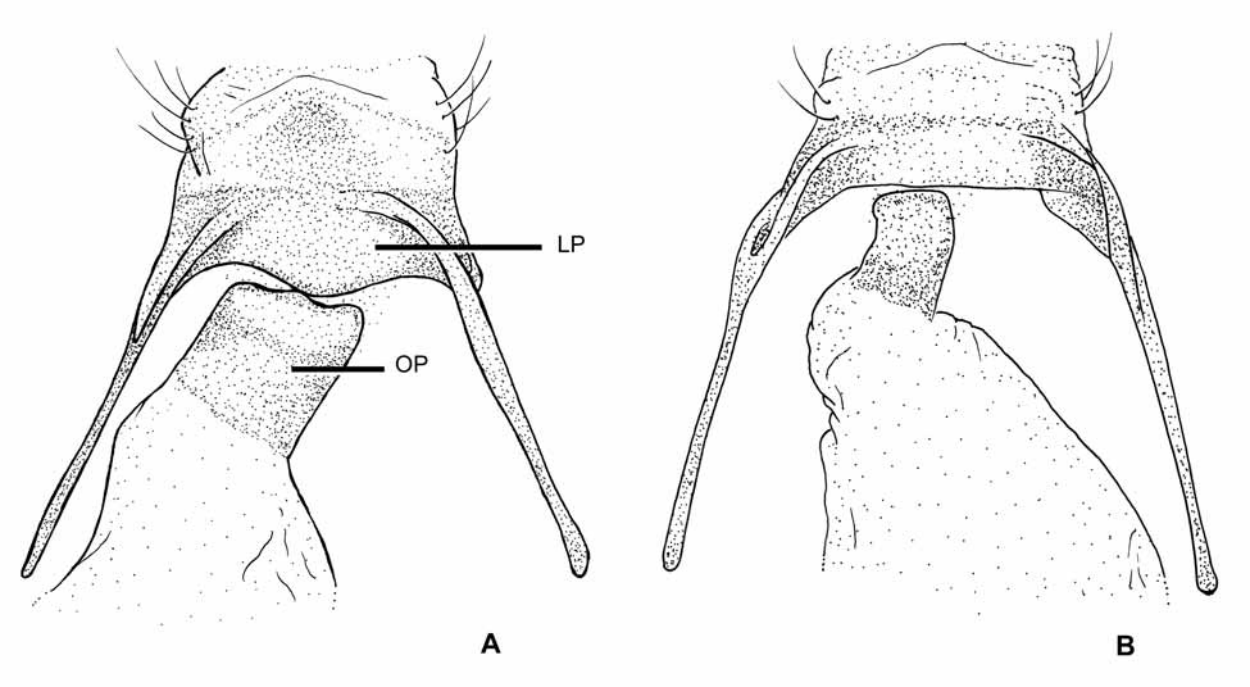

FIG. 3. Lamella postvaginalis (LP) and sclerotized ostial plate (OP) of female *H. thetis* (left) and *H. diffinis* (right).

tiated this taxon from his concept of *thetis* based on more reddish 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) described *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 orange 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). Examination 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:* "Colorado". *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 examined.

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 discussed by Kitching & Cadiou (2000), the type locality is incorrect, since Bang-Haas (1927) examined the type of minima and recognized it as the same taxon as "*senta*". Frankenbusch described 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 *Haemorhagia fuciformis jordani* Clark, 1927; Eitschberger, Danner & Surholt (1996) provided the replacement name *heppneri*.

‡ *Haemorrhagia diffinis thetis f. mcdunnoughi* Clark, 1927: 104. **Revised Synonomy**

Notes. Unavailable infrasubspecific name. Described based on 10 specimens from "Senator Mts., [Bradshaw Mtns.] Arizona, ...Cochise Co., Arizona,...Pinal Mts., Gila Co., Arizona,...southern Utah,...Congress, Arizona,...White Mts., Utah." (Clark 1927).

