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Source: The Journal of the Lepidopterists' Society, 67(4) : 241-252

Published By: The Lepidopterists' Society

URL: <https://doi.org/10.18473/lepi.v67i4.a1>

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A NEW SPECIES AND TWO NEW SUBSPECIES OF *ADELPHA* HÜBNER, [1819] FROM
THE TROPICAL ANDES (NYMPHALIDAE: LIMENITIDINAE)

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ABSTRACT. A new species, *Adelpha margarita* Willmott & Hall, **new species**, is described from Andean cloud forest habitats from southern Ecuador to Bolivia. *Adelpha margarita garleppi* Willmott, **new subspecies**, is described for southern Peruvian and Bolivian individuals, which differ from the nominate subspecies in having complete orange postdiscal bands on the dorsal surface. The new species differs from related species in the *Adelpha serpa* group in wing pattern, DNA sequence data and habitat. A lectotype is designated for *Adelpha seriphia thersasia* Fruhstorfer, because the type series of this name contains individuals of both *A. seriphia* and *A. margarita*. Neighbor-joining and maximum parsimony analyses of 579 bp of the mitochondrial *cytochrome oxidase I* (COI) 'barcode' region, for 27 *Adelpha* specimens representing 9 species and 13 taxa, suggest that the closest relative to *A. margarita* is the Central American to west Andean taxon *A. seriphia godmani* Fruhstorfer. The DNA sequence data, coupled with a re-analysis of museum specimens, suggest that *Adelpha godmani* should be treated as a distinct species (**revised status**). Finally, a new subspecies, *Adelpha justina pichincha* Willmott & Hall, **new subspecies**, is described from Pichincha province in western Ecuador.

Additional key words: Ecuador, Peru, Bolivia, DNA barcode, COI

Like other better known mimetic butterfly genera, the diverse nymphalid genus *Adelpha* Hübner, [1819], is notable for its marked geographic wing pattern variation within species. In addition, the genus displays a frustrating simplicity and homogeneity in genital and other morphological characters that typically are used to define butterfly species. These two traits have conspired to cause much historical taxonomic confusion, and Willmott's (2003a) revision of the genus represents just the first step towards developing a firm species classification. In particular, intensive field work coupled with newly available DNA sequence data are likely to result in refinement of the taxonomy. For example, Prudic et al. (2008) provided convincing data to support recognition of the three taxa formerly placed within *Adelpha bredowii* Geyer, 1837, as distinct species. New field work demonstrated micro-sympatry of some phenotypes, and DNA sequence data show that the three taxa are reciprocally monophyletic and therefore most likely reproductively isolated. *Adelpha bredowii* is a member of the *Adelpha serpa* (Boisduval, 1836) group, one of the most taxonomically challenging in the genus, characterized elsewhere by the often extreme rarity of its species. For example, *Adelpha radiata explicator* Willmott & Hall, 1999, remains known from the entire Amazon basin by just the holotype specimen. Here, we use data from DNA sequences, new field work and a re-examination of museum specimen wing patterns to clarify relationships among tropical Andean members of the *A. serpa* group, and describe a hitherto

overlooked species of *Adelpha*, comprising two subspecies, that ranges from southern Ecuador to Bolivia. We also take the opportunity to describe an additional new subspecies of *Adelpha justina* (C. & R. Felder, 1861) from central western Ecuador.

MATERIALS AND METHODS

Adelpha specimens were examined in major public and private collections in Europe, North and South America, as listed in Willmott (2003a), to record distributional data, study morphological variation, assess taxonomic diversity and locate type specimens. In addition, we made particular efforts to obtain tissue samples for DNA analysis from the most recently collected specimens of taxonomically important *Adelpha*. Such specimens include, especially, those that can be assigned reliably to a taxon by virtue of having been collected near type localities. Unprepared, papered specimens were an especially valuable resource because the rehydration needed to spread and pin such specimens appears to degrade DNA significantly. Acronyms used here include: BMNH: Natural History Museum, London, UK; FLMNH: Florida Museum of Natural History, Gainesville, USA; HAWA: Haydon Warren-Gash collection, Pressac, France; KWJH: Keith R. Willmott & Jason P. W. Hall collection, Gainesville, FL, USA; MECN: Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; MUSM: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; PIBO: Pierre Boyer collection, Le Puy,

France; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; ZMHU: Zoologisches Museum, Humboldt Universität, Berlin, Germany.

Morphology was studied using standard techniques, with adult abdomens being soaked in hot 10% KOH for 10–15 minutes, dissected and subsequently stored in glycerin. Body morphology and dissections were studied using a binocular microscope at 50× magnification. The terminology for male genital and abdominal structures largely follows Klots (1956), nomenclature for venation follows Comstock and Needham (1918), and wing pattern elements are named as in Willmott (2003a). We use the abbreviations DFW, VFW, DHW and VHW for dorsal and ventral forewing and hind wing.

Specimens for tissue samples, distributional data and field observations for *Adelpha* were gathered by the authors during more than 650 days of field work in Ecuador between 1991 and 2011, representing 385 sites in 20 provinces, ranging from sea level to 4000 m on both Andean slopes.

We extracted genomic DNA from two legs removed from dried, papered specimens of the new species of *Adelpha* and close relatives (some spread specimens of the latter were sampled) using Qiagen's DNeasy Blood & Tissue Kit following the manufacturer's protocol, incubating samples overnight (20–24 hr) and using a final elution volume of 100 µl (50 µl for specimens older than 20 yrs). We amplified the first half of the mitochondrial gene *cytochrome oxidase I* (COI), also known as the barcode region for animals (Hebert et al. 2003), using the primers LepF1 (forward, ATTCAACCAATCATAAAGATAT) and LepR1 (reverse, TAAACTTCTGGATGTCCAAAA) (Hebert et al. 2004), or LCO (forward, GGTCAACAAATCATAAAGATATTGG and HCO (reverse, TAAACTTCAGGGTGACCAAAA AATCA) (Folmer et al. 1994). For samples that failed to amplify with these primers, we amplified two shorter, partially overlapping fragments of the barcode region using primer pairs LCO and K699 (reverse, WGGGGGGTAAACTGTTCATCC), and Ron (forward, GGATCACCTGATATAGCATTCCC) and Nancy (reverse, CCTGGTAAATTTAAAATATAAACTTC) (Monteiro & Pierce 2001, Elias et al. 2007). All PCR reactions were conducted in a 20 µl volume comprising 2 µl DNA, 0.8 µl MgCl₂ (50 mM), 13.4 µl ddH₂O, 2 µl buffer (10X), 0.8 µl dNTPs (10mM), 0.4 µl of each primer (10 µM), and 0.2 µl Platinum® Taq DNA Polymerase (5 U/µl). Reaction conditions were as follows: 1 min at 94°C followed by 5 cycles of 30 s at 94°C, 40 s at 45°C, 1 min at 72°C, followed by 35 cycles of 30 s at 94°C, 40 s at 51°C, 1 min at 72°C, followed by 5 min at 72°C. Single strands of PCR products were sequenced by University

