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'Species' from two different butterfly genera combined into one: description of a new genus of Euptychiina (Nymphalidae: Satyrinae) with unusually variable wing pattern

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ABSTRACT

Sepona Freitas and Barbosa, **gen. nov.** is proposed for the Neotropical satyrine butterfly species *Euptychia punctata* Weymer, 1911 and its junior subjective synonyms *Euptychia griseola* Weymer, 1911 and *Taygetis indecisa* Ribeiro, 1931. The new genus has a distinctive wing pattern and shape of the valvae in the male genitalia, the latter being a unique autapomorphy within the subtribe Euptychiina. Based on molecular data, this genus is not sister to any other single euptychiine genus, instead appearing as the sister to all remaining genera in the *Taygetis* clade. The present paper illustrates the complexity of the taxonomy of Euptychiina, and the importance of using different sources of evidence in taxonomic studies.

Introduction

In recent years, the highly diverse butterfly subfamily Satyrinae has been subject to several studies attempting to clarify its internal relationships and taxonomy (Murray and Prowell, 2005; Peña et al., 2006, 2010; Marín et al., 2011; Matos-Maravi et al., 2013; Siewert et al., 2013; Seraphim et al., 2014). These studies have revealed many non-monophyletic genera, and a number of complexes of cryptic species waiting to be disentangled, especially in the predominantly lowland, largely Neotropical subtribe Euptychiina (e.g. Peña et al., 2010; Freitas et al., 2012a,b; Matos-Maravi et al., 2013; Zacca et al., 2013; Siewert et al., 2013; Seraphim et al., 2014).

Including 10 genera, the "*Taygetis* clade" is one of five major groups of Euptychiina (Peña et al., 2010); a preliminary phylogeny for this clade (Matos-Maravi et al., 2013) showed that four genera, namely *Harjesia* Forster, 1964, *Pseudodebis* Forster, 1964, *Forsterinaria* R. Gray, 1973 and *Taygetis* Hübner [1819], are polyphyletic, requiring some revised generic combinations and the description of new genera. The genus *Harjesia*, as then conceived, included species placed in three different clades within the "*Taygetis* clade" (Matos-Maravi et al., 2013). In that phylogeny, *Harjesia griseola* (Weymer, 1911) appeared as sister to the entire "*Taygetis* clade" (Matos-Maravi et al., 2013), suggesting that it should be placed in a new genus.

Ongoing research into the phylogenetic relationships of another euptychiine genus, *Yphthimoides* Forster, 1964, showed that this genus is clearly polyphyletic, with several species that should be reassigned to other genera (Freitas et al., 2012b, Barbosa et al., 2015, EPB and AVLF, *in prep.*). One species in particular, *Yphthimoides punctata* (Weymer, 1911), is quite distinct from all other described *Yphthimoides*, and further morphological studies revealed that *Y. punctata* and *H. griseola* are similar enough to be considered subjective synonyms.

This study presents evidence based on an integrative taxonomic approach (e.g., Dayrat, 2005; Yeates et al., 2011; Pante et al., 2015) using both morphological and molecular data for the synonymy of *Y. punctata* and *H. griseola*, and describes a new genus to harbor the resulting single species.

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Material and methods

Adult specimens were studied in a number of American and European collections, and the following acronyms are used here: **AWLW** – Allan & Lesley Wolhuter collection, United Kingdom; **DZUP** – Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil; **FLMNH** – Florida Museum of Natural History, Gainesville, FL, USA; **KWJH** – Keith R. Willmott & Jason P. W. Hall collection, Gainesville, FL, USA; **LBCB**: L. & C. Brévignon collection, French Guiana; **MNHN** – Muséum National d'Histoire Naturelle, Paris, France; **MNRJ** – Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; **MOBE**: Mohamed Benmesbah collection, France; **MUSM** – Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; **MZUJ** – Muzeum Zoologiczne Uniwersytetu Jagiellónskiego, Kraków, Poland; **NHMUK** – The Natural History Museum, London, United Kingdom; **YUGA** – Yuvinka Gareca colletion, Santa Cruz, Bolivia; **ZSM** – Zoologische Staatssammlung München, München, Germany; **ZUEC** – Museu de Zoologia da Universidade Estadual de Campinas, Campinas, São Paulo, Brazil; **ZUEC-AVLF** – André V. L. Freitas Collection, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.