Hemaris diffinis heppneri Eitschberger, Danner & Surholt, 1996 **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* jordani Barnes & 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 caudad; 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 CNCNoctuoidea13841, CNCNoctuoidea13842, 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 sympatry (dissection numbers CNC13736, CNC13744, CNC13745; Table 1) were too old for molecular analysis, those from nearby sites expressed "diffnis" 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 euphorbiae* (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 (*Oxytropis*

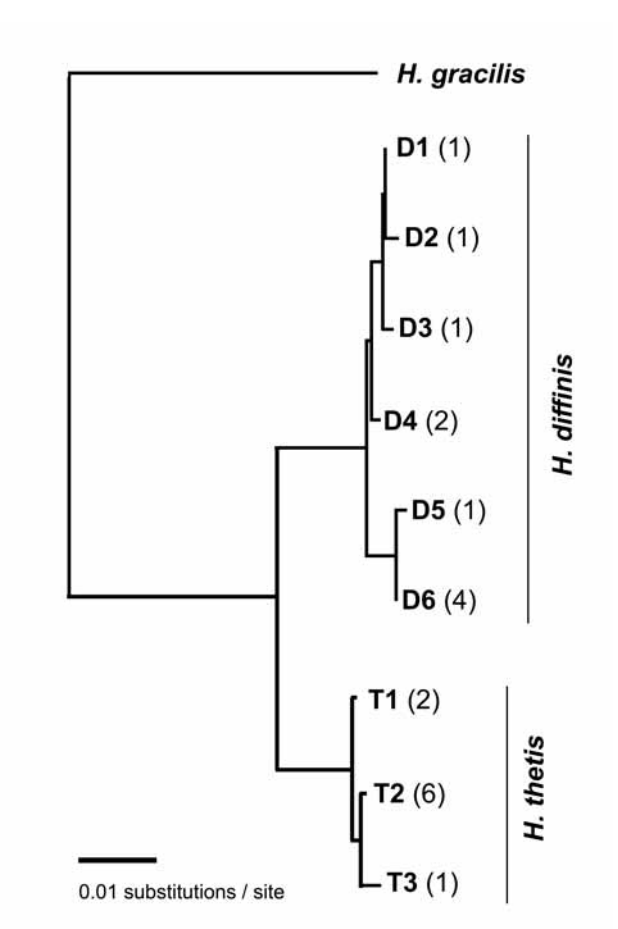

FIG. 4. Neighbor-joining tree of *Hemaris* haplotypes, based on the 658 base-pair barcode fragment of the mtDNA gene *cox1*. Haplotypes correspond to those given in Table 1, with number of individuals sharing a haplotype given in brackets.