of Florida's Interdisciplinary Center for Biotechnology Research Sanger Sequencing Group using the same primers as in the PCR. Sequences were aligned using BioEdit v. 7.1.3 (Hall, 1999) and by eye, and fragments were assembled into composite sequences where necessary. To test hypotheses of species limits based on morphology and distribution, we conducted both a neighbor-joining (NJ) analysis and a maximum parsimony (MP) analysis on the DNA sequence data. Despite criticism of NJ analyses (Goldstein & DeSalle 2011), they remain a simple way to graphically represent similarity among taxa and hence decide the most appropriate taxonomic rank, still a necessarily subjective step in almost all studies. MP analysis complements NJ by allowing the identification of putative nucleotide autapomorphies for species, which may be tested by inclusion of additional individuals. All analyses were conducted using MEGA 5.05 (Tamura et al. 2011), with the following options selected: for NJ, we used the Kimura 2-parameter substitution model and other default settings, while for MP analysis we used the Close-Neighbor-Interchange heuristic search with 100 random addition starting trees, evaluating branch support with 100 bootstrap replicates. Trees were rooted with *Adelpha californica* (Butler, 1865), which is part of a small clade sister to all other Central and South American *A. serpa* group species (Willmott 2003b). All new sequences are deposited in GenBank.

RESULTS AND DISCUSSION

DNA sequence data and the taxonomy of *Adelpha seriphia*

We amplified part of the COI barcode region for 26 *Adelpha* specimens representing 8 species and 12 taxa, and obtained sequence data for *Adelpha californica* from GenBank (Appendix 1). The final aligned dataset, after trimming to remove poor quality sequence (a problem in particular with older museum specimens), was 579 bp. Of these, 106 sites were variable and 67 were parsimony informative. The NJ analysis showed that individuals of all putative species clustered together except for *A. seriphia godmani* Fruhstorfer, 1913, which formed a paraphyletic cluster separate from other *A. seriphia* (C. & R. Felder, 1867) (Fig. 1). The three Ecuadorian *A. s. godmani* formed a cluster, even though KW-080510-01, from southwestern Ecuador, was markedly divergent from the other two northwest Ecuadorian specimens. This cluster was sister to *A. margarita* **new species**, while LEP-04017 from El Águila in west Colombia was sister to both of these clusters. The MP analysis found 2206 trees of length 326 steps, which were topologically similar to the NJ tree and also contained the clade with *A. seriphia*, *A.*

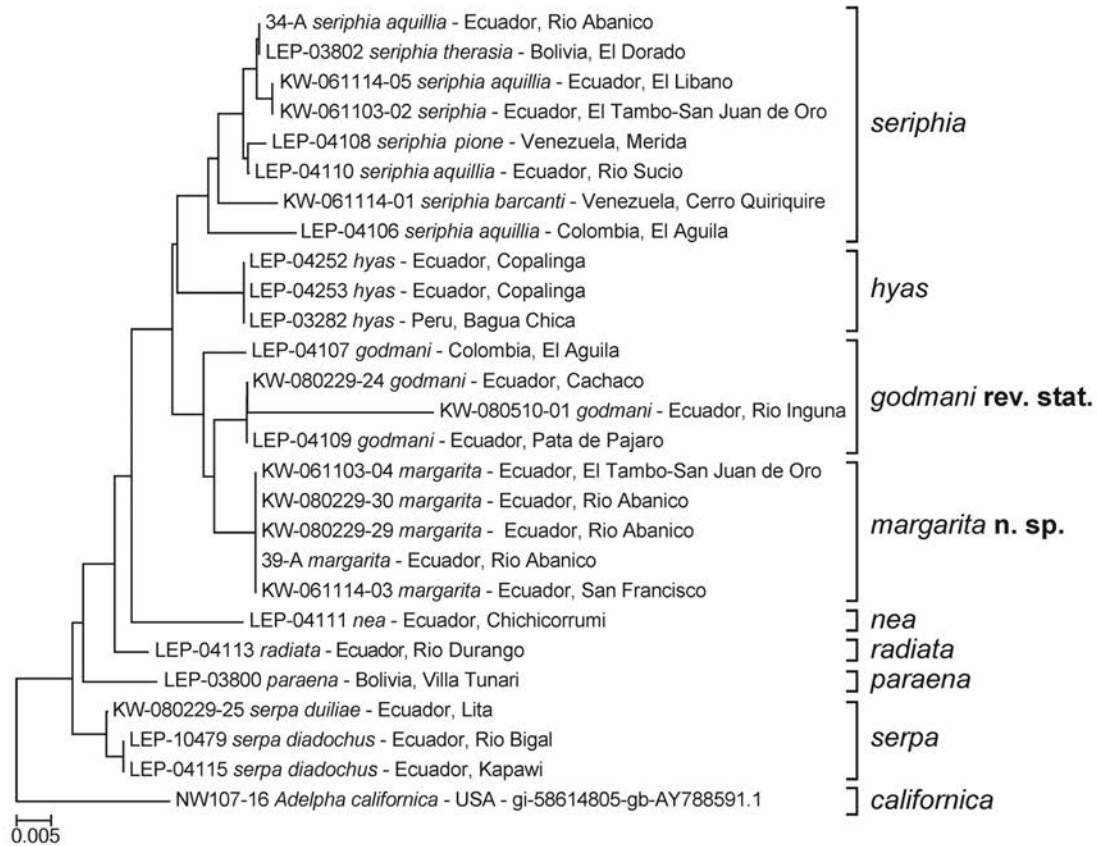


FIG. 1. Neighbor-joining tree (Kimura 2-parameter) for *Adelpha serpa* group based on 579 bp of COI (barcode region).

hyas, *A. s. godmani* and *A. margarita*. Within this clade the only conflicting result was the placement of LEP-04107 as sister to *A. margarita* in the MP analysis, rather than to *A. margarita* + *A. s. godmani* as in the NJ analysis. Bootstrap support for *A. seriphia* excluding *A. s. godmani* was 63%, for west Ecuadorian *A. s. godmani* was 98%, and for all other species represented by multiple individuals was > 90%. Reasonable bootstrap support (82%) was found for a sister relationship between *A. s. godmani* and *A. margarita*.