Morphology

Dissections were made using standard techniques. Legs, palpi and abdomens were soaked in hot 10% potassium hydroxide for nearly 10 minutes before dissection, and dissected parts were stored in glycerol. In order to see the venation, wings were diaphanized by soaking them in alcohol and NaClO solution (bleach). Taxonomic nomenclature follows Lamas (2004a,b), modified by Peña et al. (2006) and Wahlberg et al. (2009). Drawings and measurements of wings, legs and palpi were made using a Leica® MZ7.5 stereomicroscope equipped with a micrometric scale and a drawing tube. Photographs of the male and female genitalia were taken using a Zeiss Discovery V20 Stereomicroscope. The following abbreviations are used: (FW) forewing, (HW) hind wing, (D) dorsal, (V) ventral.

Phylogenetic inference

Genomic DNA was extracted from two legs of adults by using the DNeasy Blood & Tissue Kit protocol (QIAGEN, Düsseldorf, Germany). DNA was stored in TE buffer at −20 °C. The mitochondrial gene cytochrome c oxidase I (Cox1, ca. 658 bp, corresponding to the 'DNA barcode' region) for all specimens and the nuclear genes GAPDH for one specimen (YPH-0240) and RpS5 for the outgroups were amplified, purified and sequenced using standard techniques (see Silva-Brandão et al., 2005; Wahlberg and Wheat, 2008). The sequences of nuclear gene RpS5 for *Harjesia griseola* were obtained from GenBank.

All the sequences were aligned by eye with sequences obtained previously and available on GenBank by using BioEdit v. 7.2.4 (Hall, 2013, available at http://www.mbio.ncsu.edu/bioedit/bioedit.html#downloads). The final matrix comprised 32 specimens from species of 10 genera (including 11 specimens from the new genus *Sepona*) and three species used as outgroups, namely *Hermeuptychia maimoune* (A. Butler, 1870), *Paryphthimoides grimon* (Godart [1824]) and *Splendeuptychia doxes* (Godart [1824]) (see Table 1 for the sequence codes).

The phylogenetic relationships of the new species were estimated using maximum likelihood. Analyses were run using RAXML (Stamatakis et al., 2008) with 1000 rapid bootstrap replicates and a search for the maximum likelihood topology on the CIPRES portal (Miller et al., 2010). The data were modeled according to the GTR + G model for each partition independently.

Table 1
Species of Euptychiina with code, sampling site data, and GenBank accession numbers for sequenced genes.

