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DNA barcodes uncover hidden taxonomic diversity behind the variable wing patterns in the Neotropical butterfly genus *Zaretis* (Lepidoptera: Nymphalidae: Charaxinae)

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The leafwing butterflies of the genus *Zaretis* Hübner, [1819] are revised based on morphological and molecular data. Species were delimited using morphology and 396 'DNA barcode' sequences. Intraspecific and interspecific genetic distances, along with neighbor-joining, maximum likelihood and Bayesian inference analyses, were used to infer putative species limits and monophyly. Additionally, a Poisson-tree-processes model was used to infer putative species boundaries based on the best-scoring maximum likelihood tree. Fifteen species are recognized, two of which are included in a new genus, ***Phantos*** Dias **gen. nov.**, erected to include ***Phantos callidryas*** **comb. nov.** and ***Phantos opalina*** **stat. rev.**, **comb. nov.** *Zaretis strigosus* is formally recognized as a valid species, and four new species, namely ***Zaretis hurin*** Dias **sp. nov.**, ***Zaretis elianahenrichae*** Dias **sp. nov.**, ***Zaretis mirandaenrichae*** Dias **sp. nov.** and ***Zaretis crawfordhilli*** Dias **sp. nov.**, are described. In addition, nine lectotypes are designated, five new synonyms and two new combinations are proposed, and two preoccupied names, five infrasubspecific names and three *nomina nuda* are recognized. Species are critically discussed, and an identification key, distribution maps and illustrations of habitus and male and female genitalia for all species, where available for study, are provided.

ADDITIONAL KEYWORDS: *Coenophlebia* – DNA barcoding – morphology – Salicaceae – *Siderone* – Zaretidinae.

INTRODUCTION

Zaretis Hübner, [1819] is a neotropical genus of leafwing butterflies widely distributed throughout the Central and South Americas (Comstock, 1961; Willmott & Hall, 2004). More than 40 years after the preceding revision of the genus (Comstock, 1961), and 50 years since the previous description of a new species (Bryk, 1953), the taxonomy of *Zaretis* was succinctly reviewed by Willmott & Hall (2004), and three new species (Willmott & Hall, 2004; Choimet, 2009; Dias, Casagrande & Mielke, 2012) and two subspecies (Brévignon, 2006) were described. Additionally, two taxonomic names, one previously in synonymy and another recognized as a subspecies, were recognized as valid species (Dias *et al.*, 2012, 2015), increasing the number of valid species to ten. Nevertheless, only three of those ten species are easily recognizable: *Zaretis syene* (Hewitson, 1856), *Zaretis callidryas* (R. Felder, 1869) and *Zaretis delassisei* Choimet, 2009. The identification of the remaining species is complicated by a lack of consistent external diagnostic characters, owing to the high level of intraspecific variation in both sexes that occurs both within a single locality and throughout the distributional range of these

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species (Pyrcz & Neild, 1996; Willmott & Hall, 2004). D'Abrera (1988) regarded *Zaretis* as 'the most variable of the neotropical butterflies'. A lack of obvious interspecific differences in male genitalia and the marked sexual dimorphism complicate identification further (Willmott & Hall, 2004). In the past, these issues caused differing views on the number of valid species and resulted in the description of 27 debatable species-level taxonomic names (e.g. Comstock, 1961; Vane-Wright, 1975; Lamas, 2004; Willmott & Hall, 2004). Despite recent efforts to facilitate the identification of some taxa (Willmott & Hall, 2004; Dias *et al.*, 2012, 2015), the correct association of most of those names and the species diversity within the genus have remained uncertain.

Traditional morphological taxonomic studies can be extremely time consuming or even unproductive in certain groups, especially when the subject species are superficially similar or highly variable. Such is the case with most of the species of *Zaretis*. To overcome these shortcomings in taxonomy as a whole, Hebert *et al.* (2003a) suggested the use of 'DNA barcodes'; a short, standardized DNA fragment from the mitochondrial cytochrome c oxidase subunit I (COI) gene to facilitate the identification and discovery of new species based on differences in their sequences. Although there is some dispute on both practical and theoretical grounds about the exclusive use of this method in taxonomic studies and difficulties caused by hybridization, gene introgression and *Wolbachia* infections (e.g. Brower, 2006; Cong *et al.*, 2017), the effectiveness of DNA barcodes has been confirmed repeatedly by the successful identification and discovery of species in numerous animal groups (e.g. Hebert, Ratnasingham & deWaard, 2003b; Huemer *et al.*, 2014; Dumas *et al.*, 2015). The use of standard phylogenetic analyses and novel statistics to infer species delimitation with single-locus molecular data, such as Poisson-tree-processes (PTP; Zhang *et al.*, 2013) and generalized mixed Yule coalescent (GMYC) methods (Fujisawa & Barraclough, 2013), provides further statistical support for DNA barcode species delimitation. Thus, the aim of this study was to complement morphological and molecular data and use different statistical methods to resolve the chaotic species-level taxonomy of the genus *Zaretis*.

MATERIAL AND METHODS

Material examined

About 2200 specimens of *Zaretis* were examined directly or indirectly, deposited in the following collections: CBF, Coleccíon Boliviana de Fauna, La Paz, Bolivia; CFR, Colección Familia Romero, Maracay, Venezuela; CM, Coleção Carlos Guilherme Costa Mielke, Ponta Grossa, Brazil; DZUP, Coleção Entomológica Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Brazil; ECOSUR, El Colegio de la Frontera Sur, Chetumal, Mexico; FLMNH, McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, FL, USA; INBIO, Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; IOC, Instituto Oswaldo Cruz, Rio de Janeiro, Brazil; JS, Collectión Julian Adolfo Salazar-Escobar, Manizales, Colombia; LCB, Collection L. et C. Brévignon, Cayenne, Guyane; MECN, Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MNCR, Museu Nacional de Costa Rica, San José, Costa Rica; MNHNUC, Museo de Historia Natural de la Universidad de Caldas, Manizales, Colombia; MNRJ, Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; NHM, Natural History Museum, Vienna, Austria; NHMUK, The Natural History Museum, London, UK; NMI, National Museum of Ireland, Dublin, Ireland; OM, Coleção Olaf Hermann Hendrik Mielke, Curitiba, Brazil; PUCE, Pontificia Universidad Católica de Ecuador, Quito, Ecuador; RMS, Naturhistorska Riksmuseet, Stockholm, Sweden; SRTI, Smithsonian Tropical Research Institute, Barro Colourado, Panamá; USNM, National Museum of Natural History, Washington, DC, USA; UNAM, Universidad Nacional Autónoma de México, Ciudad de México, Mexico; UPENN, University of Pennsylvania, PA, USA; XC, Collection Xavier Choimet, Saint-Nazaire, France; ZIN, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia; ZMHU, Museum fur Naturkunde Leibniz-Institut für Evolutions und Biodiversitatsforschung an der Humboldt-Universitat zu Berlin, Berlin, Germany. Specimens directly examined are listed in the Supporting Information (Appendix S1), and dissected specimens are marked with an asterisk. Barcoded specimens are listed separately in Supporting Information (Appendix S2). Distribution maps were prepared in SimpleMappr (Shorthouse, 2010), extrapolated from the georeferenced labels of examined specimens (Supporting Information, Appendix S1).

The abdomens of dissected specimens (92 in total) were detached and soaked in 10% potassium hydroxide solution in a test tube heated in a bain-marie for ~3–10 min. Afterwards, the abdomen was dissected and the genitalia were removed. The genitalia were examined under a stereoscopic microscope, and illustrations were prepared with the aid of a camera lucida. In the illustrations, continuous lines represent sclerotized structures; thin lines, membranous structures; and dotted lines, structures visible through transparency. The terminology by Kristensen (2003), with some minor modifications, is used for structures of the genitalia, the terminology

of Comstock & Needham (1898), for the venation of the wings, and the terminology of Nijhout (1991) for elements of wing pattern, as interpreted by Schwanwitsch (1940) and Descimon (1986) for *Zaretis*. Adults are illustrated at life size, and scale bars are provided. Higher and species-level taxonomy follows Lamas (2004), with the latter updated with subsequent species descriptions and taxonomic acts (Willmott & Hall, 2004; Brévignon, 2006; Choimet, 2009; Dias *et al.*, 2012, 2015). Names deemed to be infrasubspecific conform to the provisions of article 45.6, and names recognized as *nomina nuda* fail to conform to articles 12 and/or 13 of the ICZN (1999). Characteristic labels will be added in all types designated here. Taxonomic accounts are arranged in chronological order. A literature review was also performed, based mostly on the bibliography of the Neotropical butterflies listed by Lamas (2017) (Supporting Information, Appendix S6). In the taxonomic catalogues (Supporting Information, Appendix S6), most literature records could not be assigned to a species with certainty, given the confused species-level taxonomy, misidentifications and different interpretations of species validity; records tentatively assigned to a species are marked with an asterisk. Descriptions of new taxa are based on males.

DNA PROCESSING AND TAXON SAMPLING

Extraction, amplification, and sequencing of 658 bp of the 'DNA barcode' of the mitochondrial cytochrome oxidase *c* subunit I of all *Zaretis* specimens from ECOSUR, DZUP, INBIO, STRI, UNAM, UPENN and some from FLMNH were carried out at the Canadian Center for DNA Barcoding, Biodiversity Institute of Ontario, University of Guelph, ON, Canada and followed the protocol described by Hebert *et al.* (2004). The remaining specimens from FLMNH were processed at the McGuire Center for Lepidoptera, as described by Ortiz-Acevedo & Willmott (2013). Additional sequences were obtained from online databases (Benson *et al.*, 2005; Ratnasingham & Hebert, 2007). In total, 396 DNA barcodes were selected for the molecular study, including one sequence of *Coenophlebia archidona* (Hewitson, 1860) and two sequences of two species of *Siderone* Hübner, [1823] as outgroups, and 393 sequences of specimens of *Zaretis* (Supporting Information, Appendix S2). The number of sequences of each putative species of *Zaretis* in the analyses was selected to include an extensive variety of phenotypes and was based on the distinctiveness and range of the putative species, such that more distinctive species with smaller ranges are less represented in the analyses than complex and similar putative species with larger ranges (Table 1). Also, a number of female specimens were selected to help correctly match the sexes of the putative species. The sequences were aligned manually in MEGA6 (Tamura *et al.*, 2013). Accession numbers for the sequences are given in the Supporting Information (Appendix S2) and are available at http://www.boldsystems.com (Ratnasingham & Hebert, 2007) and GenBank (Benson *et al.*, 2005).

Table 1. Estimates of average evolutionary divergence (AED) and respective standard error (SE) over sequence pairs within species of ***Phantos*** Dias **gen. nov.** and *Zaretis* Hübner, [1819]

Genus	Species	AED	SE	*N*
Zaretis	***crawfordhilli* sp. nov.**	0.004	0.001	38
Zaretis	*delassisei*	0.010	0.005	2
Zaretis	***elianahenrichae* sp. nov.**	0.002	0.001	25
Zaretis	*ellops*	0.001	< 0.001	103
Zaretis	***mirandahenrichae* sp. nov.**	0.001	< 0.001	32
Zaretis	*falcis*	0.008	0.002	12
Zaretis	***hurin* sp. nov.**	0.008	0.002	44
Zaretis	*isidora*	0.011	0.002	41
Zaretis	*itylus*	0.000	< 0.001	2
Zaretis	*itys*	0.005	0.001	19
Zaretis	*pythagoras*	0.000	< 0.001	4
Zaretis	*strigosus*	0.005	0.001	54
Zaretis	*syene*	0.000	< 0.001	3
Phantos	***callidryas* comb. nov.**	0.000	< 0.001	12
Phantos	***opalina* comb. nov., stat. rev.**	0.000	< 0.001	2

N, number of specimens analysed.

ANALYSES OF MOLECULAR DATA

Distance analyses

Distance analyses of intraspecific mean divergence, interspecific mean divergence, net interspecific mean divergence, and construction of a neighbor-joining (NJ) (Saitou & Nei, 1987) tree were performed in MEGA6, using the substitution model determined by JModelTest 0.1.1 (Darriba *et al.*, 2012), according to the corrected Akaike information criterion (AICc). This metric selected Tamura–Nei with a proportion of invariable sites as the substitution model. Clade support was assessed using 1000 bootstrap (BS) replicates and considered strongly supported when > 70%.

Maximum likelihood

The maximum likelihood (ML) analysis was performed in RAxML v8.2 (Stamatakis, 2014) using a heuristic search implementing 100 random-addition replicates. As RAxML v8.2 is limited to parameter-rich models of the GTR ("Generalised Time-Reversible", Tavaré 1986) family, the GTR-CAT ("Bayesian mixture model", Lartillot & Philippe, 2004) substitution model was selected. This model performs faster searches with better ML substitution values, incorporates rate heterogeneity, and follows the argument, by Stamatakis

(2014), against the use of the proportion of invariable sites in ML searches. Clade support was assessed using 1000 non-parametric BS replicates and considered strongly supported when > 70% (Hillis & Bull, 1993).

Bayesian inference

Bayesian inference (BI) analysis was performed in MrBayes v3.2.5 (Ronquist & Huelsenbeck, 2003). As MrBayes supports only a limited number of substitution models, and the exact model selected by JModelTest 0.1.1 using the Bayesian information criterion (BIC) metric was not supported by MrBayes, the mixed model was selected. This model removes the need for a priori model testing, allowing MrBayes to sample across the substitution model space in the Markov chains Monte Carlo (MCMC) analysis itself (e.g. Dumas *et al.*, 2015). Two independent runs with four MCMC chains, one cold and three heated, ran for a number of generations, sampling trees every 1000 generations. The runs were periodically sampled to assess convergence of the log-likelihood curves and the split-frequencies in Tracer v1.6.0 (Rambaut *et al.*, 2014), with a burn-in of 10%. The run was stopped after examining the trace plots, and when the average standard deviation in split frequencies was < 0.01 and the effective sample size was > 200. A burn-in of 25% was applied to summarize statistics for parameters and trees sampled in the Bayesian MCMC analysis. Clade support was assessed by posterior probabilities (PP) directly estimated from the majority-rule consensus topology, and considered strongly supported when > 95% (Erixon *et al.*, 2003).

Poisson-tree-processes molecular species delimitation

Following the recommendations of Tang *et al.* (2014), the best tree recovered from the ML analyses in RAxML was used to perform a Poisson-tree-processes single-locus molecular species delimitation (Zhang *et al.*, 2013). A visualization of the PTP molecular species delimitation result, combining principal coordinates analysis (PCoA), PTP and species tree mapping, was performed by PhyloMap-PTP (Zhang *et al.*, 2011). These analyses were conducted on the Exelixis Lab web server (http://species.h-its.org/ptp/), with default settings. The findings were evaluated by examining the trace plots.

RESULTS AND DISCUSSION

DNA BARCODE DISTANCE ANALYSES, PHYLOGENETIC INFERENCES AND SPECIES DELIMITATION

The distance analyses showed that the intergeneric average evolutionary divergence (AED) estimate between species of *Zaretis*, *Coenophlebia* and *Siderone* ranged from 8.6% (*Z. itylus* vs. *S. galanthis*) to 11.6% (*Z. delassisei* vs. *C. archidona*) (Table 2). Similar AED estimates were recovered between *Phantos callidryas* comb. nov. and *Phantos opalina* stat. rev., comb. nov. and species of the above cited genera. These estimates further corroborate the description of a new genus to include these two species. Nevertheless, the lowest interspecific AED among all species analysed was between *P. callidryas* comb. nov. and *P. opalina* stat. rev., comb. nov., with 2% (SE = 0.006) AED. The most divergent species of *Zaretis* in relationship to other species of the genus was *Z. syene*, with interspecific AED ranging from 7.1% (*Z. syene* vs. *Zaretis pythagoras*) to 8.7% (*Z. syene* vs. *Zaretis crawfordhilli* Dias sp. nov.). The interspecific AEDs between most of species were well above 2%, suggested as an appropriate threshold for species delimitation in Lepidoptera (Hebert *et al.*, 2003a; Huemer *et al.*, 2014). The net AED estimates provided generally similar results (Table 3). The intraspecific AEDs were < 1% in all species, except *Zaretis isidora*, with 1.1% (SE = 0.002; Table 1). This relatively large intraspecific AED might be the result of restricted gene flow between currently isolated populations occurring in the Amazon basin and along the eastern coast of Brazil. Except for two other species, *Zaretis hurin* Dias sp. nov. and *Zaretis falcis*, with 0.8% (SE = 0.002), the remaining 11 species of *Zaretis* had AED estimates ranging from 0.0 to 0.5%. Comparison of inter- and intraspecific AEDs suggests the existence of a distinct DNA barcode gap, with little to no overlap for species of these genera.

Neighbor-joining, ML and BI analyses (Figs 1–3; Supporting Information, Appendices S3–S5) recovered 15 monophyletic clades corresponding to the putative species (based on Willmott & Hall, 2004; Dias *et al.*, 2012, 2015) and four previously unrecognized species, described below. Two species formerly in *Zaretis* are here transferred to the new genus *Phantos* Dias gen. nov., described below, and *P. opalina* stat. rev., comb. nov. was recovered as a valid species. Most species were strongly supported by all analyses, although there are some differences between the results. In the NJ analysis, all species were strongly supported by high BS values except *Z. itylus* (BS = 45) and *Z. hurin* sp. nov. (BS = 65). *Zaretis isidora* was recovered with moderate support (BS = 82), and the remaining species were recovered with strong support, with BS values > 90. Conversely, in the ML and BI analyses, *Z. isidora* did not receive strong support (BS = 65, PP = 87), whereas *Z. hurin* sp. nov. (BS = 90, PP = 100) was strongly supported. Two specimens morphologically identified as *Zaretis ellops* (highlighted in Supporting Information, Appendices S3–S5) were recovered as related to *Zaretis strigosus* in the NJ analysis, with low support (BS = 48), and to *Z. ellops* in the ML and BI analyses, with strong support (ML, BS = 84; BI, PP = 97). The clade formed by all specimens morphologically identified as *Z. strigosus* was strongly supported in NJ analysis (BS = 97; Supporting Information, Appendix S3). *Zaretis itylus*,

Table 2. Estimates of evolutionary divergence (below the diagonal) and respective standard errors (above the diagonal) over sequence pairs between species of *Coenophlebia* C. Felder & R. Felder, 1862, *Siderone* Hübner, [1823], ***Phantos*** Dias **gen. nov.** and *Zaretis* Hübner, [1819]

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	*archidona*		0.013	0.013	0.013	0.012	0.013	0.012	0.013	0.012	0.011	0.018	0.011	0.011	0.013	0.012	0.012	0.013	0.013
2	*callidryas*	0.099		0.013	0.013	0.012	0.012	0.012	0.013	0.012	0.012	0.015	0.012	0.012	0.006	0.012	0.012	0.013	0.013
3	*crawfordhilli*	0.108	0.100		0.010	0.009	0.009	0.008	0.013	0.009	0.007	0.011	0.008	0.008	0.013	0.009	0.010	0.013	0.015
4	*delassisei*	0.116	0.106	0.065		0.009	0.010	0.009	0.014	0.008	0.009	0.014	0.009	0.009	0.013	0.008	0.009	0.012	0.014
5	*elianahenrichae*	0.094	0.088	0.058	0.056		0.009	0.008	0.012	0.008	0.006	0.009	0.007	0.006	0.012	0.008	0.007	0.012	0.012
6	*ellops*	0.097	0.090	0.059	0.069	0.048		0.008	0.012	0.009	0.008	0.009	0.009	0.008	0.012	0.008	0.007	0.012	0.013
7	*falcis*	0.095	0.079	0.051	0.061	0.048	0.048		0.013	0.008	0.007	0.010	0.007	0.007	0.011	0.008	0.008	0.012	0.013
8	*galanthis*	0.099	0.102	0.103	0.113	0.086	0.094	0.096		0.014	0.012	0.017	0.012	0.011	0.014	0.013	0.012	0.013	0.013
9	*hurin*	0.103	0.090	0.059	0.048	0.046	0.057	0.050	0.104		0.008	0.010	0.008	0.007	0.012	0.008	0.009	0.012	0.014
10	*isidora*	0.091	0.083	0.045	0.060	0.029	0.049	0.040	0.095	0.048		0.009	0.007	0.005	0.012	0.008	0.007	0.011	0.012
11	*itylus*	0.089	0.064	0.038	0.050	0.021	0.025	0.033	0.086	0.032	0.030		0.008	0.009	0.013	0.008	0.010	0.014	0.017
12	*itys*	0.091	0.091	0.047	0.058	0.030	0.049	0.041	0.090	0.048	0.036	0.021		0.006	0.012	0.008	0.007	0.011	0.013
13	*mirandahenrichae*	0.090	0.085	0.046	0.051	0.025	0.045	0.038	0.081	0.039	0.025	0.023	0.029		0.012	0.007	0.008	0.011	0.013
14	*opalina*	0.101	0.020	0.097	0.110	0.088	0.089	0.073	0.108	0.089	0.084	0.053	0.091	0.085		0.012	0.012	0.013	0.014
15	*pythagoras*	0.101	0.092	0.047	0.050	0.039	0.043	0.046	0.101	0.043	0.042	0.023	0.041	0.034	0.089		0.008	0.011	0.013
16	*strigosus*	0.098	0.093	0.060	0.059	0.034	0.033	0.045	0.094	0.052	0.039	0.033	0.037	0.038	0.092	0.043		0.011	0.013
17	*syene*	0.104	0.095	0.087	0.080	0.078	0.084	0.080	0.100	0.083	0.077	0.059	0.073	0.072	0.099	0.071	0.074		0.014
18	*syntyche*	0.115	0.103	0.115	0.110	0.092	0.101	0.103	0.094	0.111	0.099	0.090	0.102	0.097	0.109	0.100	0.097	0.102	

Table 3. Estimates of net evolutionary divergence (below the diagonal) and respective standard errors (above the diagonal) over sequence pairs between species of *Coenophlebia* C. Felder & R. Felder, 1862, *Siderone* Hübner, [1823], ***Phantos*** Dias **gen. nov.** and *Zaretis* Hübner, [1819]

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	*archidona*		0.013	0.013	0.013	0.011	0.013	0.012	0.013	0.012	0.011	0.018	0.011	0.011	0.013	0.013	0.013	0.013	0.014
2	*callidryas*	0.099		0.013	0.013	0.012	0.012	0.011	0.013	0.012	0.011	0.015	0.012	0.012	0.006	0.013	0.013	0.013	0.012
3	*crawfordhilli*	0.106	0.098		0.010	0.009	0.009	0.008	0.013	0.009	0.007	0.011	0.008	0.008	0.012	0.008	0.009	0.013	0.013
4	*delassisei*	0.111	0.101	0.058		0.009	0.010	0.009	0.014	0.008	0.008	0.013	0.009	0.009	0.013	0.008	0.009	0.012	0.013
5	*elianahenrichae*	0.094	0.088	0.056	0.051		0.009	0.008	0.011	0.008	0.005	0.008	0.006	0.006	0.012	0.008	0.007	0.012	0.012
6	*ellops*	0.096	0.090	0.057	0.064	0.048		0.008	0.013	0.009	0.008	0.009	0.008	0.008	0.012	0.008	0.007	0.012	0.012
7	*falcis*	0.091	0.075	0.045	0.052	0.043	0.043		0.012	0.008	0.006	0.010	0.007	0.007	0.011	0.008	0.008	0.012	0.012
8	*galanthis*	0.099	0.102	0.101	0.108	0.086	0.093	0.092		0.013	0.011	0.016	0.012	0.011	0.013	0.013	0.012	0.013	0.013
9	*hurin*	0.099	0.086	0.053	0.039	0.041	0.052	0.042	0.100		0.007	0.010	0.008	0.007	0.012	0.008	0.008	0.012	0.013
10	*isidora*	0.085	0.077	0.038	0.049	0.023	0.043	0.030	0.089	0.038		0.008	0.006	0.005	0.011	0.007	0.006	0.011	0.011
11	*itylus*	0.089	0.064	0.036	0.045	0.021	0.025	0.029	0.086	0.028	0.024		0.007	0.008	0.013	0.009	0.010	0.015	0.018
12	*itys*	0.088	0.088	0.043	0.050	0.027	0.046	0.034	0.087	0.041	0.028	0.018		0.006	0.012	0.007	0.007	0.011	0.012
13	*mirandahenrichae*	0.089	0.084	0.043	0.045	0.024	0.043	0.032	0.080	0.033	0.018	0.022	0.026		0.012	0.007	0.007	0.011	0.012
14	*opalina*	0.101	0.020	0.095	0.105	0.088	0.088	0.069	0.108	0.084	0.079	0.053	0.088	0.084		0.012	0.012	0.013	0.013
15	*pythagoras*	0.101	0.092	0.045	0.045	0.038	0.043	0.042	0.101	0.039	0.037	0.023	0.039	0.033	0.089		0.008	0.011	0.013
16	*strigosus*	0.096	0.090	0.056	0.051	0.031	0.030	0.038	0.092	0.046	0.031	0.031	0.032	0.034	0.089	0.041		0.011	0.012
17	*syene*	0.104	0.095	0.085	0.075	0.078	0.084	0.076	0.100	0.079	0.072	0.059	0.070	0.071	0.099	0.071	0.071		0.013
18	*syntyche*	0.115	0.103	0.113	0.105	0.091	0.101	0.099	0.094	0.107	0.094	0.090	0.099	0.096	0.109	0.100	0.095	0.102	

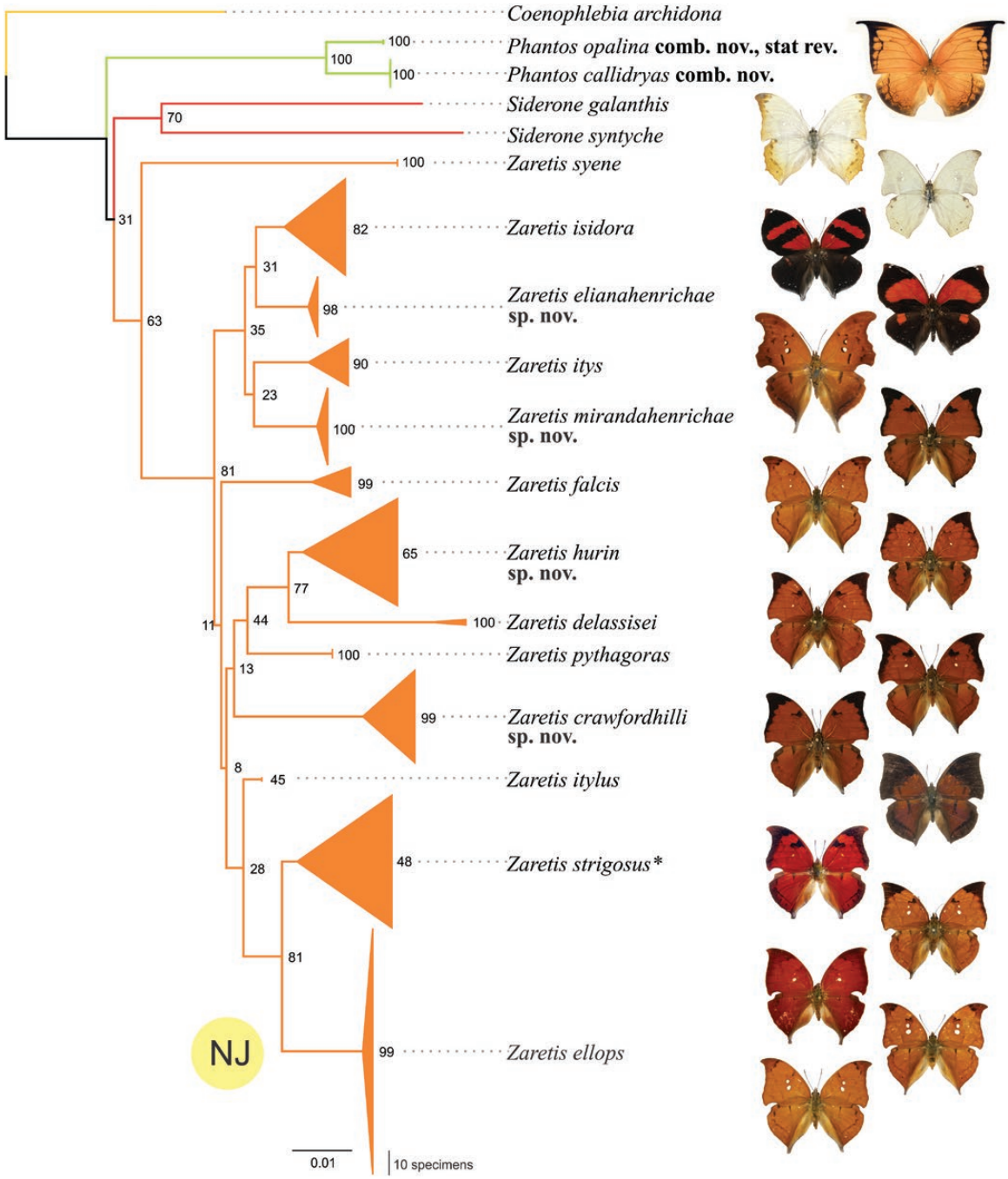

Figure 1. Neighbor-joining (NJ) tree based on 396 *COI* 'barcode' sequences of specimens of *Coenophlebia* C. Felder & R. Felder, 1862 (yellow), ***Phantos*** Dias **gen. nov.** (green), *Siderone* Hübner, [1823] (red) and *Zaretis* Hübner, [1819] (orange). Numbers in the nodes indicate bootstrap support; horizontal scale bar indicates number of substitutions per site; vertical scale bar indicates the number of specimens analysed in each clade. *Includes two specimens morphologically identified as *Z. ellops* (Ménétriés, 1855).

although moderately supported in the ML analyses (BS = 85), was not recovered at all by the BI. However, *Z. itylus*, a distinctive and rather rare species occurring along the east coast of Brazil (Dias *et al.*, 2012), was represented by only two sequences extracted from old specimens, with about half the total length of the DNA barcode sequence of the *COI*.

Although the NJ, ML and BI analyses were not intended to infer the phylogeny in the present study, some relationships recovered in all or most of the

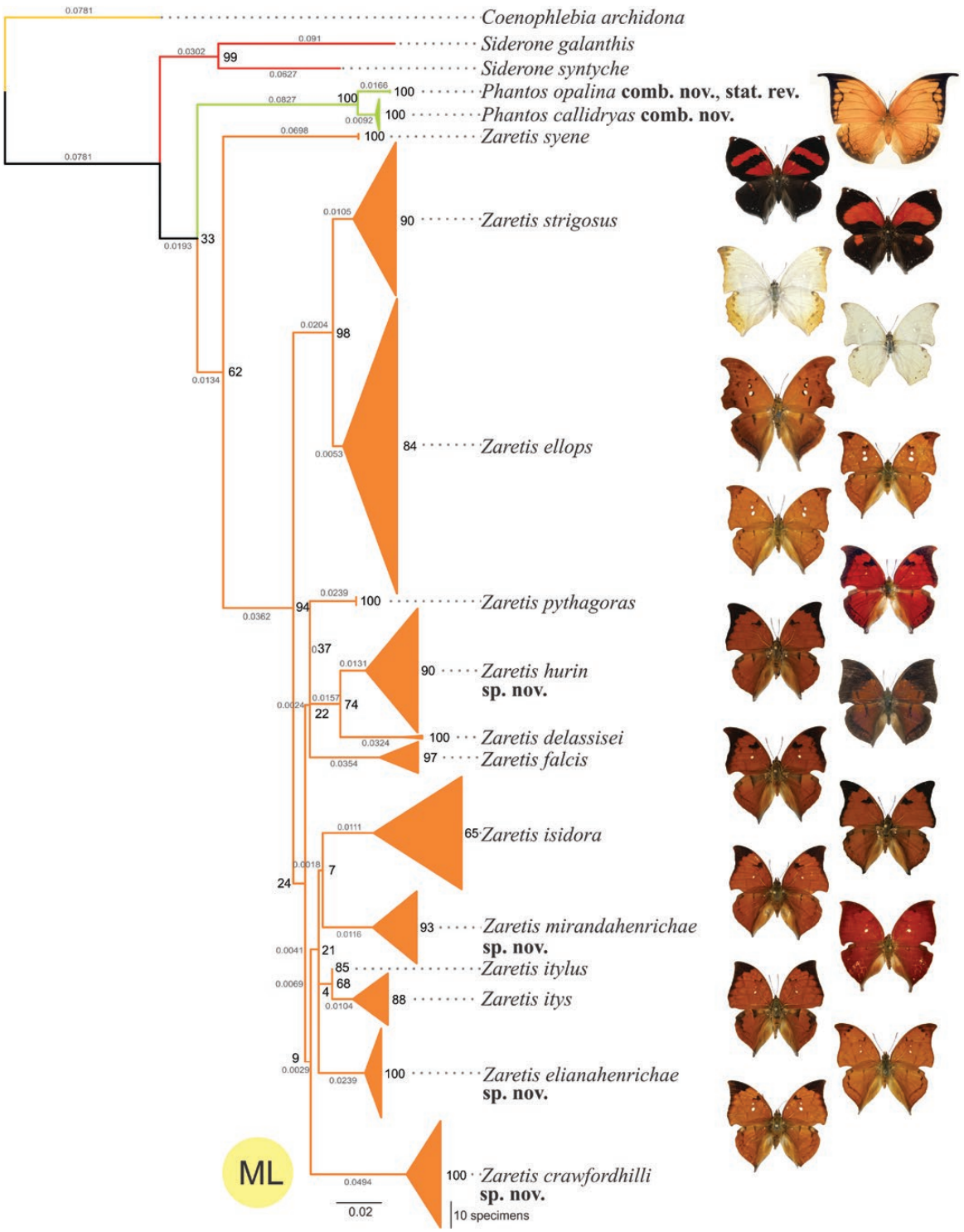

Figure 2. Maximum likelihood (ML) tree based on 396 *COI* 'barcode' sequences of specimens of *Coenophlebia* C. Felder & R. Felder, 1862 (yellow), ***Phantos*** Dias **gen. nov.** (green), *Siderone* Hübner, [1823] (red) and *Zaretis* Hübner, [1819] (orange). Numbers in the nodes indicate bootstrap support; numbers above branches indicate branch lengths; horizontal scale bar indicates number of substitutions per site; vertical scale bar indicates the number of specimens analysed in each clade.

