NABA-NC 2016-19 Adelpha bredowii

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Adelpha bredowii in USA: putative misidentification and subdivision

“most Lepidopterists will persist in labelling this species as H. Bredowii of Hübner: the latter is a perfectly distinct species” (Arthur G. Butler, 1865)

In recent years many lepidopterists have accepted a proposal that the California Sister, a butterfly included on the NABA checklist under the scientific name Adelpha bredowii, is divisible into three distinct species: the true California Sister, A. californica (Butler, 1865), A. eulalia (Doubleday, 1848), and A. bredowii Geyer, 1837 – this last being found only in Mexico. The three taxa collectively form a very well-marked clade (Willmott, 2003b: 286), and the two U.S. taxa are parapatric in distribution. Thus the question of taxonomic rank involves a matter of judgement. This case examines the evidence for adopting or not adopting such changes for the NABA list.

The current NABA list includes three species of the limenitidine genus Adelpha: A. fessonia, A. basiloïdes and A. bredowii. Of these, only the last, the California Sister, can be regarded as a well-established member of the U.S. butterfly fauna. Carpenter. & Hobby (1945), including the nominate race, recognized four subspecies of A. bredowii: bredowii, californica, eulalia and guatemalensis (Carpenter & Hobby, 1945). Within the U.S., Scott (1986: 263, as Limenitis bredowii) divided this butterfly into two seemingly well-marked subspecies, A. bredowii californica, found in California, Oregon and NW Nevada (Austin & Leary, 2008: 124), and A. bredowii bredowii, in SE Nevada, Texas and Mexico. Willmott (2003a: 50–55), however, on formally synonymizing guatemalensis with eulalia, recognized three races (two of which were in effect conflated by Scott within the nominate subspecies). According to Willmott, A. bredowii eulalia occurs in extreme southwest California, Arizona, Utah, Texas, New Mexico, Colorado and Nevada, through Mexico to eastern Guatemala, and possibly western Honduras. In Mexico and Guatemala it is mainly restricted to the Atlantic slopes. True bredowii bredowii, according to Willmott, is only found on the Pacific slopes of western central Mexico, never USA, with “Michoacán … the only state … where there are not also records of A. b. eulalia”.

Based in part on molecular evidence, Prudic et al. (2008) proposed that all three subspecies as recognized by Willmott (2003a) should be reinstated as full species (as, historically, they were first proposed). If accepted, this would entail removing the well-known name Adelpha bredowii from the NABA list, to be replaced by two separate species: Adelpha californica and A. eulalia. Before going on to examine the case for and against making such a change, or any other possible changes, the formal synonymies of the genus and the three taxa involved are presented below.

Adelpha Hübner, 1819

Nymphalis of authors, nec Nymphalis Kluk, 1780 (type species, by selection of Hemming: Papilio polychloros Linnaeus, 1758), nec Nymphalis Latreille, 1804 (type species, by monotypy: Papilio
atalanta Linnaeus, 1758); nec Nymphalis Felder, 1861 (type species, by selection of Hemming: Papilio astyanax Fabricius, 1775).

Limenitis of authors, nec Limenitis Fabricius, 1807 (type species, by selection of Dalman: Papilio populi Linnaeus, 1758).

Adelpha Hübner, 1819. Type species, by selection of Scudder: Papilio mesentina Cramer, 1777.

Heterochroa Boisduval, 1836. Type species by monotypy: Heterochroa serpa Boisduval, 1836.

As ably discussed by Willmott (2003a: 5), the many species currently included in Adelpha for long “oscillated” between Adelpha, Heterochroa (junior subjective synonym) and Limenitis (the related genus for various ‘admirals’, now universally accepted as separate). In the 19th century a number of species were also described in the omnibus genus Nymphalis Latreille, 1804 – an invalid junior homonym of Nymphalis Kluk, 1780, the genus for the Mourning Cloak, N. antiopa, and its allies (type species: Papilio polychloros L., 1758). Currently, as extensively discussed by Willmott (2003b), there is no dispute regarding inclusion of the species in question here within the genus Adelpha; if required, citations for all these generic names can be accessed at the website of Pitkin & Jenkins (2016).