The DNA sequence data, coupled with a re-analysis of museum specimens, suggest that *Adelpha godmani* should be treated as a distinct species (**revised status**). Specimens of *A. godmani* were, on average, 3.1% divergent from remaining *A. seriphia*, and both NJ and MP analyses suggest that *A. hyas hewitsoni* Willmott & Hall, 1999, which occurs on the east Andean slopes with *A. seriphia* but at lower elevations, is more closely related to *A. seriphia* than is *A. godmani*. Furthermore,

there is evidence that *A. godmani* and *A. seriphia* are sympatric in west Colombia. Two specimens in the FLMNH, one male and one female, from Colombia, Caldas, El Águila, 1700 m, appear to represent *A. seriphia aquillia* Fruhstorfer, 1915, and *A. godmani*, respectively. In common with other, east Andean *A. seriphia*, the male has dark orange interneural stripes intruding into the pale orange subapical marking on the VFW, the white submarginal series on the VFW in cells Cu_1-M_1 are reduced, and the FW postdiscal band is narrow with dislocated spots. The female resembles west Ecuadorian *A. godmani* in having a clean pale orange subapical marking on the VFW, the white VFW submarginal series expressed throughout the wing, and the FW postdiscal spots less dislocated. The female sequence (LEP-04107) did not cluster conclusively with remaining *A. godmani*, but given the unusually high variation within west Ecuadorian *A. godmani* (1.8%), it is premature to speculate whether this result is



FIG. 2. *Adelpha* specimens, left half dorsal surface, right half ventral surface. **A)** *A. margarita margarita* **new species**, **holotype** ♂, Ecuador, MECN; **B)** *A. margarita margarita* **new species**, paratype ♀, Ecuador, FLMNH; **C)** *A. margarita garleppi* **new subspecies**, holotype ♂, Peru, MUSM; **D)** *A. margarita garleppi* **new subspecies**, paratype ♀, Peru, BMNH (mirror image of specimen); **E)** *A. seriphia aquillia*, ♂, Ecuador, FLMNH; **F)** *A. seriphia aquillia*, ♀, Ecuador, PIBO; **G)** *A. seriphia therasia*, ♂, Peru, MUSM (mirror image of specimen); **H)** *A. seriphia therasia*, **lectotype** ♀, ZMHU; **I)** *A. godmani*, ♂, Ecuador, FLMNH; **J)** *A. godmani*, ♀, Ecuador, FLMNH; **K)** *A. justina pichincha* **new species**, **holotype** ♂, Ecuador, MECN; **L)** *A. justina pichincha* **new subspecies**, paratype ♀, Ecuador, FLMNH. Scale bar near middle at bottom of figure applies to all specimens except K, L, which are represented by scale bar at bottom right.

meaningful; more sequences of *A. godmani* are clearly needed from west Colombia, and throughout Central America, to test the current hypothesis. In addition to wing pattern (see Willmott 2003a) and DNA sequence differences, in Ecuador *A. godmani* occurs at significantly lower elevations (750–2020 m, mean 1339 m, n=14 localities) than *A. seriphia aquillia* (1350–2500 m, mean 1755 m, n=15 localities) (*t*-test, $p < 0.01$) (Willmott & Hall unpublished). The DNA sequence data otherwise confirm the existing classification, showing remaining *A. seriphia* taxa to form a single cluster with specimens from northern Venezuela to Bolivia. Given that there have been a number of changes to the classification of the *Adelpha serpa* group, based on findings of Prudic et al. (2008) and this paper, we present an updated classification for these species in Appendix 2.

Descriptions of new taxa

Adelpha margarita Willmott & Hall, new species

Figs. 1, 2A–D, 3, 4C

Diagnosis and identification: Numerous wing pattern and male genital characters (see Willmott 2003b), especially the 'V'-shaped 3rd discal cell bar on the VFW and lack of a clunicula (spinose process on inner basal edge of valva), place *Adelpha margarita* new species within the *A. serpa* group, within a clade of species including *A. zea* (Hewitson, 1850), *A. paroeca* (Bates, 1864), *A. nea* (Hewitson, 1847), *A. paraena* (Bates, 1865), *A. serpa*, *A. radiata* Fruhstorfer, 1915, *A. seriphia*, *A. godmani* (**revised status**) and *A. hyas* (Doyère, [1840]). The new species is distinguished from all of these species by the paired markings of the white VHW inner submarginal series in cell M_3-M_2 being faded in comparison with the markings in adjacent cells, with this part of the cell thus appearing blackish. The species is further distinguished from *A. zea*, *A. paroeca*, *A. nea* and *A. paraena* by having the white VHW submarginal series spots divided in each cell. In comparison with the most phenotypically similar remaining species, *A. hyas*, *A. seriphia* and *A. godmani*, it is further distinguished by the white HW postdiscal band being slightly constricted in cells M_2-Rs and the reddish orange postdiscal band on the VHW being correspondingly displaced basally in these cells. The VHW reddish orange postdiscal band is parallel and close to the inner edge of the white submarginal series, without a broadened, blackish space visible in cells Cu_2-M_1 as in *A. seriphia* (Fig. 2E–H) and *A. godmani* (Fig. 2I, J). In comparison with other members of the *A. serpa* group and based on the limited data available, the following five DNA nucleotides appear to be

autapomorphies for *A. margarita* (position from alignment with *Bombyx mori* (Linnaeus, 1758) mitochondrial genome, NCBI Reference Sequence NC_002355.1): position 11986: C (not T); position 12157: C (not T); position 12298: G (not A); position 12397: C (not T); position 12463: C (not T).

Description: MALE: (Fig. 2A): Forewing length 27–29mm (mean 27.4 mm, n=15). *Wing shape:* triangular, slightly produced at apex. *Dorsal surface:* Ground color dark grayish brown. Forewing discal cell with dark reddish, narrow dash at base, a dark reddish band in middle between thinner black first and second discal cell bars, and a dark reddish band covering discocellulars, dirty whitish marking between second and third discal cell bar; white postdiscal band with faint turquoise tinge present as dislocated spots between anal margin and vein M_3 , decreasing in width anteriorly; postdiscal band present anterior of vein M_3 as dashes of paler ground color; subapical orange spot formed of fused postdiscal series extending and tapering from costa to anterior half cell Cu_1-M_3 . Hind wing with postdiscal band similar to forewing extending from costa into cell 2A– Cu_2 , slightly constricted in cells M_1-Rs , broadest in discal cell and tapering to rounded point towards tornus; dark, curved, orange dash (representing postdiscal series) in cell 2A– Cu_2 ; submarginal series visible as dashes of paler ground color. Ventral surface: Ground color dark blackish brown. Forewing with orange stripe along costa from base to mid-discal cell; discal cell silvery white with four black cell bars, first curved basally at posterior edge cell, second slightly bent in middle, third 'V'-shaped and touching second in middle, fourth straight, dark orange between first and second bar and forming band over discocellulars; base cell 2A– Cu_3 with orange spot ringed in white, then thin black bar, white bar, black bar, basal to pale postdiscal band, base cell Cu_2-Cu_1 with white spot split by black line; postdiscal band as on dorsal surface except continuing as clear white dashes to costa anterior of vein M_3 ; pale orange subapical spot formed of fused postdiscal series as on FW but with indistinct edges, especially in cell M_1-Rs , with spot in each cell split by interneural darker orange stripe; fused postdiscal series continue as three dark orange dashes in cells Cu_1-M_3 , Cu_2-Cu_1 and 2A– Cu_2 ; submarginal series silvery white, inner twice width of outer, divided in each cell by black interneural stripe, almost absent in cells Cu_1-M_2 , inner series basal edge fused with subapical orange spot in cells M_3-M_1 , dark division between inner and outer series indistinct. Hind wing basal area white except for black stripe from wing base to tip subcostal vein, distal edge anal margin lined with black, black discal stripe from $Sc+R_1$ extending across cell then down through 3A–2A just anterior of and parallel to vein 3A; black discal stripe bordered distally by dark orange band, this bordered distally by black stripe extending from costa through discocellulars and along vein 2A to tornus; pale postdiscal band as on dorsal surface; postdiscal series fused forming a dark orange line from costa to tornus, convex except indented basally in cell M_1-Rs ; submarginal series silvery white, inner two to three times width of outer, divided in each cell by black interneural stripe, white scaling much reduced in cell M_3-M_2 , dark division between inner and outer series indistinct. *Head:* eyes dark brown with short setae; dense white scales at ventral base of eyes; antennae black, head with white scales at ventral base of antennae; labial palpi white with broad black inner and outer lateral stripe and dorsal surface, latter also with black hairs; top of head with chestnut brown scales, frons with brown hairs. *Thorax:* dorsal surface black with short dark brown hairs, ventral surface white with black stripes where legs rest against thorax, forelegs white, mid and hind legs black except for white ventral femur. *Abdomen:* dorsal surface black with short dark brown hairs, ventral surface white, then with dark gray lateral stripe, then white lateral stripe. *Genitalia* (Fig. 3A): saccus broad, similar in length to tegumen; valva triangular in lateral view tapering smoothly to posterior tip, with short spines at tip extending about one quarter distance along ventral edge; clunicula (spinose process on inner basal edge of valva) absent; aedeagus short, approximately straight except for slight 'spoon'-shaped curve at posterior tip, small spinose pad inside vesica near tip.