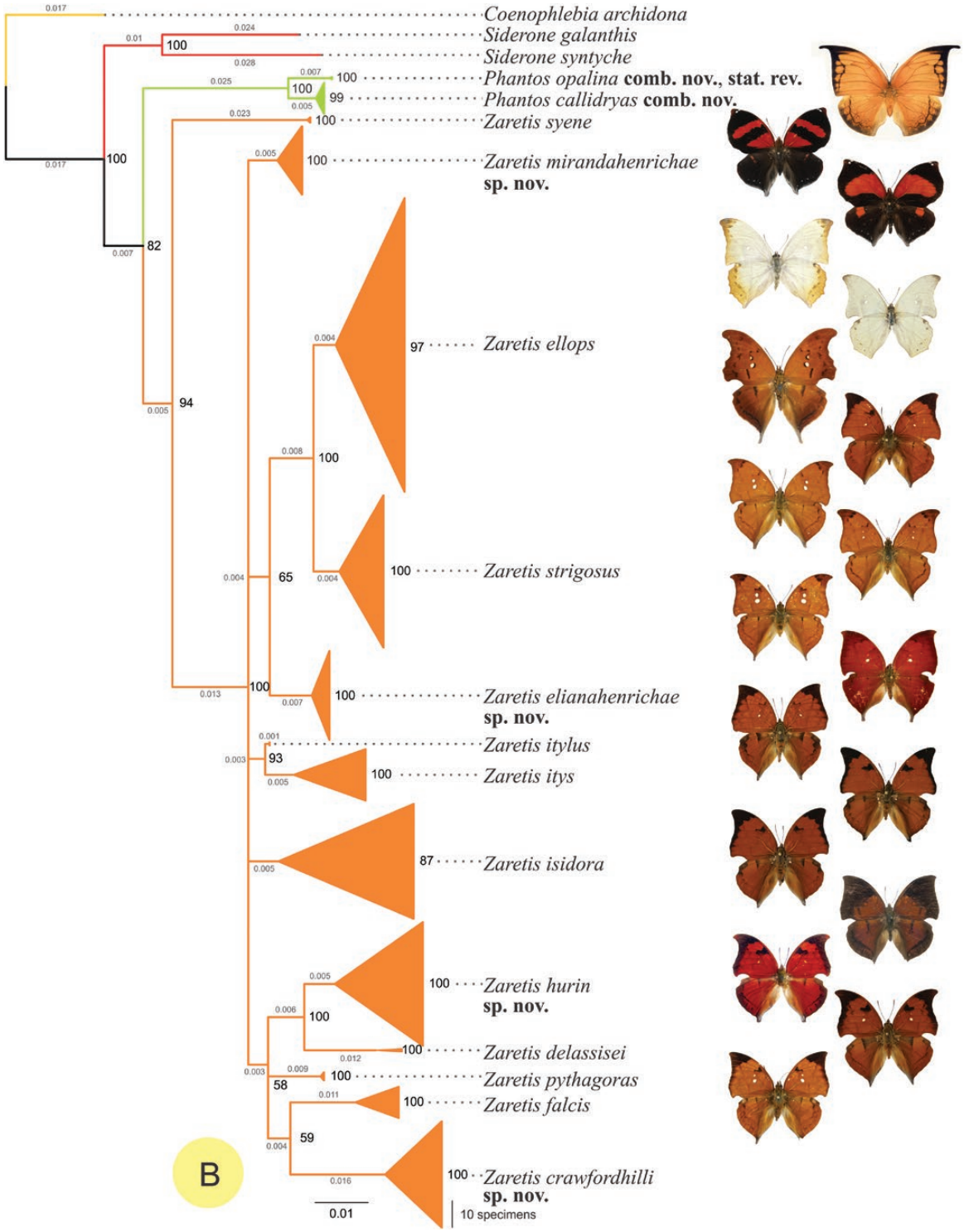

Figure 3. Bayesian inference (BI) tree based on 396 *COI* 'barcode' sequences of specimens of *Coenophlebia* C. Felder & R. Felder, 1862 (yellow), ***Phantos*** Dias **gen. nov.** (green), *Siderone* Hübner, [1823] (red) and *Zaretis* Hübner, [1819] (orange). Numbers in the nodes indicate posterior probabilities; numbers above branches indicate branch lengths; horizontal scale bar indicates number of substitutions per site; vertical scale bar indicates the number of specimens analysed in each clade.

analyses are presented and discussed. In the NJ analysis, the two species included here in *Phantos* gen. nov. were recovered as a monophyletic clade sister to *Siderone* + *Zaretis*. A parallel study conducted on the molecular phylogeny of the Anaeini (Toussaint *et al.*, in preparation) with four additional molecular markers also recovered a similar result, and here, in the single-locus ML and BI analyses, the new genus was recovered as a monophyletic clade sister to *Zaretis*. *Zaretis syene* was always recovered as sister to the remainder of the species of *Zaretis*, with strong support in the BI analysis (PP = 94). The clade *Z. ellops* + *Z. strigosus* was recovered in all analyses with strong support (NJ, BS = 81; ML, BS = 98; BI, PP = 100), a relationship that is supported by the morphology of both the male and the female genitalia (see below). *Zaretis strigosus* was formerly synonymized with *Z. isidora* (Lamas, 2004; Willmott & Hall, 2004), although it was later informally resurrected by a number of authors in faunistic studies (see Dias *et al.*, 2015). The clade *Z. hurin* sp. nov. + *Z. delassisei* was also strongly supported in all analyses (NJ, BS = 77; ML, BS = 74; BI, PP = 100), usually related to *Z. pythagoras*, *Z. falcis* and/or *Z. crawfordhilli* sp. nov. *Zaretis itys* was recovered as sister to *Z. itylus* in the ML analysis, but not in the BI analysis, probably because of the above cited shortcomings; these two species were formerly considered conspecific (Lamas, 2004; Willmott & Hall, 2004), probably owing to the similarity between females.

The PTP analysis models speciation or branching events in terms of the number of substitutions, using a clustering algorithm applied to single-locus sequences (Zhang *et al.*, 2013). Therefore, the entities output by PTP are, in theory, species under the phylogenetic species concept. This analysis recovered nearly all putative species that were recovered as monophyletic by the NJ, ML and BI analyses. Yet, the analysis indicated the existence of two more species: *Z. hurin* sp. nov. and *Z. ellops* were each split into two species, both clustering morphologically similar specimens from Andean and western Amazon areas as one species (represented by three and two specimens in the analysis, respectively) and the remaining specimens as another species (highlighted terminals in Supporting Information, Appendices S3–S5). Although in the tree above the specimens of *Z. hurin* sp. nov. always grouped with their conspecific specimens in all other analyses, the relationships between the clade formed by the two specimens of *Z. ellops* and other specimens varied across methods (see above and Supporting Information, Appendices S3–S5). These results might indicate the existence of additional unrecognized taxa or some restriction to the gene flow between populations occurring in these particular areas and the remainder of their populations.

In the PhyloMap visualization of the PTP results (Fig. 4), each circle in the plot represents a specimen, and clusters of different colours represent different species. The original topology recovered by the ML analysis is given by the lines connecting the clusters, although greatly distorted. Thicker lines indicate that the branch length in the original ML tree was longer than the branch in the PhyloMap visualization, revealing the true longer branch lengths leading to *C. archidona*, species of *Siderone* and *Z. syene*. Each axis explains a certain amount of variance in the data set: the horizontal axis represents 28.31% and the vertical, 26.27%. Normally, one axis separates outgroup taxa from other related taxa (Zhang *et al.*, 2011). Here, species of *Coenophlebia*, *Siderone*, *P. callidryas* comb. nov. and *P. opalina* stat. rev., comb. nov. are removed to the top of the plot. This result further corroborates the description of a new genus for the latter two species. The position of *Z. syene* also indicates relatively greater molecular divergence consistent with its phenotypic distinctiveness in comparison to other species of *Zaretis*. On the horizontal axis, two noticeable clusters are clearly recognizable, one smaller cluster including *Z. ellops* and *Z. strigosus*, and another large cluster including the remaining species of *Zaretis*. However, in this type of visualization the neighbouring taxa in the PCoA might not appear close to each other, and their true distances should be measured by the length and thickness of the branches connecting those taxa (Zhang *et al.*, 2011).

TAXONOMY OF *ZARETIS* AND *PHANTOS* GEN. NOV.

ZARETIS HÜBNER, [1819]

(FIGS 5–21; SUPPORTING INFORMATION, APPENDIX S6)

Type species: *Papilio isidora* Cramer, 1779 by subsequent designation (Scudder, 1875).

Diagnosis

Zaretis are brushfoot (Nymphalidae) leafwings (Charaxinae), and therefore are butterflies with reduced forelegs and sclerotized parapatagia. The tribe Anaeini, in which *Zaretis* is placed, currently does not have any clearly defined synapomorphies. Yet, species of *Zaretis* can be distinguished from the Preponini, and most species of related Anaeini genera, by the characteristic underside wing pattern resembling dead leaves, labial palpus (Reuter, 1896; Rydon, 1971), wing venation (Röber, 1892; Comstock, 1961; Rydon, 1971), male genitalia (Mielke, Mielke & Casagrande, 2004), and a number of other characters of the immature stages (e.g. Rydon, 1971; Dias, Casagrande & Mielke, 2010). Many of these characters are shared with species of *Coenophlebia* (whose immature stages are unknown), *Siderone* and *Phantos* gen

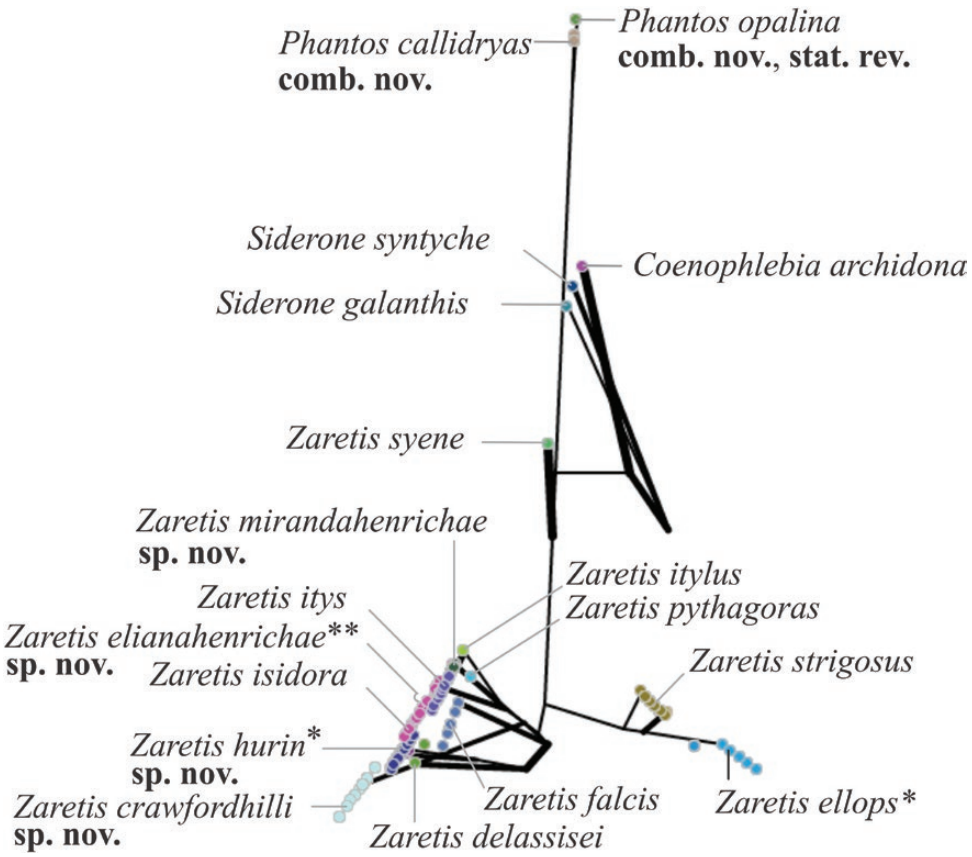

Figure 4. Phylomap visualization of the Poisson-tree-processes (PTP) molecular species delimitation result based on 396 *COI* 'barcode' sequences of specimens of *Coenophlebia* C. Felder & R. Felder, 1862, ***Phantos*** Dias **gen. nov.**, *Siderone* Hübner, [1823] and *Zaretis* Hübner, [1819]. Specimens (circles) of the same species are coloured alike. See text for further details. *Recovered as two distinct species. **Concealed by circles of other species.

nov. However, species of *Zaretis* can be distinguished easily from *Coenophlebia*, represented by *C. archidona*, by the presence of deep emarginations in the inner margin near the tornus of the forewing (FW) and between Sc+R and M_1 of the hindwing (HW), and a developed tornal projection at 2A on the HW. Additionally, in *C. archidona*, M_1 and M_2 arise from a common stalk, but separately from the discal cell in species of *Zaretis*, *Siderone* and *Phantos* gen. nov.

Zaretis can be distinguished from *Siderone* and *Phantos* gen. nov. by the wing shape, colour and pattern, which is variable, but always ranges from pale yellow to reddish brown in both wings, with reddish brown to dark brown markings on the upperside, and the male genitalia, with a conspicuous projection between the costa and the harpe (except for *Z. syene*, in which this projection is reduced and similar to species of *Siderone* and *Phantos* gen. nov.).

Zaretis can be distinguished from *Siderone* chiefly by the wing shape, colour and pattern. The wings are never as rounded at the outer margin or bear black with scarlet red bands or markings in species of *Zaretis* as in *Siderone*. *Zaretis* also has FW vein R_4 ending at the costal margin before the apex, marked sexual dimorphism, the head capsule scoli of the larvae lacking protrusions, and pupae without lateral indentations.

Zaretis can be distinguished from *Phantos* gen. nov. by the stronger development of the thorax, the wing colour and pattern, with the wings never being pearly white or yellowish white on the wing upper side, by R_1, R_2 and R_3 running free to the costal margin of the FW, by the presence of a marked discal spot (element 'e') on the forewing dorsum (FWD), the absence of projections at M_3 beyond the external margin of the HW in both sexes, the stronger development of the tornal projection at 2A, and by the relative size and shape of the head capsule scoli of the larvae, which are straight and of the same size or shorter than the height of the head capsule. A key to species of *Zaretis* is presented below.

Redescription

Head: Eyes reddish brown and naked (Fig. 6A); labial palpus creamy white ventrally, pale orange to reddish brown dorsally and at the tip (Figs 5D,

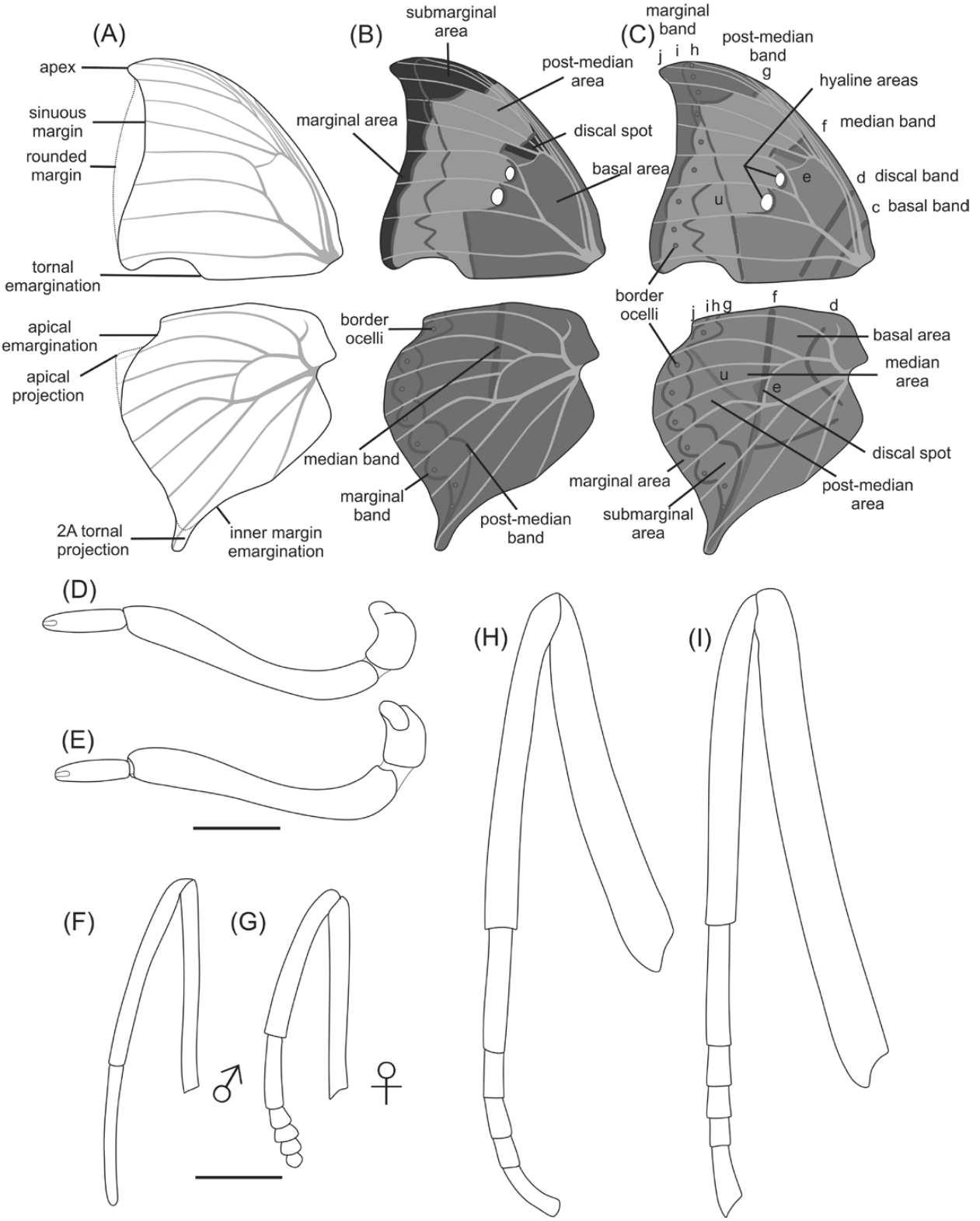

Figure 5. Labial palpus and thoracic appendages of *Zaretis* Hübner, [1819]; morphology and terminology. A–C, wings. A, venation. B, C, colour pattern. B, upperside. C, underside. D, E, labial palpus. D, inner surface. E, outer surface. F, G, foreleg, lateral. F, male. G, female. H, mid-legs, lateral. I, hindlegs, lateral. Scale bars represent 1 mm.

Figure 6. Head and thoracic appendices *Zaretis* Hübner, [1819]. A, head and labial palpus, ventral. B, C, labial palpus. B, outer. C, inner. D, E, foreleg, lateral. D, male. E, female.

E, 6A–C); antennal length about one-third of the forewing length, segments dark brown with some ventral creamy white scaling; club slender and elongated, tips usually lighter. Female as in male, but usually lighter in colour, pale yellow to reddish brown, depending on the species.

Thorax: Dorsally pale orange to reddish brown with scattered brownish and greenish scaling; ventrally pale orange to dark brown, with area between legs creamy white; forelegs with creamy white scales in the tarsus (Figs 5F, G, 6D, E); mid- and hindleg femora, tibiae and tarsi and creamy white speckled with pale orange to dark brown scales, respectively (Fig. 5H, I). Female as in male, but usually lighter in colour, pale yellow to reddish brown, depending on the species.

Wing size and shape (Fig. 5A): Forewing length 2.4–4.6 cm. Forewing costal margin convex; apex usually pointed, rounded in one species, slightly to strongly falcate; outer margin usually sinuous, but almost straight or rounded in some species, smooth to crenulated; inner margin straight, emargination before tornus slightly to strongly developed. Hindwing with emargination at Sc–Rs, outer margin rounded, smooth to crenulated, with a long and rounded projection at 2A; inner margin slightly emarginated near the tornus. Female larger than male, and wing shape usually different; outer margin usually straighter or rounder, depending on the species; emargination before tornus always developed; hindwing proportionately larger than male; emargination at Sc–Rs always developed; apex always projected at Rs; outer margin usually straighter than male; inner margin moderately to strongly emarginated near the tornus.

Wing colour and pattern, upper side (Fig. 5B): Ground colour of both wings beige to reddish brown with light to dark brown markings, fore- and hindwings usually of similar ground colour, but of different colours in some species. Forewing usually with three distinct bands, formed by light brown to dark brown continuous or interrupted markings: a median band, formed by the discal spot (element 'e') and the distal band of the central symmetry system (element 'f'); a post-median band, formed by the proximal band of the border symmetry system (element 'g'); and a marginal band, formed by the parafocal element (element 'i'). Even when the median band is absent, the discal spot is always present, light to dark brown in colour. The border ocelli and the submarginal and marginal bands (elements 'h', 'i' and 'j') are either indistinct or coalesced with the parafocal element. These three bands delimit four distinct areas of the forewing upperside: the basal area, from the base of the wing to the median line; the post-median area, from the median band to the post-median band; the submarginal area, from the post-median band to the submarginal band; and the marginal area, from the submarginal band to the outer margin. Marginal area is usually darker than other areas, from light to dark brown, similar in colour to the colour of the discal spot; submarginal area, when distinct, of the same colour as the post-median band posterior to M_2, along the outer margin, and coalesced with the marginal band distal to M_2, near the apex; intraspecifically variable presence of hyaline areas (although they occur more frequently in some species than others) in M_3–CuA_1 and CuA_1–CuA_2 on or immediately anterior to the median band. Hindwing usually with three distinct bands, similar to those on the forewing. However, in

the hindwing the median band runs only to the discal cell, and the discal spot is reduced or absent; the post-median and submarginal bands run almost regularly along the outer margin to the tornal projection at 2A, frequently with rudimentary border ocelli (element 'h') between them; anal fold usually lighter in colour, from pale beige to reddish brown; tornal projection at 2A usually darker, with creamy white scales. The hindwing upperside areas are delimited by the bands of the hindwing underside in five distinct areas, described below: basal, median, post-median, submarginal and marginal areas. Long and thin scales of the same colour of the background, in the discal cell, at the base of CuA_1–CuA_2, and throughout the length of 2A and 3A. Female with bands and areas of both wings as in male, but frequently different in colour, usually lighter.

Wing colour and pattern, underside (Fig. 5C): Ground colour of both wings beige to reddish brown, with random speckles of scales lighter and darker than the ground colour ('ripple pattern'), usually resembling a skeletonized dead leaf. Forewing pattern of bands and areas similar to the upper side, but with two additional faint bands, formed by light brown to dark brown scales darker than the ground colour: a basal band, formed by part of the central symmetry system (element 'c'); and a discal band, formed by the proximal band of the basal symmetry system (element 'd'). The umbra connects the median band to the post-median band at CuA_1–CuA_2, forming a continuous line similar to the midrib of a dead leaf. Hindwing pattern of bands and areas are similar to the upperside, but with an additional faint band, the discal band, formed by the proximal band of the basal symmetry system (element 'd'), as in the forewing. Anterior part of the median band and posterior part of the umbra form a continuous line similar to the midrib of a dead leaf; the anterior part of the umbra, the posterior part of the median band and the post-median band complete the masquerade. Part of the median band posterior to CuA_2 and marginal band are usually not as developed as the others; border ocelli rudimentary, dark brown and surrounded by creamy white scales; apical ocelli usually as scattered creamy white scales. Hindwing with five distinct areas: the basal area, from the base of the wing to the continuous line formed by the medial band and the umbra; the median area, from the medial band to the umbra; the post-median area, from the umbra to the post-median band; the submarginal area, from the post-median band to the marginal band; and the marginal area, from the marginal band to the outer marigin. Female bands and areas of both wings are as in the male, but frequently different in colour, usually lighter.

Abdomen: Dorsally uniform pale orange to reddish brown; ventrally uniform light brown to reddish brown. Female as in male, but lighter in colour, dorsally pale yellow to reddish orange, ventrally beige to reddish brown, depending on the species.

Male genitalia (Fig. 15A–L): Tegumen trapezoidal in lateral view, dorsally wider and humped posteriad, strongly attached to the uncus, and attached to the gnathos only by membranes; appendix angularis hooked; saccus short, not projected anteriorly; dorsal projection of the saccus 'C' shaped and projected dorsad at a right angle. Uncus semitubular, almost straight or slightly curved, with a well-developed median dorsal ridge and distally hooked, usually with a distal callus; gnathos laterally slightly curved, dorsally thin or wide, produced ventrad, arms parallel, with ventral part of the gnathos bar shaped and fused medially; valva externally covered with short setae, costa long and curved, developed anteriad, two projections of varying shapes and development, one between the costa and the harpe, and another at the end of the harpe, sacculus triangular, ampulla developed and rounded; aedeagus varying slightly in length and width, cylindrical and bifid distally, without cornuti; manica inserted slightly anterior to the half of the aedeagus; fultura inferior thin, bar shaped.

Female genitalia (Figs 16A–L, 17A–J): Tergum VIII triangular, ventrally attached to the sides of the lamella postvaginalis and dorsally to the lamella antevaginalis by a varying sclerotized loop; papilla analis round and with short setae, projecting the apophysis posterioris; lamella antevaginalis assymetrical and variable, connected to the sides of the lamella postvaginalis by projections of varying sclerotization; lamella antevaginalis left side usually larger than the right; lamella postvaginalis varying in width and length; posterior edge of the lamella postvaginalis straight, rounded, smooth, bilobed or medially indented; seminal duct close to the base of the ductus bursae; corpus bursae rounded or laterally compressed, half the length or shorter than the ductus bursae, bearing two parallel signa; these are thin and long, formed by minute sclerotized bumps.

Immature stages (Fig. 18): All species with known immature stages (namely, *Z. strigosus*, *Z. ellops*, *Z. crawfordhilli* sp. nov., *Z. mirandahenrichae* Dias sp. nov. and *Z. elianahenrichae* Dias sp. nov.) are similar to those recently described by Dias *et al.* (2015) (Müller, 1886; Muyshondt, 1973; Janzen & Hallwachs, 2017); host plants are mostly in the Salicaceae, chiefly on species of *Casearia*, but also on species of *Laetia*, *Ryania*, *Xylosma* and *Zuelania* (Beccaloni *et al.*, 2008; Dias *et al.*, 2015; Janzen & Hallwachs, 2017); records for species of *Zaretis* on Rhamnaceae and Piperaceae are doubtful and need confirmation (Beccaloni *et al.*, 2008).

Discussion

Zaretis was erected by Hübner ([1819]) to include *Papilio isidora* Cramer, 1779 and the Indo-australian nymphaline species *Papilio polibete* Cramer, 1779. Inexplicably, Hübner ([1819]), placed *Papilio itys* Cramer, 1777 in *Apatura* (Hübner, [1819]). The type species of the genus, *P. isidora* Cramer, 1779, was subsequently designated by Scudder (1875). Early authors combined and described species currently in *Zaretis* in *Papilio* (sometimes in the sections 'Danaus', 'Festivus' and 'Nobilis' of the Linnean system), *Nymphalis* (once in the section 'Gemmatus' of the Linnean system) and *Paphia*, as a genus or as a subgenus of *Maniola*. However, in the middle of the 19th century, several authors, recognizing the similarities between species in *Zaretis* and *Siderone*, regarded the former as synonymous with the latter, an arrangement preferred by some authors to the present day (e.g. Brévignon, 2006). Nevertheless, *Zaretis* (Hübner, [1819]) has priority over *Siderone* (Hübner, [1823]). The misspelling *Zaretes* [sic], probably introduced by Röber (1892), was widely adopted in the late 19th and beginning of the 20th century by several authors who were unaware of the name *Zaretis* or who did not agree with the synonymization of *Zaretis* with *Siderone*. Although others (e.g. Scudder, 1875) had already noted the misspelling, the correct spelling was widely adopted after the catalogue by Stichel (1939). Comstock (1961), in his revision of species currently in Anaeini, regarded *Zaretis* as a subgenus of *Anaea*. However, this arrangement was never popular, and later authors tended to lump all species of Anaeini in *Anaea* or, more frequently, regarded each one of Comstock's (1961) subgenera as genera. The latter view was strongly backed up by the most comprehensive taxonomic study of the Charaxinae to date, by Rydon (1971), and it is currently the most widely accepted arrangement (e.g. Lamas, 2004; Willmott & Hall, 2004). From early on, the species included here in *Phantos* gen. nov. were kept apart from species currently in *Zaretis* by many authors, most notably Röber (1916) and Stichel (1939), who retained them in *Anaea* owing to their distinctiveness.

Zaretis is currently placed in Anaeini (Lamas, 2004), but adults and immature stages are different from most of the genera included in that tribe. Even though the monophyly of Anaeini is contested by some authors (e.g. Rydon, 1971; Pyrcz & Neild, 1996), the tribe is usually treated as monophyletic (e.g. Comstock, 1961; DeVries, 1987; Lamas, 2004), despite the lack of unambiguous synapomorphies. Species of *Zaretis*, *Siderone*, *Coenophlebia* and *Phantos* gen. nov. share several common and distinct characters (particularly in the immature stages). Therefore, Rydon (1971) erected the taxon 'Zaretidinae' (i.e. Zaretidini), following the lead of previous authors (e.g. Röber, 1892; Reuter, 1896) in considering species of the above genera 'transitional' between Preponini and Anaeini. Rydon's (1971) 'Zaretidinae' is most likely to be monophyletic, although probably sister to the remainder of Anaeini (Wahlberg *et al.*, 2009).

Distribution

Neotropical, in forest habitats from Mexico to Argentina, except most of the Antilles (occurring only on the island of Trinidad) and Chile, from sea level to 2200 m (Figs 19–21). Of the 12 species included, five are Trans-Andean, three are widespread in Central America and Trans-Andean South America, and two occur on the western slopes of the Andes. One is restricted to middle elevations of the Andes, and the remaining six species occur in Cis-Andean South America. Of these, one is widespread in all suitable habitats, two occur exclusively in the Amazon basin and eastern slopes of the Andes, two occur in other South American forests further from the Amazon basin, and one is restricted to dense ombrophilous forests on the southeastern coast of Brazil.

ZARETIS ITYS (CRAMER, 1777)

(FIGS 7A–D, 15A, 16A,B, 19; SUPPORTING INFORMATION, APPENDIX S6)

Type material

Female lectotype of *Papilio itys* Cramer, 1777 with the following labels: / Surinam[e] Coll[ection] [C. van] Len[n]ep/ Felder Coll[ection]/ Lectotype/ B.M.TYPE No. Rh 17307/ *Papilio itys* Cramer det. R. I. Vane-Wright 1972 LECTOTYPE #f/ (NHMUK).

Diagnosis

Zaretis itys, as with most species of the genus, is somewhat variable, but more-or-less distinctive. The species was recently redescribed and diagnosed by Dias *et al.* (2012), but that diagnosis focused on a comparison with one of the most similar species, *Z. itylus*, which is not sympatric with *Z. itys*. *Zaretis itys* is sympatric with *Z. isidora*, *Z. strigosus*, *Z. hurin* sp. nov. and *Z. falcis* in the Amazon basin and the Guianas. Males (Fig. 7A, B) can be distinguished from the above species by the less-developed emargination of the inner margin at the forewing tornus. Females (Fig. 7C, D) can be distinguished by the shape of the FW, with the outer margin always smooth and rounded, slightly falcate at the apex, and by the contrasting colour and pattern.

Discussion

Papilio itys Cramer, 1777 was the first taxon associated with *Zaretis* to be described and, therefore, is the preferred name for authors who follow a very conservative line and treat all other available names applied to *Zaretis*, with the exception of *Z. syene* and *P. callidryas* comb. nov., as junior subjective synonyms (e.g. Comstock, 1961; Vane-Wright, 1975). This species was recently circumscribed

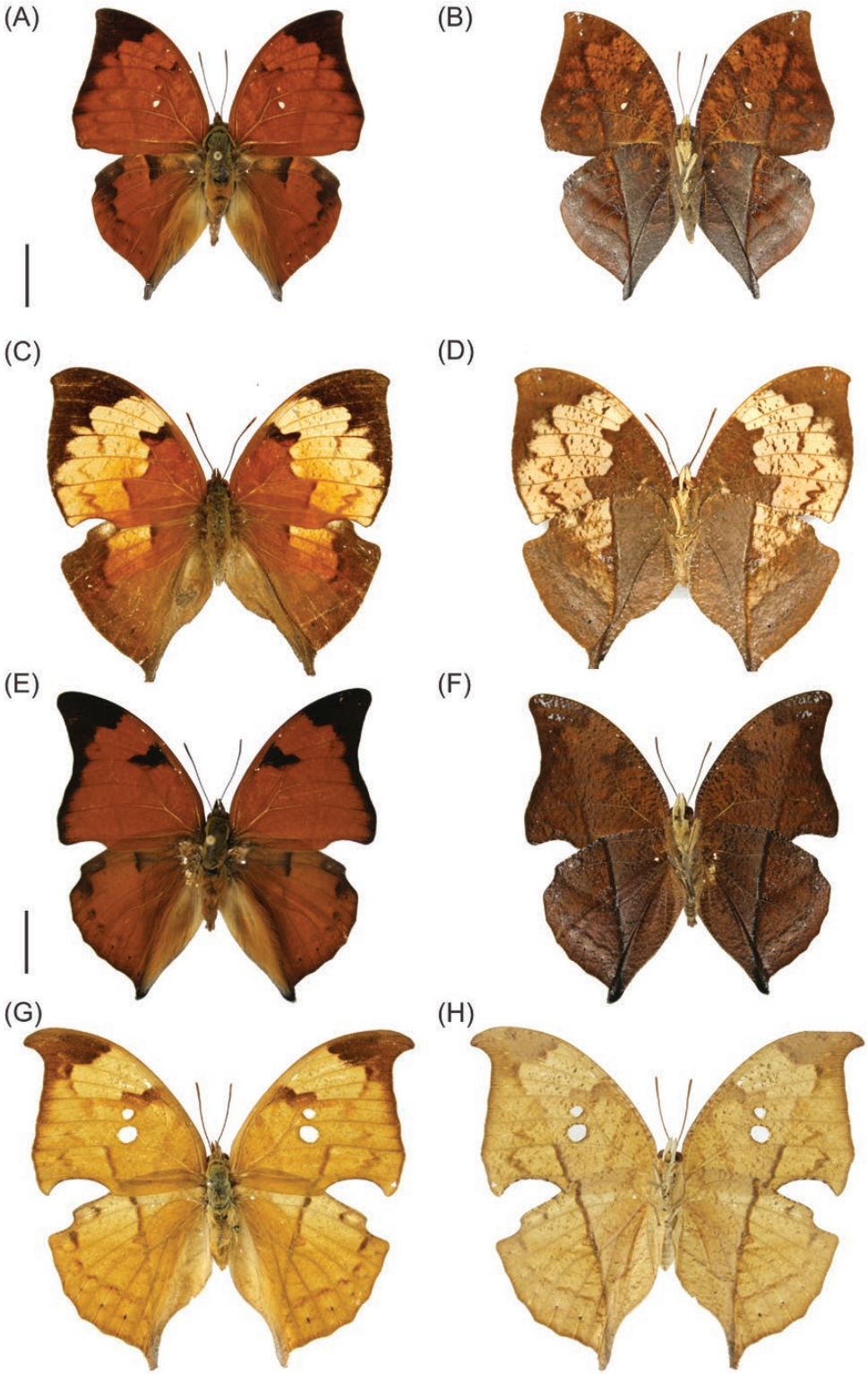

Figure 7. Imagoes of species of *Zaretis* Hübner, [1819], dorsal and ventral. A–D, *Z. itys* (Cramer, [1777]). A, B, male. C, D, female. E–H, *Z. isidora* (Cramer, [1779]). E, F, male. G, H, female. Scale bars represent 1 cm.