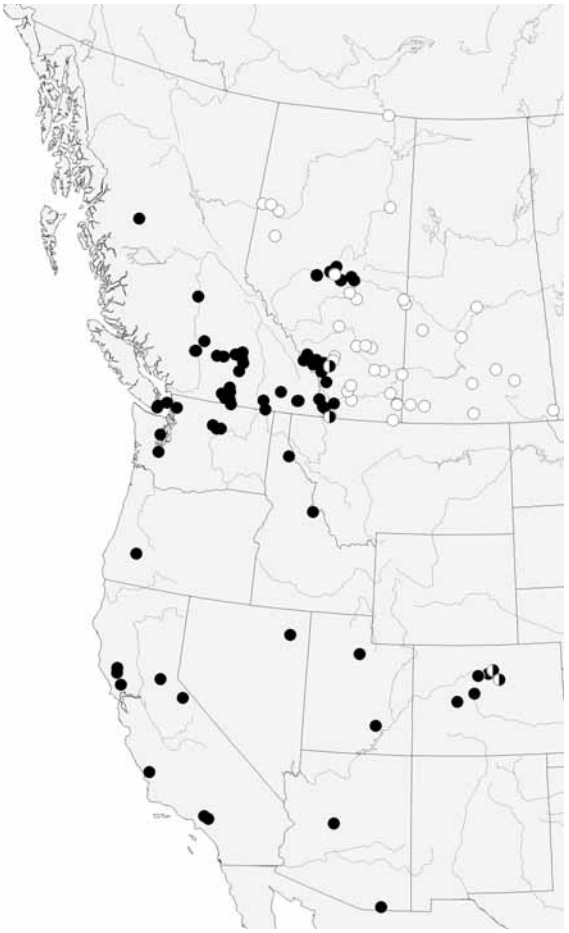

FIG. 5. Distribution of examined specimens of *H. thetis* (black) and western North American *H. diffinis* (white). Half-filled circles indicate records of both species at the same site (Alberta), or adjacent sites too close to map separately (Colorado).

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 *thetis* should be re-assessed in light of the confusion with *diffinis*. Snowberry (*Symphoricarpos* species, Caprifoliaceae) is undoubtedly referable to *thetis* (host records for *senta*, (Tuttle 2007); also reared CNC specimens). A female *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 *thetis* specimen from a larval collection on "*Chiogenes* sp." (1956; CNC) points to the same host, since *G. hispidula* is the only native BC species that was previously placed in *Chiogenes*. This plant inhabits wet, boggy areas – perhaps boreal populations of *thetis* utilize ericaceous hosts (which are also used by *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 *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 *diffinis* should be investigated.

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. *Hemaris diffinis* is generally found in warmer, drier

Table 1. Specimen data for molecular and dissection voucher specimens.

Species	Country	Province	Locality	Latitude	Longitude	Date	Collector	Depository	Sex	Disection #	DNA voucher #	GenBank #	Haplotype
Hemaris diffinis	CAN	AB	Edmonton	53.55	-113.47	5-May-42	Bowman, K.	CNC	m	CNC_13736	-	-	-
Hemaris diffinis	CAN	AB	Elkwater Park	49.66	-110.28	5-Jun-52	Konotopetz, L.A.	CNC	m	CNC_13752	-	-	-
Hemaris diffinis	CAN	AB	Fort McMurray	56.73	-111.38	6-Jun-63	Brown, W.J.	CNC	f	CNC_13762	-	-	-
Hemaris diffinis	CAN	AB	Lethbridge	49.70	-112.82	6-Jun-29	Pepper, J.H.	CNC	f	CNC_13737	-	-	-
Hemaris diffinis	CAN	AB	Waterton Lakes NP, Rowe L. trail, 5500' - 6500'	49.05	-114.00	17-Jun-61	Milliron, H.E.	CNC	f	CNC_13744	-	-	-