Adelpha bredowii Geyer, 1837


Heterochroa bredowii: Westwood, 1850: 278 [in part].


Adelpha bredowi [sic]: Godman & Salvin, 1884: 301.


Limenitis bredowii bredowii: de la Maza, 1987: 119, pl. 47, fig. 8.


Adelpha californica (Butler, 1865)

Heterochroa californica Butler, 1865: 485. Type locality: California. Type material NHMUK, examined by Willmott (2003a: 53). Female syntype noted by Willmott figured at: http://butterfliesofamerica.com/L/ih/adelpha0097_i.htm [and 98]

Limenitis bredowii: Edwards, 1868: Limenitis 4, 3 figs. [Misidentification; eulalia and californica as synonyms.]


Adelpha bredowii: Glassberg, 2001: 193; Prudic et al., 2002. [Misidentifications; californica not mentioned.]

Adelpha eulalia (Doubleday, 1848)

Limenitis eulalia Doubleday, 1848: pl. 36, fig. 1. Type locality: “Venezuela” (Westwood, 1852: viii [erroneous; currently interpreted as central Mexico]). Putative syntype in NHMUK, London, as determined by G.D.H. Carpenter and examined by Willmott (2003a: 52), designated lectotype by Prudic et al. (2008: 12), and figured at http://butterfliesofamerica.com/L/ih/adelpha0099_i.htm [and 100] [Note: this specimen evidently originated from the collection of French entomologist Achille Guenée (1809–1880), which reached London in the 1920s via the Oberthür collection; despite the argumentation of Carpenter & Hobby, 1945: 316, this is a most unlikely provenance for a Doubleday type; however, we agree that the pl. 36 Hewitson image of eulalia upperside fits the current interpretation of that species better than either bredowii or californica, and corresponds well with the ex Guenée specimen currently regarded as the lectotype.]


Heterochroa eulalia: Westwood, 1850: 276 (“native of Venezuela”).

Heterochroa bredowii: Westwood, 1850: 278 (eulalia Doubleday MS, as synonym; “Mexico”). [Misidentification.]

Adelpha bredowii: Kirby, 1871: 235 (eulalia as synonym). [Misidentification.]

Adelpha bredowi [sic]: Godman & Salvin, 1884: 301 (eulalia as synonym) [Misidentification.]


Limenitis bredowia eulalia: de la Maza, 1987: 119, pl. 47, fig. 7.


Adelpha californica: Kirby, 1871: 741 (A. eulalia as a synonym) [Misidentification.]


Willmott 2003

As already indicated, Willmott (2003a: 50–55), largely accepting the status quo at the time, divided Adelpha bredowii into three subspecies: A. bredowii bredowii (Mexico), A. b. eulalia (southern USA to central America; to include guatemalensis), and A. b. californica (mostly California and Oregon; the second and third come close to overlapping in southern California). The last of these looks particularly distinct from eulalia but Willmott (2003a,b), apparently impressed by the distinctiveness of the clade as a whole within Adelpha, opted to maintain A. bredowii as a single, polytypic species.

Prudic, Warren & Llorente-Bousquets 2008

Prudic, Warren & Llorente-Bousquets (2008), based on molecular, morphological, colour pattern and distributional data, concluded that the three subspecies recognized by Willmott (2003a,b) should all be returned to full species rank, as they had originally been proposed. Their results are summarized in their own words: “In recent decades … Adelpha bredowii … known in the USA as the California Sister, has been considered to be a polytypic array of taxa, composed of two, three or four subspecies. The most recent review … recognized three: A. b. bredowii, A. b. eulalia (=
guatemalensis) and A. b. californica. We used mitochondrial (COII) and nuclear (Tpi) DNA sequence data, coupled with a re-evaluation of traditional morphological characters, to determine the phylogenetic relationships between members of the A. bredowii complex, and to elucidate their taxonomic status. Phylogenetic analysis of molecular data corroborated the monophyly of each of the three subspecies (sensu Willmott), with the following topology: (bredowii + (eulalia + californica)). Average levels of COII variation among these taxa were much greater than the average variation within each taxon (3.4% vs. 0.2%, respectively). There were no shared alleles among these taxa, even from localities where two lineages (bredowii and eulalia) were collected in exact sympatry and synchrony. The degree of genetic divergence, reciprocal monophyly, and absence of shared alleles between taxa, coupled with unique morphological and distributional attributes of each, strongly suggest that A. bredowii, A. eulalia and A. californica are all species-level taxa.” (Prudic et al., 2008: 1).