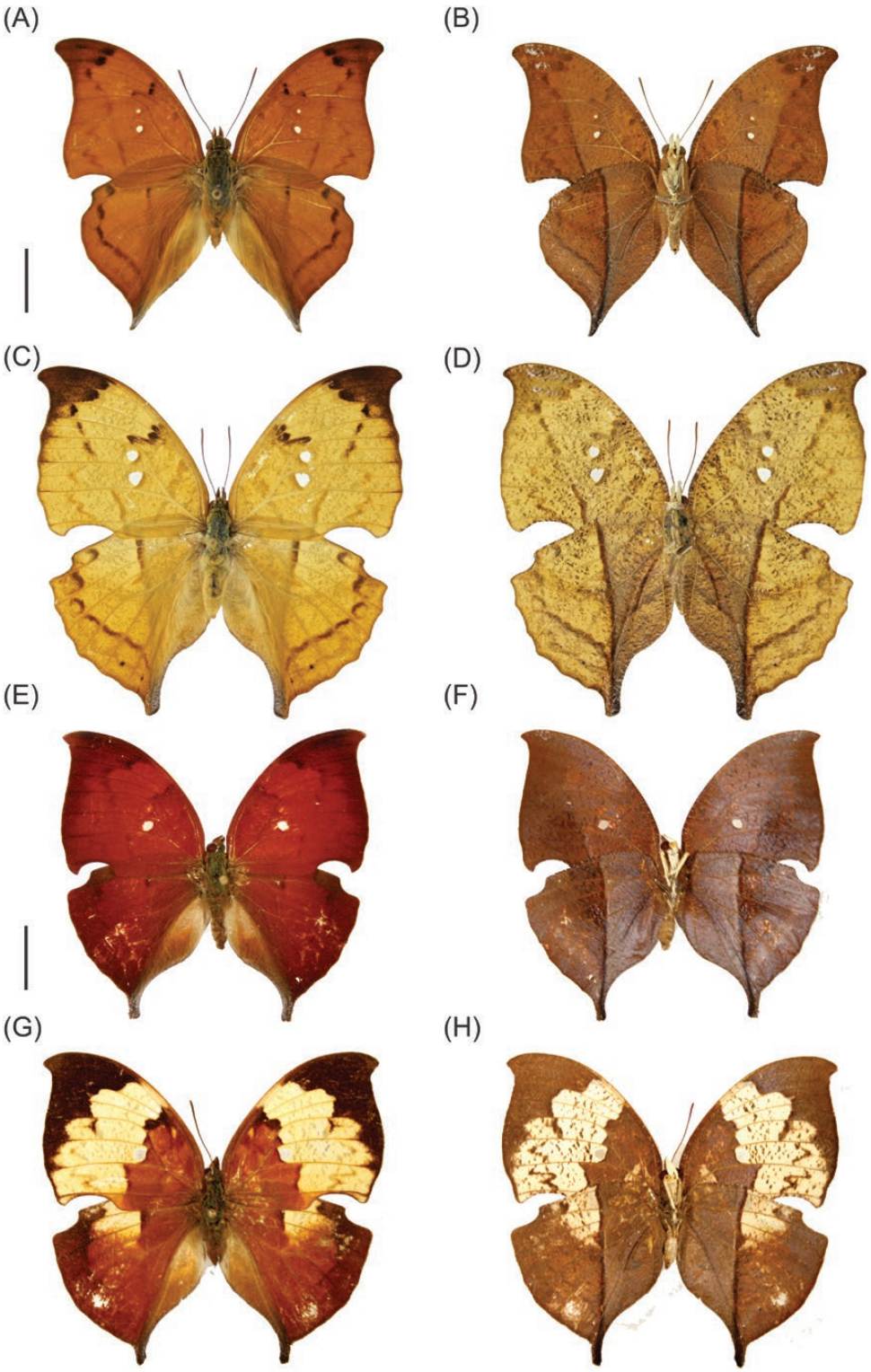

Figure 8. Imagoes of species of *Zaretis* Hübner, [1819], dorsal and ventral. A–D, *Z. strigosus* (Gmelin, [1790]). A, B, male. C, D, female. E–H, *Z. itylus* (Westwood, 1850). E, F, male. G, H, female. Scale bars represent 1 cm.

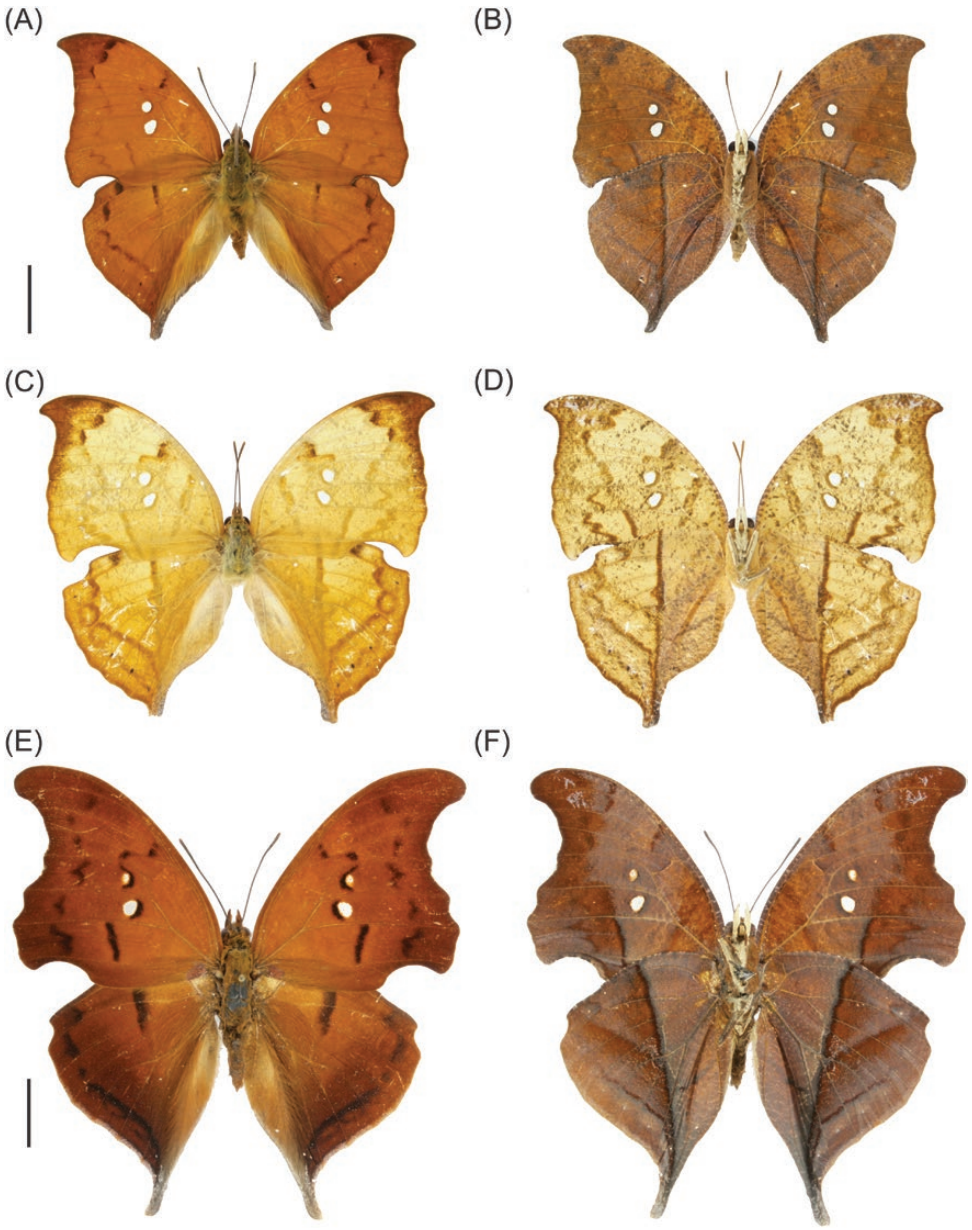

Figure 9. Imagoes of species of *Zaretis* Hübner, [1819], dorsal and ventral. A–D, *Z. ellops* (Ménétriés, 1855). A, B, male. C, D, female. E, F, *Z. syene* (Hewitson, 1856), male. Scale bars represent 1 cm.

and discussed by Dias *et al.* (2012), recognizing *Z. itys* as a distinctive species of Amazonian distribution with distinctive characters. The species was described based on an unstated number of female specimens from Suriname. A single female from Lennep's collection, source of many of Cramer's specimens from Suriname, compares closely with Cramer's original illustrations (Cramer, 1777: plate 119, fig. F, G). This specimen was designated as a lectotype of *P. itys* Cramer, 1777 by Vane-Wright (1975) when he was reviewing the butterflies named by Gmelin. This specimen is not in the NHMUK type collection; Vane-Wright (1975) and later Pyrcz & Neild (1996) affirmed that this specimen is deposited at the NHMUK in the Rothschild collection. Nevertheless, the lectotype, illustrated by Pyrcz & Neild (1996) and Warren *et al.* (2016), compares perfectly with female specimens of *Z. itys*, as recognized by Dias *et al.* (2012) and here.

Distribution

It is widespread in the Amazon basin and the Guianas, usually in low to mid-altitudes, occurring from about sea level to 1500 m on the eastern slopes of the Andes, in Bolivia, Brazil (Acre, Amazonas, Rondônia, Roraima, Mato Grosso, Mato Grosso do Sul, Pará), Colombia, Ecuador,

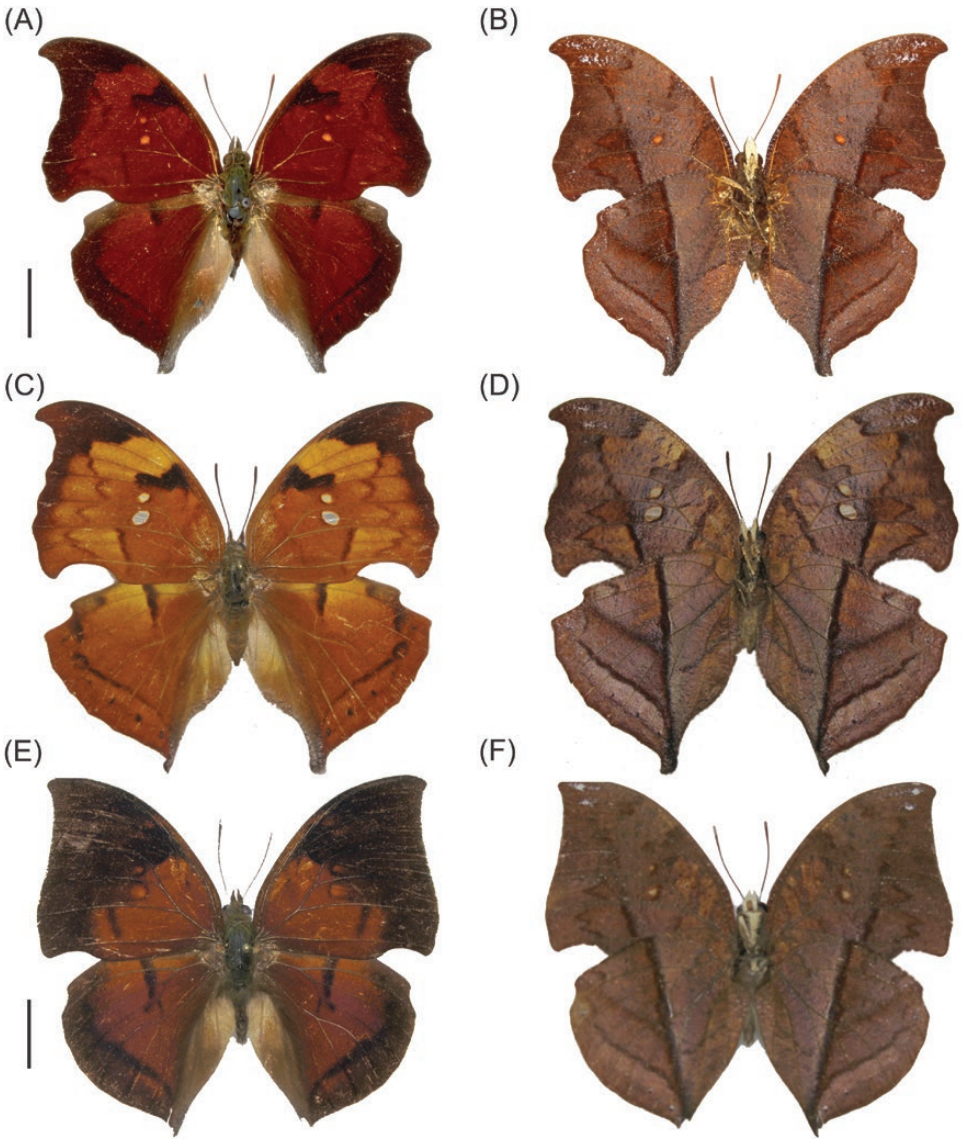

Figure 10. Imagoes of species of *Zaretis* Hübner, [1819], dorsal and ventral. A–D, *Z. pythagoras* Willmott & Hall, 2004. A, B, male. C, D, female. E, F, *Z. delassisei* Choimet, 2009, male. Scale bars represent 1 cm.

French Guiana, Guyana, Peru, Suriname and Venezuela (Fig. 19). It may occur in northwestern Argentina (i.e. Catamarca, Jujuy, Salta and Tucumán) and further south and east in Brazil (i.e. Goiás, Tocantins and Maranhão).

Examined material

See Supporting Information, Appendix S1.

ZARETIS ISIDORA (CRAMER, 1779)

(FIGS 7E–H, 15B, 16C, D, 20; SUPPORTING INFORMATION, APPENDIX S6)

Type material

Male lectotype of *Papilio isidora* Cramer, 1779, here designated, with the following labels: / N. 35 ISIDORA Cr[amer]. III.235.A.B.E.F/ Surinam[e] Coll[ection]. [C. van] Len[n]ep/ Felder Coll[ectio]n./ *Papilio isidora* Cramer det. R.I. Vane-Wright, 1972/? SYNTYPE #m/ (NHMUK).

Male holotype of *Siderone zethus* Westwood, 1850 with the following labels: /Type/ Para [Pará, Brazil]/ B.M. TYPE No. Rh.10379 *Siderone zethus*, #m Hew[itson]./ *Siderone zethus* Westwood det. R.I. Vane-Wright, 1972 HOLOTYPE #m/*zethus* Westwo[od] G[enera of]. D[iurnal]. L[epidoptera]. [volume] 5 [page] 321/ (NHMUK).

Male lectotype of *Siderone isidora* var. *cacica* Staudinger, 1887, here designated, with the following labels: /Origin / Chanchamayo[, Peru] Thamm [leg.]/ *cacica* Stgr.[Staudinger]/ *Sid*[*erone*]. spec[ies]. [illegible] ign[ota]./ (ZMHU).

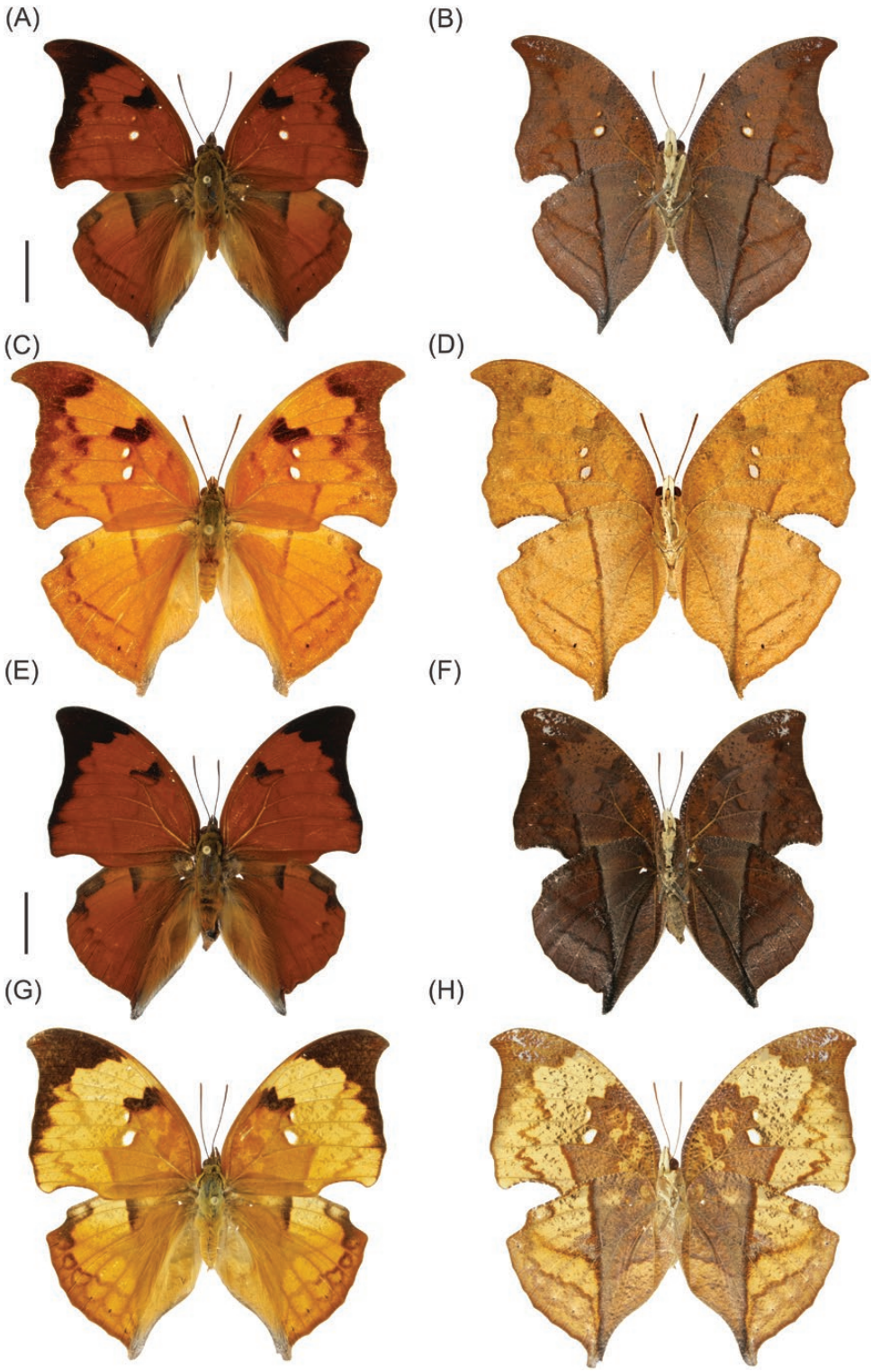

Figure 11. Imagoes of species of *Zaretis* Hübner, [1819], dorsal and ventral. A–D, *Z. falcis* Dias, Casagrande & Mielke, 2012. A, B, male. C, D, female. E–H, ***Z. hurin*** Dias **sp. nov.** E, F, male, paratype. G, H, female, paratype. Scale bars represent 1 cm.

Figure 12. Aberration of *Z. falcis* Dias, Casagrande & Mielke, 2012, male dorsal, from Óbidos, Pará, Brasil, deposited at the MNRJ. Scale bar represents 1 cm.

Zaretes [sic] *isidora isidora* f. *bisaltina* Fruhstorfer, 1909 does not have a formal type because it is an infrasubspecific entity. However, the specimen described by Fruhstorfer (1909b) is a female with the following labels: /Type / Type / SYN-TYPE/ Fruhstorfer Coll. B.M. 1987-285. /Obidos [Pará, Brazil] Amazonenstrom [Amazon river] VIII-IX [18]99 ex coll. H. Fruhstorfer/ *isidora* #f forma *bisaltina* Fruhst[orfer]./ (NHMUK).

Male lectotype of *Zaretes* [sic] *isidora leopoldina* Fruhstorfer, 1909, here designated, with the following labels: /Paratype / Fruhstorfer Coll. B.M. 1987-285. / Espírito Santo Brasil ex coll. Fruhstorfer/ *Zaretes* [*sic*] *isidora leopoldina* Fruh[storfer]. det. R.I. Vane-Wright, 1972 #m SYNTYPE./ leopoldina Fruhst[orfer]./ (NHMUK).

Zaretis itys itys forma *monops* Bryk, 1953 does not have a formal type because it is an infrasubspecific entity. However, the specimen described by Bryk (1953) is a male with the following labels: /*Zaretis itys itys* f[orm]a. *monops* m[ale] F. Bryk det. 194[blank]/ Sv. Amaz[on]. Exp[editon]. Roman/ Manáos [Manaus, Amazonas, Brazil]/ 24.nov[ember]/ (RMS).

The male holotype of *Siderone isidora naama* Brévignon, 2006 was not examined, but has the following label data: French Guiana, Saint-Georges de l'Oyapock, 13.IV.1984, Number 48 (Trap captured) (Bévignon, 2006) (LCB).

Diagnosis

Zaretis isidora, as with most species of the genus, is extremely variable and similar to its congeners. This species is sympatric with *Z. itys*, *Z. strigosus*, *Z. falcis* and *Z. hurin* sp. nov. in the Amazon basin and the Guianas, and with *Z. strigosus* and *Z. itylus* in Atlantic forests. Males (Fig. 7E, F) can be distinguished from *Z. itys* by the well-developed emargination of the inner margin at the FW tornus; from *Z. falcis* by the FW apex, which is considerably less falcate, and by the FW outer margin being less crenulated; from *Z. hurin* sp. nov. by the absence of a purplish sheen on the FWD of *Z. isidora* when viewed obliquely; from *Z. itylus* by the shape of the outer margin of the FW, which is sinuous, and HW not strongly emarginated in Sc–Rs and projected at Rs at the apex as in *Z. itylus*; and from *Z. strigosus* by the generally darker and more homogeneous coloration, with post-median and submarginal bands absent or weakly developed on both wings on the upperside. Owing to the extreme variation of males of *Z. isidora* and *Z. strigosus*, the identification of the males can be confirmed only by examining the genitalia; in *Z. isidora*, the uncus is longer, thinner and curved, with a distal callus, and the gnathos is not enlarged at the dorsal half (Fig. 15B). Females of *Z. isidora* (Fig. 7G, H) can be distinguished from females of *Z. itys* and *Z. itylus* by the shape of the outer margin of the FW, which is sinuous, and by the upperside of the wings' basal and post-median areas, never reddish brown and beige to pale yellow, as in *Z. itys* and *Z. itylus*, repectively; from *Z. falcis* by the FW apex, which is considerably less falcate, by the outer margin not being crenulated, and by the FW post-median band, which is usually weakly developed; from *Z. hurin* sp. nov. by the generally lighter coloration, especially at the wing base, and by the upperside of the wings bands being usually more weakly developed; and from *Z. strigosus* by the two-tone pattern of the wing underside, which is variably darker in the basal, submarginal area near the apex and marginal areas, in contrast to lighter post-median and submarginal areas along the outer margin. Nevertheless, owing to the extreme variation of females of *Z. isidora* and the latter two species, identification with respect to *Z. strigosus* can be confirmed only by the examination of the genitalia; in *Z. isidora*, the lamella postvaginalis is longer than wider, with the edge slightly indented medially (Fig. 16C, D); identification with respect to *Z. hurin* sp. nov. can be reliably confirmed only with molecular data, although there may be slight differences between the genitalia of the species.

Discussion

Zaretis isidora is the type species of the genus *Zaretis*, selected by subsequent designation by Scudder (1875). Therefore, the resolution of its taxonomic status is paramount. *Papilio isidora* Cramer, 1779 was described based on an unstated number of specimens from Suriname, known to be at least two, one male and one female [illustrated by Cramer (1779) in plate 235, fig. A, B, E, F]. Vane-Wright (1975) found two specimens, one male and one female, from

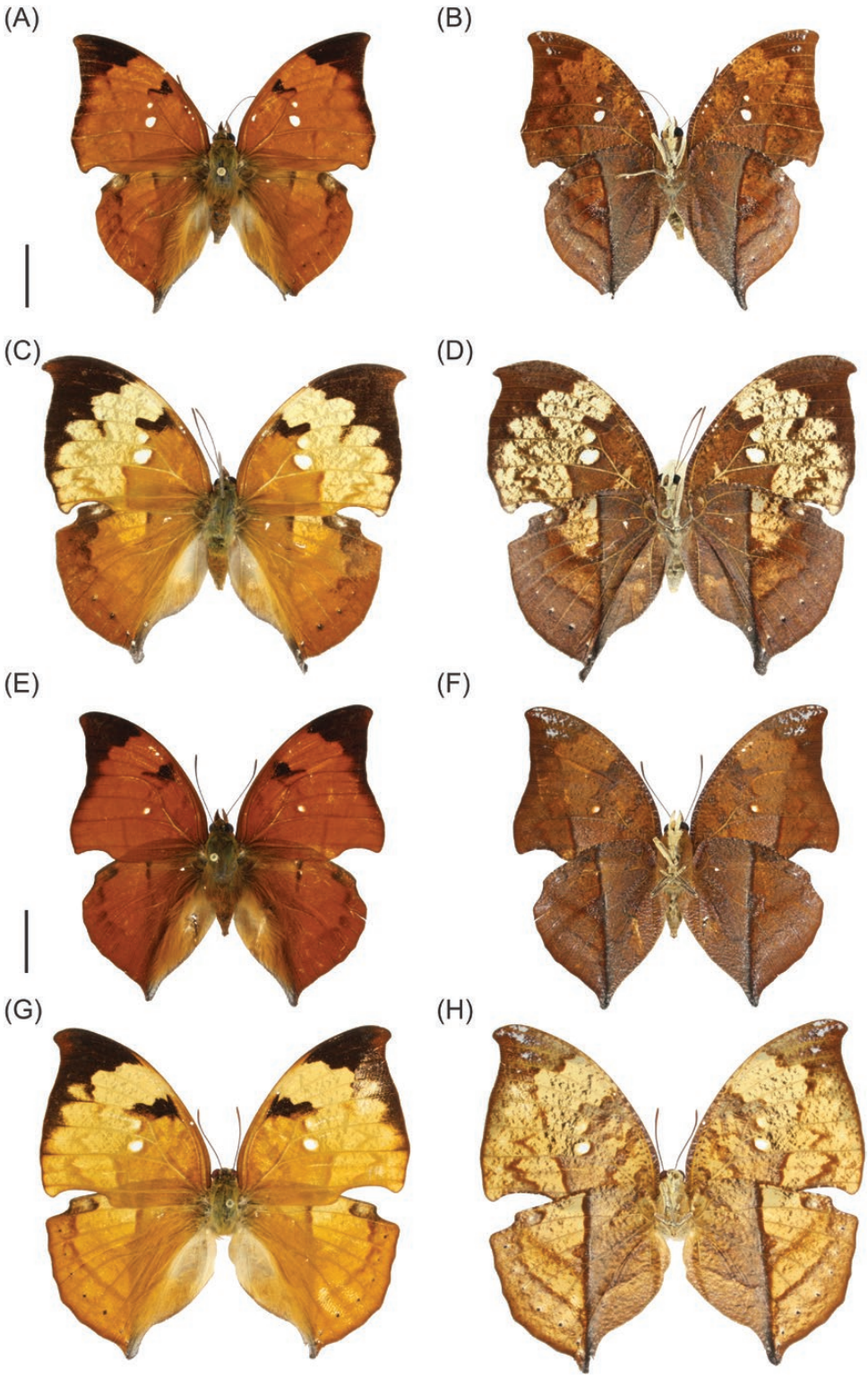

Figure 13. Imagoes of species of *Zaretis* Hübner, [1819], dorsal and ventral. A–D, ***Z. crawfordhilli*** Dias **sp. nov.** A, B, male, holotype. C, D, female, allotype. E–H, ***Z. mirandahenrichae*** Dias **sp. nov.** E, F, male, holotype. G, H, female, allotype. Scale bars represent 1 cm.

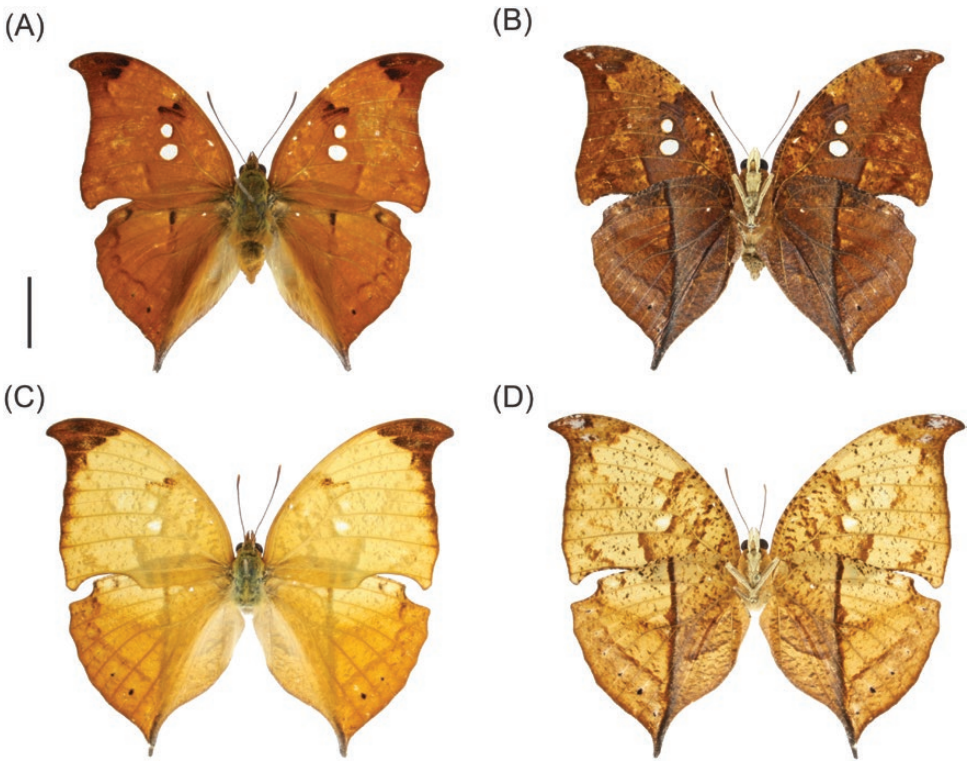

Figure 14. Imagoes of ***Zaretis elianahenrichae*** Dias **sp. nov.** A, B, male, holotype. C, D, female, allotype. Scale bar represents 1 cm.

Suriname similar to the illustrations, in the C. van Lennep collection at the NHMUK and labelled these specimens as potential syntypes ('?SYNTYPE'). Van Lennep's collection was the source of many of Cramer's specimens; his collection was later acquired by the Felders, then by Rothschild, and finally by the NHMUK. None of these specimens could be located by us in the type collection of the NHMUK, and they must be deposited in the main collection. However, the male specimen was illustrated by Pyrcz & Neild (1996) and Warren *et al.* (2016) and is closely comparable with Cramer's original illustrations and with specimens of *Z. isidora* from Suriname, the Guianas and the Amazon basin. Therefore, in the present study, this specimen is designated as the lectotype to reduce present and future taxonomic uncertainty. *Siderone zethus* Westwood, 1850 was described based on a single specimen from Pará, examined by Vane-Wright (1975) and illustrated by Warren *et al.* (2016). The phenotype of the holotype compares almost perfectly with specimens of *Z. isidora* from the Amazon basin and the Guianas, but with a rather falcate FW apex. This specimen is similar in this regard to the somewhat distinctive *Z. falcis*, but other characters of wing shape and coloration clearly identify it as *Z. isidora*.

Siderone isidora v. *cacica* Staudinger, 1887 was described based on a 'small number' of specimens from Chanchamayo, Peru (Staudinger, 1887). This name refers to the typical phenotype of *Z. isidora* from certain parts of Peru and Bolivia, with suffused reddish brown on the upperside submarginal area near the apex and marginal areas, and which is larger than typical *Z. isidora* from the Amazon basin. Five male syntypes with the Staudinger's typical pink 'Origin' label collected by Mr Thamm in Chanchamayo, Peru, were located at the ZMHU. Of these, only two agree with the species description, two are specimens of *Z. strigosus*, and one certainly is a mislabelled specimen of *Z. itylus*. Therefore, one of the specimens that agrees perfectly with the species description and was illustrated by Warren *et al.* (2016) is here designated as the lectotype.