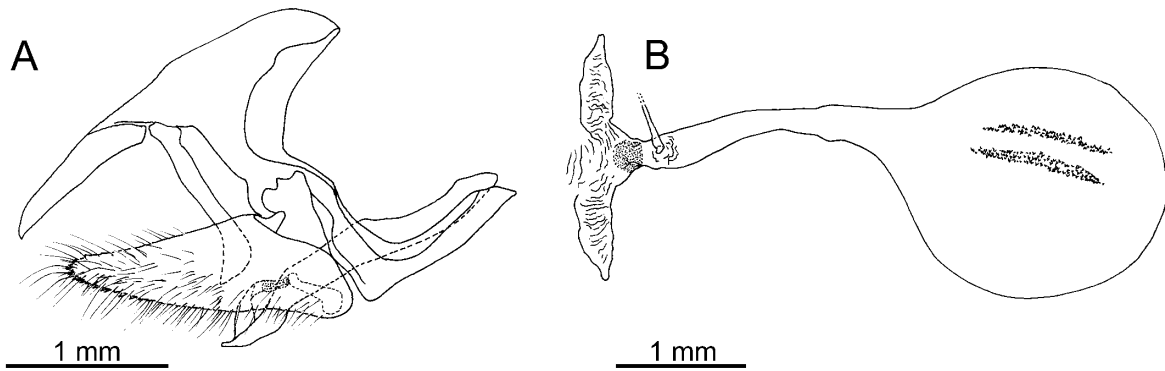


FIG. 3. Genitalia of *Adelpha margarita* new species A) Paratype ♂, lateral view, Ecuador, FLMNH; B) Paratype ♀, dorsal view, Ecuador, FLMNH.

FEMALE: (Fig. 2B): *Forewing length* 28–29 mm (mean 28.5 mm, $n=2$). *Wing shape*: similar to male except slightly broader. *Dorsal surface*: similar to male except slightly paler ground color, postdiscal band slightly broader, pale dashes of upper postdiscal band more distinct. *Ventral surface*: similar to male except for broader postdiscal band, and submarginal series more strongly fused. *Head, thorax, abdomen*: similar to male. *Genitalia* (Fig. 3B): lamella postvaginalis a narrow, laterally elongated, weakly sclerotized, wrinkled plate; ostium bursae a sclerotized simple tube incomplete dorsally; ductus seminalis origin on dorsal surface of ductus bursae, near ostium bursae; ductus bursae a simple tube; corpus bursae round, of similar length to ductus bursae, with two parallel bands of small, teeth-like signae in middle of dorsal surface.

Types: HOLOTYPE ♂: **ECUADOR:** *Zamora-Chinchipe*: km 3.5 El Tambo-San Juan del Oro, [3°57'9"S, 79°3'33"W], 1900m, (K.R. Willmott, R. Aldaz), 3 November, [FLMNH-MGCL-111890], (FLMNH, to be deposited in MECN).

PARATYPES (19 ♂, 2 ♀): **ECUADOR:** *Loja*: 'above Yangana' [=La Entrada], [4°25'6"S, 79°9'18"W], 2500m, (I. Aldas), October, 2 ♂, (PIBO), (I. Aldas), Oct-Nov, 5 ♂, (KWJH); *Morona-Santiago*: Condor Mirador, [3°37'42"S, 78°23'40"W], 1972m, (J. Radford), 22 August, 1 ♂ [CON45], (FLMNH) (CULEPEX Expedition); Condor Mirador, [3°37'42"S, 78°23'41"W], 1972m, (J. Radford), 23 August, 1 ♂ [CON111], 1 ♂ [CON113], (FLMNH) (CULEPEX Expedition), 1 ♂ [CON112], (MECN); Condor Mirador, [3°37'43"S, 78°23'40"W], 1972m, (J. Radford), 27 August, 1 ♂ [CON288], (FLMNH) (CULEPEX Expedition); Condor Mirador, [3°38'44"S, 78°23'44"W], 1973m, (E. Hartley), 27 August, 1 ♂ [CON276], (FLMNH) (CULEPEX Expedition), (K. Buckland), 27 August, 1 ♂ [CON262], (FLMNH) (CULEPEX Expedition); km 19 Macas-Nueve de Octubre rd., Río Abanico, [2°15'18"S, 78°12'0"W], 1600m, (I. Aldas), September, 1 ♂, (KWJH); km 19 Macas-Nueve de Octubre rd., Río Abanico, [2°15'18"S, 78°12'0"W], 2200m, (I. Aldas), September, 2 ♂, (KWJH); *Zamora-Chinchipe*: km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S, 79°5'42"W], 2000–2100m, (K. Willmott), 3 December, 1 ♀ [FLMNH-MGCL-111893], (FLMNH), (K. Willmott, R. Aldaz), 14 October, 1 ♀ [FLMNH-MGCL-111892], (FLMNH), 15 October, 1 ♂ [FLMNH-MGCL-111891], (FLMNH); km 3.5 El Tambo-San Juan del Oro, [3°57'9"S, 79°3'33"W], 1900m, (K. Willmott, R. Aldaz), 3 November, 1 ♂ [FLMNH-MGCL-111889], (FLMNH).