The molecular evidence
Prudic et al. (2008) examined 60 specimens of the A. bredowii-complex for an analysis of cytochrome oxidase subunit II (COII) variation: 17 A. bredowii, 25 A. californica, and 18 A. eulalia, from across their geographic ranges. Specimens of A. bredowii and A. eulalia from overlap or potential hybrid zones in Mexico were included, to assess the possibility of shared alleles between taxa. Three other Adelpha species were used as outgroups: A. lycoreias, A. mesentina, and A. phylaca. Sixteen specimens were also sequenced to evaluate variation within the nuclear gene triosephosphate isomerase (Tpi).

For COII the final aligned sequence yielded 658 characters, of which 72 were considered phylogenetically informative. The maximum reported sequence divergence was 4.2% between A. bredowii and A. californica, 2.4% between A. bredowii and A. eulalia, and 3.7% between A. eulalia and A. californica. Twenty-four different haplotypes were found, A. californica having 14, A. bredowii 4 and A. eulalia 6. In 60 specimens examined, none of the taxa shared haplotypes, even when collected from the same locality, and no clear geographic patterns were correlated with haplotype variation within any taxon. The intron for Tpi ranged from 50–121 bp dependent on species, with direct sequencing and alignment apparently being straightforward. The final aligned sequence yielded 324 characters, 42 of which were considered phylogenetically informative. The maximum reported sequence divergence for this nuclear gene was 1.7% between A. bredowii and A. eulalia, and 1.4% between A. bredowii/californica and A. californica/eulalia. Seven different Tpi alleles were found. Based on the subset of 16 specimens for Tpi analysis, none of the taxa shared alleles, and no clear geographic patterns were correlated with the allelic variation within any taxon (Prudic et al., 2008).

Morphological differences
Genitalia. Prudic et al. (2008) examined the genitalia of 8 male, 1 female A. bredowii (Mexico), 12 male, 4 female A. eulalia (3 male, 1 female from USA), and 8 male, 2 female A. californica (all California). Despite extensive variation seen in valve teeth number in all three taxa, the overall shape of the valvae, and of other male genitalic structures, were considered consistent within each species, and of diagnostic value. According the authors’ results, the valvae of A. bredowii and A. californica tend to be
evenly upturned throughout their length, whereas in *A. eulalia* the distal tips tend to be abruptly upturned. While a subtle difference, this was seen to be consistent for the 12 *A. eulalia* examined. The genital capsule of *A. bredowii* was considered smaller than that of *A. eulalia* and *A. californica*, in lateral view with a distinctly rounded proximal edge to the tegumen. Males of *A. eulalia* were considered to have a proportionally longer phallus than *A. bredowii* and *A. californica*. The authors acknowledged that an insufficient number of females were dissected to be confident that observed differences were diagnostic. However, as with the males, the female genitalia of *A. bredowii* appeared smaller than *A. eulalia* or *A. californica*, probably reflecting overall smaller body size. The sterigma and lamella antevaginalis of *A. californica* were seen as broad and well developed, reduced in *A. bredowii* and intermediate in *A. eulalia*. The ductus bursae and corpus bursae were considered proportionally longer in *A. californica* than in *A. bredowii* or *A. eulalia*, which appeared similar to each other in this respect.