Zaretes [sic] *isidora isidora* f. *bisaltina* Fruhstorfer, 1909 was described as a 'female form', denoting an infrasubspecific entity. Therefore, the name is invalid and without a formal type, but it corresponds to a distinct phenotype of females of *Z. isidora* from the lower Amazon river basin, with the anterior part of the post-median band, between M_3 and the costal margin, yellowish and separated from the rest of the post-marginal band by a dark brown bar, which connects the discal spot to the submarginal and marginal areas. Thus,

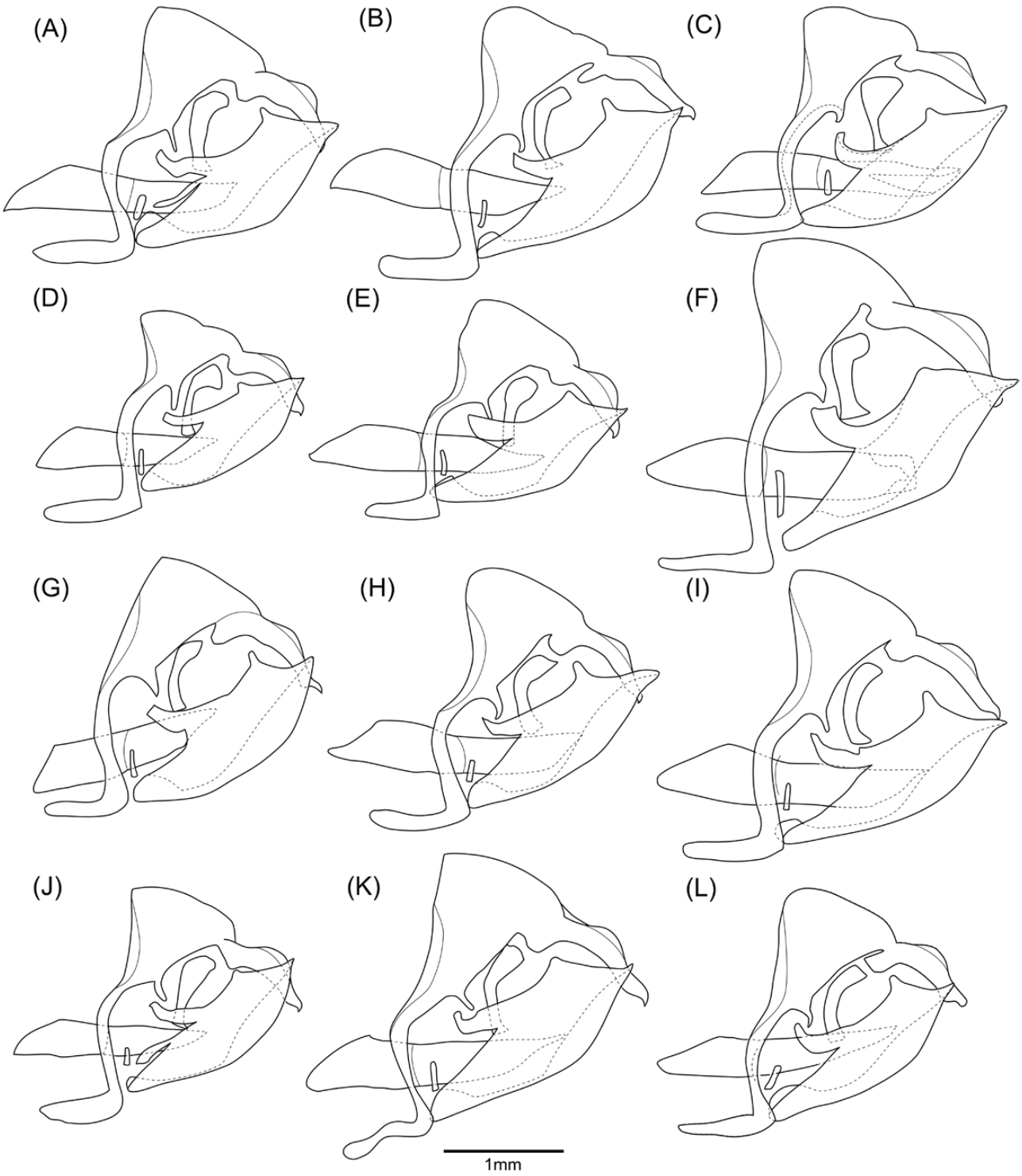

Figure 15. Male genitalia of species of *Zaretis* Hübner, [1819], lateral. A, *Z. itys* (Cramer, [1777]). B, *Z. isidora* (Cramer, [1779]). C, *Z. strigosus* (Gmelin, [1790]). D, *Z. itylus* (Westwood, 1850). E, *Z. ellops* (Ménétriés, 1855). F, *Z. syene* (Hewitson, 1856). G, *Z. pythagoras* Willmott & Hall, 2004. H, *Z. falcis* Dias, Casagrande & Mielke, 2012. I, ***Z. hurin*** Dias **sp. nov.** J, ***Z. crawfordhilli*** Dias **sp. nov.** K, ***Z. mirandahenrichae*** Dias **sp. nov.** L, ***Z. elianahenrichae*** Dias **sp. nov.**

it is similar in appearance to species of *Doleschallia* C. Felder & R. Felder, 1860, especially *Doleschallia bisaltide* (Cramer, 1777) (Nymphalinae). One of Fruhstorfer's specimens, illustrated by Warren *et al.* (2016), is kept at the type collection of the NHMUK.

Zaretes [sic] *isidora leopoldina* Fruhstorfer, 1909, was described based on an unstated number of specimens from Espírito Santo, Brazil. Only one syntype was located by Vane-Wright (1975) and by us in the NHMUK type collection. The specimen agrees perfectly with specimens of *Z. isidora* from the dense ombrophilous forests along the Brazilian coast, differing from the much more common *Z. strigosus*, as the upperside of the wings has a generally darker ground colour and the post-median and submarginal bands are absent or faint, not reaching the tornus in the hindwing dorsum (HWD). Therefore, this specimen, illustrated by Warren *et al.* (2016), is here designated as the lectotype.

Zaretis itys itys f. *monops* (Bryk, 1953) was described from a single specimen from Manaus, Amazonas, Brazil. However, it was described denoting an infrasubspecific entity and, therefore, the name is invalid and does not have a formal type. This specimen, similar to the type of *P. isidora* Cramer, 1779 and specimens of *Z. isidora* occurring in the Amazon basin, was inadvertently described based on the presence of only one hyaline area (thus '*monops*', 'single eye') in the post-median area of the FW, in CuA_1–CuA_2. However, the presence or absence of hyaline areas in the FW is variable in species of *Zaretis*.

Siderone isidora naama Brévignon, 2006 was described based on nine specimens from French Guiana, five males and four females. The holotype is similar to the type of *P. isidora* Cramer, 1779 and specimens of *Z. isidora* from the Amazon basin and Guianas; the allotype is similar to Fruhstorfer's infrasubspecific female form '*bisaltina*' (Fruhstorfer, 1909b), similar to specimens from the lower Amazon River basin. Therefore, this name is here considered to refer to a species of the genus *Zaretis* and treated as a junior subjective synonym of *Z. isidora* (comb. nov., syn. nov.).

Distribution

Widespread in the Amazon basin and the Guianas, usually occurring in low to mid-altitudes from sea level to 1400 m elevation in the eastern slopes of the Andes, in Bolivia, Brazil (Acre, Amazonas, Rondônia, Mato Grosso and Pará), Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname and Venezuela; and, disjointly, in Atlantic forests of Brazil (Alagoas, Bahia, Espírito Santo, Distrito Federal, Minas Gerais, Rio de Janeiro, São Paulo and Pernambuco) (Fig. 20). It may occur in northwestern Argentina (i.e. Catamarca, Jujuy, Salta and Tucumán) and further south and east in Brazil (i.e. Goiás, Maranhão, Mato Grosso do Sul, Paraná, Tocantins and Roraima).

Examined material

See Supporting Information, Appendix S1.

ZARETIS STRIGOSUS (GMELIN, [1790])

(FIGS 8A–D, 15C, 16E, F, 20; SUPPORTING INFORMATION, APPENDIX S6)

Type material

Female lectotype of *Papilio strigosus* Gmelin, [1790] with the following labels: / 55 *strigosus*, Gmel[in] type specimen/ Lectotype/ *Papilio strigosus* Gmelin det. R.I. Vane-Wright, 1971 LECTOTYPE #f/ (NMI).

Male lectotype of *Siderone isidora* var. *strigosa* Staudinger, 1886, here designated, with the following label: / Blumenau [18]85 Mull[er]/ (ZMHU).

Male lectotype of *Zaretes* [sic] *isidora russeus* Fruhstorfer, 1909, here designated, with the following labels: / Type/ Type/ Fruhstorfer Coll. B.M. 1937-285./ Columbien [Colombia] ex coll. H. Fruhstorfer/ russeus Fruhst[orfer]./ *Zaretes isidora russeus* Fruh[storfer]. det. R.I. Vane-Wright, 1972 #m SYNTYPE/ (NHMUK).

Male lectotype of *Zaretes* [sic] *isidora vulpecula* Fruhstorfer, 1909, here designated, with the following labels: / Type/ Type / Fruhstorfer Coll. B.M. 1937-285./ Bahia Brasilia [Brazil] Fruhstorfer/ *isidora vulpecula* Fruhst[orfer]./ *Zaretes isidora vulpecula* Fruh[storfer]. det. R.I. Vane-Wright, 1972 #m SYNTYPE/ (NHMUK).

Female lectotype of *Zaretes* [sic] *isidora vulpina* Fruhstorfer, 1909, here designated, with the following labels: / Type/ Type / Fruhstorfer Coll. B.M. 1937-285./ Paraguay ex coll. H. Fruhstorfer/ *Zaretes isidora vulpina* Fruh[storfer]. det. R.I. Vane-Wright, 1972 #f SYNTYPE/ (NHMUK).

Zaretes [sic] *isidora isidora* f. *foliacea* Fruhstorfer, 1909 does not have a formal type because it is an infrasubspecific entity. However, the specimen described by Fruhstorfer (1909b) is a female with the following labels: / SYN-TYPE/ Type/ Type/ Fruhstorfer Coll. B.M. 1937-285./ Obidos [Pará] Amazonenstrom VIII-IX.99 ex. coll. H. Fruhstorfer/ foliacea 18–70 Fruh[storfer]./ (NHMUK).

The male holotype of *Siderone ellops mellita* Brévignon, 2006 was not examined, but has the following label data: French Guiana, Saint-Georges de l'Oyapock, 30.V.1984, Number 46 (Brévignon, 2006) (LCB).

Diagnosis

Zaretis strigosus is the most variable species of the genus and, as with other species of *Zaretis*, it is extremely similar to many of its congeners. This species is sympatric with *Z. itys*, *Z. isidora*, *Z. falcis* and *Z. hurin* sp. nov. in the Amazon basin and the Guianas, and with *Z. isidora*, *Z. itylus* and *Z. hurin* sp. nov. in the Atlantic forest. However, the male genitalia of

this species are distinct (Fig. 15C), comparable only to *Z. ellops*, a Trans-Andean species. Differing from all the above cited species, in *Z. strigosus* the uncus is almost straight, short, thick, medially keeled and without a distal callus, and the dorsal half of the gnathos is larger than the ventral. Males (Fig. 8A, B) can be externally distinguished from *Z. itys* by the developed emargination of the inner margin at the tornus; from *Z. falcis* by the FW apex, only slightly to moderately falcate, outer margin not crenulated, and discal spot, marginal area and submarginal area near the apex never as developed and dark brown; from *Z. itylus* by the shape of the outer margin of the FW, sinuous, and HW not strongly emarginated in Sc–Rs and projected at Rs at the apex; from *Z. isidora*, throughout its distribution, and from *Z. hurin* sp. nov., in Atlantic forests, by generally much lighter and speckled coloration, with post-median and submarginal bands usually developed in both uppersides of the wings, especially the HWD post-median band, which usually runs to the tornal projection at 2A; and from *Z. hurin* sp. nov., in the Amazon basin and Guianas, by the absence of a purplish sheen on the FWD when viewed obliquely. Females (Fig. 8C, D) can be distinguished from *Z. itys* and *Z. itylus* by the shape of the FW, sinuous, and upperside of the wings basal and post-median areas, never reddish brown and beige to pale yellow, respectively, and the lighter and homogeneous coloration of basal, post-median area and submarginal areas along the outer margin in both wings upper and undersides; from *Z. falcis* by the FW apex, considerably less falcate; and from *Z. hurin* sp. nov. and *Z. isidora* by the generally lighter and homogeneous coloration of basal, post-median and submarginal areas in both wings upper and undersides. Owing to the extreme variation of females of *Z. strigosus* and the latter two species, the identification only be confirmed can by the examination of the genitalia; in *Z. strigosus*, the lamella postvaginalis is wider than long, and its posterior edge is bilobed (Fig. 16E, F).

Discussion

The name *Z. strigosus* was evaluated by Vane-Wright (1975) and briefly discussed by Dias *et al.* (2015). The species it represents is the most taxonomically problematic of the genus. The lectotype of *Papilio strigosus* Gmelin, [1790], designated by Vane-Wright (1975), is a heavily worn female specimen with several repairs; the left antenna was replaced by a bristle. According to Kirby (1879), that specimen was described by Zschach (1788) as 'species 55' of the Museum Leske and afterwards properly named by Gmelin ([1790]). The exact origin of this specimen was unknown by both Zschach and Gmelin (cited as '*Exoticus*' and '*extra Europam*'). However, as discussed by Vane-Wright (1975), it probably came from Suriname, the generally accepted locality for the Leske material. The lectotype agrees perfectly with specimens of *Z. strigosus* from the Amazon basin and the Guianas, with the upperside of the wings having a homogeneous pale orange to orange ground colour.

Siderone isidora v. *strigosa* Staudinger, 1887 was described based on an unstated number of specimens from Brazil ('Rio de Janeiro to Rio Grande do Sul'). Staudinger (1887) was unsure whether *S. isidora* v. *strigosa* Staudinger, 1887 was equivalent to *P. strigosus* Gmelin, [1790], and suggested that Gmelin's poorly described species might not even belong in the genus, wrongly assuming that the type was missing. Vane-Wright (1975) correctly recognized *S. isidora* v. *strigosa* Staudinger, 1887 as a subsequent secondary homonym of *P. strigosus* Gmelin, [1790]. No specimens can be recognized unequivocally as pertaining to the type series of *S. isidora* v. *strigosa* Staudinger, 1887, as none of the potential syntypes at the ZMHU (i.e. one female from Rio de Janeiro, two males from São Paulo, two males and one female from Santa Catarina, one male, collected by Mr Bescke, and one female, collected by Mr Sommer, from unknown localities in Brazil) have Staudinger's typical pink 'Origin' label. However, he frequently did not include this label on many of his 'varieties' (G. Lamas, personal communication). One of the potential syntypes, from Casa Branca, São Paulo, Brazil, collected by Mr Garbe in 1887 and illustrated by Warren *et al.* (2016), is labelled 'SYNTYPUS'. It is improbable that this specimen is part of the type series of *S. isidora* v. *strigosa* Staudinger, 1887, as it seems unlikely that this specimen could have been collected by Mr Ernst Garbe and sent to Europe early in 1887, reaching Staudinger in time to prepare and publish that part of the series, presented in mid-March 1887 (Lamas, 2017). At least one of the potential syntypes, a female collected in 'Brazil' by Mr Sommer, does not belong to *Z. strigosus* as here conceived. A male specimen from Blumenau, Santa Catarina, Brazil, collected in 1885 by Mr F. Müller, is here designated as the lectotype.

Zaretes [sic] *isidora russeus* Fruhstorfer, 1909 was described based on an unstated number of specimens from 'Colombia'. Only one syntype was located by Vane-Wright (1975) and by us at the NHMUK type collection. This specimen was not dissected, but agrees perfectly with specimens of *Z. strigosus* from the Amazon basin and Guianas, being generally darker than specimens from the Atlantic forests, but having the post-median and submarginal bands usually developed on the upperside of both wings, especially the HWD post-median band, which runs to the tornal projection at 2A. This specimen, illustrated by Warren *et al.* (2016), is here designated as the lectotype.

Zaretes [sic] *isidora isidora* f. *foliacea* Fruhstorfer, 1909 was described as a 'female form' denoting an

infrasubspecific entity; therefore, the name is invalid and without a formal type. Nevertheless, it corresponds to a distinct phenotype of females of *Z. strigosus* from the Amazon basin, with rounded and crenulated outer margins. One of these specimens, illustrated by Warren *et al.* (2016), is kept at the NHMUK type collection.

Zaretes [sic] *isidora vulpecula* Fruhstorfer, 1909 was described based on four specimens (three males and one female) from Bahia, Brazil, collected by Mr Haensch. All four specimens were located by Vane-Wright (1975) at the NHMUK, but we had access to only one male. This specimen, which agrees perfectly with the pale orange phenotype of specimens of *Z. strigosus* from the northeastern states of Brazil, is here designated as the lectotype.

Zaretes [sic] *isidora vulpina* Fruhstorfer, 1909 was described based on an unstated number of specimens from Paraguay. Fruhstorfer (1909b) claimed he had access to a large quantity of specimens, but Vane-Wright (1975) found only eight syntypes (seven males and one female) at the NHMUK. Only two of these (one male and one female) were located by us. The male specimen could not be dissected, but it is rather different from the most common phenotype of *Z. strigosus* in Paraguay, even though the female certainly represents *Z. strigosus*. There is a strong possibility that the type series contains multiple species. Nevertheless, the species description and the picture and description (Fruhstorfer, 1909b: 167–168, fig. 4) of the male genitalia clearly agree with *Z. strigosus*, one of the few species of the genus that can be identified reliably by the examination of the genitalia. Therefore, the above cited female specimen, which agrees perfectly with specimens of *Z. strigosus* from Paraguay, deposited in the NHMUK type collection, is designated here as the lectotype.

Siderone ellops melita Brévignon, 2006 was described based on nine specimens from French Guiana, two males and seven females. The male paratype illustrated (Brévignon, 2006: p. 300, figs 9, 10) is unlike most specimens of *Z. strigosus* from the Amazon basin and Guianas, but the species description and the plates of the male genitalia unequivocally identify this name as *Z. strigosus*. The female specimen illustrated is similar to the type of *Z. strigosus* and to specimens from the Amazon basin and Guianas, with pale orange to orange ground colour on the upperside of the wings. Therefore, this name is treated here as a junior subjective synonym of *Z. strigosus* (comb. nov., syn. nov.).

The immature stages of *Z. strigosus* are typical of the genus and were described by Müller (1886) and Dias *et al.* (2015) from Santa Catarina, Rio de Janeiro and Paraná and Santa Catarina in Brazil, respectively. Several authors recorded host plants for what is assumed to be *Z. strigosus*, the most common species of the *Zaretis* in Cis-Andean South America. Most authors cite host plants in the Salicaceae: unidentified species of *Casearia* (F. Müller, 1878; Otero & Marigo, 1990; Brown, 1992; Freitas *apud* Beccaloni *et al.*, 2008) and *Casearia sylvestris* (Müller, 1886; Mabilde, 1896; Costa-Lima, 1928, 1936; Ronna, 1933; Biezanko, Ruffinelli & Carbonell, 1966; Silva *et al.*, 1968; Hayward, 1969; Biezanko, Ruffinelli & Link, 1974; Bizarro *apud* Beccaloni *et al.*, 2008); records of species of *Colubrina* and *Colubrina glandulosa* (Rhamnaceae), provided by Silva *et al.* (1968) and Zikán & Zikán (1968), are uncertain and in need of confirmation.

Distribution

Widespread in the Amazon basin and the Guianas, usually in low to mid-altitudes, occurring from about the sea level to 1400 m on the eastern slopes of the Andes, in Argentina, Bolivia, Brazil (Acre, Amazonas, Rondônia, Maranhão, Mato Grosso, Mato Grosso do Sul and Pará), Colombia, Ecuador (Orellana and Morona-Santiago), French Guiana, Guyana, Paraguay, Peru, Suriname, Uruguay and Venezuela; and in Atlantic forests of Brazil (Alagoas, Bahia, Ceará, Espírito Santo, Distrito Federal, Goiás, Minas Gerais, Rio de Janeiro, Rio Grande do Sul, São Paulo, Santa Catarina, Paraíba and Pernambuco) (Fig. 20). It may occur in northwestern Argentina (i.e. Catamarca, Jujuy, Salta and Tucumán) and in all remaining states of Brazil.

Examined material

See Supporting Information, Appendix S1.

ZARETIS ITYLUS (WESTWOOD, 1850) (FIGS 8E–H, 15D, 16G, H, 19; SUPPORTING INFORMATION, APPENDIX S6)

Type material

Male holotype of *Siderone itylus* Westwood, 1850 with the following labels: / Type/ Rio/ B.M.TYPE No. Rh 10378 *Siderone itylus* #m Westw[ood]./ *Siderone itylus* Westwood det. R.I. Vane-Wright, 1972 Holotype #m/ *Itylus* Westw[ood] G.D.L. p.321/ (NHMUK).

Male lectotype of *Zaretes* [sic] *itys pseuditys* Fruhstorfer, 1909 and consequently of *Zaretes* [sic] *pseuditys* Fruhstorfer, 1909 with the following labels: / Espírito Santo Brasil ex. coll. Fruhstorfer/ Fruhstorfer Coll. B.M. 1937-285/ Type/ Type/ *Zaretes itys pseuditys* Fruh[storfer]. Det. R.I. Vane-Wright 1972 #m SYNTYPE/ *pseuditys* Fruhst[orfer]./ LECTOTYPE *Zaretes itys pseuditys* Fruhstorfer, 1909 Dias, Casagrande & Mielke, det. 2012/ LECTOTYPUS/ (NHMUK).

Diagnosis

Zaretis itylus, as with most species of the genus, is somewhat variable, but more-or-less distinctive. The

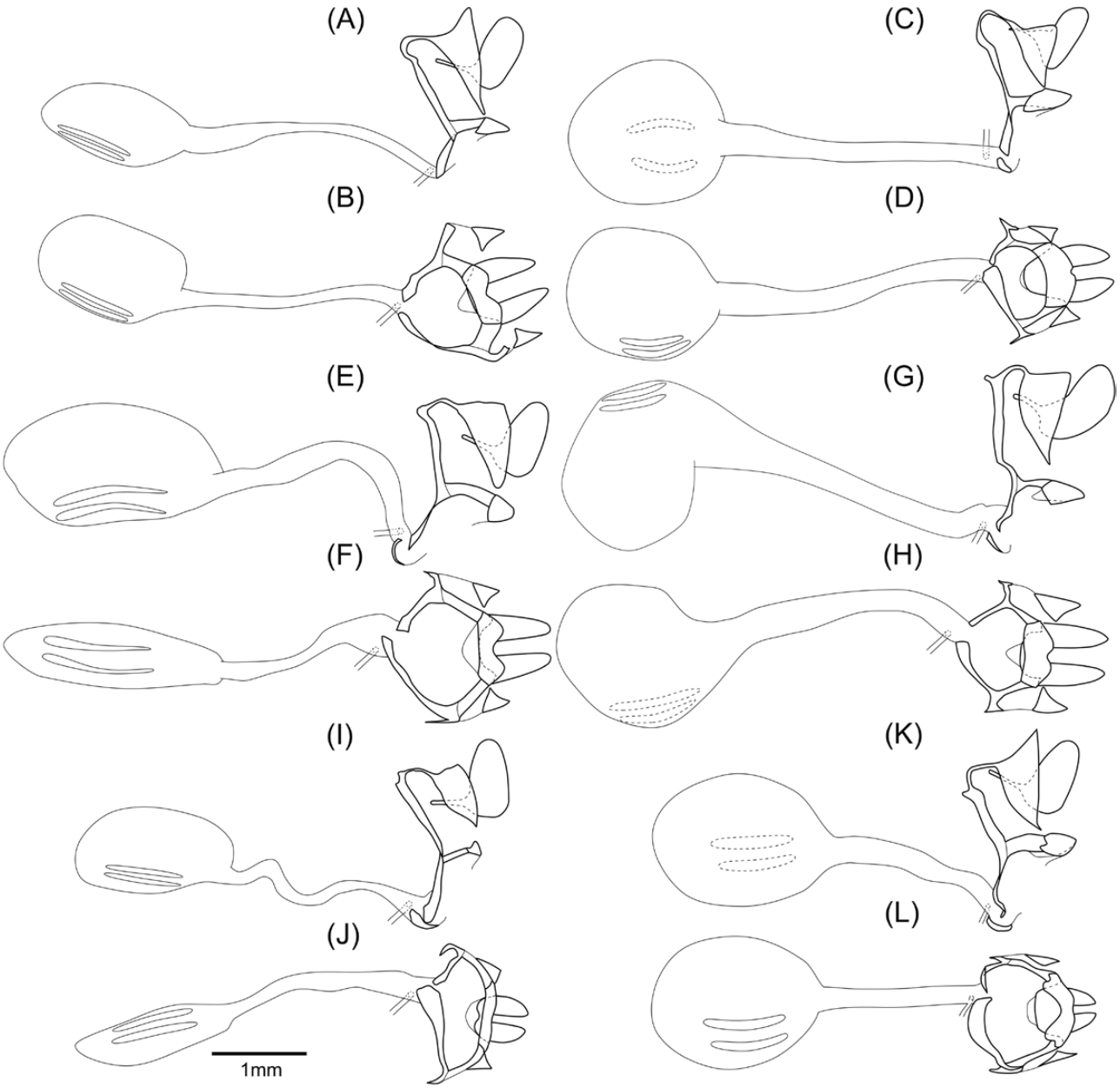

Figure 16. Female genitalia of species of *Zaretis* Hübner, [1819], lateral and ventral. A, B, *Z. itys* (Cramer, [1777]). C, D, *Z. isidora* (Cramer, [1779]). E, F. *Z. strigosus* (Gmelin, [1790]). G, H, *Z. itylus* (Westwood, 1850). I, J, *Z. ellops* (Ménétriés, 1855). K, L, *Z. pythagoras* Willmott & Hall, 2004.

species was recently redescribed and diagnosed by Dias *et al.* (2012), but the diagnosis focused on a comparison with one of the most similar and likely sister species, *Z. itys*, which is not sympatric with *Z. itylus*. *Zaretis itylus* is sympatric only with *Z. isidora* and *Z. strigosus* in the coastal Atlantic forests of Brazil. Males (Fig. 8E, F) can be distinguished from the above species by the shape of the FW, which is similar to that of the female, with the outer margin evenly rounded until just before the apex; the colour of the upperside of the wings, which is reddish brown, with the marginal and submarginal areas suffused with reddish brown; and the shape of the HW, which is strongly emarginated at Sc–Rs and projected at Rs, resembling the wing shape of a female. Females (Fig. 8G, H) are similar to *Z. itys*, but the FWD and HWD basal areas are generally darker, and the FW discal spot less developed; nevertheless, they can be distinguished from *Z. isidora* and *Z. strigosus* (and from *Z. crawfordhilli* sp. nov.) by the same set of characters.

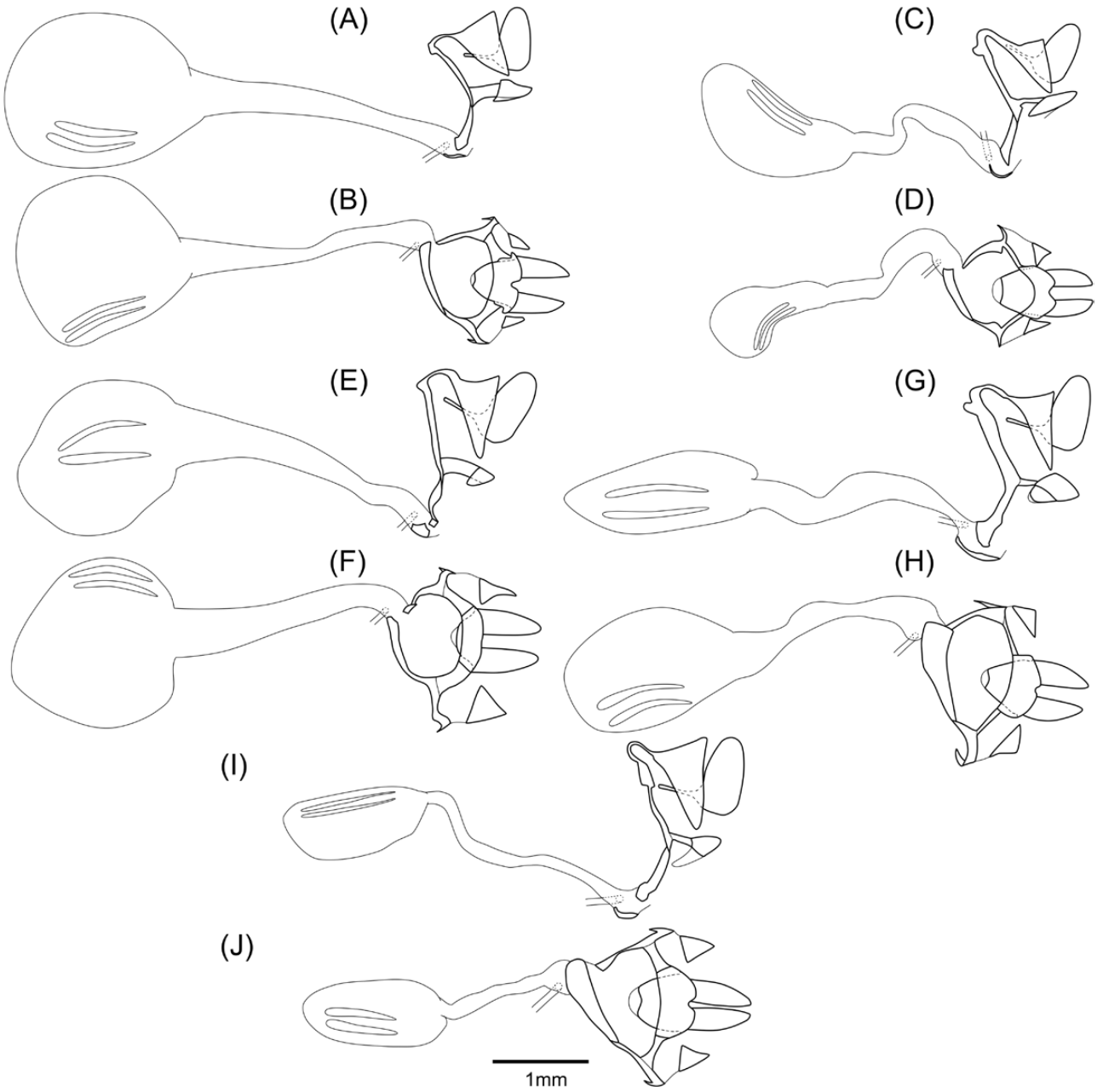

Figure 17. Female genitalia of species of *Zaretis* Hübner, [1819], lateral and ventral. A, B, *Z. falcis* Dias, Casagrande & Mielke, 2012. C, D, ***Z. hurin*** Dias **sp. nov.** E, F, ***Z. crawfordhilli*** Dias **sp. nov.** G, H, ***Z. mirandahenrichae*** Dias **sp. nov.** I, J, ***Z. elianahenrichae*** Dias **sp. nov.**

Discussion

Zaretis itylus was recently redescribed and discussed by Dias *et al.* (2012). This name was widely misused in the past by several authors, who presumably, owing to its type locality, assumed it to represent the phenotype of *Zaretis* occurring in southern and southeastern Brazil. However, *Z. itylus* represents a distinctive, rare and restricted species. Numerous citations to *Z. itylus* in fact represent *Z. strigosus* or *Z. isidora* (see Dias *et al.*, 2012).

Siderone itylus Westwood, 1850 was described from a single male specimen (Hemming, 1941), thought to be a female by Westwood owing to the lack of forelegs in the holotype and the unusual wing shape (Dias *et al.*, 2012). The species represented by the names *Zaretes* [sic] *pseuditys* Fruhstorfer, 1909 and *Zaretes* [sic] *itys pseuditys* Fruhstorfer, 1909 was described twice by Fruhstorfer (1909a, b; certainly by a *lapsus memoriae*), first as a species (Fruhstorfer, 1909a), based on an unstated number

Figure 18. Immature stages of some species of *Zaretis* Hübner, [1819]. A, B, fifth instar of ***Z. crawfordhilli*** Dias **sp. nov.** (03-SRNP-21184), dorsal and lateral. C, D, fifth instar of ***Z. elianahenrichae*** Dias **sp. nov.** (10-SRNP-73168), dorsal and lateral. E, fifth instar of *Z. ellops* (Ménétriés, 1855) (81-SRNP-1120), dorsal. F, fifth instar of *Z. ellops* (83-SRNP-1200), parasitized by Tachinidae (Exoristinae, *Winthemia* Wood03; no voucher code). G, second instar of ***Z. mirandahenrichae*** Dias **sp. nov.** (04-SRNP-55931) parasitized by Braconidae (Euphorinae, *Meteorus* Janzen23; voucher DHJPAR0021248). H, third instar of ***Z. crawfordhilli*** Dias **sp. nov.** (09-SRNP-32288) parasitized by Braconidae (Microgastrinae, *Cotesia* Whitfield93, voucher DHJPAR0039886). Voucher codes by Janzen & Hallwachs (2017).

of specimens from Espírito Santo, Brazil, and later as a subspecies (Fruhstorfer, 1909b), based on four specimens from the same locality. Most probably, both descriptions were based on the same three males and one female specimen collected by Mr J. Michaelis and cited in the latter publication. Therefore, the male lectotype designated by Dias *et al.* (2012) applies to both names. Although Willmott & Hall (2004) found all four of Fruhstorfer's syntypes in the NHMUK, Vane-Wright (1975) located only two males and one female. Only two of those specimens are currently in the NHMUK type collection, the male lectotype designated by Dias *et al.* (2012) from Espírito Santo, Brazil, illustrated by Warren *et al.* (2016), and one female paralectotype from the same locality.