Other examined specimens: **PERU:** *San Martín*: Jorge Chávez, [5°41.0'S, 77°40.0'W], 1450m, (Calderón, B.), May, 1 ♂, (PIBO).

Etymology: This species is named for Margaret Robinson, in gratitude for all her friendship and support. The name is formed from the feminine Latin noun 'margarita', meaning 'pearl', and thus also alludes to the variegated black and silvery white submarginal markings

on the ventral surface which are such a distinctive feature of this species.

Taxonomy and variation: The only specimens examined by Willmott (2003a) of this species were two of the type specimens of *A. m. garleppi* new subspecies, described here, which were treated as representing a form of *A. seriphia thersasia* Fruhstorfer, 1915. Subsequently, however, we and others have collected series of specimens of both *A. margarita margarita* and *A. seriphia aquillia* at five sites in central and southern Ecuador, from Morona-Santiago to Loja (Río Abanico, San Francisco, El Tambo-San Juan del Oro rd., Cóndor Mirador, La Entrada above Yangana) (Fig. 4B, C). These specimens show consistent wing pattern differences as described above under the Diagnosis, and COI sequence data confirm the hypothesis of *A. margarita* as a species distinct from *A. seriphia aquillia*. In fact, the data suggest that the closest relative of *A. margarita* is the allopatric west Andean-Central American *A. godmani* (Fig. 4A). Mean DNA sequence divergence between *A. margarita* and *A. godmani* is 2 %, similar to differences between *A. nea* and *A. radiata* (2.4 %), *A. serpa* and *A. radiata* (1.5 %) and *A. seriphia* and *A. hyas* (2.3%), all sympatric or elevationally parapatric species pairs. *Adelpha margarita* and *A. godmani* both occur on the west Andean slopes in southern Ecuador (Fig. 4A) but at different elevations, with the former known only from 2500 m and the latter from below 1400 m (Willmott & Hall unpublished).

Adelpha margarita margarita shows variation in the width of the postdiscal band and DFW orange marking, which may be slightly narrower than in the holotype, and in the intensity of white scaling in the ventral submarginal series, which may appear more blackish than the holotype in some specimens. Some specimens show a trace of orange scaling in the DFW postdiscal series.

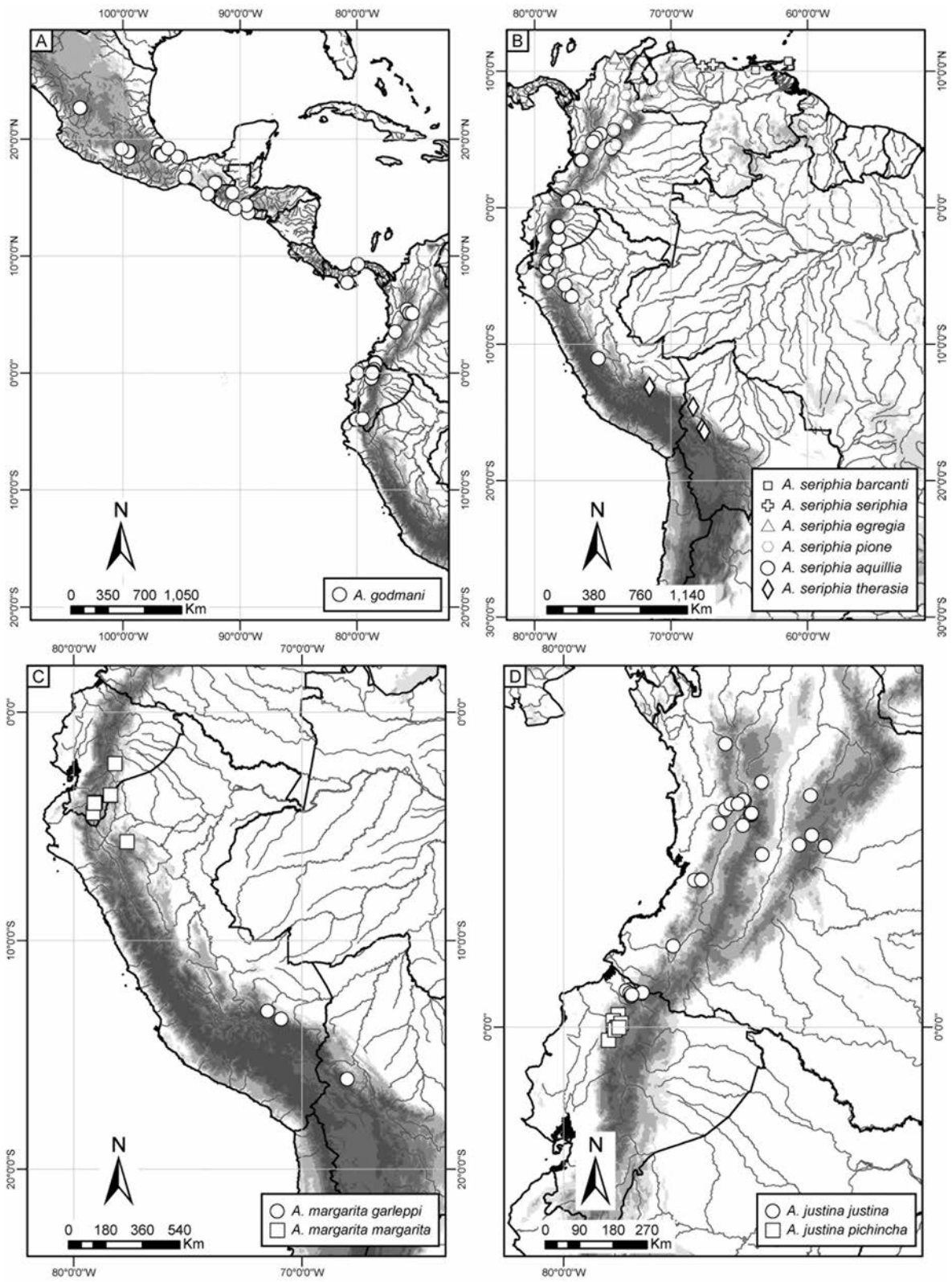


FIG. 4. Distribution of *Adelpha* taxa. A) *A. godmani*; B) *A. seriphia*; C) *A. margarita* new species; D) *A. justina justina* and *A. justina pichincha* new subspecies.

Distribution: *Adelpha margarita margarita* is known from the eastern Andes from central Ecuador (Morona-Santiago, Río Abanico) to northern Peru (San Martín, Jorge Chávez) (Fig. 4C). It has also been collected on the west Andean slopes in southern Ecuador, on the road from Yangana to Valladolid.

Habitat and adult ecology: This species is known from 7 localities, most of which are hilltops or ridge tops in cloud forest, with reliable elevation data ranging from 1900–2500 m. At the lower limit of its elevation *A. margarita* occurs at the same sites as *A. seriphia*, but otherwise the two species appear to replace one another in elevation. We found males perching on the tops of small trees 8 m above the ground at 11:00 hrs in bright sun. During approximately 6 months of trapping we also collected one male and the two known females in canopy traps baited with rotting fish, c. 15 m above the ground, in undisturbed cloud forest on a hillside above the Río San Francisco.