Wing pattern differences. Prudic et al. (2008: 7–9, tab. 3) evaluated numerous wing pattern characters, with emphasis on those used by Carpenter & Hobby (1945). Perhaps most notably, as earlier described by Skinner (1911), Willmott (2003a) and Stout (2005), they observed that *A. californica* differs from the other two taxa in having two longitudinal orange bars in the hindwing discal cell area. The additional orange bar represents Discalis I of Schwanwitsch (1924) (or the orange zone between the black “third cell bar” and black “postcellular bar” of Willmott, 2003a: fig.3). In *A. bredowii* and *A. eulalia* there is only the more basal orange band in this region of the ventral hindwing, representing Discalis II of Schwanwitsch (or the orange zone between the first and second black cells bars of Willmott) – a feature apparently plesiomorphic to all three taxa (see figures in Stout, 2005). [Note: the hindwing of *Adelpha* has an open discal cell, there being no m2-m3 cross vein; however, Discalis I marks without doubt the course of this vein obsolete in the adult, but almost certainly expressed earlier in development.]

Among several other wing characters, Prudic et al. (2008) discuss differences in forewing shape, the forewing upperside apical orange patch, and the white postdiscal band. They note that, although the coloration of the bluish markings of the hindwing underside exhibit some geographic variation in *A. bredowii* and *A. eulalia*, in these two taxa they are distinctly bluish, but violet in *A. californica*. Also subject to some geographical variation, the coloration and shape of the ventral hindwing submarginal dark areas differs in all three taxa: “The dark submarginal area on *A. bredowii* is nearly linear, and ochraceous-brown in color, while on *A. californica* the dark area is irregularly shaped and rather broad throughout, with a duller brownish color; the dark region on *A. eulalia* is similar to that of *A. bredowii*, but somewhat broader, darker, and more irregularly-shaped” (Prudic et al., 2008: 8).

A key for separation of the three taxa

In light of the differences enumerated by Willmott (2003a), Stout (2005), Prudic et al. (2008) and Glassberg (2012), it is possible to present a seemingly reliable key for separation of the three taxa, both from each other and from all other known *Adelpha*, based very largely on wing pattern characters alone:
Eyes smooth (viewed macroscopically); upperside of hindwing with a complete white discal band from costa to cell 1A+2A; distal bluish band of forewing underside discal cell divided into two almost equal areas by dark antero-posterior line; upperside forewing with postdiscal white band divided by darkened veins; upperside forewing discal cell with red scaling, including at base; upperside forewing with large subapical orange area (bredowii complex)

-- Not as above other Adelpha species

2 Hindwing underside postdiscal white band margined distally with an almost straight, distinct dark line which itself is edged with a continuous line of bluish scales, extending from costa to vein 1A+2A; hindwing underside discal cell area crossed by a single orange band; forewing apex rounded or more acuminate

-- Hindwing underside postdiscal white band edged distally with a comparatively curvilinear and less distinct dark line that is only discontinuously margined with bluish scales, most prominently in posterior cells CuA₁ and CuA₂; hindwing underside discal cell area crossed by two orange bands; forewing apex relatively rounded

3 Forewing apex less acuminate; upperside forewing preapical orange area broader and shorter, not extending posteriorly into cell M₃

-- Forewing apex more acuminate; upperside forewing preapical orange area narrower and longer, extending narrowly into cell M₃

Thus in the USA, the California and Arizona sisters are readily and reliably differentiated by the hindwing underside discal cell area, which has two orange bars in A. californica, but only one in A. eulalia (and the Mexican A. bredowii).

Views expressed since publication of Prudic et al. 2008

The proposal to divide Adelpha bredowii sensu lato into three separate species appears to have gained rapid acceptance within the wider lepidopterological community, with a considerable number of recent papers, local lists and websites treating all three as distinct. A few of these publications give information on how to separate the taxa on the basis of wing coloration (e.g. Glassberg, 2012; Butterflies and Moths of North America, 2016), and Willmott & Hall (2013) endorse the Prudic et al. (2008) separations. However, we have been unable to find any additional evidence-based arguments, for or against, since the appearance of Prudic et al. (2008).

What is to be decided?

If the conclusions of Prudic et al. (2008) are accepted, the name Adelpha bredowii no longer applies to a species found in America north of Mexico. Thus the questions to be resolved now are (a): is the evidence for separate species status of the three subspecies recognised by Willmott (2003a), as proposed by Prudic et al. (2008), convincing or not, and (b): if the evidence is convincing, are the names A. californica and A. eulalia properly applied to the California Sister and Arizona Sister, respectively? Additionally, if separate species status is accepted, the English Names Committee will also need to address this case.
References