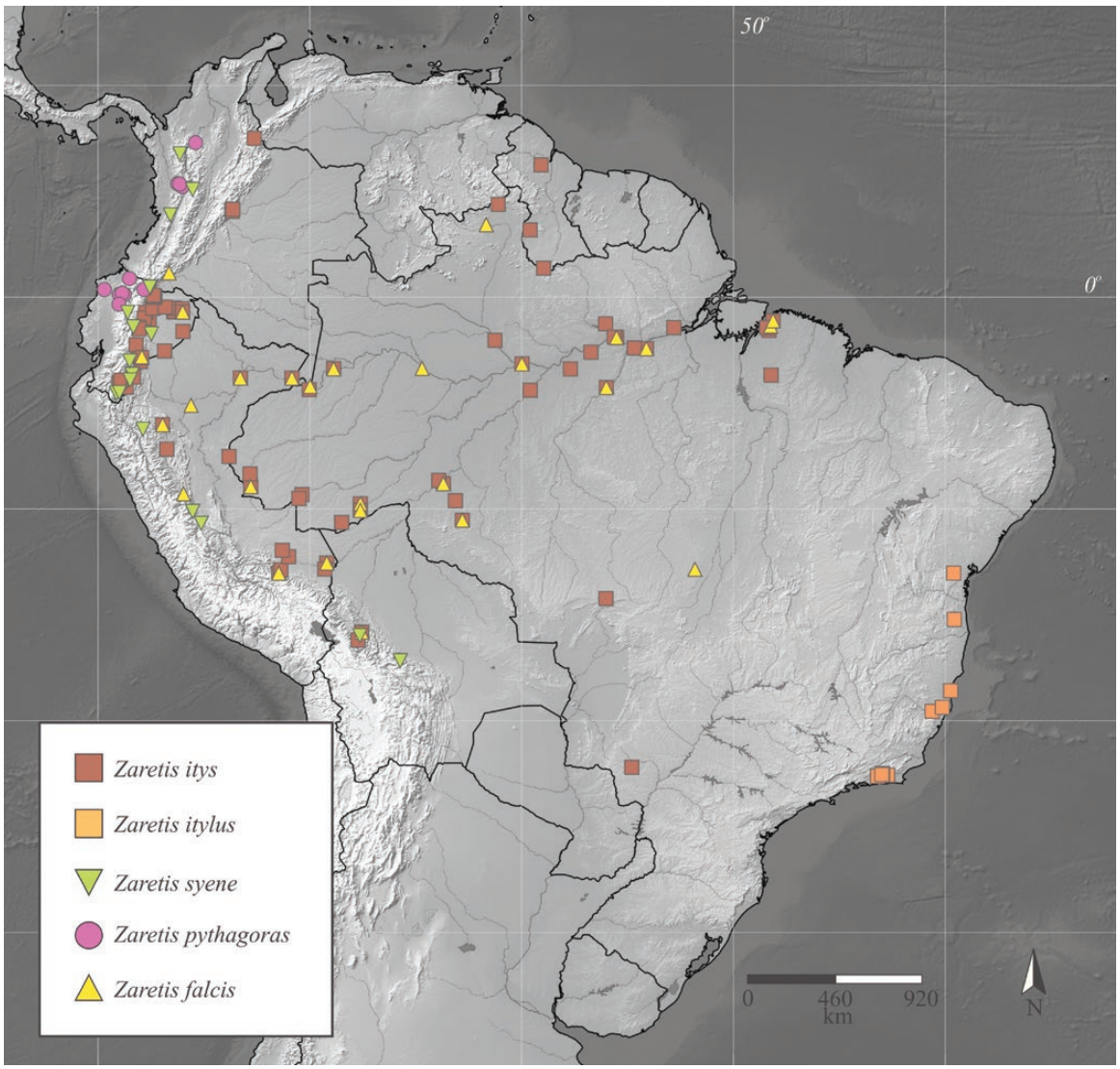

Figure 19. Distribution of *Zaretis itys* (Cramer, [1777]). *Z. itylus* (Westwood, 1850). *Z. syene* (Hewitson, 1856), *Z. pythagoras* Willmott & Hall, 2004, and *Z. falcis* Dias, Casagrande & Mielke, 2012, based on the labels of the examined specimens.

Distribution Restricted to dense ombrophilous forests of coastal Brazil (Rio de Janeiro, Espírito Santo, Bahia; Fig. 19). It is not known whether this species occurs further north or south along the Brazilian coast, where it might be expected based on the distributions of endemic species with which it occurs.

Examined material See Supporting Information, Appendix S1.

ZARETIS ELLOPS (MÉNÉTRIÉS, 1855)

(FIGS 9A–D, 15E, 16I, J, 18E, F, 21; SUPPORTING INFORMATION, APPENDIX S6)

Type material

The type series of *Siderone ellops* Ménétriés, 1855 was not examined, but it is presumably housed at ZIN.

Male lectotype of *Zaretes* [sic] *isidora anzuletta* Fruhstorfer, 1909, here designated, with the following labels: / Type/ Type/ Fruhstorfer Coll. B.M. 1937-285 /Mexico Fruhstorfer/ *Zaretes isidora anzuletta* Fruh[storfer]. Det. R.I. Vane-Wright 1972 #m SYNTYPE/ *isidora anzuletta* Fruhst[orfer]./ (NHMUK).

Diagnosis

Zaretis ellops, as with most species of the genus, is somewhat variable and similar to its congeners. This species is likely to be sympatric with *Z. pythagoras*, *Z. delassisei*, *Z. crawfordhilli* sp. nov., *Z. elianahenrichae* sp. nov. and *Z. mirandahenrichae* sp. nov., in Central America and Trans-Andean South America. The species strikingly resembles *Z. elianahenrichae*

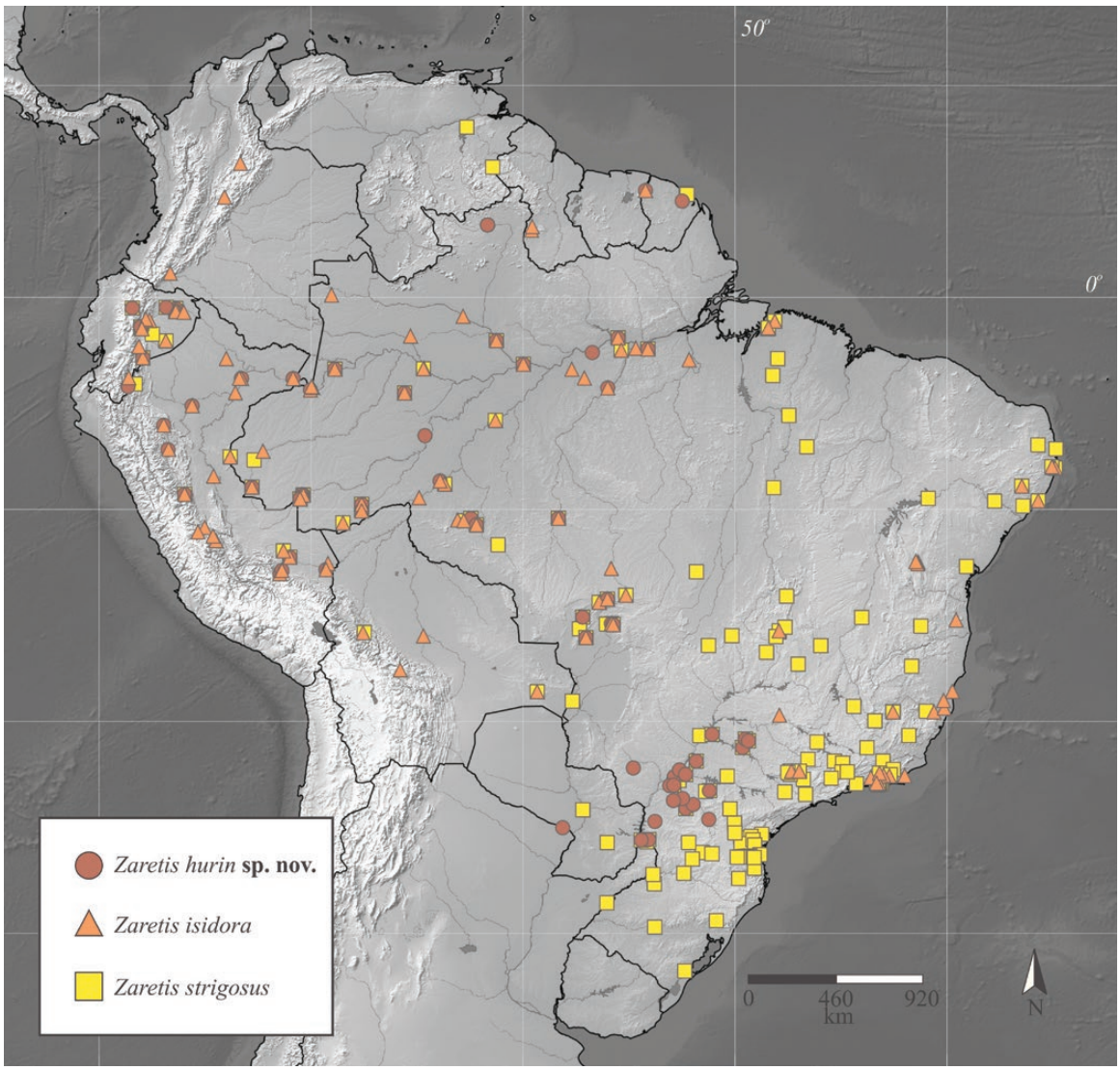

Figure 20. Distribution of ***Zaretis hurin*** Dias **sp. nov.**, *Z. isidora* (Cramer, [1779]) and *Z. strigosus* (Gmelin, [1790]), based on the labels of the examined specimens.

sp. nov., but the male genitalia of *Z. ellops* are distinct, comparable only to the South American *Z. strigosus*. In contrast to the above species, in *Z. ellops* the uncus is almost straight, short, thick, medially keeled and without a distal callus, and the dorsal half of the gnathos is slightly larger than the ventral (Fig. 15E). Males (Fig. 9A, B) can be externally distinguished from *Z. crawfordhilli* sp. nov. and *Z. mirandahenrichae* sp. nov. by the generally much lighter and speckled coloration, with post-median and submarginal bands usually present in the upperside of both wings, especially the HWD post-median band, which usually runs to the tornal projection at 2A; additionally, *Z. ellops* can be distinguished from *Z. crawfordhilli* sp. nov. by the more strongly developed emargination of the inner margin of the FW at the tornus; from *Z. elianahenrichae* sp. nov. by the shape of the FW apex, which is slightly to moderately falcate; by the coloration of the submarginal area near the apex and the marginal area, which is suffused with pale orange to orange scales near the apex; by the bands of the upperside of the wings being generally lighter and less developed, orange to light brown; and by the HW tornal projection at 2A being shorter and wider; and from *Z. pythagoras* and *Z. delassisei* by the absence of a purplish sheen on the FWD when viewed obliquely. Additionally, it can be distinguished from *Z. pythagoras* by the lighter colour of the upperside of the wings, pale orange to orange; and from *Z. delassisei* by the FWD pale orange to orange coloration not being restricted to the basal and part of the post-median

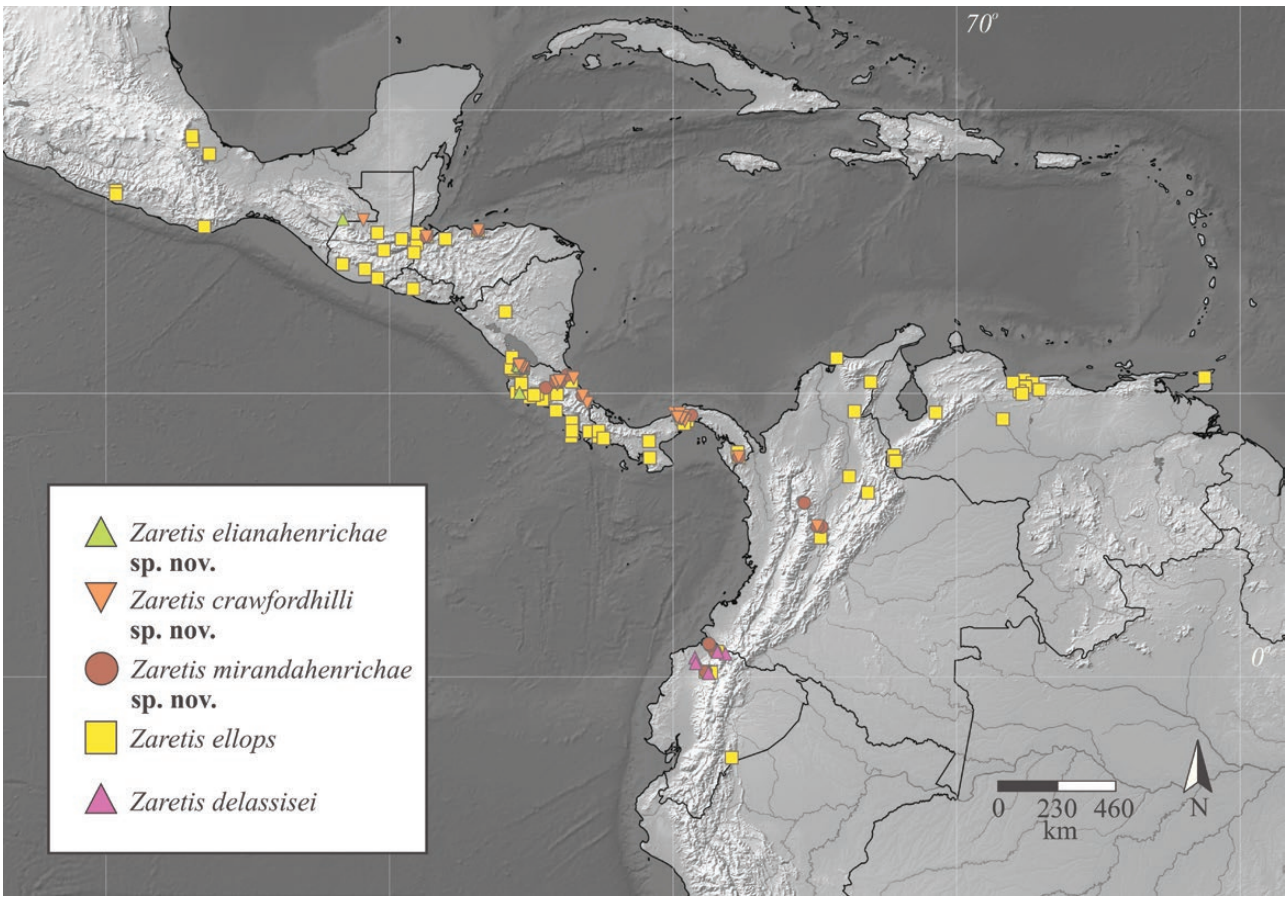

Figure 21. Distribution of ***Zaretis elianahenrichae*** Dias **sp. nov.**, ***Z. crawfordhilli*** Dias **sp. nov.**, ***Z. mirandahenrichae*** Dias **sp. nov.**, *Z. ellops* (Ménétriés, 1855) and *Z. delassisei* Choimet, 2009, based on the labels of the examined specimens.

areas and by the HW tornal projection at 2A being longer. Females (Fig. 9C, D) can be distinguished from *Z. crawfordhilli* sp. nov. and *Z. mirandahenrichae* sp. nov. by the generally lighter and homogeneous coloration of basal, post-median and submarginal areas along the outer margin on both wing surfaces; from *Z. elianahenrichae* sp. nov. by the coloration of the submarginal area near the apex and the marginal area, which is suffused with pale yellow to yellow scales near the apex; by the FWD and HWD basal and post-median areas and submarginal area along the outer margin being similar in colour, pale yellow to yellow, and by the HW tornal projection at 2A being shorter and wider; and from *Z. pythagoras* by the colour of the post-median area and submarginal area along the outer margin of the FW, which is never suffused with yellowish orange; females of *Z. delassisei* are unknown.

Discussion

Zaretis ellops is the most common and widely distributed species of *Zaretis* in Trans-Andean Neotropics, being the replacement of *Z. strigosus* in that area.

Siderone ellops Ménétriés, 1855 was described based on an unstated number of males and females from Nicaragua, presumably deposited at the ZIN. No specimens of the type series were examined. However, the illustration provided by Ménétriés (1855) clearly represents *Z. ellops*, as recognized here, by the coloration of the submarginal area near the apex and the marginal area, which is washed out and suffused with pale orange scales, by the bands of the upperside of the wings being faint, and by the HW tornal projection at 2A being short and wide.

Zaretes [sic] *isidora anzuletta* Fruhstorfer, 1909 was described based on an unstated number of males and females from Mexico, deposited at the NHMUK. Vane-Wright (1975) located two syntypes, one male and one female, probably the same specimens located by us in the NHMUK type collection. The male specimen is very similar to the illustration of *Siderone ellops* Ménétriés, 1855 and specimens of *Z. ellops* from Mexico and neighbouring countries. Therefore, the

male specimen deposited at the NHMUK type collection and illustrated by Warren *et al.* (2016) is designated here as the lectotype.

The immature stages of *Z. ellops* (Fig. 18E, F) are typical of the genus, were described by Muyshondt (1976) in El Salvador, and illustrated by Janzen & Hallwachs (2017) in Costa Rica. Several authors recorded host plants for what is assumed to be *Z. ellops*, the most common species of *Zaretis* to the north of the Andes. All records are in the Salicaceae, on undetermined (Comstock & Vázquez, 1961; DeVries, 1987) or determined species of *Casearia*: *Casearia guianensis* (Orellana *apud* Beccaloni *et al.*, 2008), *Casearia nitida* (Muyshondt, 1973), *Casearia sylvestris* (Muyshondt, 1976) and species of *Xylosma* (Fox *apud* Beccaloni *et al.*, 2008). This species was frequently reared by Janzen & Hallwachs (2017), on *Casearia arguta*, *Casearia corymbosa*, *C. nitida*, *Casearia praecox*, *C. sylvestris*, *Casearia tremula*, *C. corymbosa* and *Zuelania guidonia*. Most immature stages used *C. corymbosa* (~60% of the records) and *C. arguta* (~30% of the records), which are not used or only rarely used by the three other *Zaretis* species collected as larvae in the area.

Distribution

Widespread in Central America, except the Antilles, and Trans-Andean South America, Belize, northwestern and western Colombia, Costa Rica, Ecuador (Carchi, Pichincha and, by a single record, on the eastern slopes of the Andes in Morona-Santiago), El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panamá, Trinidad and northwestern Venezuela; occurs mostly in dry forests from near sea level to 800 m (Fig. 21). It may occur in northwestern Peru. In Costa Rica, occurs only on the Pacific slope, whereas the Atlantic slope is shared by three other species of the genus (DeVries, 1987; Janzen & Hallwachs, 2017). Detailed distributional data for Mexico are provided by Vargas *et al.* (2008).

Examined material

See Supporting Information, Appendix S1.

Zaretis syene (Hewitson, 1856)

(Figs 9E, F, 15F, 19; Supporting Information, Appendix S6)

Type material

Male holotype of *Siderone syene* Hewitson, 1856 with the following labels: / Type/ SYN-TYPE/ B.M. TYPE No. Rh 10380 *Siderone syene* [#f] #m Hew[itson]./ N. Granada. Hewitson Coll. 79-69 *Siderone syrene* [sic], 2./ (NHMUK).

Diagnosis

Zaretis syene is highly distinctive and can be distinguished easily from all other species of *Zaretis* by the wing shape, coloration and male genitalia (Figs 9E, F, 15F). This species is probably elevationally allopatric with respect to other species of the genus. It can be distinguished from all species of the genus by the FW apex being strongly falcate, wide and rounded; by the FW outer margin being strongly crenulated at M_3, CuA_1 and CuA_2; by the HW apex emarginated at Sc–R–Rs, and HW outer margin slightly projected at Rs; and by the HW tornal projection at 2A being strongly developed. The wing pattern is typical of the genus, but the upperside of the wings has an orange ground colour, including the submarginal and marginal areas, and well-developed dark brown markings; the pattern is obscured by a variable dark brown suffusion along the outer margin, particularly on the HWD; wing underside homogeneously brown in all areas, bands and umbra dark brown; male genitalia relatively larger when compared with other species; projection between the costa and the harpe weak, similar to species of *Siderone* and *Phantos* gen. nov.

Discussion

Siderone syene Hewitson, 1856 is a distinctive and rare species, described based on an unstated number of specimens from Nueva Granada, i.e. Colombia. However, the wording of the description clearly implies that the description of *S. syene* Hewitson, 1856 was based on single specimen, thought to be a female by Hewitson (1856). The true sex of Hewitson's specimen was revealed only many years later by Gabriel (1927); as far as we know, females of this species are still unknown. The holotype is illustrated by Warren *et al.* (2016) and is deposited in the NHMUK type collection. Salazar (1995) indicated the presence of this species on all three Colombian cordilleras, regarding the occurrence of *Z. syene* as an indicator of well-preserved humid forests in Colombia.

Distribution

Restricted to premontane cloud forests from 1000 to 2500 m in Bolivia, Colombia, Ecuador and Peru (Fig. 19). The records for Brazil provided by Comstock (1961) and label data of specimens at the USNM are certainly mistaken.

Examined material

See Supporting Information, Appendix S1.

Zaretis pythagoras Willmott & Hall, 2004

(Figs 10A–D, 15G, 16K,L, 19; Supporting Information, Appendix S6)

Type material

The holotype of *Zaretis pythagoras* Willmott & Hall, 2004 has the following label data: Ecuador, Pichincha, Santo Domingo, Rio Taguaza (misspelled 'Tatuaza' in

the original description), 23.VIII.1973 (Willmott & Hall, 2004) (NHMUK).

Diagnosis

Zaretis pythagoras, unlike most species of the genus, is not very variable and is relatively distinctive. This species was recently described and diagnosed by Willmott & Hall (2004), but females were not known at the time of the description. *Zaretis pythagoras* is likely to be sympatric with *Z. ellops*, *Z. delassisei*, *Z. crawfordhilli* sp. nov., *Z. elianahenrichae* sp. nov. and *Z. mirandahenrichae* sp. nov. in Trans-Andean South America. Males (Fig. 10A, B) can be distinguished from the above species by the shape of the FW apex, which is more falcate; by the outer margin always being crenulated; by the colour of the basal, post-median and submarginal areas along the outer margin being reddish brown; by the wide dark brown marginal area along the outer margin; and by the presence of a purplish sheen on the upperside of the wings when viewed obliquely. It can be distinguished further from *Z. delassisei* by the presence of reddish brown post-median area anterior to CuA_1 and the developed HW projection of the tornus at 2A; and from *Z. crawfordhilli* sp. nov. by the developed emargination of the inner margin of the FW at the tornus. Females (Fig. 10C, D) can be distinguished from all sympatric species by the shape of the FW apex, which is more falcate; by the outer margin, which is always crenulated; by the colour of the FW basal area, which is dark orange, with post-median and submarginal areas along the outer margin dark orange with a yellowish orange suffusion; by the colour of the HW areas, which are mostly dark orange, with a yellowish orange suffusion near the inner margin in the basal and median areas; and by the wing undersides being mostly homogeneously dark brown, yellowish in the basal and post-median areas of the FW and in the median area of the HW; females of *Z. delassisei* are unknown.

Discussion

Zaretis pythagoras was recently described and discussed by Willmott & Hall (2004) and Dias *et al.* (2012). This species was referred as '*Z. violacea*' nom. nud. by Salazar & Constantino (2001) and listed as '*Zaretis* sp. nov.' by Lamas (2004) before its description. *Zaretis pythagoras* was described based on eight male specimens from western Ecuador and Colombia. Male specimens were further illustrated by Constantino & Salazar (2007: figs 23, 24) and Checa (2008: 38, fig. 3). The female was described and incorrectly indicated as 'female allotype' by Choimet (2009) from a single specimen collected in western Ecuador at 1000 m. As can be deduced from the limited number of known specimens, there is little intraspecific variation in this species. Willmott & Hall (2004) indicated that specimens of *Z. pythagoras* were usually collected towards the end of the wet season in Ecuador, along forested rivers, where males were locally common in traps baited with rotting fish.

Distribution

Restricted to Trans-Andean South America wet rainforest habitats, from 300 to 1000 m, in western Colombia and northwestern Ecuador (Fig. 19).

Examined material

See Supporting Information, Appendix S1.

ZARETIS DELASSISEI CHOIMET, 2009 (FIGS 10E, F, 21; SUPPORTING INFORMATION, APPENDIX S6)

Type material

The holotype of *Zaretis delassisei* Choimet, 2009 was not examined, but it has the following label data: Ecuador, Pichincha, Pacto, 1000 m, VI-2008, Delassise *leg.* (Choimet, 2009) (XC).

Diagnosis

Zaretis delassisei is highly distinctive and can be distinguished easily from all other species of *Zaretis* by the wing shape and coloration (Fig. 10E, F). This species is likely to be sympatric with *Z. ellops*, *Z. pythagoras*, *Z. crawfordhilli* sp. nov., *Z. elianahenrichae* sp. nov. and *Z. mirandahenrichae* sp. nov., in Trans-Andean South America. Males can be distinguished from all above cited species by the wing shape, with the FW apex slightly falcate and the HW tornal projection at 2A being weakly developed; by the wing coloration, with the FW basal area reddish brown, and most of the post-median, and all submarginal and marginal areas coalesced, dark brown, and the HW basal, median and post-median areas reddish brown, suffused with variable dark brown along the outer margin; by the post-median band being dark brown and continuous; and by the wings having a purplish sheen on the upperside when viewed obliquely; the female is unknown.

Discussion

Zaretis delassisei is a distinctive species, described based on a single specimen collected in western Ecuador and deposited in the XC. One specimen of this species was illustrated by Checa (2008: 38, fig. 4) before its description, identified as '*Zaretis* sp.'. *Zaretis delassisei* appears to be rare and localized. There is little intraspecific variation, as can be deduced from the limited series of specimens available. As far as we know, the female remains unknown.

Distribution

Restricted to Trans-Andean South America wet rainforest habitats in western Ecuador, from ~400 to 1000 m elevation. It is likely to occur in southwestern Colombia in similar environments (Fig. 21).

Examined material
See Supporting Information, Appendix S1.

ZARETIS FALCIS DIAS, CASAGRANDE & MIELKE, 2012

(FIGS 11A–D, 12, 15H, 17A, B, 19; SUPPORTING INFORMATION, APPENDIX S6)

Type material
Male holotype of *Zaretis falcis* Dias, Casagrande & Mielke, 2012 with the following labels: / Holotypus/ 23–28-II-1988 – Ilha de Maracá, Alto Alegre, RR [Roraima, Brazil] Mielke & Casagrande/ HOLOTYPE *Zaretis falcis* Dias, Casagrande & Mielke, det. 2012/ DZ 19.625/ (DZUP); allotype female with the following labels: / Allotypus/ 23–28-II-1988 - Ilha de Maracá, Alto Alegre, RR [Roraima, Brazil] Mielke & Casagrande/ ALLOTYPE *Zaretis falcis* Dias, Casagrande & Mielke, det. 2012/ DZ 19.478/ (DZUP).

Diagnosis
Zaretis falcis, as with most species of the genus, is somewhat variable but more-or-less distinctive. The species was recently described and diagnosed by Dias *et al.* (2012), but the diagnosis focused on a comparison with one of the most similar species, *Z. pythagoras*, which is not sympatric with *Z. falcis*. *Zaretis falcis* is sympatric with *Z. itys*, *Z. isidora*, *Z. strigosus* and *Z. hurin* sp. nov. in the Amazon basin and the Guianas. Both sexes can be distinguished from the above species by the distinctly falcate FW apex and the always crenulated outer margins. It can be distinguished further from *Z. itys* by the developed emargination of the inner margin at the tornus; and from *Z. hurin* sp. nov. by the absence of a purplish sheen on the FWD when viewed obliquely (Fig. 11A–D). Males of *Z. strigosus* and *Z. isidora* can be extremely similar in colour and pattern to *Z. falcis*, and can be distinguished further from the last species by the male genitalia; in *Z. falcis*, the harpe is conspicuously longer and posteriorly directed (Fig. 15H). Females (Fig. 11C, D) can be distinguished further from *Z. itys*, *Z. isidora* and *Z. hurin* sp. nov. by the coloration of the basal, post-median and submarginal areas along the outer margin of the wings being uniformly orange on the upperside, and homogeneous beige to light brown on the underside; females of *Z. strigosus* can be extremely similar in colour and pattern to *Z. falcis*, which is distinguished externally only by the strongly falcate apex of the FW. However, *Z. falcis* can be distinguished by the longer than wide lamella postvaginalis, which is medially indented at its posterior edge (Fig. 17A, B).

Discussion
Zaretis falcis was described based on the male holotype and the female allotype from Roraima, Brazil, collected by O. Mielke and M. Casagrande in 1988. Fifteen further specimens deposited at the DZUP and USNM were examined, but not explicitly designated as paratypes. Several other specimens were located at FLMNH, MNRJ, OM and other collections, after the description of *Z. falcis*, confirming its widespread Amazonian distribution. Dias *et al.* (2012) indicated that *Z. falcis* was probably not recognized as a distinct species in the past because of the infraspecific variation of species of *Zaretis*, but acknowledged its distinctiveness and stability of phenotype. The examination of these additional specimens and specimens figured in publications (e.g. Witt, 1970: figs 3, 6; Pyrcz & Neild, 1996: pl. 20, fig. 848) confirms this assumption. An aberrant male from Bolívar, Venezuela, illustrated by Pyrcz & Neild (1996: pl. 20, fig. 851), was recognized as corresponding to *Z. falcis* in the taxonomic catalogue, but not discussed further by Dias *et al.* (2012). Two additional male specimens with corresponding phenotype were found at the MNRJ, collected in the beginning of the 20th century, from Óbidos and Itaituba, Pará, Brazil (Fig. 12). Further studies with more recently collected specimens and analyses of their DNA barcodes could confirm whether these specimens correspond in fact to *Z. falcis* or to an undescribed species.

Distribution
Widespread in the Amazon basin and the Guianas, in low-elevation forests in Bolivia, Brazil (Acre, Amazonas, Distrito Federal, Mato Grosso, Pará, Rondônia and Roraima), Colombia, Ecuador, French Guiana and Peru (Fig. 19). It may occur in Suriname, Guyana, northwestern Argentina (i.e. Catamarca, Jujuy, Salta and Tucumán) and further south and east in Brazil (i.e. Goiás, Maranhão, Mato Grosso do Sul and Tocantins).

Examined material
See Supporting Information, Appendix S1.

ZARETIS HURIN DIAS SP. NOV.

(FIGS 11E–H, 15I, 17C, D, 20; SUPPORTING INFORMATION, APPENDIX S6)

[urn:lsid:zoobank.org:act:1FDFEB50-90C0-4D7B-BA9A-5941623321F6]

Type material
Male holotype with the following labels: /HOLOTYPUS/ HOLOTYPE *Zaretis hurin* Dias det. 2016 /17-XII-2009 /FAZ[enda]. Matão 25 KM L de [east of] LOANDA, Paraná, 400 m [23°1′24″S, 53°4′52″W], CARNEIRO & DOLIBAINA LEG. /DNA FER003 wg, EF1a, CAD /DZ 19.467 /BC-DZ / (DZUP). Female allotype with the following labels: /ALLOTYPUS / ALLOTYPE *Zaretis hurin* Dias det. 2016 /14-XII-2009 /FAZ[enda]. Matão 25 KM L de [east of] LOANDA, Paraná, 400 m [23°1′24″S, 53°4′52″W], MIELKE, MAIA, CARNEIRO & DOLIBAINA LEG. /DZ 19.801 /BC-DZ / (DZUP).

Paratypes: **ARGENTINA, Formosa**, Laguna Blanca, *Parque Nacional Rio Pilcomayo, Parador Yaguarete (orilla Rio Pilcomayo)*, 82 m, 2 #m, 30.V.2011, Núñez-Bustos & Kopuchian leg., MACN-Bar-Lep-ct 02714, MACN-Bar-Lep-ct 02744 (MACN); **Misiones,** Gal. Belgrano, *Almirante Brown, Reserva Yacutinga,* 4 #m, 2–5.III.2007, Mielke & Casagrande leg., DZ 15.516, DZ 15.530, DZ 23.675, DZ 23.775 (DZUP); **BRASIL, Acre,** Senador Guiomard, *Reserva Catuaba*, 1 #f, 1,3–5.X.2006, Mielke & Casagrande leg., DZ 20.439 (DZUP); **Amazonas,** Canutama, *Fazenda 3 Coqueiros, 12 km West, km 90 Estrada P. Velho-Humaitá,* 1 #m, 30.VI.2001, Mielke leg., OM 53.721 (OM); **Mato Grosso,** Diamantino, *Alto Rio Arinos, Faz. São João,* 1 #m, 22.I.1978, Mielke & Furtado leg., DZ 22.902 (DZUP); Chapada dos Guimarães, *Buriti, Colégio Buriti,* 600 m, #m, 25.VI.1972, Mielke & Brown leg., DZ 22.742 (DZUP); Cáceres, 1 #f, 16.XI.1984, Buzzi, Mielke, Elias & Casagrande leg., DZ 22.692 (DZUP); 2 #m, 18.XI.1984, Buzzi, Mielke, Elias & Casagrande leg., DZ 15.554, DZ 19.926 (DZUP); 1 #m, 15.XI.1984, Buzzi, Mielke, Elias & Casagrande leg., DZ 19.547 (DZUP); **Paraná,** Diamante do Norte, *EE Caiuá,* 300 m, 1 #m, 12.IV.2011, Dolibaina & Salik leg., DZ 19.596 (DZUP); Loanda, *RPPN Faz. Matão,* 400m, 1 #f, 11.X.2009, Carneiro, Leite, Dias & Dolibaina leg., DZ 22.672 (DZUP); 1 #m, 18–21.IV.2008, Dolibaina leg., DZ 23.645 (DZUP); Planaltina do Paraná, *RPPN Duas Barras,* 1 #m & #f, 13.V.2009, Dolibana & Carneiro, DZ 19.388, DZ 22.482 (DZUP); **Rondônia,** Jaru, 250 m, #m, 4–12.IX.1977, Gifford & Negrett leg., DZ 15.582 (DZUP); Ouro Preto do Oeste, 1 #m, 17–31.VIII.1987, Elias leg., DZ 20.391 (DZUP); **Roraima,** Alto Alegre, *Ilha de Maracá,* 3 #m & 2 #f, 24–31.VIII.1987, Mielke & Casagrande leg., DZ 19.529, DZ 20.166, DZ 15.575, DZ 22.582, DZ 23.685 (DZUP); 1 #f, 23–28.II.1986, Mielke & Casagrande leg., DZ 20.417 (DZUP); **São Paulo,** Teodoro Sampaio, *Parque Estadual Morro do Diabo,* 1 #m, 17–19.VIII.1989, Mielke & Casagrande leg., DZ 22.592 (DZUP); **ECUADOR, Morona-Santiago,** *forest ridge nr. Yaupi, 400 m,* 1 #m, 20.VI.2009, Gallice leg., LEP-14967 (FLMNH); *Río Wampis,* 300–450 m, 1 #m, 22.VI.2009, Gallice leg., LEP-14961 (FLMNH); **Orellana,** *Boca del Río Añangu, Río Napo*, 220 m–300 m, 2 #m, 6.XI.2005, 15.XI.2005, Willmott leg., LEP-06365, LEP-06368 (FLMNH); *Estación Científica Yasuní,* 400 m, 1 #m, 4.VI.2004, Gallice leg., LEP-14966 (FLMNH); *Estación Científica Yasuní, parcela 50 Ha,* 250–270 m, 1 #m, 5.VII.2014, Willmott & Paez leg., LEP-14950 (FLMNH); *Napo Wildlife Center, Napo trail,* 250 m, 1 #m, 22.X.2005, Elias leg., LEP-06364 (FLMNH); *Yarina,* 250 m, 1 #m, VIII–IX.2012, Gallice leg., LEP-14922 (FLMNH); 1 #m, 2010, no collector, LEP-17608 (FLMNH); **Zamora-Chinchipe,** *Quebrada Maycú,* 900 m, 1 #m, 30.VI.2014, Willmott leg., LEP-14948 (FLMNH); **Pastaza,** *Puyo via Tena,* 750 m, 1 #m, no collector, OM 71.145 (OM); *Rio Anzu,* 1 #m, 30.XI.1998, no collector, OM 71.123 (OM); **PERU, Cuzco,** Chontachaca, *Cosñipata Valley,* 950m, 1 #f, 2012, no collector, OM 71.167 (OM); **Loreto,** *Quebrada Polis, Momón River,* 1 #m, X.2009, Ramírez leg., DZ 19.624 (DZUP); *San Juan de Poli, Momón River,* 1 #m, X.2009, Ramírez leg., DZ 19.229 (DZUP) **San Martin,** Juanjuí, 700m, 1 #m, 28.VIII.2011, Tafur Novoa leg., OM 71.791 (OM).