***Adelpha margarita garleppi* Willmott,
new subspecies
Figs. 2C,D, 4C**

Description and Diagnosis: This subspecies differs from the nominate subspecies in having the fused postdiscal series on the DFW visible as a broad orange band extending from the subapical orange marking on the FW to the tornal orange spot on the DHW. The postdiscal band is also slightly narrower in *A. m. garleppi*. This taxon is also very similar to the sympatric *A. s. therasia* (Fig. 2G,H), but may be distinguished by characters discussed under the Diagnosis of *A. margarita margarita*. Most obviously, *A. m. garleppi* has very broad, almost fused silvery white submarginal series on the VHW which closely border the orange postdiscal band, without the broad black area which separates these two pattern elements in the middle of the wing in *A. s. therasia*.

Types: HOLOTYPE ♂: PERU: Cuzco: [Valle de Cosñipata], El Mirador, 1720m, 13° 04'S, 71° 33'W, 11 February 2011, M[ichael] McInnis (MUSM).

PARATYPES (1 ♀): PERU: Cuzco: Marcapata, [13°26.0'S, 70°55.0'W], 4500 ft, 1 ♀, (BMNH). BOLIVIA: La Paz: Río Zongo, [16°3.40'S, 68°1.2'W], 1200m, (Garlepp), 1896, 1 ♂ (ZMHU).

Etymology: This subspecies is named for Otto Garlepp, who collected the Bolivian paratype, in addition to many other important specimens of Bolivian butterflies, including the lectotype of *A. s. therasia*.

Taxonomy and variation: Willmott (2003a) included the BMNH and ZMHU type specimens of *A. m. garleppi* under *A. seriphia therasia*, and illustrated the male under this name (Willmott 2003a: Fig. 41i,j). However, all of the wing pattern characters discussed above to distinguish *A. margarita margarita* from other *Adelpha* also occur in the three type specimens of *A. m. garleppi*, and suggest that these two taxa are conspecific. Willmott (2003a) listed two Bolivian specimens in the ZMHU as possible syntypes of *A. s. therasia*, a female from Coroico labeled as a syntype by G. Lamas (Fig. 2H), and a male from Río Zongo (Fig. 2C), both

collected by Garlepp. The former represents *A. seriphia*, the latter *A. margarita*. Neither specimen was labeled as a type by Fruhstorfer, but that is also true of other ZMHU Fruhstorfer *Adelpha* types, such as the Ocaña paralectotype of *A. seriphia aquillia* referred to specifically by Fruhstorfer (1915: 531) as being in the “coll. Staudinger in the Berlin Museum” (Willmott 2003a). Fruhstorfer clearly, therefore, had examined the Staudinger material in the ZMHU, and it seems reasonable to conclude that this also included the putative syntype specimens of *A. s. therasia* collected by Garlepp. Although Fruhstorfer (1915) stated that the *A. s. therasia* type specimens were collected by Fassl, it seems most likely that this was a mistake, because neither we ourselves nor G. Lamas (pers. comm.) have located any other similar Bolivian specimens collected by Fassl in world collections. The female syntype (Fig. 2H), in particular, closely matches the original description in having very narrow postdiscal bands and the “white zone of the hind wings besides more pregnantly bordered in black” (Fruhstorfer, 1915: 531). To fix the identity of *A. s. therasia*, while minimizing nomenclatural change, we therefore designate this female specimen in the ZMHU, with the following labels, as the lectotype of *Adelpha seriphia therasia* Fruhstorfer (Fig. 2H): “Corvico [sic] ca. 2000 m. Bolivia (Yungas) 1895 (2-5) Garlepp”, “SYNTYPE ♀ *Adelpha seriphia therasia* Fruhstorfer G. Lamas det. '87”, “SYNTYPE”.

Distribution: This subspecies is currently known only from the three type specimens from southern Peru (Cuzco) and northern Bolivia (La Paz) (Fig. 4C).

Habitat and adult ecology: According to G. Lamas and M. McInnis (in litt.), the holotype specimen was collected on a bend of the road from Acjanaco to Pilcopata which overlooks a cliff. The specimen was feeding on flowers of *Miconia* (Melastomataceae) trees, along with a number of other rarely collected Lycaenidae and Riodinidae. The rarity of the taxon otherwise suggests that it flies at similarly poorly collected elevations and heights above the ground as the nominate subspecies. The similarity of the dorsal wing patterns of *A. m. garleppi* and *A. s. therasia* and other presumably sympatric *Adelpha*, such as *A. alala* (Hewitson, 1847) and *A. aricia* (Hewitson, 1847), suggests that these species may be involved in mimicry.

***Adelpha justina pichincha* Willmott & Hall,
new subspecies
Figs. 2K,L, 4D**

Description and Diagnosis: This subspecies (Fig. 2K,L) is most similar to the nominate subspecies (see Willmott, 2003a, Fig. 114a,b), but distinguished from it by the narrower DFW orange postdiscal

band. The ratio of the width of the band measured along vein Cu_1 to the forewing length varied from 0.046 to 0.106 in 7 specimens (mean 0.084), while in the most phenotypically similar subspecies, *A. justina justina*, this ratio varied from 0.139 to 0.201 in 11 specimens from Ecuador and Colombia (mean 0.170). A *t*-test indicates this difference to be significant ($p < 0.01$).

Types: HOLOTYPE ♂: **ECUADOR:** *Imbabura:* km 26 Chontal Bajo-Chontal Alto, Chontal Alto, [0°17'48"N, 78°42'3"W], 1550–1650m, (K. Willmott & J. Hall), 10 August, [FLMNH-MGCL-149747], (FLMNH), to be deposited in MECN).