Hemaris diffinis	CAN	AB	Red Deer River, 10km N Jenner	50.83	-111.16	19-May-00	Schmidt, B.C.	CNC	m	-	CNCNoctuoidea 13840	EU646623	D6
Hemaris diffinis	CAN	AB	Grande Prairie region, Kleskun Hill	55.25	-118.53	3-Jun-00	Schmidt, B.C.	UASM	m	-	UASM58219	EU646618	D6
Hemaris diffinis	CAN	AB	Grande Prairie region, Kleskun Hill	55.25	-118.53	3-Jun-00	Schmidt, B.C.	UASM	m	-	UASM58222	EU646619	D6
Hemaris diffinis	CAN	AB	Jenner, 10 km N	50.83	-111.16	3-Jun-04	Schmidt, B.C.	UASM	m	-	UASM99164	EU646621	D6
Hemaris diffinis	CAN	AB	Grande Prairie region, Kleskun Hill	55.25	-118.53	3-Jun-00	Schmidt, B.C.	UASM	m	-	UASM58220	EU646620	D5
Hemaris diffinis	CAN	AB	Jenner, 10 km N	50.83	-111.16	3-Jun-04	Schmidt, B.C.	UASM	m	-	UASM99165	EU646622	D1
Hemaris diffinis	CAN	AB	Red Deer River, 10km N Jenner	50.83	-111.16	19-May-00	Schmidt, B.C.	CNC	m	-	LEP041271	-	D4
Hemaris diffinis	CAN	MB	Miniota	50.13	-101.03	10-Jun-37		CNC	f	CNC_13763	-	-	-
Hemaris diffinis	CAN	MB	Norway House	53.99	-97.82	24-Jun-38	Brown, W.J.	CNC	f	CNC_13757	-	-	-
Hemaris diffinis	CAN	MB	Riding Mountain NP, Gorge Ck.	50.88	-100.25	25-Jun-79	Miller, S.J.	CNC	m	CNC_13760	-	-	-
Hemaris diffinis	CAN	NT	Fort Smith	60.04	-111.96	22-Jun-50		CNC	m	CNC_13751	-	-	-
Hemaris diffinis	CAN	ON	Constance Bay	45.49	-76.08	14-May-42	Freeman, T.N.	CNC	m	CNC_13746	-	-	-
Hemaris diffinis	CAN	ON	Manitoulin Dist., Misery Bay	45.79	-82.73	15-Jun-96	Morton, J.	CNC	m	CNC_13753	-	-	-
Hemaris diffinis	CAN	ON	Marmora	44.48	-77.68	10-May-52	Vockeroth, J.R.	CNC	f	CNC_13767	-	-	-
Hemaris diffinis	CAN	ON	Nipigon	49.01	-88.27	11-Jul-07	Fletcher, J.	CNC	f	CNC_13761	-	-	-
Hemaris diffinis	CAN	SK	Eaglehill Ck.	52.35	-108.97	18-May-69	Brooks, A.R.	CNC	m	CNC_13739	-	-	-
Hemaris diffinis	CAN	SK	Harlan	53.60	-109.92	11-Jun-47	Bruggeman, P.F.	CNC	m	CNC_13738	-	-	-
Hemaris diffinis	CAN	SK	Storthoaks	49.38	-101.60	14-Apr-05	Noble, T.M.	CNC	m	CNC_13740	-	-	-
Hemaris diffinis	CAN	SK	13 km NNE Eastend, Pine Cree Campground	49.62	-108.76	29-May-03	Schmidt, B.C.	CNC		-	CNCNoctuoidea 13846	EU646624	D4