Diagnosis

Zaretis hurin sp. nov., as with most species of the genus, is extremely variable and extremely similar to its congeners. This species is sympatric with *Z. itys*, *Z. isidora*, *Z. strigosus* and *Z. falcis* in the Amazon basin and the Guianas, and with *Z. strigosus* in the Atlantic forest. Males (Fig. 11E, F) can be distinguished from all sympatric species occurring in the Amazon basin and the Guianas by the presence of a purplish sheen on the FW upperside when viewed obliquely. It can be distinguished further from *Z. itys* by the more strongly developed emargination of the inner margin at the FW tornus; from *Z. isidora* by the coloration of the wings, which are generally darker; and from *Z. falcis* by the coloration of the wings, which are generally darker and with more homogeneous dark orange to reddish brown areas and have a less falcate FW apex. In the Atlantic forest, where the characteristic purplish sheen of *Z. hurin* sp. nov. is absent, the species can be distinguished from *Z. strigosus* by the coloration, which is generally darker and more homogeneous; the post-median band of the FWD and submarginal bands of the both wings are faint or absent and the post-median band of the HWD is usually strongly developed. Owing to the variation in males of *Z. hurin* sp. nov. and *Z. strigosus*, certain identification in Atlantic forest can be achieved only by examination of the genitalia; in *Z. hurin* sp. nov., the uncus is longer, thinner and curved, with a small distal callus, and the gnathos is not enlarged at the dorsal half (Fig. 15I). Females (Fig. 11G, H) are similar to *Z. isidora* and can be distinguished from *Z. itys*, *Z. falcis* and *Z. strigosus* by the same set of characters. Owing to the variation in females of *Z. hurin* sp. nov., *Z. isidora* and *Z. strigosus*, identification with respect to *Z. strigosus* can be confirmed only by examination of the genitalia; in *Z. hurin* sp. nov., the lamella postvaginalis is longer than wide, with a bilobed posterior edge (Fig. 17C, D). Identification with respect to *Z. isidora* can be confirmed only with molecular data; although the uppersides of the wing basal areas are usually darker and the post-median band of the HWD is usually more strongly developed in *Z. hurin* sp. nov., there are only minor differences between the genitalia of both species.

Description

Head: Eyes reddish brown and naked; labial palpus creamy white ventrally, dark orange to reddish brown dorsally and at the tip; antennal length about one-third of the forewing length, segments dark brown with some ventral creamy white scaling; club slender and elongated, tip dark orange to reddish brown. Female as in male, but usually lighter in colour, orange to dark orange.

Thorax: Dorsally dark orange to reddish brown with scattered brownish and greenish scaling; ventrally dark orange to reddish brown, with area between legs creamy white; forelegs with creamy white scales in the tarsus; mid-leg femora, tibiae and tarsi and hindleg tibiae and tarsi creamy white, speckled with dark orange to reddish brown scales. Female as in male, but usually lighter in colour, orange to dark orange.

Wing size and shape: Forewing length, typical for genus. Forewing costal margin convex; apex slightly pointed and falcate; outer margin sinuous, smooth to slightly crenulated; inner margin straight, emargination before tornus developed, about one-third the length of the inner margin. Hindwing with slight emargination at Sc–Rs; outer margin rounded, smooth to slightly crenulated, with a developed projection at 2A; inner margin almost straight. Female larger than male, and FW shape rounder and more falcate; emargination before tornus developed; hindwing proportionately larger than male; emargination at Sc–Rs developed; apex projected at Rs; outer margin straighter than male; inner margin moderatedly emarginated near the tornus.

Wing colour and pattern, upper side: Ground colour of both wings dark orange to reddish brown with brown to dark brown markings, fore- and hindwings of similar ground colour. Forewing basal, median and submarginal area along the outer margin usually coalesced; median and post-median bands faint or absent; submarginal area near the apex and marginal area coalesced, brown to dark brown, along the outer margin to the apex; discal spot of the same colour, usually large; presence of hyaline areas in M_3–CuA_1 and CuA_1–CuA_2 on the median band variable, but usually faint or absent. Hindwing areas of the same colour, orange to reddish brown; median band usually developed, from the costal margin to the discal cell; discal spot absent; post-median and submarginal bands faint, more noticeable near the costal margin; apex suffused with dark brown; border ocelli faint or absent; anal fold lighter in colour; tornal projection at 2A usually darker with some creamy white scaling. Female forewing basal area darker than post-median area and submarginal area along the outer margin orange to dark orange; post-median area and submarginal area along the outer margin pale yellow to yellow; discal spot, submarginal area near the apex and marginal area brown to dark brown, the two latter coalesced; median and post-median bands usually faint, orange to dark orange. Hindwing basal and marginal areas usually darker than median, post-median and submarginal areas, orange to dark orange; median, post-median and submarginal areas pale yellow to yellowish orange; median band usually developed, from the costal margin to the discal cell; the discal spot absent; post-median and submarginal bands faint, more noticeable near the costal margin; apex suffused with dark brown; border ocelli faint or absent; anal fold lighter in colour; tornal projection at 2A usually darker with some creamy white scaling.

Wing colour and pattern, underside: Ground colour of both wings reddish brown to brown, with random speckles of scales lighter and darker than the ground colour in a ripple pattern. Forewing areas of similar colour, post-median and submarginal areas along the outer margin slightly lighter; all bands noticeable, slightly darker than the ground colour, but submaginal band from the inner margin to CuA_1 darker and more distinct; border ocelli faint, formed by dark brown and creamy white scales, scattered near the apex. Hindwing areas similar in colour to the FW; all bands noticeable, slightly darker than the ground colour, but median and post-median bands and the posterior part of umbra darker and more distinct. Female forewing basal, submarginal area near the apex and marginal areas darker than other areas and similar in colour, orange to brown; post-median and submarginal areas along the outer margin, beige to pale yellow; all bands noticeable, orange to brown. Hindwing basal area darker, orange to brown; median, post-median and submarginal areas beige to pale yellow; marginal area pale yellow to orange; all bands notiaceable, orange to brown, but median and post-median bands and the posterior part of umbra darker and more distinct; border ocelli faint, formed by dark brown and creamy white scales; tornal projection at 2A usually with some creamy white scaling.

Abdomen: Dorsally uniform dark orange to reddish brown; ventrally lighter in colour. Female as in male, but lighter in colour, orange to dark orange.

Male genitalia (Fig. 15I): Tegumen trapezoidal in lateral view, dorsally wider, strongly attached to the uncus, and only attached to the gnathos by membranes; appendix angularis hooked; saccus short, not projected anteriorly; dorsal projection of the saccus 'C' shaped and projected dorsad at a right angle; uncus about the same siza as the tegumen, semitubular, thin and lightly curved, with a well-developed median dorsal ridge, distally hooked and with a ventral callus; gnathos laterally

slightly curved, dorsally thin, produced ventrad, arms parallel; ventral part of the gnathos bar shaped and fused medially; valva externally covered with short setae, costa long and curved, developed anteriad, with two developed projections, one between the costa and the harpe, and another at the end of the harpe; sacculus triangular, ampulla developed and rounded; aedeagus as long as the length of the tegumen and uncus combined, cylindrical and bifid distally, without cornuti; manica inserted slightly anterior to the half of the aedeagus; fultura inferior thin, bar shaped.

Female genitalia (Fig. 17C, D): Tergum VIII triangular, ventrally attached to the sides of the lamella postvaginalis and dorsally to the lamella antevaginalis by a strong dorsally projected loop, this with a small anterior projection; papilla analis rounded and with short setae, projecting the apophysis posterioris; lamella antevaginalis asymmetrical, connected to the sides of the lamella postvaginalis by lightly sclerotized projections, left side larger than the right; lamella postvaginalis longer than wide, anterior area with a small membranous area, and posterior edge bilobed; seminal duct close to the base of the ductus bursae; posterior half of the ductus bursae bulbous; corpus bursae laterally compressed, about the same length of the ductus bursae, bearing two parallel signa, which are thin and long, formed by minute sclerotized bumps.

Discussion

The description of *Z. hurin* sp. nov. is based on 46 barcoded specimens, ten male specimens from Ecuador (Orellana, Zamora-Chinchipe and Morona-Santiago), deposited at the FLMNH, and 26 male and ten female specimens from Argentina (Formosa, Misiones), Brazil (Acre, Mato Grosso, Pará, Paraná, Rondônia, Roraima and São Paulo), Ecuador (Pastaza) and Peru (Cuzco, San Martin) deposited at the DZUP and MACN. Only barcoded specimens are designated as paratypes, although several other specimens were examined in other collections. *Zaretis hurin* sp. nov. probably failed to be identified as a distinct species in the past because of its similarity to other species of *Zaretis*; its distinctive characters were most likely to be regarded as intraspecific variations. Nevertheless, clear differences are noticeable when long series of specimens are available for examination. Despite the number of specific names proposed in the genus, no previously proposed name corresponds to *Z. hurin* sp. nov., although many authors recognized the coexistence of two distinctive 'phenotypes' or 'genotypes' of *Zaretis* in Argentina (Formosa, Misiones), southern Brazil and eastern Paraguay (Sharpe, 1890; Köhler, 1923; Kivirikko, 1936; Hayward, 1964; Nuñez-Bustos, 2008, 2009; Lavinia *et al.*, 2017). One of these corresponds to *Z. strigosus* and the other to *Z. hurin* sp. nov. This species occurs in two distinct phenotypes, in the Amazon basin and the Guianas, with a purple sheen when viewed obliquely, and without such a sheen in interior Atlantic forests to the south. The Brazilian state of Mato Grosso marks the transition between these two phenotypes. As far as we know, specimens of *Z. hurin* sp. nov. without a purplish sheen only occur sympatrically with both *Z. isidora* and *Z. strigosus* in this state, where the distinction between those three species can be difficult. Specimens of *Z. strigosus* can be distinguished easily by the examination of the male genitalia; bowever, both sexes of *Z. isidora* can be difficult to distinguish, especially females. Some specimens can be identified safely only by analysis of their DNA barcodes.

Distribution

Widespread in the Amazon basin and the Guianas, usually from low to mid-elevations in the eastern slopes of the Andes, in Brazil (Acre, Amazonas, Mato Grosso, Pará, Rondônia and Roraima), Ecuador and Peru; and in seasonal semidecidual forests in Argentina (Formosa and Misiones), Brazil (Paraná, São Paulo and Mato Grosso do Sul) (Fig. 20). The species probably occurs in the remaining coutries of the Amazon basin and the Guianas and may occur in northwestern Argentina (i.e. Catamarca, Jujuy, Salta and Tucumán) and in other parts of western and southern Brazil (i.e. Rio Grande do Sul and Santa Catarina) and eastern Paraguay.

Etymology

The name of the new species is derived from the Quendi word '*hurin*', meaning 'hidden' or 'concealed' in Quenya, the constructed language devised by J. R. R. Tolkien (ISO 639-3: qya). The name is given in reference to the elusive nature of the species-level taxonomy of *Zaretis* and is proposed as a noun in apposition.

Examined material

See Supporting Information, Appendix S1.

ZARETIS CRAWFORDHILLI DIAS SP. NOV.

(FIGS 13A–D, 15J, 17E, F, 18A, B, 18H, 21; SUPPORTING INFORMATION, APPENDIX S6)

[urn:lsid:zoobank.org:act:A68CBEB3-C98B-4590-BB4D-8F7B67E1102E]

Type material

Male holotype with the following labels: / HOLOTYPUS /HOLOTYPE *Zaretis crawfordhilli* Dias det. 2016 /Voucher: D.H. Janzen & Winnie Hallwachs caterpillar (Lepidoptera) database, Area de Conservación Guanacaste, Costa Rica [Alajuela, Área de Conservación Guanacaste, Sector Rincón Rain Forest, Vado Rio Francia, 400 m, (10.90093, –85.28915) [10°54′3″N, 85°17′21″W], 4-VII-2001, Pérez *leg. ex larvae* in *Casearia arborea*], http://janzen.sas.upenn.

edu 01-SRNP-5303 /LEGS AWAY FOR DNA / DZ 30.200 / (DZUP). Allotype female with the following labels: /ALLOTYPUS /ALLOTYPE *Zaretis crawfordhilli* Dias det. 2016 /Voucher: D.H. Janzen & Winnie Hallwachs caterpillar (Lepidoptera) database, Area de Conservación Guanacaste, Costa Rica [Alajuela, Área de Conservación Guanacaste, Sector Rincón Rain Forest, Sendero Rincón, 430 m, (10.8962, –85.27769 [10°53′46″N, 85°16′40″W]), 12-X-2002, Pérez *leg. ex larvae* in *Casearia arborea*], http://janzen.sas.upenn.edu 02-SRNP-21246 /LEGS AWAY FOR DNA /DZ 30.204 / (DZUP).

Paratypes: **COSTARICA, Alajuela,** Área de Conservación Guanacaste, *Rincón Rain Forest, Camino Rio Francia*, 410 m, 1 m# & 1 #f, 19.VIII.2005, Pérez leg., 05-SRNP-42266, 05-SRNP-42267 (UPENN); 1 #m, 19.VIII.2005, Carmona leg., DZ 30.201 (DZUP); *Rincón Rain Forest, Finca Hugo*, 540 m, 1 #m, 21.VI.2011, Pérez leg., 11-SRNP-42929 (UPENN); *Rincón Rain Forest, Quebrada Guarumo*, 400 m, 1 #f, 20.VIII.2001, Pérez leg., 01-SRNP-5693 (UPENN); 1 #f, 8.X.2012, Calderon leg.,12-SRNP-85888 (UPENN); *Rain Forest, Río Francia Arriba*, 400 m, 1 #m, M 8.XI.2012, Pérez leg., 12-SRNP-86533 (UPENN); *Rincón Rain Forest, San Lucas*, 320 m, 1 #m, 30.VI.2011, Córdoba leg., 11-SRNP-43136 (UPENN); 1 #m, 26.VI.2012, Córdoba leg., 12-SRNP-43156 (UPENN); *Rincón Rain Forest, Selva*, 410 m, 29.IV.2010, Briceño leg., 10-SRNP-69622 (UPENN); 1 #m, 8.V.2010, Briceño leg., 10-SRNP-69643 (UPENN); *Rincón Rain Forest, Sendero Juntas*, 400 m, 1 #m, 8.XI.2006, Araya leg., 06-SRNP-44414 (UPENN); *Rincón Rain Forest, Sendero Llano*, 400 m, 1 #f, 10.IX.2007, Carmona leg., 07-SRNP-42457 (UPENN); *Rincón Rain Forest, Sendero Parcelas*, 375 m, 1 #m, 07.XII.2005, Carmona leg., 05-SRNP-41764 (UPENN); 375 m, 1 #f, 12.VII.2005, Carmona leg., 05-SRNP-41763 (UPENN); *Rincón Rain Forest, Sendero Rincón*, 430 m, 2 #m, 8.IV.2003, Pérez leg., 03-SRNP-10614, 03-SRNP-10615 (UPENN); 1 #m, 16.I.2005, Pérez leg., 05-SRNP-40138 (UPENN); 1 #m, 16.I.2005, Pérez leg., 05-SRNP-40139 (UPENN); 1 #m, 9.V.2012, Córdoba leg., 12-SRNP-41969 (UPENN); 1 #f, 3.X.2005, Pérez leg., 05-SRNP-42926 (UPENN); 1 #f, 12.I.2007, Pérez leg., 07-SRNP-40155 (UPENN); 1 #f, 5.IX.2011, Umaña leg., 11-SRNP-44034 (UPENN); *Rincón Rain Forest, Sendero Rincón*, 410 m, 1 #m, 29.IV.2010, Briceño leg., 10-SRNP-69621 (UPENN); *San Cristóbal, Puente Palma*, 460 m, 1 #f, 21.IX.2006, Cano leg., DZ 30.205 (DZUP); *San Cristóbal, Sendero Huerta*, 527 m, 1 #m, 3.X.2006, Cano leg., 06-SRNP-8208 (UPENN); 1 #m & 1 #f, 17.IV.2007, Sihezar leg., 07-SRNP-1798, 07-SRNP-1797 (UPENN); 1 f#, 4.IV.2012, Cano leg., 12-SRNP-1391 (UPENN); **Guanacaste,** Área de Conservación Guanacaste, *Pitilla, Pasmompa*, 440 m, 1 #m, 15.X.2003, Rios leg., 03-SRNP-21420 (UPENN); 1 #f, 9.X.2010, Rios leg., 10-SRNP-32187 (UPENN); *Pitilla, Sendero Evangelista*, 660 m, 1 #f, 29.IX.2011, Rios leg., 11-SRNP-32971 (UPENN); *Pitilla, Sendero Mismo*, 680 m, 1 #m, 22.IX.2003, Rios leg., 03-SRNP-21183 (UPENN); **Heredia,** *Sarapiquí, Agrícola Sofia*, 0–100 m, 2 #m, 3.VII.2010, Brenes & Paniagua leg., DZ 30.106 (DZUP), INB00042773401 (INBIO); 1 #m, 5.IV.2009, Brenes & Paniagua leg., INB0004269668 (INBIO); *Sarapiquí*, *Estacíon Biológica La Tirimbina*, 169 m, 1 #m, 6.VII.2010, Miranda & Rojas leg., DZ 30.202 (DZUP); 230 m, 1 #m, 6.VII.2010, Miranda & Rojas leg., INB0004277310 (INBIO); *Sarapiquí, Starke*, 0–100 m, 2 #m, 3.VIII.2009, Calderón & Cruz leg., INB0004269384, INB0004269662 (INBIO); 1 #m, 29.VI.2010 Calderón & Cruz leg., INB0004277350 (INBIO); 1 #f, 30.VI.2010, Calderón & Cruz leg., DZ 30.208 (DZUP); **Limón,** Veragua, *Rainforest Restaurant*, 400–440 m, 1 #f, 14.XI.2008, Villalobos leg., DZ 30.107 (DZUP); **MEXICO, Chiapas,** Ocosingo, *Chajul*, 200 m, 1 #f, 20.VIII.1996, Ibarra leg., AIV193 (UNAM); **PANAMA, Panamá Oeste,** *Barro Colourado Island*, 150 m, 1 #f, 15.V.2012, Bobadilla leg., YB-BCI56036 (STRI); 1 #f, 25.VI.2012, Rivera leg. YB-BCI68924 (STRI).

Diagnosis

Zaretis crawfordhilli sp. nov., as with most species of the genus, is somewhat variable and similar to its congeners. The species is sympatric with *Z. ellops*, *Z. pythagoras*, *Z. delassisei*, *Z. elianahenrichae* sp. nov. and *Z. mirandahenrichae* sp. nov. Males (Fig. 13A, B) can be distinguished from all above cited species by the less well-developed emargination of the inner margin at the FW tornus, which is different in comparison to that of *Z. itys*. Females (Fig. 13C, D) can be distinguished from the above species by the shape of the FW, the outer margin always being smooth and rounded, and slightly falcate at the apex; and by the colour and pattern. Forewing dorsum basal area dark orange to reddish brown, post-median area beige to pale yellow, submarginal area beige to pale yellow along the outer margin and dark brown, coalesced with the marginal area near the apex; marginal area dark brown; post-median band usually reddish brown, between post-median and submarginal areas; forewing ventrum (FWV) similar to the upperside, but basal, submarginal areas near the apex almost solid brown to dark brown, post-median and submarginal areas along the outer margin pale beige to beige; FWV basal and discal bands usually indistinct, post-median band as in the upperside; hindwing dorsum (HWD) basal area reddish brown, and median area, submarginal and marginal areas reddish brown suffused with dark brown; hindwing ventrum similar to upperside, with basal, submarginal and marginal areas almost solid brown to dark brown, median area suffused with pale beige to

beige from the inner margin, post-median area brown to light brown, usually lighter than basal, submarginal and marginal areas; females of *Z. delassisei* are unknown.

Description

Head: Eyes reddish brown and naked; labial palpus creamy white ventrally, orange to dark orange dorsally and at the tip; antennal length about one-third of the forewing length, segments brown with some ventral creamy white scaling; club slender and elongated, tip orange to dark orange. Female as in male, but usually lighter in colour, orange to dark orange.

Thorax: Dorsally orange to dark orange with scattered brownish and greenish scaling; ventrally orange to reddish brown, with area between legs creamy white; forelegs with creamy white scales in the tarsus; midleg femora, tibiae and tarsi and hindleg tibiae and tarsi creamy white, speckled with pale orange to reddish brown scales. Female as in male, but usually lighter in colour, orange to dark orange.

Wing size and shape: Forewing length, medium. Forewing costal margin convex; apex pointed and falcate; outer margin sinuous, smooth to slightly crenulated; inner margin straight, emargination before tornus underdeveloped, about one-quarter of the length of the inner margin. Hindwing with slight emargination at Sc–Rs; outer margin rounded, smooth to slightly crenulated, with a developed projection at 2A; inner margin almost straight. Female larger than male, and FW rounded and more falcate at the apex; emargination before tornus developed; hindwing proportionately larger than male; emargination at Sc–Rs developed; apex projected at Rs; outer margin rounded; inner margin emarginated near the tornus.

Wing colour and pattern, upper side: Ground colour of both wings orange to dark orange with brown to dark brown markings, fore- and hindwings of similar ground colour. Forewing basal, median and submarginal areas along the outer margin usually of the same colour; median and post-median bands faint; submarginal area near the apex and marginal area coalesced, brown to dark brown, along the outer margin to the apex; discal spot of the same colour; presence of hyaline areas in M_3–CuA_1 and CuA_1–CuA_2 on the median band variable, but usually present. Hindwing areas of the same colour, orange to reddish brown; median, post-median and submarginal bands faint, more noticeable near the costal margin; discal spot absent; border ocelli faint or absent; anal fold lighter in colour; tornal projection at 2A usually darker with some creamy white scaling. Female forewing basal area darker than post-median and submarginal areas along the outer margin, orange to dark orange; post-median and submarginal areas along the outer margin pale beige to pale yellow; discal spot, submarginal area near the apex and marginal area brown to dark brown, the two latter coalesced; median and post-median bands usually faint, orange to dark orange. Hindwing basal and marginal areas usually darker than median, post-median and submarginal areas, orange to dark orange; median, post-median and submarginal areas pale yellow to yellowish orange; median band usually developed from the costal margin to the discal cell; the discal spot absent; post-median and submarginal bands faint, more noticeable near the costal margin; apex suffused with dark brown; border ocelli faint or absent; anal fold lighter in colour; tornal projection at 2A usually darker with some creamy white scaling.

Wing colour and pattern, underside: Ground colour of both wings brown to reddish brown, with random speckles of scales lighter and darker than the ground colour in a ripple pattern. Forewing areas of similar colour, with post-median and submarginal areas along the outer margin slightly lighter; all bands noticeable, slightly darker than the ground colour; border ocelli faint, formed by dark brown and creamy white scales, scattered near the apex. Hindwing areas similar in colour to the FW; all bands noticeable, slightly darker than the ground colour, but median and post-median bands and the posterior part of umbra darker and more distinct. Female forewing basal, submarginal area near the apex and marginal areas darker than other areas and similar in colour, reddish brown to dark brown; post-median and submarginal areas along the outer margin beige to pale yellow; all bands noticeable, orange to brown. Hindwing basal and marginal areas darker, reddish brown to dark brown; median area beige to pale yellow; post-median and submarginal areas lighter than basal and marginal areas, but darker than medial area; all bands notiaceable, orange to brown, but median and post-median bands and the posterior part of umbra darker and more distinct; border ocelli faint, formed by dark brown and creamy white scales; tornal projection at 2A usually with some creamy white scaling.

Abdomen: Dorsally uniform orange to dark orange; ventrally brown to reddish brown. Female dorsally orange to dark orange; ventrally reddish brown to dark brown.

Male genitalia (Fig. 15J): Tegumen trapezoidal in lateral view, dorsally wider and posteriorly bulged, strongly attached to the uncus, and attached to the gnathos only by membranes; appendix angularis hooked; saccus short, not projected anteriorly, dorsal projection of the saccus 'C' shaped and projected dorsad at a right angle; uncus semitubular, slightly shorter than the tegumen, slightly curved, with a

well-developed median dorsal ridge, distally hooked and with a ventral callus; gnathos laterally slightly curved, dorsally slightly larger than ventrally, produced ventrad, arms parallel; ventral part of the gnathos bar shaped and fused medially; valva externally covered with short setae; costa long and curved, developed anteriad, two projections, one smaller projection between the costa and the harpe, and another at the end of the harpe; sacculus triangular, ampulla developed and rounded; aedeagus as long as the length of the tegumen and uncus combined, cylindrical and bifid distally, without cornuti; manica inserted slightly anterior to the half of the aedeagus; fultura inferior thin, bar shaped.

Female genitalia (Fig. 17E, F): Tergum VIII triangular, ventrally attached to the sides of the lamella postvaginalis and dorsally to the lamella antevaginalis by a strong projected loop; this with a small anterior projection; papilla analis rounded and with short setae, projecting the apophysis posterioris; lamella antevaginalis assymetrical, connected to the sides of the lamella postvaginalis by wide sclerotized projections, with left side larger than the right; lamella postvaginalis wider than long, anterior area with a small membranous area, and posterior rounded to slightly bilobed; seminal duct close to the base of the ductus bursae; corpus bursae rounded, about half the length of ductus bursae, bearing two parallel signa, which are thin and long, formed by minute sclerotized bumps.

Discussion

The description of *Z. crawfordhilli* sp. nov. is based on 48 barcoded specimens, 29 male and 16 female specimens from Costa Rica (Alajuela, Guanacaste and Heredia) deposited at the DZUP, INBIO and UPENN, one female from México (Chiapas) deposited at the UNAM, and two females from Panamá, deposited at the STRI. Only barcoded specimens are designated as paratypes, although several other specimens were examined at the INBIO and USNM. This species is similar to and has been frequently identified as the Amazonian *Z. itys*, which it resembles in the weakly developed emargination of the FW at the tornus, and the somewhat similar wing shape and coloration of the female. Nevertheless, *Z. crawfordhilli* sp. nov. is not recovered as closely related to *Z. itys* in any of our analyses. Additionally, the shape of the underdeveloped emargination of the inner margin at the FW tornus is clearly different for these two species, being shorter but similarly deep in *Z. crawfordhilli* sp. nov., whereas it is shorter and considerably shallower in *Z. itys*. The female wings are broader, and the coloration of the upperside is usually lighter than in *Z. itys*. This species, according to the data presented by DeVries (1987) and Janzen & Hallwachs (2017), is rather common, second only to *Z. ellops* in Costa Rica, but occurring mostly on the Atlantic slopes, whereas *Z. ellops* occurs mostly on the Pacific slopes. DeVries (1987) found this species to be most common in baited traps during the dry season.

DeVries (1987) described the immature stages of *Z. crawfordhilli* sp. nov. (identified as *Z. itys*; Fig. 18A, B), indicating several differences between that species and *Z. ellops*: 'thoracic hump [A2 enlargement] and the rhomboid shapes on the dorsum highlighted in green; last segment [A9 + 10] is splayed into a short fan; head horns [head capsule scoli] curve inward toward each other; and the entire head is dotted in green granules'. It is not certain whether he was using the latter name to refer to *Z. elianahenrichae* sp. nov. or *Z. mirandahenrichae* sp. nov., because he was unaware of the existence of further species in Costa Rica. However, it is safe to assume that *Z. crawfordhilli* sp. nov. is the species under consideration, given his species description and figures (DeVries, 1987; pl. 14, figs 12–14), and by the fact that this species is the second most common species of *Zaretis* in Costa Rica, whereas *Z. elianahenrichae* sp. nov. and *Z. mirandahenrichae* sp. nov. are much scarcer. Several authors recorded host plants for what is assumed to be *Z. crawfordhilli* sp. nov. Most citations are on Salicaceae: on undetermined species of the family (Marquis, 1991; Dyer, 1995), undetermined (DeVries, 1987; Mallet *apud* Beccaloni *et al.*, 2008) and determined species of *Casearia*: *C. arborea* (DeVries, 1986; Gentry & Dyer *apud* Beccaloni *et al.*, 2008), *C. arguta* (DeVries, 1986), *C. sylvestris* (DeVries apud Beccaloni *et al.*, 2008), and species of *Laetia* and *Ryanea* (DeVries, 1987), on *Laetia procera* (DeVries, 1986; Gentry & Dyer *apud* Beccaloni *et al.*, 2008) and *Ryanea speciosa* (DeVries, 1986). The record for *Piper trigonun* (Piperaceae) provided by DeVries (1986) is doubtful and needs confirmation. This species was frequently reared by Janzen & Hallwachs (2017) on *C. arborea*, *C. corymbosa* and *C. sylvestris*. Most immature stages used *C. arborea* (~78% of the records) and *C. sylvestris* (~10% of the records), which are likewise used by *Z. elianahenrichae* sp. nov. and *Z. mirandahenrichae* sp. nov., but never or rarely used by *Z. ellops*.

Distribution

The species occurs in forest habitats from low to mid-elevations and is probably widespread in Central America and Trans-Andean South America, in Belize, northwestern and western Colombia, Costa Rica, western Ecuador, Guatemala, Honduras, southern Mexico, Nicaragua and Panamá; it occurs in forest habitats from low to mid-elevations (Fig. 21). It may occur in the remaining countries of Central America, except the Antilles, western Ecuador and northwestern Peru and northwestern Venezuela.

Etymology
Zaretis crawfordhilli sp. nov. is named in honour of Crawford Hill of Philadelphia, USA, in recognition of his decades of teaching biodiversity to high school students and his serious support and encouragement for exposing those same students to new locations and especially, to Área de Conservación Guanacaste, where *Z. crawfordhilli* sp. nov. is prominent.

Examined material
See Supporting Information, Appendix S1.

ZARETIS MIRANDAHENRICHAE DIAS SP. NOV.

(FIGS 13E, F, 15K, 17G, H, 18G, 21; SUPPORTING INFORMATION, APPENDIX S6)

[urn:lsid:zoobank.org:act:737B7B83-B06E-41C4-A773-4A9FE3429885]

Type material
Male holotype with the following labels: /HOLOTYPUS /HOLOTYPE *Zaretis mirandahenrichae* Dias det. 2016 /COSTA RICA. Prov. Heredia, Sarapiquí, Est. Biol. La Tirimbina, Mirador, 167 m [10°25′6″N, 84°7′7″W], 24 ABR [IV] 2009, I. Chacón, A. Barrientos [*leg.*], Tp. Luz. [light trap] L_N_266268_523359 #96598/ [barcode] INB0004211690 INBIOCRI COSTA RICA/ Zaretis isidora DHJ02/ Legs away for DNA I. A. Chacón 2010/ DZ 30.206/ (DZUP). Female allotype with the following labels: /ALLOTYPUS /ALLOTYPE *Zaretis mirandahenrichae* Dias det. 2016 / COSTA RICA. Prov. Heredia, Sarapiquí, Starke. O a 100 m [10°26′16″N, 84°0′43″W]. 29 JUN [VI] 2010. E. Calderón, M. Cruz [*leg.*]. Tp. de Fruta [fruit-baited trap] #15 (Dosel [canopy]) L_N_269206_536862 #101206 /[barcode] INB0004277346 / Costa Rica-Heredia, Sarapiquí, Starke TA 15- 10°26.485′N 83° 59.684 Eduardo Calderón Espinoza & Miguel Cruz Artavia 6/29/2010 Zaretis isidora, Hembra Det. I.A. Chacón Julio 2010 / Legs away for DNA I.A. Chacón 2010/ Zaretis isidora DHJ02 Det: I.A. Chacón feb[uary] 2013/ DZ 30.211/. (DZUP).