PARATYPES (15 ♂, 3 ♀): **ECUADOR:** *Imbabura:* km 26 Chontal Bajo-Chontal Alto, Chontal Alto, [0°17'48"N, 78°42'3"W], 1550–1650m, (K. Willmott & J. Hall), 10 August, 1 ♂ [FLMNH-MGCL-149745], 1 ♂ [FLMNH-MGCL-149746], 1 ♂ [FLMNH-MGCL-149748], 1 ♂ [FLMNH-MGCL-149749], (FLMNH); *Pichincha:* 7 km SW Las Tolas, [0°3'26"N, 78°49'6"W], 1350m, (K. Willmott & J. Hall), 3 August, 1 ♂ [FLMNH-MGCL-149735], 1 ♂ [FLMNH-MGCL-149736], 1 ♂ [FLMNH-MGCL-149737], (FLMNH); c. 1 km S Nanegalito, Hostería El Rosal, [0°3'27"N, 78°40'53"W], 2000m, (Warren-Gash, H.), 5 September, 1 ♂, (HAWA); km 9 Pacto-Guayabillas rd., [0°9'18"N, 78°49'14"W], 1630m, (K. Willmott & J. Hall), 5, 6 August, 1 ♂ [FLMNH-MGCL-149743], 1 ♂ [FLMNH-MGCL-149744], (FLMNH); Mindo, Río Napombillo, [0°3'49"S, 78°47'0"W], 1200m, (K. Willmott), 13 November, 1 ♂, (KWJH); old Quito-Nono rd., Tandayapa, [0°0'24"S, 78°41'2"W], 1600–1800m, (Boyer, P.), 30 January, 1 ♀, (PIBO); Quito-Sto. Domingo old rd., Hacienda Santa Isabel, [0°18'48"S, 78°56'0"W], 1200m, (K. Willmott & J. Hall), 2 September, 1 ♂, (KWJH); Reserva Las Gralarias, [0°0'39"S, 78°43'50"W], (T. Kell), 25 February, 1 ♂ [FLMNH-MGCL-151113], (FLMNH); Reserva Las Gralarias, Quebrada Santa Rosa, [0°0'28"S, 78°43'27"W], 1800m, (K. Willmott & J. Hall), 4 August, 1 ♂ [FLMNH-MGCL-149738], 1 ♀ [FLMNH-MGCL-149739], 1 ♀ [FLMNH-MGCL-149740], 1 ♀ [FLMNH-MGCL-149741], (FLMNH); Reserva Las Gralarias, Quebrada Santa Rosa, [0°0'28"S, 78°43'27"W], 1950m, (K. Willmott & J. Hall), 4 August, 1 ♂ [FLMNH-MGCL-149742], (FLMNH).

Etymology: This subspecies is named for the province of Pichincha, itself named for Volcán Pichincha, whence comes the majority of specimens of this subspecies.

Taxonomy and variation: Willmott (2003a: Fig. 114c,d) figured a specimen of this subspecies under *A. justina justina* and discussed the possibility that it might represent a distinct subspecies, but refrained from describing it because only a single specimen was then known. Specimens are now known from 9 sites up to 72 km apart, from southern Imbabura, just north of the Río Guayllabamba, to southern Pichincha, along the Alóag-Santo Domingo road (Fig. 4D). There is some variation within populations in the width of the orange DFW postdiscal band, but this band is always considerably narrower than in the nominate subspecies, especially in comparison with neighboring northwest Ecuadorian specimens which have the broadest bands (Willmott 2003a). The extent of the white DHW postdiscal spot is also variable, and in fact most specimens have more extensive white than the geographically closest specimens of *A. justina justina*, from northwestern Ecuador, but show little difference in this character in comparison with Colombian specimens of the nominate subspecies.

Distribution: This subspecies is known only from the western Andes of Ecuador, from southern Imbabura to southern Pichincha province (Fig. 4D). In addition to the localities listed above, Raguso and Gloster (1996) also reported '*Adelpha justina*' from Reserva Maquipucuna (Ecuador, Pichincha, Río Alambi, c. 0°5'42"N, 78°38'0"W, 1600 m), presumably based on specimens of this subspecies.

Habitat and adult ecology: *Adelpha justina pichincha* occurs in relatively undisturbed cloud forest from 1200–2000 m. We have collected males in traps baited with rotting fish from 1–15 m above the ground along ridge tops. The majority of males that we have encountered have been perching along ridge tops from 3–15 m above the ground, in small to large light gaps, from 10:00 hrs to 13:00 hrs. We also observed a single male perching and patrolling a small area above a river 5–8 m above the water from 13:15–13:30 hrs. At the same site and time, three females were encountered gliding downstream, 1–2 m above the water in a slightly shaded area. The latter observation is particularly unusual given the extreme rarity of females of this species; out of 211 specimens of *A. justina* located by Willmott (2003a) in collections, only 2 were females, and we have yet to observe a female of the nominate subspecies.

Use of DNA sequence data in Neotropical butterfly taxonomy

One of the first studies to use DNA sequence data to support the recognition and description of a new butterfly species was Brower (1996), and since then there has been an exponential increase in publications using such data in systematics. Nevertheless, although a number of generic-level studies have inadvertently revealed problems in species taxonomy (e.g., Mallarino et al. 2005, Elias et al. 2009, and Mullen et al. 2010), surprisingly few publications have deliberately employed DNA sequence data to solve species-level taxonomic issues. DNA sequence data are clearly of value in revealing potential cryptic species within intensive inventories of particular regions (e.g., Janzen et al. 2011), as illustrated by Chacón et al.'s (2012) recent description of a new species of *Opsiophanes* Doubleday, [1849], from Costa Rica. However, delimiting sympatric morpho-species is usually just the first step in species taxonomy, with the second, critical, issue being the association of allopatric taxa (e.g., Silva-Brandão et al. 2008). Not only is this second step necessary for a sound understanding of species distributions and diversity, but it is also essential for the stable application of taxonomic names. In the case of our study, the separation between *A. seriphia* and *A. margarita* was reasonably clear, but the relationships of

A. margarita to other *Adelpha* taxa were not. Broad geographic sampling is therefore essential in most studies, as illustrated by Prudic et al. (2008), Sourakov and Zakharov (2011), and Bonebrake et al. (2011). Such sampling is especially challenging in large, highly diverse and biologically complex regions such as the tropical Andes, and the lack of recently collected specimens amenable to molecular study is no doubt a major factor hindering the incorporation of molecular data into species-level taxonomic research. The acquisition of new material and appropriately preserved tissue samples from geographically diverse regions, including those that have been historically well-collected, should therefore remain a top priority for museums.

ACKNOWLEDGEMENTS

We thank the museum curators who allowed us to examine the *Adelpha* collections under their care, and in particular R. Eastwood, B. Huertas and W. Mey for providing photos of specimens. Gerardo Lamas provided typically wise and helpful advice concerning the identity of the *therasia* syntypes and information about MUSM specimens of *A. margarita*. We thank S. Villamarín, the MECN and Ecuadorian Ministerio del Ambiente for arranging the necessary permits for research in Ecuador. We thank the following for contributing information and/or specimens for study: I. Aldas, C. Brévignon, M. Costa, J. Radford, J. Salazar and C. Whelan. For their careful mentoring in the molecular lab we thank M. Elias, C. Jiggins, S. Mullen and G. Paulay, and we especially thank L. Xiao for her work in generating and editing the majority of the sequences used in this study. Museum and field work was funded in part by the Leverhulme Trust, the Darwin Initiative, the National Science Foundation (# 0847582) and the FLMNH Museum Associates, and field work by the National Geographic Society (Research and Exploration Grant # 5751-96) and NSF (# 0103746, #0639977, #0639861). Finally, we thank G. Lamas and A. Aiello for their helpful comments and suggestions which significantly improved the paper.

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Submitted for publication 4 January 2013; revised and accepted 22 February 2013.

APPENDIX I. Voucher specimen information for DNA sequence data.