Table 1. Continued on next page

Table 1. Continued

Species	Country	Province	Locality	Latitude	Longitude	Date	Collector	Depository	Sex	Disection #	DNA voucher #	GenBank #	Haplotype
Hemaris diffinis	USA	CO	Boulder, 4.5 mi N, 5500'	40.08	-105.27	19-Jun-61	Stainer, J.R.	CNC	m	CNC_13745	-	-	-
Hemaris diffinis	USA	GA	Gordon Co., Calhoun	34.50	-84.95	14-Sep-07	Adams, J.K.	CNC	m	-	LEP041279	-	D2
Hemaris diffinis	USA	OK	Comanche Co., Fort Sill	34.67	-98.38	26-Jul-03	Garhart, M.C.	CSU	m	-	NOC14993	-	D3
Hemaris gracilis	CAN	AB	Richardson Dunes Wild. Pk.	58.21	-111.39	14-Jun-00	Schmidt, B.C.	UASM	f	-	UASM19688	EU646625	-
Hemaris thetis	CAN	AB	Calgary, Head of Pine Ck.	50.86	-114.22	18-Jun-14	Dod, F.H.W.	CNC	m	CNC_13734	-	-	-
Hemaris thetis	CAN	AB	Crowsnest Pass	49.63	-114.63	7-Jun-40	Pepper, J.H.	CNC	f	CNC_13735	-	-	-
Hemaris thetis	CAN	AB	Waterton Lakes	49.05	-113.91	18-Jun-56	Sterns, E.E.	CNC	m	CNC_13741	-	-	-
Hemaris thetis	CAN	AB	Waterton Lakes	49.05	-113.91	18-Jun-56	Sterns, E.E.	CNC	m	CNC_13742	-	-	-
Hemaris thetis	CAN	AB	Waterton Lakes	49.05	-113.91	18-Jun-56	Sterns, E.E.	CNC	m	CNC_13743	-	-	-
Hemaris thetis	CAN	AB	Opal Natural Area	54.01	-113.27	5-Jun-03	Schmidt, B.C.	CNC	f	CNC_13759	CNCNoctuoidea 13841	EU646630	T1
Hemaris thetis	CAN	AB	West Castle R. Road, 15km SW Beaver Mines	49.38	-114.37	22-May-99	Schmidt, B.C.	CNC	m	-	CNCNoctuoidea 13842	EU646631	T2
Hemaris thetis	CAN	AB	Beaver Mines, 15 km W	49.34	-114.42	22-May-99	Anweiler, G.G.	UASM	m	-	UASM58223	EU646627	T2
Hemaris thetis	CAN	AB	Beaver Mines, 15 km W	49.34	-114.42	22-May-99	Anweiler, G.G.	UASM	m	-	UASM58404	EU646626	T2
Hemaris thetis	CAN	BC	Summerland	49.61	-119.68	26-May-90	Troubridge, J.	CNC	m	CNC_13754	-	-	-
Hemaris thetis	CAN	BC	Riondel, 2km S	49.76	-116.85	24-May-02	Schmidt, B.C.	CNC	m	-	CNCNoctuoidea 13843	EU646632	T2
Hemaris thetis	CAN	BC	Riondel, 2km S	49.76	-116.85	17-May-04	Schmidt, B.C.	UASM	m	-	UASM99166	EU646628	T2
Hemaris thetis	CAN	BC	Riondel, 2km S	49.76	-116.85	17-May-04	Schmidt, B.C.	UASM	m	-	UASM99167	EU646629	T2
Hemaris thetis	USA	AZ	Cochise Co.			1-Jul-26		CNC	f	CNC_13765	-	-	-
Hemaris thetis	USA	CA	Glendora	34.14	-117.86	31-Jul-35		CNC	m	CNC_13756	-	-	-
Hemaris thetis	USA	CA	Lake Co., Kelseyville	38.98	-122.84	20-Jun-38	Macheboeuf, C.	CNC	f	CNC_13766	-	-	-
Hemaris thetis	USA	CA	El Dorado Co., Georgetown	38.91	-120.84	31-Jul-06	Robinson, P.	CSU	f	-	NOC14990	-	T3
Hemaris thetis	USA	CO	Boulder, 4 mi NW 6900'	40.06	-105.32	17-Jun-61	Mann, C.H.	CNC	m	CNC_13747	-	-	-
Hemaris thetis	USA	CO	Boulder, 4 mi NW 6900'	40.06	-105.32	8-Jun-61	Mann, C.H.	CNC	m	CNC_13748	-	-	-
Hemaris thetis	USA	CO	Boulder, 4 mi NW 6900'	40.06	-105.32	17-Jun-61	Mann, C.H.	CNC	f	CNC_13749	-	-	-
Hemaris thetis	USA	CO	Boulder, 4 mi NW 6900'	40.06	-105.32	17-Jun-61	Mann, C.H.	CNC	f	CNC_13750	-	-	-
Hemaris thetis	USA	CO	Grand Co., Maryvale	39.93	-105.79	28-May-02	Bowman, D.E.	DEB	m	-	LEP041991	-	T1
Hemaris thetis	USA	WA	Belfast	48.55	-122.34	22-May-49	Frechin, D.P.	CNC	f	CNC_13758	-	-	-
Hemaris thetis	USA	WA	Tenino [Thurston Co.]	46.86	-122.85	30-May-51	Frechin, D.P.	CNC	m	CNC_13755	-	-	-

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 *thetis* ranged 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 *thetis*, but this requires confirmation. By comparison, *H. diffinis* 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 Mountain foothills. In the southern portion of the AB Rocky 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 *thetis*. Structurally, these southern, summer *thetis* are identical to northern populations (and AZ *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 *thetis* would shed additional light on these variation patterns. In a pattern parallel to that in *thetis*, summer generation *diffinis* from the northwestern parts of the range vary only slightly from the spring phenotype, where 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 *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.

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