Paratypes: **COSTA RICA, Alajuela,** Área de Conservación Guanacaste, *Rincón Rain Forest, Camino Río Francia*, 410 m, 1 #m, 11.X.2003, Carmona leg., DZ 30.114 (DZUP); *Rincón Rain Forest, Quebrada Escondida*, 420 m, 2 #m, 22.III.2005, Pérez leg., DZ 30.111 (DZUP), 05-SRNP-40837 (UPENN); *Rincón Rain Forest, Quebrada Guarumo*, 400 m, 1 #f, 30.VIII.2001, Vargas leg., 01-SRNP-5691 (UPENN); *Rincón Rain Forest, Sendero Rincón*, 430 m, 1 #f, 18.X.2011, Córdoba leg., 11-SRNP-44587 (UPENN); 1#m & 1 #f, 25.XI.2002, Pérez leg., 02-SRNP-21453, 02-SRNP-21455 (UPENN); *San Cristobal, Sendero Huerta*, 527 m, 1 #m & 1#f 10.V.2012, Cano leg., 12-SRNP-1873, 12-SRNP-1874 (UPENN); **Guanacaste,** *Pitilia, Sendero Paleta*, 570 m, #f, 23.VIII.2004, Moraga leg., 04-SRNP-34810 (UPENN); *Pitilla, Bullas*, 440 m, 1 #m, 15.VI.2012, Calero leg., 12-SRNP-71413 (UPENN); *Pitilla, Ingas*, 580 m, #m, 7.III.2009, Moraga leg., 09-SRNP-30712 (UPENN); 1 #m, no date, Rios leg., DZ 30. 210 (DZUP); Pitilla, Loaiciga, 445 m, #m, 29.IX.2005, Espinosa leg., 05-SRNP-34151 (UPENN); *Pitilla, Manguera*, 470 m, #f, 4.III.2010, Moraga leg., 10-SRNP-71089 (UPENN); *Pitilla, Medrano*, 380 m, 1 #m & 1 #f, 8.IX.2012, Calero leg., 12-SRNP-72116, 12-SRNP-72117 (UPENN); *Pitilla, Pasmompa*, 440 m, 1 #m, 16.II.2012, Rios leg., 12-SRNP-30532 (UPENN); *Pitilla, Sendero Evangelista*, 660 m, 1 #m, 13.VII.2002, Moraga leg., 02-SRNP-28460 (UPENN); 1 #m, 28.X.2004, Moraga leg., 04-SRNP-55932 (UPENN); *Pitilla, Sendero Laguna*, 680 m, 1 #m, 11.VIII.2007, Rios leg., 07-SRNP-32980 (UPENN); *Pitilla, Sendero Nacho*, 710 m, 1 #m, 14.X.2003, Rios leg., 03-SRNP-21390 (UPENN); *Pitilla, Sendero Mismo*, 680 m, 1 #f, 18.VIII.2004, Rios leg., DZ 30.110 (DZUP); **Heredia,** *Sarapiquí, Agrícola Sofia*, 0–100 m, 1 #m, 6.VI.2009, Brenes & Paniagua leg., DZ 30.207 (DZUP); 2 #f, 5.VI.2009, Brenes & Paniagua leg., INB0004273125, INB0004273119 (INBIO); *Sarapiquí, Estación Biológica La Tirimbina*, 100–200 m, 1 #m, 5.IV.2010, Miranda & Rojas leg., INB0004278034 (INBIO); *Sarapiquí, Starke*, 0–100 m, 1 #f, 2.VI.2009, Calderón & Cruz leg., INB0004273143 (INBIO); 1 #m & 1 #f, 5.VI.2009, Calderón & Cruz leg., INB0004269382, INB0004273198 (INBIO); 1 #f, 9.V.2009, Calderón & Cruz leg., INB0004273139 (INBIO); **ECUADOR, Esmeraldas,** *Río Chuchuví*, 1 #m, 2010, Aldaz leg, R67 (FLMNH); *San Francisco ridge*, 1 #m, 2010, Aldaz leg., R11 (FLMNH); *San Lorenzo-Lita rd. Tundaloma Lodge 100m*, 100 m, 1 #m, 17–19.VII.2011, Willmott & Hall leg., LEP-09963 (FLMNH); *Tundaloma Lodge*, 100 m, 1 #m, 17–19.VII.2011, Willmott & Hall leg., LEP-17613 (FLMNH); 2, #m, 22.VII.2014, Willmott leg., LEP-14943, LEP-14947 (FLMNH); **Pichincha,** *km 20 Pacto-Guayabillas rd.*, 900 m, 1#m & 1 #f, 7–8.VIII.2011, Willmott & Hall leg., LEP-17612, LEP-17614 (FLMNH); *km 21 Pacto-Guayabillas rd., Sardinas*, 850 m, 1 #m, 7–8.VIII.2011, Willmott & Hall leg., LEP-09961 (FLMNH).

Diagnosis
Zaretis mirandahenrichae sp. nov., as with most species of the genus, is somewhat variable and similar to its congeners. The species is sympatric with *Z. ellops*, *Z. pythagoras*, *Z. delassisei*, *Z. elianahenrichae* sp. nov. and *Zaretis crawfordhilli* sp. nov. Males (Fig. 13E, F) can be distinguished from *Z. crawfordhilli* sp. nov. by the fully developed emargination of the inner margin at the FW tornus; from *Z. phytagoras* by the FW apex, which is considerably less falcate, and the outer margin, which is not crenulated; from *Z. pythagoras* and *Z. delassisei* sp. nov. by the absence of a purplish sheen

on the FWD when viewed obliquely; from *Z. ellops* and *Z. elianahenrichae* sp. nov. by the FW, which is similarly falcate but less pointed; by the generally darker and homogeneous orange coloration, with post-median and submarginal bands absent or weakly developed on the upperside of both wings; FW submarginal area near the apex and marginal area along the outer margin coalesced, wider and dark brown. Females (Fig. 13G, H) can be distinguished from females of *Z. crawfordhilli* sp. nov. by the upperside of the wings basal and post-median areas along the outer margin, orange to dark orange and yellow to yellowish orange, repectively, and two-tone wing underside pattern not as evident; from *Z. pythagoras* by the FW apex, considerably less falcate; from *Z. ellops* and *Z. elianahenrichae* sp. nov. by the wing upper and underside basal and post-median areas, and marginal and submarginal areas near the apex notably darker than other areas, with a two-tone pattern of coloration, although subtler than in *Z. crawfordhilli* sp. nov., variably darker in those areas.

Description

Head: Eyes reddish brown and naked; labial palpus creamy white ventrally, dark orange to reddish brown dorsally and at the tip; antennal length about one-third of the forewing length, segments dark brown with some ventral creamy white scaling; club slender and elongated, tip dark orange to reddish brown. Female as in male, but usually lighter in colour, pale orange to orange.

Thorax: Dorsally orange to dark orange with scattered brownish and greenish scaling; ventrally orange to dark orange, with area between legs creamy white; forelegs with creamy white scales in the tarsus; mid-leg femora, tibiae and tarsi and hindleg tibiae and tarsi creamy white, speckled with pale orange to reddish brown scales. Female as in male, but usually lighter in colour, pale orange to orange.

Wing size and shape: Forewing length, medium. Forewing costal margin convex; apex pointed and falcate; outer margin sinuous, smooth to slightly crenulated; inner margin straight, emargination before tornus developed, about one-third the length of the inner margin. Hindwing with slight emargination at Sc–Rs; outer margin rounded, smooth to slightly crenulated, with a developed projection at 2A; inner margin almost straight. Female larger than male, and FW shape rounder and more falcate; emargination before tornus developed; hindwing proportionately larger than male; emargination at Sc–Rs developed; apex projected at Rs; outer margin straighter than male; inner margin moderatedly emarginated near the tornus.

Wing colour and pattern, upper side: Ground colour of both wings orange to dark orange with brown to dark brown markings, fore- and hindwings of similar ground colour. Forewing basal, median and submarginal area along the outer margin usually coalesced; median and post-median bands faint or absent; submarginal area near the apex and marginal area coalesced, brown to dark brown, along the outer margin to the apex; discal spot of the same colour, usually large; presence of hyaline areas in M_3–CuA_1 and CuA_1–CuA_2 on the median band variable, but usually faint or absent. Hindwing areas of the same colour, orange to dark orange; median band slightly developed; discal spot absent; post-median and submarginal bands faint, more noticeable near the costal margin; border ocelli faint or absent; anal fold lighter in colour; tornal projection at 2A usually darker with some creamy white scaling. Female forewing basal area darker than post-median and submarginal areas along the outer margin, orange to dark orange; post-median and submarginal areas along the outer margin yellow to pale orange; discal spot, submarginal area near the apex and marginal area brown to dark brown, the two latter coalesced; median and post-median bands usually faint, so that the basal and post-median band intermingle. Hindwing basal, median, post-median, submarginal and submarginal areas orange to dark orange; median, post-median and submarginal areas usually lighter, yellowish orange to orange; median, post-median and submarginal bands faint, more noticeable near the costal margin; discal spot absent; apex suffused with dark brown; border ocelli faint or absent; anal fold lighter in colour; tornal projection at 2A usually darker with some creamy white scaling.

Wing colour and pattern, underside: Ground colour of both wings reddish brown to brown, with random speckles of scales lighter and darker than the ground colour in a ripple pattern. Forewing areas of similar colour, with post-median and submarginal areas along the outer margin slightly lighter; all bands noticeable, slightly darker than the ground colour, but submaginal band from the inner margin to CuA_1 darker and more distinct; border ocelli faint, formed by dark brown and creamy white scales, scattered near the apex. Hindwing areas similar in colour to the FW; all bands noticeable, slightly darker than the ground colour, but median and post-median bands and the posterior part of umbra darker and more distinct. Female forewing basal, submarginal area near the apex and marginal area slightly darker than other areas and similar in colour, orange to brown; post-median and submarginal areas along the outer margin, pale yellow to yellow; all bands noticeable, orange to brown. Hindwing basal area darker, light brown to brown; median, post-median and submarginal areas pale yellow to yellow; marginal area yellow to orange; all bands notiaceable, orange to brown, but median and post-median bands and the posterior part of umbra darker and more

distinct; border ocelli faint, formed by dark brown and creamy white scales; tornal projection at 2A usually with some creamy white scaling.

Abdomen: Dorsally uniform orange to dark orange; ventrally reddish brown to brown. Female orange to dark orange, ventrally orange to brown.

Male genitalia (Fig. 15K): Tegumen trapezoidal in lateral view, dorsally wider, strongly attached to the uncus, and attached to the gnathos only by membranes; appendix angularis hooked; saccus short, not projected anteriorly, dorsal projection of the saccus 'C' shaped and projected dorsad at a right angle; uncus about the same size as the tegumen, semitubular, thin and lightly curved, with a well-developed median dorsal ridge, distally hooked and with a ventral callus; gnathos laterally curved, dorsally thin, produced ventrad, arms parallel, with ventral part of the gnathos bar shaped and fused medially; valva externally covered with short setae; costa long and curved, developed anteriad, with two projections, one smaller, between the costa and the harpe, and another at the end of the harpe; sacculus triangular, ampulla developed and rounded; aedeagus as long as the length of the tegumen and uncus combined, cylindrical and bifid distally, without cornuti; manica inserted slightly anterior to the half of the aedeagus; fultura inferior thin, bar shaped.

Female genitalia (Fig. 17G, H): Tergum VIII triangular, ventrally attached to the sides of the lamella postvaginalis and dorsally to the lamella antevaginalis by a strong dorsally projected loop, this with a small anterior projection; papilla analis rounded and with short setae, projecting the apophysis posterioris; lamella antevaginalis assymetrical, connected to the sides of the lamella postvaginalis by lightly sclerotized projections, left side much wider and larger than the right; lamella postvaginalis longer than wide, anterior area tapering and with a small membranous area, posterior edge slightly indented; seminal duct close to the base of the ductus bursae; posterior half of the ductus bursae bulbous, with corpus bursae laterally compressed, about the same length of the ductus bursae, bearing two parallel signa, which are thin and long, formed by minute sclerotized bumps.

Discussion

The description of *Z. mirandahenrichae* sp. nov. is based on 42 barcoded specimens, 19 males and 14 females, from Costa Rica (Alajuela, Guanacaste and Heredia), deposited at the DZUP, INBIO and UPENN, and nine barcoded specimens, eight males and one female, from Ecuador deposited at the FLMNH. Only barcoded specimens are designated as paratypes, although other specimens were examined at the INBIO and USNM. This species is similar to and frequently misidentified as *Z. isidora* from the Amazon basin, Guianas and Atlantic forests owing to the somewhat similar wing shape and coloration of the wing upper and undersides. This species, according to the data presented by Janzen & Hallwachs (2017), is not as common as *Z. ellops* and *Z. crawfordhilli* sp. nov. and, similarly to *Z. crawfordhilli* sp. nov. and *Z. elianahenrichae* sp. nov., it occurs on the Atlantic slopes of Costa Rica. This species was reared multiple times by Janzen & Hallwachs (2017), on *C. arborea*, *C. corymbosa* and *C. sylvestris*. Most immature stages used *C. arborea* (~82% of the records), which is likewise the preferred host plant of *Z. elianahenrichae* sp. nov. and *Z. crawfordhilli* sp. nov, but it is never used by *Z. ellops* in Costa Rica.

Distribution

Probably widespread in Central America, except the Antilles, and Trans-Andean South America, in northwestern and western Colombia, Costa Rica, western Ecuador, Mexico and Panamá; occurring in forest habitats from low to mid-elevations (Fig. 21). It may occur in the remaining countries of Central America, except the Antilles, western Peru and northwestern Venezuela.

Etymology

Zaretis mirandahenrichae sp. nov. is named for Miranda Henrich in recognition of her mother Charlotte Hill's generous support for taxonomic resolution of the caterpillar parasitoids of this and many other species of Lepidoptera inhabiting the Área de Conservación Guanacaste rain forest.

Examined material

See Supporting Information, Appendix S1.

ZARETIS ELIANAHENRICHAE DIAS SP. NOV.

(FIGS 14A–D, 15L, 17I, J, 18C, D, 21; SUPPORTING INFORMATION, APPENDIX S6)

[urn:lsid:zoobank.org:act:430E1AD4-BD48-4F5B-A906-30B2A47FD113]

Type material

Male holotype with the following labels: /HOLOTYPUS /HOLOTYPE *Zaretis elianahenrichae* Dias det. 2016 / Voucher: D.H. Janzen & Winnie Hallwachs caterpillar (Lepidoptera) DB: http://janzen.sas.upenn.edu Área de Conservación Guanacaste, Costa Rica [Guanacaste, Área de Conservación Guanacaste, Sector Pitilla, Sendero Orosilito, 900 m (10.98332, –85.43623 [10°58′60″N, 85°26′10″W]), 8-XI-2003, Rios *leg. ex larvae* in *Casearia arborea*], 03-SRNP-21709 / LEGS AWAY FOR DNA / DZ 30.203 / (DZUP). Allotype female with the following labels: /ALLOTYPUS / ALLOTYPE *Zaretis elianahenrichae* Dias det. 2016 / Voucher: D.H. Janzen & Winnie Hallwachs caterpillar (Lepidoptera) DB: http://janzen.sas.upenn.edu Area de

Conservación Guanacaste, Costa Rica [Guanacaste, Área de Conservación Guanacaste, Sector Del Oro, Sendero Puertas, 400 m (11.01087, –85.48817 [11°0′39″N, 85°29′17″W]), 18-VI-2003, Garcia *leg. ex larvae* in *Casearia sylvestris*], http://janzen.sas.upenn.edu 03-SRNP-15898 /LEGS AWAY FOR DNA / DNA FER036 wg, EF1a, CAD /DZ 30.113 / (DZUP).

Paratypes: **COSTA RICA, Alajuela,** Área de Conservación Guanacaste, *San Cristobal, Buenos Aires*, 400 m, 1 #m, 24.XI.2006, Cano leg., 06-SRNP-9573 (UPENN); *San Cristobal, Puente Palma*, 460 m, 1 #m, 28.XI.2006, Córdoba leg., 06-SRNP-9681 (UPENN); **Guanacaste,** Área de Conservación Guanacaste, *Brasilia, Morales*, 440 m, 1 #m, 10.XI.2011, Carmona leg., 11-SRNP-66261 (UPENN); *Del Oro, Sendero Puertas*, 400 m, 1#m & 2 #f, 19.IX.2003, Rios leg., 03-SRNP-28921, 03-SRNP-15897, 04-SRNP-27147 (UPENN); *Del Oro, Sendero Puertas*, 400 m, 1 #f, 19.IX.2003, Rios leg., 03-SRNP-28921 (UPENN); 1 #f, 26.IX.2005, Cantillano leg., 05-SRNP-24281 (UPENN); *Pitilla, Bullas*, 440 m, 1 #f, 29.VI.2012, Calero leg., 12-SRNP-71521 (UPENN); *Pitilla, Ingas*, 580 m, 1 #f, 5.VII.2012, Rios leg., 12-SRNP-31086 (UPENN); *Pitilla, Loaiciga*, 445 m, 1 #m, 29.VI.2004, Rios leg., DZ 30.112 (DZUP); 1 #f, 21.VII.2003, Moraga leg., 03-SRNP-20263 (UPENN); *Pitilla, Medrano*, 380 m, 1 #m & #f, 11.IX.2012, Calero leg., 12-SRNP-72120, 12-SRNP-72121 (UPENN); 1 #m, 4.VII.2012, Calero leg., 12-SRNP-71601 (UPENN); 1 #m, 4.VII.2012, Martínez leg., 12-SRNP-71603 (UPENN); 1 #m, 5.VII.2012, Calero leg., 12-SRNP-71664 (UPENN); *Pitilla, Pasmompa*, 440 m, 1 #m, 30.III.2003, Cantillano leg., 03-SRNP-1845 (UPENN); *Pitilla, Quebradona*, 475 m, 1 #f, 24.X.2010, Calero leg., 10-SRNP-73168 (UPENN); *Pitilla, Sendero Evangelista*, 660 m, 1 #m, 15.X.2004, Rios leg., 04-SRNP-55792 (UPENN); *Pitilla, Sendero Memos*, 740 m, 1#m & 1 #f, 21.IV.2005, Rios leg., DZ 30.209 (DZUP), 05-SRNP-31614 (UPENN); *San Cristobal*, 460 m, 1 #m, 4.IX.2006, Sihezar leg., 06-SRNP-7337 (UPENN); **MEXICO, Chiapas,** La Independencia, *San Antonio Buena Vista,* 1 #m, 1.VIII.1992, Ibarra leg., AIV194 (UNAM).

Diagnosis

Zaretis elianahenrichae sp. nov., as with most species of the genus, is somewhat variable and similar to its congeners. This species is likely to be sympatric with *Z. ellops*, *Z. pythagoras*, *Z. delassisei*, *Z. crawfordhilli* sp. nov. and *Z. mirandahenrichae* sp. nov. *Zaretis elianahenrichae* sp. nov. strikingly resembles *Z. ellops*, but the male genitalia are distinct; the uncus is longer, thinner and curved, with a small distal callus; and the dorsal and ventral halves of the gnathos are about the same size (Fig. 15L). Males (Fig. 14A, B) can be externally distinguished from *Z. crawfordhilli* sp. nov. and *Z. mirandahenrichae* sp. nov. by the generally much lighter and speckled coloration, with post-median and submarginal bands usually present in both uppersides of the wings, especially the HWD post-median band, which usually runs to the tornal projection at 2A; additionally, *Z. elianahenrichae* sp. nov. can be distinguished from *Z. crawfordhilli* sp. nov. by the fully developed emargination of the inner margin of the FW at the tornus; and from *Z. pythagoras* and *Z. delassisei* by the absence of a purplish sheen on the FWD when viewed obliquely. Additionally, it can be distinguished from *Z. pythagoras* by the lighter colour of the upperside of the wings, pale orange to orange; and from *Z. delassisei* by the FWD pale orange to orange coloration not restricted to the basal and part of the post-median areas and the HW tornal projection at 2A longer; and from *Z. ellops* by the shape of the FW apex, moderately to strongly falcate; coloration of the submarginal area near the apex and the marginal area, solid pale orange to orange; bands of the wings upperside generally darker and developed, orange to brown; and HW tornal projection at 2A shorter and wider. Females (Fig. 14C, D) can be distinguished from *Z. crawfordhilli* sp. nov. and *Z. mirandahenrichae* sp. nov. by the generally lighter and homogeneous coloration of basal, post-median and submarginal areas along the outer margin of the upper and undersides of the wings; from *Z. pythagoras* by the shape of the FW apex, considerably less falcate, and the coloration of the post-median and submarginal areas along the outer margin of the FW, lighter and never suffused with scales of different colour; and from *Z. ellops* by the coloration of the the submarginal area near the apex and the marginal area, solid brown to dark brown; FWD and HWD dissimilar in colour, basal and post-median areas and submarginal area along the outer margin darker in HW; and HW tornal projection at 2A longer and thinner; females of *Z. delassisei* are unknown.

Description

Head: Eyes reddish brown and naked; labial palpus creamy white ventrally, pale orange to orange dorsally and at the tip; antennal length about one-third of the forewing length, segments orange with some ventral creamy white scaling; club slender and elongated, tip pale orange to orange. Female as in male, but usually lighter in colour, pale yellow to yellow.

Thorax: Dorsally pale orange to orange with scattered brownish and greenish scaling; ventrally pale orange to orange, with area between legs creamy white; forelegs with creamy white scales in the tarsus; midleg femora, tibiae and tarsi and hindleg tibiae and tarsi creamy white, speckled with pale orange to reddish brown scales. Female as in male, but usually lighter in colour, pale yellow to yellow.

Wing size and shape: Forewing length, medium. Forewing costal margin convex; apex pointed and falcate; outer margin sinuous, slightly crenulated to crenulated; inner margin straight, emargination before tornus developed, about one-third the length of the inner margin. Hindwing with slight emargination at Sc–Rs; outer margin rounded, smooth to slightly crenulated, with a developed projection at 2A, long and thin; inner margin almost straight. Female larger than male, and FW shape rounder and more falcate; emargination before tornus developed; hindwing proportionately larger than male; emargination at Sc–Rs developed; apex projected at Rs; outer margin straighter than male; inner margin emarginated near the tornus.

Wing colour and pattern, upper side: Ground colour of both wings pale orange to orange with light brown to brown markings, fore- and hindwings of similar ground colour. Forewing basal, median and submarginal areas along the outer margin about the same colour, but post-median band slightly lighter; median and post-median bands faint; submarginal area near the apex and marginal area coalesced, brown to dark brown, along the outer margin to the apex; discal spot of the same colour, usually faint; presence of hyaline areas in M_3–CuA_1 and CuA_1–CuA_2 on the median band variable, but usually present. Hindwing areas of the same colour, orange to reddish brown; median, post-median and submarginal bands faint, more noticeable near the costal margin; discal spot absent; border ocelli faint or absent; anal fold lighter in colour; tornal projection at 2A usually darker with some creamy white scaling. Female forewing basal, post-median and submarginal area along the outer margin usually coalesced, pale yellow to yellow; discal spot, submarginal area near the apex and marginal area brown to dark brown, the two latter coalesced; median and post-median bands faint or absent. Hindwing marginal area usually darker, pale orange to orange, lighter towards the wing base; median, post-median and submarginal bands faint, more noticeable near the costal margin; discal spot absent; border ocelli faint or absent; anal fold lighter in colour; tornal projection at 2A usually darker with some creamy white scaling.

Wing colour and pattern, underside: Ground colour of both wings reddish brown to brown, with random speckles of scales lighter and darker than the ground colour in a ripple pattern. Forewing areas of similar colour, post-median and submarginal areas along the outer margin lighter, with yellowish scaling; all bands noticeable, slightly darker than the ground colour, but submaginal band from the inner margin to CuA_1 darker and more distinct; border ocelli faint, formed by dark brown and creamy white scales, scattered near the apex. Hindwing areas similar in colour to the FW; median and post-median areas lighter, with yellowish scaling; all bands noticeable, slightly darker than the ground colour, but median and post-median bands and the posterior part of umbra darker and more distinct. Female forewing basal area pale yellow to yellow; post-median and submarginal areas along the outer margin pale yellow; marginal and submarginal areas near the apex darker than other areas, orange to brown; all bands noticeable, orange to brown. Hindwing basal area darker, pale yellow to yellow; median, post-median, submarginal and marginal areas pale yellow; all bands noticeable, orange to brown, but median and post-median bands and the posterior part of umbra darker and more distinct; border ocelli faint, formed by dark brown and creamy white scales; tornal projection at 2A usually with some creamy white scaling.

Abdomen: Dorsally uniform pale orange to orange; ventrally reddish brown to brown. Female dorsally pale yellow to yellow and ventrally darker, pale yellow to yellow.

Male genitalia (Fig. 15L): Tegumen trapezoidal in lateral view, dorsally wider, strongly attached to the uncus, and attached to the gnathos only by membranes; appendix angularis hooked; saccus short, not projected anteriorly, dorsal projection of the saccus 'C' shaped and projected dorsad at a right angle; uncus about the same size as the tegumen, semitubular, thin and lightly curved, with a well-developed median dorsal ridge, distally hooked and with a developed ventral callus; gnathos laterally slightly curved, dorsally thin, produced ventrad, arms parallel, ventral part of the gnathos bar shaped and fused medially; valva externally covered with short setae; costa long and curved, developed anteriad, with two developed projections, one between the costa and the harpe, and another at the end of the harpe; sacculus triangular, ampulla developed and rounded; aedeagus longer than the length of the tegumen and uncus combined, cylindrical and bifid distally, without cornuti; manica inserted slightly anterior to the half of the aedeagus; fultura inferior thin, bar shaped.

Female genitalia (Fig. 17I, J): Tergum VIII triangular, ventrally attached to the sides of the lamella postvaginalis, and dorsally to the lamella antevaginalis by a dorsally projected loop, thickened after the loop; papilla analis rounded and with short setae, projecting the apophysis posterioris; lamella antevaginalis assymetrical, connected to the sides of the lamella postvaginalis by wide sclerotized projections; left side wider and larger than the right; lamella postvaginalis longer than wide, anterior area with a small membranous area, and posterior edge bilobed; seminal duct close to the base of the ductus bursae; corpus

bursae laterally compressed, about the half the length of the ductus bursae, bearing two parallel signa, these are thin and long, formed by minute sclerotized bumps.

Discussion

The description of *Z. elianahenrichae* sp. nov. is based on 26 barcoded specimens, 14 male and 11 female specimens from Costa Rica (Guanacaste and Alajuela) deposited in UPENN, two male and two female specimens, deposited at the DZUP, and one male deposited at the UNAM; only barcoded specimens are designated as paratypes. This species is strikingly similar to *Z. ellops*, although easily and reliably distinguished from it by examining the genitalia. *Zaretis elianahenrichae* sp. nov., according to the data presented by Janzen & Hallwachs (2017), is not as common as *Z. ellops* and *Z. crawfordhilli* sp. nov. Similar to *Z. crawfordhilli* sp. nov. and *Z. mirandahenrichae* sp. nov., it occurs on the Atlantic slopes of Costa Rica. This species was reared multiple times by Janzen & Hallwachs (2017) (Fig. 18C, D), on *C. arborea*, *C. sylvestris* and one record on *Zuelania guidonia*. Most immature stages use *C. arborea* (~56% of the records) and *C. sylvestris* (40% of the records) as host plants. The former is the preferred host plant of both *Z. mirandahenrichae* sp. nov. and *Z. crawfordhilli* sp. nov., but the latter is at best secondary to all species of *Zaretis* occurring in Costa Rica, although frequently cited as host plants of *Z. strigosus* and *Z. ellops* elsewhere.

Distribution

Probably widespread in Central America, except the Antilles, and Trans-Andean South America; however, it is currently known to occur only in forest habitats from 380 to 900 m in Costa Rica, Mexico (Chiapas) and western Ecuador (Fig. 21). It may occur in the remaining countries of Central America, except the Antilles, and other countries in Trans-Andean South America.

Etymology

Zaretis elianahenrichae sp. nov. is named for Eliana Henrich, in recognition of her mother Charlotte Hill's generous support of taxonomic resolution of the caterpillar parasitoids of this and many other species of Lepidoptera inhabiting the Área de Conservación Guanacaste rain forest.

Examined material

See Supporting Information, Appendix S1.

List of unavailable names and *nomina nuda* not assigned to any taxon

Zaretes [sic] *isidora vulpina lutulenta* Talbot, 1923: p. 52; infrasubspecific, nom. nud.

Zaretes [sic] *isidora vulpina* f. *polcarea* Talbot, 1923: p. 52; infrasubspecific, nom. nud.

PHANTOS DIAS GEN. NOV.

(FIGS 22–27; SUPPORTING INFORMATION, APPENDIX S6)

[urn:lsid:zoobank.org:act:9671D9C1-D0B0-4030-9482-BEE22AEA59DB]

Type species: *Nymphalis callidryas* R. Felder, 1869, here designated.

Diagnosis

Phantos gen. nov. is closest in appearance to *Zaretis*, and it can be distinguished from other taxa of Charaxinae by the set of characters cited above for that genus. It can be distinguished from species of *Zaretis* chiefly by the coloration of the upperside of the wings, which are pearly white or yellowish or greenish white, sometimes with an orangish or yellowish suffusion along the outer margin, with light to dark brown markings only on the submarginal and marginal areas; the underside ground colour is beige, brown, yellow or green, speckled with light and dark shades of these colours. Additionally, *Phantos* gen. nov. can be distinguished by the labial palpus, which is distally beige to light brown, speckled with creamy white scales (Fig. 23A–C); the slender thorax; veins R_1, R_2 and R_3 partly anastomosed to Sc; discal spot (element 'e') absent on the upperside (Fig. 22B); external margin of the HW at vein M_3 projected in both sexes, short and pointed in males, long and spatulate in females; tornal projection at 2A at the HW weakly to moderately developed (Fig. 22A); male genitalia with a pit between the tegumen and uncus; uncus short, curved and evenly keeled; saccus posteriorly projected; gnathos 'C' shaped, with the dorsal half always much larger than the ventral; projection between the costa and the harpe weakly developed (Fig. 25); and relative size and shape of the head capsule scoli of the larvae thin, curved posteriorly and longer than the height of the head capsule; larval colour pattern similar to species of *Siderone*, dorsally lighter posterior to the A2 hump. A key to species of *Phantos* gen. nov. is presented below.

Description

Head: Eyes reddish brown and naked; labial palpus creamy white ventrally, distally beige to light brown, speckled with creamy white scales (Fig. 23A); antennal length about one-third of the forewing length, segments orange to yellowish orange with some ventral creamy white scaling; club slender and elongated, tip orange to yellowish orange. Female as in male.

Thorax: Slender, dorsally mostly creamy white speckled with greyish scales; ventrally beige speckled with creamy white scales; legs mostly beige speckled with creamy white scales, tibiae and tarsi creamy white or speckled with creamy white scales (Fig. 23D, E). Female as in male.

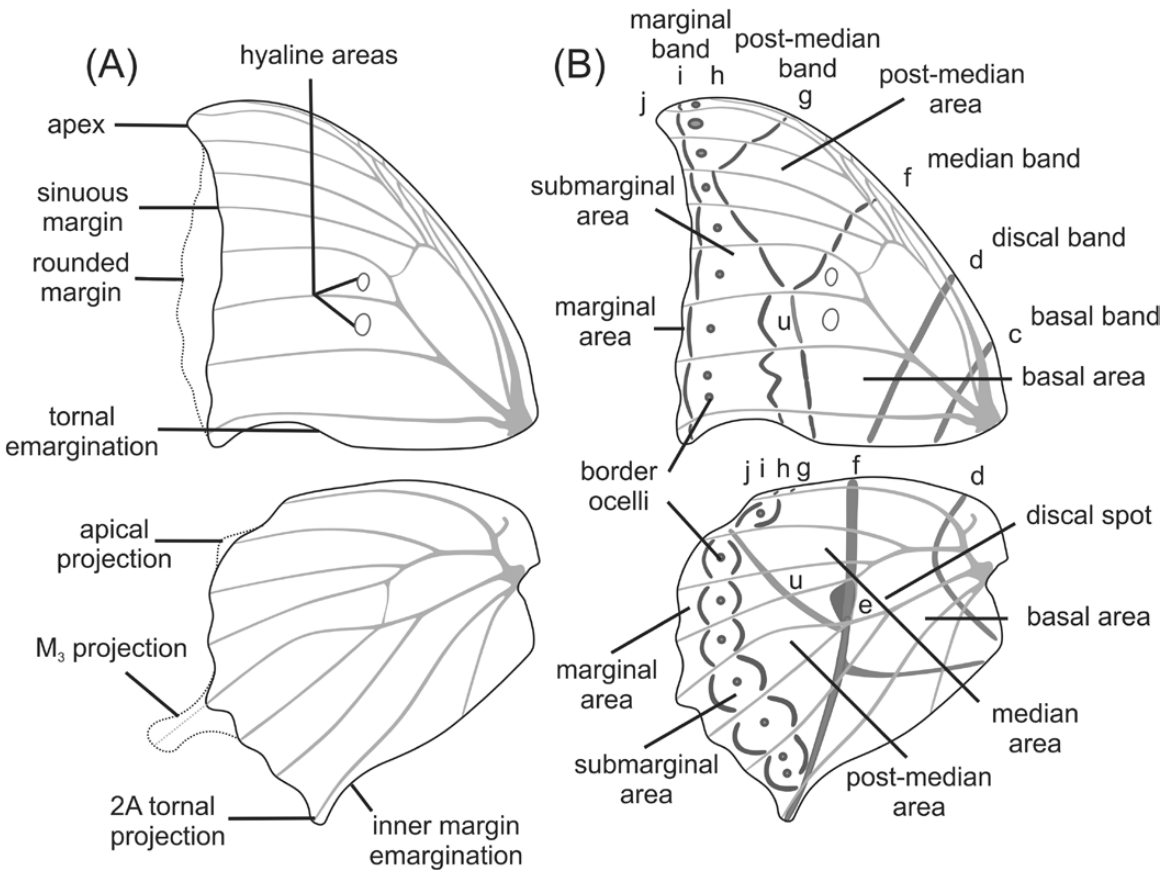

Figure 22. Wings of ***Phantos*** Dias **gen. nov.**; morphology and terminology. A, venation. B, colour pattern of the underside.

Figure 23. Head and thoracic appendices of ***Phantos*** Dias **gen. nov.** A, head and labial palpus, ventral. B, C, labial palpus. B, outer. C, inner. D, E, foreleg, lateral. D, male. E, female.