Taxon	Locality (decimal latitude and longitude)	DNA Voucher number	GenBank number
<i>Adelpha californica</i>	USA: Oregon: Benton Co. (44.467, -123.483)	NW107-16	AY788591.1
<i>Adelpha godmani</i>	Colombia: Caldas: El Águila, Neira (5.105, -75.506)	LEP-04107	KC681843
<i>Adelpha godmani</i>	Ecuador: Imbabura: Cachaco, ridge to south (0.813, -78.417)	KW-080229-24	KC681845
<i>Adelpha godmani</i>	Ecuador: Loja: Río Inguna, km 5 Zambí-Piñas rd. (-3.907, -79.532)	KW-080510-01	KC681846
<i>Adelpha godmani</i>	Ecuador: Manabí: Cerro Pata de Pájaro (0.011, -79.968)	LEP-04109	KC681844
<i>Adelpha hyas hewitsoni</i>	Ecuador: Zamora-Chinchipec: Cabañas Ecológicas Copalinga, Río Bombuscaro (-4.091, -78.959)	LEP-04252	KC681827
<i>Adelpha hyas hewitsoni</i>	Ecuador: Zamora-Chinchipec: Cabañas Ecológicas Copalinga, Río Bombuscaro (-4.091, -78.959)	LEP-04253	KC681828
<i>Adelpha hyas hewitsoni</i>	Peru: Amazonas: Bagua Chica (-5.633, -78.533)	LEP-03282	KC681829
<i>Adelpha m. margarita</i>	Ecuador: Morona-Santiago: Río Abanico (-2.255, -78.2)	39-A	KC681840
<i>Adelpha m. margarita</i>	Ecuador: Morona-Santiago: Río Abanico (-2.255, -78.2)	KW-080229-29	KC681839
<i>Adelpha m. margarita</i>	Ecuador: Morona-Santiago: Río Abanico (-2.255, -78.2)	KW-080229-30	KC681838
<i>Adelpha m. margarita</i>	Ecuador: Zamora-Chinchipec: km 3.5 El Tambo-San Juan del Oro (-3.952, -79.059)	KW-061103-04	KC681842
<i>Adelpha m. margarita</i>	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	KW-061114-03	KC681841
<i>Adelpha nea nea</i>	Ecuador: Napo: Chichicorrumi (-1.07, -77.629)	LEP-04111	KC681821
<i>Adelpha paraena paraena</i>	Bolivia: Cochabamba: Villa Tunari (-16.95, -65.418)	LEP-03800	KC681822
<i>Adelpha radiata aiellae</i>	Ecuador: Esmeraldas: Río Durango (1.038, -78.617)	LEP-04113	KC681823
<i>Adelpha seriphia aquillia</i>	Colombia: Caldas: El Águila, Neira (5.105, -75.506)	LEP-04106	KC681832
<i>Adelpha seriphia aquillia</i>	Ecuador: Morona-Santiago: Río Abanico (-2.255, -78.2)	34-A	KC681834
<i>Adelpha seriphia aquillia</i>	Ecuador: Sucumbíos: Río Sucio (0.475, -77.555)	LEP-04110	KC681833
<i>Adelpha seriphia aquillia</i>	Ecuador: Zamora-Chinchipec: El Líbano (-4.08, -78.969)	KW-061114-05	KC681835
<i>Adelpha seriphia aquillia</i>	Ecuador: Zamora-Chinchipec: km 3.5 El Tambo-San Juan del Oro (-3.952, -79.059)	KW-061103-02	KC681836
<i>Adelpha seriphia barcantii</i>	Venezuela: Monagas: Cerro Quiriquire (10.102, -63.809)	KW-061114-01	KC681830
<i>Adelpha seriphia pione</i>	Venezuela: Mérida: Mérida (8.6, -71.133)	LEP-04108	KC681831
<i>Adelpha seriphia therasia</i>	Bolivia: Cochabamba: El Dorado (-17.158, -65.767)	LEP-03802	KC681837
<i>Adelpha serpa diadochus</i>	Ecuador: Orellana: Reserva Biológica del Río Bigal, main campsite (-0.525, -77.418)	LEP-10479	KC681825
<i>Adelpha serpa diadochus</i>	Ecuador: Pastaza: Kapawi village (-2.538, -76.836)	LEP-04115	KC681826
<i>Adelpha serpa duilliae</i>	Ecuador: Carchi: Lita, ridge east of Río Baboso (0.888, -78.438)	KW-080229-25	KC681824

APPENDIX 2. Updated classification for members of the *Adelpha serpa* group following Prudic et al. (2008) and this paper. A single dash before a name indicates a valid subspecific name, two dashes indicates a synonym, and three dashes indicates an unavailable name.

- bredowii* Geyer, 1837
eulalia (Doubleday, [1848]) (raised to species rank by Prudic et al. (2008))
 --*guatemalensis* (Carpenter & Hobby, 1944)
californica (Butler, 1865) (raised to species rank by Prudic et al. (2008))
diocles Godman & Salvin, 1878
 - *creton* Godman, 1901
herbita Weymer, 1907
zea (Hewitson, 1850)
 --*serpentina* Fruhstorfer, 1915
 --*tarpeia* Fruhstorfer, 1915
paroeca (Bates, 1864)
 --*emathia* (R. Felder, 1869)
 - *pseudodonyssa* Salazar, 2000
nea (Hewitson, 1847)
 --*campeda* Fruhstorfer, 1915
 - *sentia* Godman & Salvin, 1884
paraena (Bates, 1865)
 - *massilia* (C. Felder & R. Felder, 1867)
 - *reji* Neild, 1996
 - *lecromi* Willmott, 2003
radiata Fruhstorfer, 1915
 - *myrlea* Fruhstorfer, 1915
 - *gilletella* Brévignon, 1995
 - *aiellae* Willmott & Hall, 1999
 - *explicator* Willmott & Hall, 1999
 - *romeroi* Willmott & Neild, 2003
- serpa* (Boisduval, 1836)
 --*damon* Fruhstorfer, 1913
 --*ornamenta* Fruhstorfer, 1915
 - *celerio* (Bates, 1864)
 --*diademeta* Fruhstorfer, 1913
 --*phintias* Fruhstorfer, 1913
 - *duiliae* Fruhstorfer, 1913
 - *diadochus* Fruhstorfer, 1915
 --*timehri* Hall, 1938
 --*floreia* Brévignon, 1995
seriphia (C. Felder & R. Felder, 1867)
 - *pione* Godman & Salvin, 1884
 - *aquillia* Fruhstorfer, 1915
 --*naryce* Fruhstorfer, 1915
 - *therasia* Fruhstorfer, 1915
 - *egregia* Röber, 1927
 - *barcanti* Willmott, 2003
godmani Fruhstorfer, 1913, **revised status**
 --*syrna* Steinhauser, 1974
 ---*syrna* Fruhstorfer, 1915
margarita Willmott & Hall, **new species**
 - *garleppi* Willmott, **new subspecies**
hyas (Doyère, [1840])
 - *viracocha* Hall, 1938
 - *hewitsoni* Willmott & Hall, 1999