Wing size and shape (Fig. 22A): Forewing length, 3.1–3.9 cm. Forewing costal margin convex; apex pointed, slightly to moderately falcate; outer margin slightly sinuous to sinuous, smooth to slightly crenulated; inner margin straight, emargination before tornus shallow and long, about one-third of the length of the inner margin. Hindwing with emargination at Sc–Rs, outer margin angled and projected beyond the outer

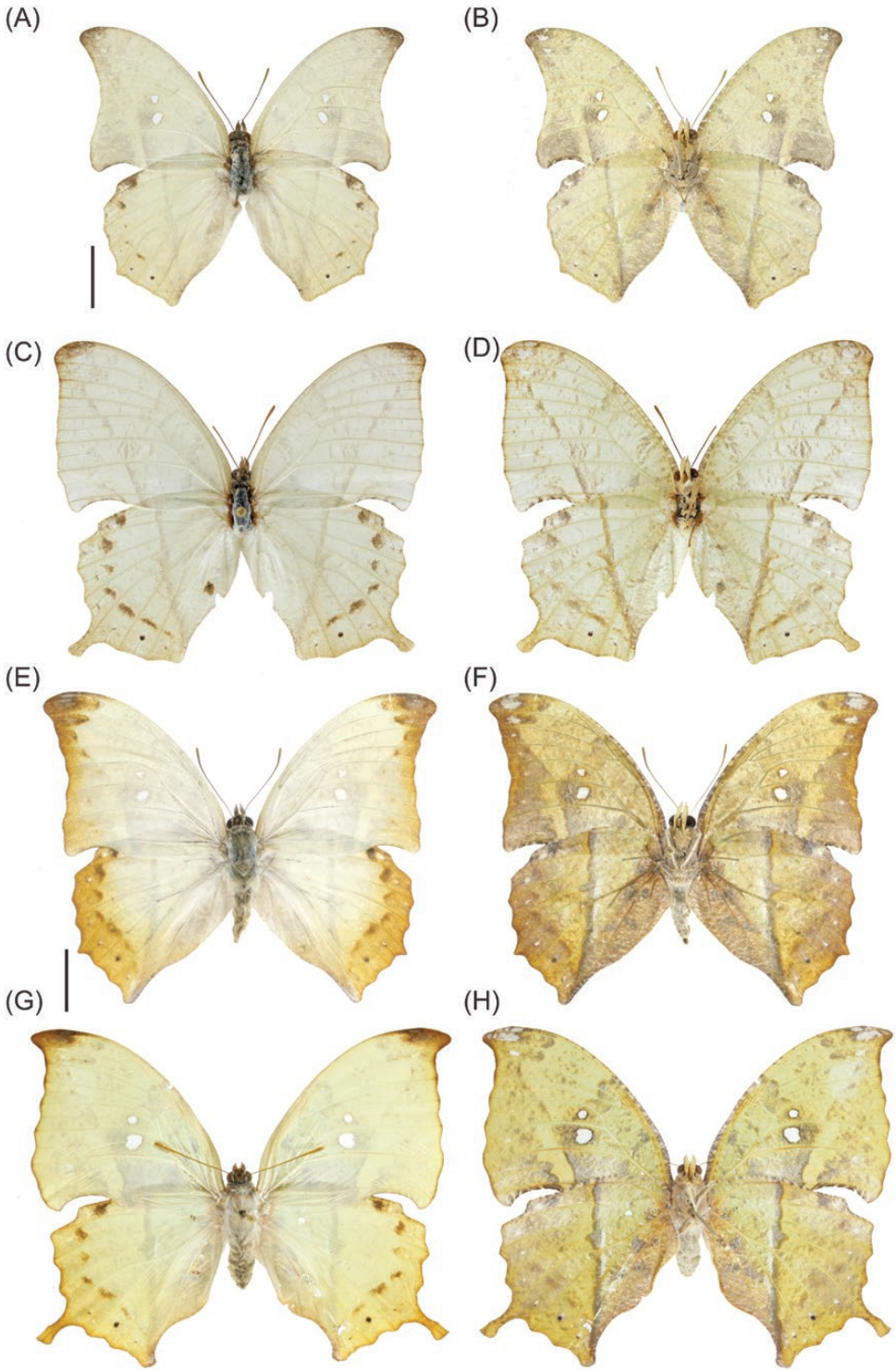

Figure 24. Imagoes of species of ***Phantos*** Dias **gen. nov.**, dorsal and ventral. A–D, ***P. callidryas*** (R. Felder, 1869) **comb. nov.** A, B, male. C, D, female. E–H, ***P. opalina*** (Godman & Salvin, [1884]) **comb. nov.**, **stat. rev.** E, F, male. G, H, female. Scale bars represent 1 cm.

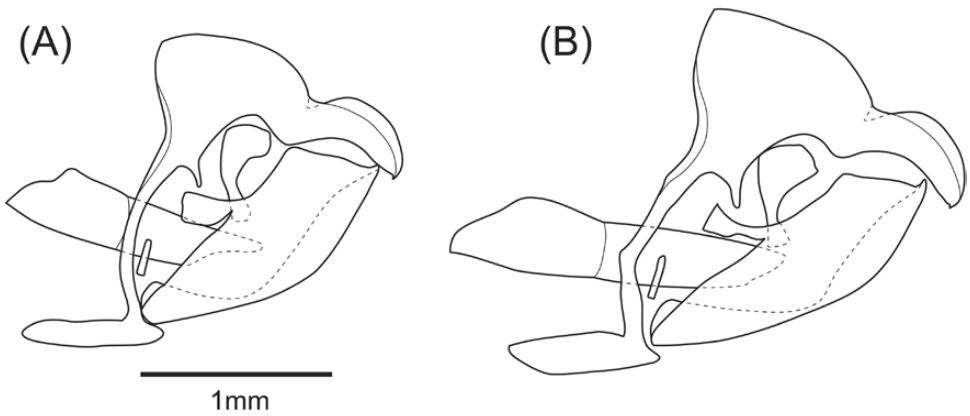

Figure 25. Male genitalia of species of ***Phantos*** Dias **gen. nov.**, lateral. A, ***P. callidryas*** (R. Felder, 1869) **comb. nov.** B, ***P. opalina*** (Godman & Salvin, [1884]) **comb. nov.**, **stat. rev.**

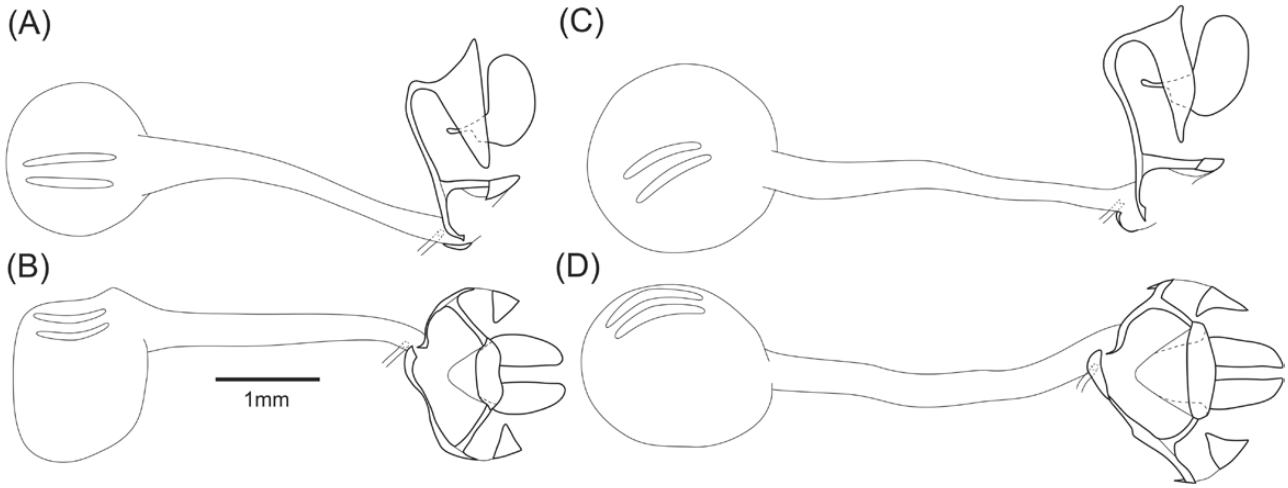

Figure 26. Female genitalia of species of ***Phantos*** Dias **gen. nov.** lateral and ventral. A, B, ***P. callidryas*** (R. Felder, 1869) **comb. nov.** C, D, ***P. opalina*** (Godman & Salvin, [1884]) **comb. nov.**, **stat. rev.**

margin at M_3, smooth to crenulated; tornus slightly to moderately projected at 2A; inner margin slightly emarginated near the tornus. Female larger than male, and wing shape different; FW outer margin rounded; HW emargination at Sc–Rs developed; apex projected at Rs; outer margin rounder, with a long, spatulated projection at M_3, crenulated; inner margin moderatedly to strongly emarginated near the tornus.

Wing colour and pattern, upper side: Bands and areas equivalent to *Zaretis*, but pattern much reduced; ground colour of both wings mostly pearly white or yellowish white, with or without an orangish or yellowish suffusion along the outer margin. Marginal and submarginal areas light to dark brown, formed by the coalesced part of the post-median band (element 'g') at the apex and the marginal band (elements 'h', 'i' and 'j') along the outer margin. Hindwing usually with two distinct bands, formed by interrupted light to dark brown markings; the post-median and submarginal bands run regularly along the outer margin to the inner margin before the tornal projection at 2A, frequently with rudimentary border ocelli (element 'h') between them; anal fold similar in colour to the rest of the HW, with some beige scaling. Female as in male, but usually lighter in colour.

Wing colour and pattern, underside (Fig. 22B): Ground colour of both wings beige, brown, yellow or green, speckled with light and dark shades of these colours ('ripple pattern'). Forewing pattern of bands and areas equivalent to *Zaretis*; basal, discal, median (including the discal spot), post-median and marginal bands subtle, beige to brown; median and post-median bands close to each from the outer margin to CuA_1; ground colour of the different areas variable, but the basal, submarginal and marginal areas usually darker than post-median area; border ocelli in R_3–R_4, R_4–R_5

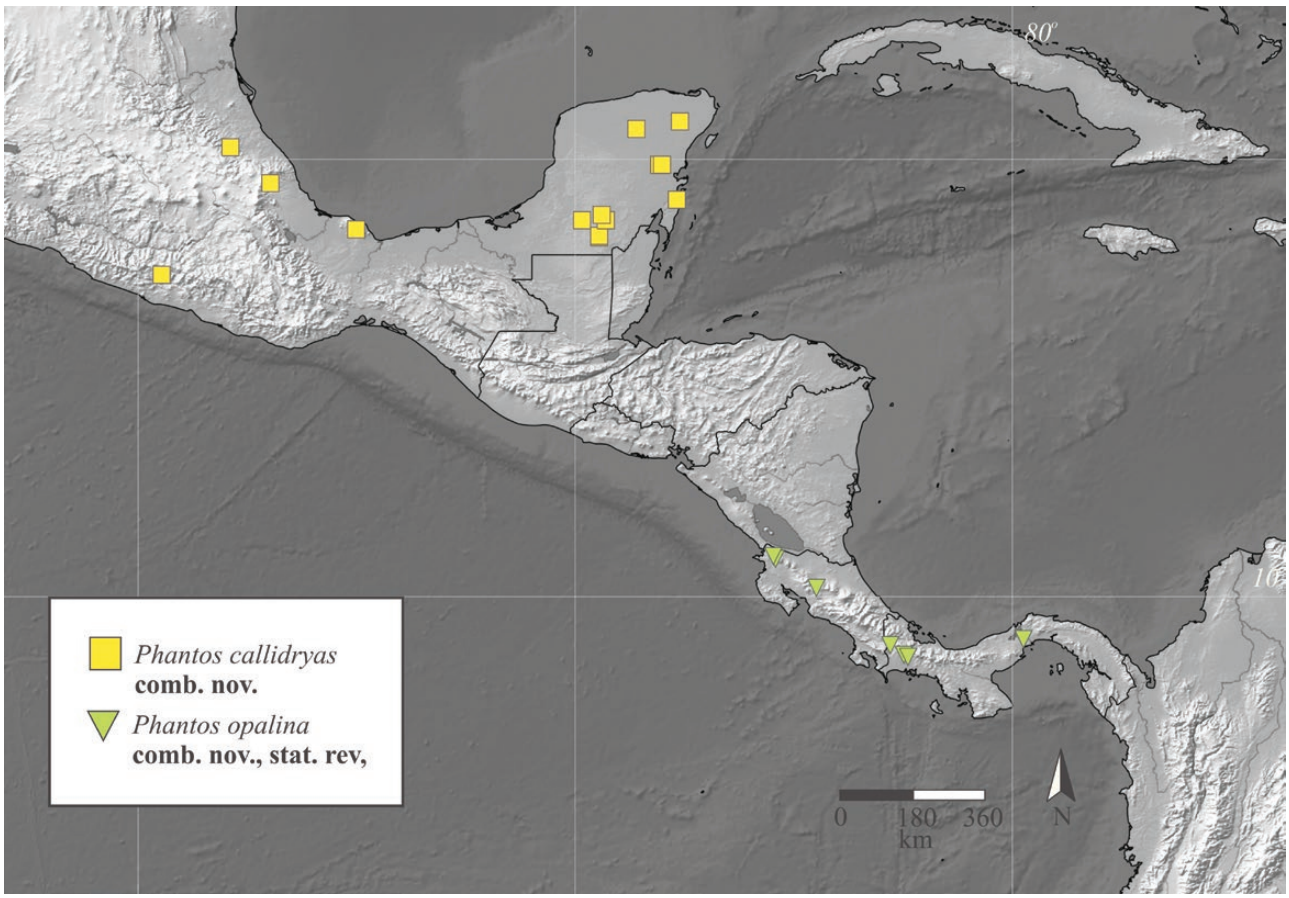

Figure 27. Distribution of ***Phantos callidryas*** (R. Felder, 1869) **comb. nov.** and ***P. opalina*** (Godman & Salvin, [1884]) **comb. nov.**, **stat. rev.**, based on the labels of the examined specimens.

and R_5–M_1 usually greatly enlarged. Hindwing pattern of bands and areas equivalent to *Zaretis*; anterior part of the median band and posterior part of the umbra forming a continuous and marked line from the costal to the inner margin, similar to the midrib of a dead leaf; discal, post-median and marginal bands and the remainder of the median band and umbra subtle, beige to brown; rudimentary border ocelli between post-median and submarginal bands. Female as in male, but usually lighter in colour.

Abdomen: Dorsally and laterally creamy white speckled with thin grey scales; ventrally beige speckled with creamy white scales. Female as in male.

Male genitalia (Fig. 25): Tegumen trapezoidal in lateral view, dorsally wider and humped, attached to the anterior part of the uncus forming a median pit, and attached to the gnathos only by membranes; appendix angularis hooked; saccus short, projected anteriorly, dorsal projection of the saccus 'C' shaped and projected dorsad at about a right angle; uncus semitubular and curved, with a well-developed and even keel and distally pointed; gnathos laterally slightly curved, dorsal half wider than ventral, produced ventrad, arms parallel, ventral part of the gnathos bar shaped, slighty angled in ventral view and fused medially; valva externally covered with short setae, costa long and curved, developed anteriad, end of the harpe pointed, angled between the costa and the harpe, sacculus triangular, ampulla developed and rounded; aedeagus short, cylindrical and bifid distally; vesica without cornuti; manica inserted about the half of the aedeagus; fultura inferior thin, bar shaped.

Female genitalia (Fig. 26): Tergum VIII triangular and thin, dosally and anteriorly projected, posteriorly attached to the lamella antevaginalis by a sclerotized loop, ventrally attached to the sides of the lamella postvaginalis; papilla analis rounded and with short setae, projecting the apophysis posterioris; lamella antevaginalis assymetrical, connected to the sides of the lamella postvaginalis by slightly sclerotized prejections; lamella antevaginalis thin, left side larger than the right; lamella postvaginalis wider

than long, with a membranous posterior projection longer than the lamella postvaginalis, posterior edge of the lamella postvaginalis slightly convex to slightly bilobed; seminal duct close to the base of the ductus bursae; corpus bursae rounded, half the length of the ductus bursae, bearing two parallel signa, which are thin and long, formed by minute sclerotized bumps.

Immature stages: Generally similar to species of *Zaretis* and *Siderone* (Lichy, 1976; Muyshondt, 1976, 2005). Early instars almost indistinguishable from species of *Zaretis* and *Siderone*, but fifth instar head capsule smoother, scoli curved backwards, longer and thinner in comparison with species of *Zaretis*; projections of A2 smaller and dorsal coloration posterior to A2 lighter than from T1 to A2, and from the same area of species of *Zaretis*; pupa similar to species of *Zaretis*; host plant records all on the Salicaceae, with reliable records on two species of *Casearia*, *C. sylvestris* and *C. nitida* (Lichy, 1976; Muyshondt, 1976; DeVries, 1987; Beccaloni *et al.*, 2008; Janzen & Hallwachs, 2017).

Discussion

Phantos gen. nov. is erected to include two species, *P. callidryas* comb. nov., here designated as the type species of the genus, and *P. opalina* comb. nov., stat. rev., removed from synonymy; *Siderone clara* Staudinger, 1886 is recognized as a junior subjective synonym of the latter name. These species are superficially similar to species of *Zaretis* and, to some extent, of *Siderone*. However, since the middle of the 19th century, several authors have already combined and described species here included in *Phantos* gen. nov. in *Nymphalis*, *Paphia* or *Anaea* because of their peculiar morphology. The anastomosis of R_1, R_2 and R_3 with Sc in the FW, and the presence of projections in M_3 on the HW of males and females, similar to many other species of Anaeini, certainly encouraged authors, such as Godman & Salvin (1884) and Staudinger (1887), to retain them in the catch-all genus *Anaea*, together with other species of uncertain affinity, instead of including them in *Zaretis*. Rydon (1971), in contrast, included the species in *Zaretis*, with some doubts. Nevertheless, it is clear that the genus represents a distinct lineage of Anaeini closely related to *Zaretis* and *Siderone*. Molecular analyses, as shown by the NJ analysis and by EFA Toussaint, FMS Dias, OHH Mielke, MM Casagrande, CP Sañudo-Restrepo, A Lam, J Morinière, M Balke, and R Vila (unpublished data), suggest that *Phantos* gen. nov. is probably sister to *Zaretis* + *Siderone*, rendering *Zaretis*, *sensu* Lamas (2004) and Willmott & Hall (2004), polyphyletic. The description of a new genus to include these species is advisable to convey more information and be less disruptive to taxonomy than the alternative of synonymizing *Zaretis* with *Siderone*.

Etymology

The name of the new genus is derived from the greek word φαντός (‘*phantós*’), meaning ‘visible’, ‘present to the eye or mind’, treated as a singular, masculine noun in the nominative case (ICZN 1999, Art. 11.8). The word ‘*phantós*’ is the root to several English words, such as ‘phantom’ and ‘fantasy’. The name of the new genus is intended to make reference to the popular name of the species included, ghost leafwings (Glassberg, 2007), a name probably given because of their pale colour and swift flight, and additionally to pay tribute to new molecular methods that ‘make visible’ many cryptic species and genera.

Distribution

Neotropical, in forests from about sea level to 1200 m throughout Central America except the Antilles, from Mexico to Panama (Fig. 27).

PHANTOS CALLIDRYAS (R. FELDER, 1869) **COMB. NOV.**

(FIGS 24A–D, 25A, 26A, B, 27; SUPPORTING INFORMATION, APPENDIX S6)

Type material

Probable male syntype of *Nymphalis callidryas* R. Felder, 1869 with the following labels: / 214/ Hedemann Mexico 1870/ *Nymphalis callidryas* Type Feld[er]/ LECTOTYPE #m *Nymphalis callidryas* R. Felder, 1869 by G. Lamas ‘90/ (NHM).

Diagnosis

Phantos callidryas comb. nov. is similar to *P. opalina* comb. nov., stat. rev., but males (Fig. 24A, B) can be distinguished by the shape of the outer margin of the FW, which is strongly sinuous, although the apex is only slightly projected and somewhat rounded in both sexes; in both sexes, outer margins smooth or only slightly crenulated; HW projections at M_3 and at the tornus at 2A comparatively less developed; colour of the wings paler, pearly white, greenish white or yellowish white; yellow or yellowish orange suffusion along the outer margins absent or very faint, especially in males; FWD markings reduced, restricted to the apex anterior to M_1; HWD markings reduced, especially in males; HW inner margin slightly emarginated near the tornus in both sexes (Fig. 24A–D).

Discussion

Phantos callidryas comb. nov. was described based on an unstated number of specimens, but given the wording of the description, it was probably based on a single male specimen, collected in Córdoba, Veracruz, Mexico, by Mr Nieto, during the summer. One specimen that may represent this type is deposited at the NHM and was examined by Godman & Salvin ([1884]) in the second half of the 19th century. A specimen deposited in the above-cited collection with a ‘*Nymphalis callidryas* Type Feld’ label in R. Felder’s handwriting was

informally selected as the lectotype by Gerardo Lamas (unpublished data). However, another label in different handwriting indicates that the specimen was collected by Mr Hedemann in 1870, after the description date. This specimen, the single specimen of this species at the NHM, could have been collected by Mr Hedemann, but given to R. Felder by Mr Nieto. If Mr Hedemann is the true collector, then the date on the black script label is not the collecting date, as Mr Hedemann left Mexico after the execution of Emperor Maximilian in 1867. Perhaps the specimen was brought to the museum after the description of the species, and misleadingly labelled with the collector's name and the date of receipt (S. Gaal-Haszler, personal communication). In view of this conflicting information, no specimen is designated as the lectotype at this time. Rudolf Felder (1869) named this species because of its resemblance to species of pierids of the genus *Callidryas* Boisduval & Le Conte, [1830], now regarded as a junior subjective synonym of *Phoebis* Hübner, [1819] (Pieridae). This similarity was further recognized by Druce (1877), Röber (1916) and D'Abrera (1984), who acknowledged that this species could be mistaken for large pierids when in flight. Immature stages of *P. callidryas* comb. nov. were reared by Muyshondt (1976) on *C. nitida* and *C. sylvestris* and by Lichy (1976) on *C. sylvestris*.

Distribution

From Mexico (Campeche, Colima, Guerrero, Jalisco, Michoacán, Nayarit, Oaxaca, Puebla, Quintana Roo, San Luis Potosí, Sinaloa, Veracruz and Yucatán), Guatemala, Belize, El Salvador and northwestern Honduras, on both the Atlantic and Pacific slopes ('Mesoamerican dominion' *sensu* Morrone, 2014) (Fig. 27). It is not known whether this species is sympatric with *P. opalina* comb. nov., stat. rev., which occurs further south. Detailed distributional data for Mexico was provided by Vargas *et al.* (2008).

Examined material

See Supporting Information, Appendix S1.

PHANTOS OPALINA (GODMAN & SALVIN, [1884]) **COMB. NOV., STAT. REV.**

(FIGS 24E–H, 25B, 26C, D, 27; SUPPORTING INFORMATION, APPENDIX S6)

Type material

Male holotype of *Anaea opalina* Godman & Salvin [1884] with the following labels: /Type HT/ #m/B.M. TYPE Rh 10262 *Anaea opalina* #m G[odman] & S[alvin]/ V[olcán] de Chiriqui 3–400 ft. Champion [leg.]./ Sp. figured./ (NHMUK).

Male holotype of *Siderone clara* Staudinger, 1886 with the following labels: / Holotypus/ Volkan Chiriqui/ Holotype #m *Siderone clara* Staudinger/ [illegible]/ (ZMHU).

Diagnosis

Phantos opalina comb. nov., stat. rev. is similar to *P. callidryas* comb. nov., but it can be distinguished by the shape of the outer margin of the FW, which is slightly convex in males (Fig. 24E, F) and more rounded in females (Fig. 24G, H); apex falcate and pointed in both sexes, especially in females; both sexes with outer margins slightly to strongly crenulated, never smooth; HW projections on the outer margin at M_3 and on the tornus at 2A strongly developed, especially in females; outer margin with a variable, but usually developed yellowish orange suffusion along the outer margin, especially in males; FWD marginal area and submarginal area anterior to M_3 coalesced, dark brown to reddish orange in males; post-median band present but fainter posterior to M_3, orange to dark brown; HWD post-median and marginal bands markings developed, especially in males; HW inner margin strongly emarginated near the tornus in females.

Discussion

Phantos opalina comb. nov., stat. rev. was described based on a single male specimen collected by Mr Champion, on dung near the margin of a forest at 1200 m of elevation (Godman & Salvin, [1884]), on the volcano of Chiriquí (i.e. volcán Barú), Chiriquí, Panamá. This species was illustrated and erroneously identified as *P. callidryas* comb. nov. by Godman & Salvin [1884] in plate 34, figs 9, 10. They decided to describe the above cited specimen only after the examination of the type of *Nymphalis callidryas* R. Felder, 1869 deposited at the NHM, which occurred ~3 months after the publication of the above plate in the Biologia Centrali-Americana series (Lamas, 2017).

Siderone clara Staudinger, 1886 was described based on a single male specimen from the volcano in Chiriquí, Chiriquí, Panama. This specimen was presented by Mr Godman and Mr Salvin to Mr Staudinger, identified as '*Siderone* sp. nov.' Unaware of Godman and Salvin's name, Staudinger (1886) illustrated and gave the name *Siderone clara* Staudinger, 1886 to that specimen, only to correctly recognize it ~1 year later as *Anaea opalina* Godman & Salvin [1884] (Staudinger, 1887). Staudinger (1887) had access to only three males and one then-unknown female of this species; although only two of those males were located by us at the ZMHU. DeVries (1987) stated that he personally trap collected *P. opalina* comb. nov., stat. rev. on only one occasion, noting that this species is rare and very local in Costa Rica. The alleged rarity is supported by the scarcity of specimens of this species in collections and owing to the fact that after several years of intensive collection of Lepidoptera larvae in Costa Rica, *P. opalina* comb. nov., stat. rev. was reared by Janzen & Hallwachs (2017) only twice, once in 1997 and again in 2010, both times on *C. sylvestris* (voucher numbers 97-SRNP-11053 and 10-SRNP-4953).

Distribution
Nicaragua, Costa Rica and Panama (northern 'Pacific dominion' *sensu* Morrone, 2014), on the Altlantic and Pacific slopes from 500 to 1200 m of elevation, in transitional cloud forests (Fig. 27). It is not known whether this species occurs in sympatry with *P. callidryas* comb. nov. further to the north; or if it occurs to the south, beyond the Darién gap.

Examined material
See Supporting information, Appendix S1.

SYNONYMIC CHECKLIST OF *ZARETIS* AND ***PHANTOS*** **GEN. NOV.**

ZARETIS HÜBNER, [1819]

itys (Cramer, 1777) (*Papilio*)
isidora (Cramer, 1779) (*Papilio*)

zethus (Westwood, 1850) (*Siderone*)
var. *cacica* (Staudinger, 1887) (*Siderone*)
isidora leopoldina Fruhstorfer, 1909 (*Zaretes*) [sic]
isidora isidora f. *bisaltina* Fruhstorfer, 1909 (*Zaretes*) [sic] **infrasubspecific**
itys itys f. *monops* Bryk, 1953 (*Zaretis*) **infrasubspecific**
isidora naama (Brévignon, 2009) (*Siderone*) **comb. nov.**, **syn. nov.**

strigosus (Gmelin, [1790]) (*Papilio*)

isidora var. *strigosa* (Staudinger, 1887) (*Siderone*) **preoccupied**
isidora isidora f. *foliacea* Fruhstorfer, 1909 (*Zaretes*) [sic] **infrasubspecific**
isidora russeus Fruhstorfer, 1909 (*Zaretes*) [sic] **syn. nov.**
isidora vulpina Fruhstorfer, 1909 (*Zaretes*) [sic] **syn. nov.**
isidora vulpecula Fruhstorfer, 1909 (*Zaretes*) [sic] **syn. nov.**
ellops mellita (Brévignon, 2009) (*Siderone*) **comb. nov.**, **syn. nov.**

itylus (Westwood, 1850) (*Siderone*)

pseuditys Fruhstorfer, 1909 (*Zaretes*) [sic]
itys f. *pseuditys* Fruhstorfer, 1909 (*Zaretes*) [sic] **preoccupied**

ellops (Ménétriés, 1855) (*Siderone*)

isidora anzuletta Fruhstorfer, 1909 (*Zaretes*) [sic]

syene (Hewitson, 1856) (*Siderone*)
pythagoras Willmott & Hall, 2004 (*Zaretis*)

violacea Salazar & Constantino, 2001 (*Zaretis*) **nom. nud.**

delassisei Choimet, 2009 (*Zaretis*)
falcis Dias, Casagrande & Mielke, 2012 (*Zaretis*)
hurin Dias **sp. nov.**
crawfordhilli Dias **sp. nov.**
mirandahenrichae Dias **sp. nov.**
elianahenrichae Dias **sp. nov.**

PHANTOS Dias **GEN. NOV.**

callidryas (R. Felder, 1869) (*Nymphalis*) **comb. nov.**
opalina (Godman & Salvin, 1884) (*Anaea*) **comb. nov.**, **stat. rev.**
clara (Staudinger, 1886) (*Siderone*) **comb. nov.**

INCERTAE SEDIS

isidora vulpina lutulenta Talbot, 1923 (*Zaretes*) [sic] **infrasubspecific**, **nom. nud.**
isidora vulpina f. *polcarea* Talbot, 1923 (*Zaretes*) [sic] **infrasubspecific**, **nom. nud.**

KEY TO *ZARETIS* AND ***PHANTOS*** **GEN. NOV.**

1. Males and females: upperside of the wings pearly, yellowish or greenish white, sometimes with an orangish or yellowish suffusion along the outer margin, and without discal spot (element 'e'); M_3 projected beyond the external margin of the HW, short and pointed in males, long and spatulate in females ..... *Phantos* sp. nov. (2)
1′. Males and females: upperside of the wings pale yellow to reddish brown with a marked discal spot (element 'e'); M_3 not projected beyond the external margin of the HW ..... *Zaretis* (3)
2. Males and females: upperside of the wings with absent or very faint yellow or yellowish orange suffusion along the outer margins; outer margins usually smooth; FW apex somewhat rounded; FWD markings reduced, restricted to the apex. North and Central America ..... *P. callidryas*
2′. Males and females: upperside of the wings with a variably developed yellow or yellowish orange suffusion along the outer margins; outer margins usually strongly crenulated; FW apex falcate and pointed; FWD markings developed along the marginal and submarginal areas. Central America ..... *P. opalina*

3. Males: FW apex strongly falcate, apex tip wide and rounded; FW outer margin strongly crenulated. Andes. Females: unknown ..... *Z. syene*
3′. Males and females: FW apex variably falcate, but apex tip never wide and rounded; FW outer margin smooth or slightly to moderately crenulated ..... (4)
4. Males: FW basal area reddish brown, and most of the post-median and all submarginal and marginal areas coalesced, dark brown; wings upperside with a purplish sheen when viewed obliquely. Females: unknown. Trans-Andean South America ..... *Z. delassisei*
4′. FW basal and post-median areas variable in colour; post-median area never dark brown and coalesced with submarginal and marginal areas; wings usually without a purplish sheen when viewed obliquely ..... (5)
5. Males: FW with underdeveloped emargination of the inner margin at the tornus. Females: FWV basal and marginal areas (usually dark brown) strikingly contrasting in colour with post-median area (usually beige), with a large discal spot in M_1–M_2 at the end of discal cell ..... (6)
5′. Males: FW emargination of the inner margin at the tornus strongly developed, tornus always hooked. Females: FWV coloration variable, but with a short discal spot in M_1–M_2 at the end of discal cell when basal and marginal areas and post-median area are strikingly contrasting in colour ..... (7)
6. Males: FW emargination of the inner margin at the tornus very shallow, tornus rather rounded. Females: FWD basal area reddish brown. Amazon basin..... *Z. itys*
6′. Males: FW emargination of the inner margin at the tornus underdeveloped but deep, tornus hooked. Females: FWD basal area orange. Trans-Andean South and Central America..... *Z. crawfordhilli* sp. nov.
7. Males: FW basal and post-median reddish brown; HW inner margin emagination strongly developed, apex projected. Females: FWV basal and marginal areas (usually dark brown) strikingly contrasting in colour with post-median area (usually beige). Atlantic forests..... *Z. itylus*
7′. Males: FW basal and post-median areas coloration variable; HW inner margin emargination underdeveloped, apex rather rounded. Females: FWV coloration variable, but never strikingly contrasting in colour ..... (8)
8. Males and females: FW apex strongly falcate; FW marginal and submarginal areas uniformly dark brown and wide, all along the outer margin and the apex ..... (9)
8′. Males and females: FW apex variably falcate; FW marginal and submarginal areas variable in colour and usually thin, more developed near the apex..... (10)
9. Males: upperside of the wings, basal, post-median and submarginal areas along the outer margin uniformly light orange, without a purplish sheen when viewed obliquely. Females: FWD basal, post-median and submarginal areas along the outer margin of the wings uniformly orange. Amazon basin… *Z. falcis*
9′. Males: upperside of the wings, basal, post-median and submarginal areas along the outer margin reddish brown, with a purplish sheen when viewed obliquely. Females: FWD basal area dark orange, with post-median and submarginal areas along the outer margin dark orange with a yellowish orange suffusion. Trans-Andean South America ..... *Z. pythagoras*
10. Males: FW median and post-median bands usually developed; HW post-median band usually developed from the inner margin near the tornus to the 2A projection. Females: FWD and FWV basal and submarginal areas and post-median area usually homogeneous in colour ..... (11)
10′. Males: FWD median and post-median bands faint or absent; HWD post-median band usually weakly developed, not reaching the 2A projection. Females: FWD and FWV basal and submarginal areas and post-median area usually of different colours ..... (13)
11. Males: uncus almost straight, short and thick, without a distal callus; dorsal half of the gnathos larger than the ventral. Females: lamella postvaginalis wider than long, posterior edge bilobed. Central America..... (12)
11′. Males: uncus curved, longer and thinner, with a distal callus; dorsal half of the gnathos similar in size to the ventral. Females: lamella postvaginalis longer than wide, posterior edge smooth or slightly bilobed..... *Z. elianahenrichae* sp. nov.
12. Males: FWD basal, post-median and submarginal areas pale orange to orange, but usually lighter; marginal and submarginal area near the apex variable in colour, suffused with pale orange to orange. Females: HWD colour variable, but usually pale yellow to yellow with an orange suffusion along the outer margin. Trans-Andean South and Central America ..... *Z. ellops*

12′. Males: FWD basal, post-median and submarginal areas pale orange to orange, but usually darker; marginal and submarginal area near the apex variable in colour, but usually homogeneous brown to dark brown. Females: HWD colour variable, but usually homogeneous pale yellow to yellow. Cis-Andean South America ..... *Z. strigosus*

13. Males: underside of the wings light brown to brown in colour; post-median area slightly lighter than basal, submarginal and marginal areas. Females: FW basal area usually orange, gradually fading to pale orange or yellow in the post-median and submarginal areas. Trans-Andean South and Central America ..... *Z. mirandahenrichae* sp. nov.

13′. Males: underside of the wings homogeneusly dark brown in colour. Females: FWD basal area usually orange, sharply changing to pale orange or yellow in the post-median and submarginal areas after the median band. Cis-Andean South America ..... (14)

14. Males: FWD basal, post-median and submarginal areas dark orange, usually with a purplish sheen when viewed obliquely. Females: FWD basal area usually orange to dark orange. Amazon and Atlantic forests ..... *Z. hurin* sp. nov.

14′. Males: FWD basal, post-median and submarginal areas lighter, usually orange, without a purplish sheen when viewed obliquely. Females: FWD basal area lighter, usually of the same colour of the post-median and submarginal areas. Amazon and Atlantic forests ..... *Z. isidora*

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. List of examined material.
Appendix S2. List of barcoded material accession numbers.
Appendix S3. Unabridged results of the neighbor-joining analysis.
Appendix S4. Unabridged results of the maximum likelihood analysis.
Appendix S5. Unabridged results of the Bayesian inference analysis.
Appendix S6. Taxonomic and bibliographic catalogue of *Zaretis* Hübner, [1819] and ***Phantos*** Dias, 2018 **gen. nov.**