Species name	Code	Locality	COI	GAPDH	RpS5
Sepona punctata	YPH-0240	Abunã, Porto Velho, RO, Brazil	KR349480	KR349476	–
Sepona punctata	YPH-0346	Est. Eco. Alto Acre, Assis Brasil, AC, Brazil	KR349481	–	–
Sepona punctata	YPH-0494	Conceição do Mato Dentro, MG, Brazil	KR349482	–	–
Sepona punctata	YPH-0502	Est. Eco. Alto Acre, Assis Brasil, AC, Brazil	KR349483	–	–
Sepona punctata	YPH-0503	Reserva Trabijú, Pindamonhangaba, SP, Brazil	KR349484	–	–
Sepona punctata	YPH-0506	Bonito, MS, Brazil	KR349485	–	–
Sepona punctata	YPH-0507	Bonito, MS, Brazil	KR349486	–	–
Sepona punctata	YPH-0511	Porto Velho, RO, Brazil	KR349487	–	–
Sepona punctata	CP23-21	Provincia La Convención, Peru	JQ392607	JQ392838	JQ392943
Sepona punctata	CP24-01	Madre de Dios, Peru	JQ392608	–	JQ392944
Sepona punctata	CP24-02	Madre de Dios, Peru	JQ392609	–	JQ392945
Hermeuptychia maimoune	YPH-0239	Rio Madeira, Porto Velho, RO, Brazil	KR349479	KR349475	KR349472
Paryphthimoides grimon	YPH-0095	Três Lagoas, MS, Brazil	KR349477	KR349473	KR349471
Splendeuptychia doxes	YPH-0172	Serra do Japi, Jundiaí, SP, Brazil	KR349478	KR349474	–
Taygetina oreba	CP02-13	Tambopata Research Center, Madre de Dios, Peru	JQ392613	JQ392842	JQ392949
Taygetina oreba	CP-CI107	CICRA, Peru	GU205839	GU205952	GU206011
Taygetina banghaasi	LEP00435	Filo de Chumbiriatza, Zamora-Chinchipe, Ecuador	JQ392633	JQ392854	JQ392964
Taygetis weymeri	PM03-03	Magistral, Sinaloa, Mexico	JQ392708	JQ392918	JQ393027
Taygetis larua	PM14-24	–	JQ392669	JQ392885	JQ392995
Taygetis virgilia	PM02-03	Amalfí, Porcé, Antioquia, Colombia	JQ392700	JQ392912	JQ393021
Taygetis laches	PM04-13	Xingu, PA, Brazil	JQ392659	JQ392878	JQ392988
Forsterinaria quantius	PM10-05	Pq. E. Serra do Rola Moça, Nova Lima, MG, Brazil	JQ392596	JQ392829	JQ392934
Parataygetis lineata	NN58	Puente Puntayacu - Qbda. La Solitaria, Junín, Peru	JQ392618	JQ392846	JQ392953
Parataygetis albinotata	CP07-43	Chanchamayo, Junín, Peru	JQ392616	JQ392844	JQ392951
Posttaygetis penelea	CP01-06	Tambopata Research Center, Madre de Dios, Peru	JQ392620	–	JQ392955
Posttaygetis penelea	UN0403	Teodoro Sampaio, SP, Brazil	JQ392623	–	–
Pseudodebis valentina	CP01-85	Tambopata Research Center, Madre de Dios, Peru	JQ392629	–	–
Pseudodebis valentina	CP-CI25	CICRA, Peru	JQ392631	JQ392852	JQ392962
Harjesia blanda	CP01-13	Tambopata Research Center, Madre de Dios, Peru	DQ338800	GQ357436	GQ357565
Harjesia blanda	CP-CI57	CICRA, Peru	JQ392606	JQ392837	JQ392942
Harjesia obscura	CP23-22	Peru	JQ392610	JQ392839	JQ392946
Harjesia obscura	PM01-20	Paranaíta, MT, Brazil	JQ392612	JQ392841	JQ392948

Sepona Freitas & Barbosa, **gen. nov.**

Type species: *Euptychia punctata* Weymer, 1911, here designated.

Diagnosis

Molecular data (Peña et al., 2010) place this genus within the "*Taygetis* clade" of the satyrine subtribe Euptychiina. In terms of wing shape and pattern, adults are similar to those of some species of *Harjesia*, *Pseudodebis* and *Taygetina* Forster, 1964, which all have undulate rather than straight dark discal and postdiscal lines on the ventral surface, but this genus can be distinguished from all other euptychiines by the unique shape of the valvae in the male genitalia (Fig. 3A). The valvae bear a long, thin, inwardly curved projection arising abruptly from the otherwise rounded main body of the valva. See Table 2 for comparisons of additional morphological characters of *Sepona punctata* with representatives of other genera of the "*Taygetis* clade". The relationships of *Sepona* to other euptychiina genera, and justification for its recognition as a monotypic genus, are addressed further below under 'Discussion'.

Etymology

Sepona is an arbitrary combination of letters, derived from the Latin transitive verb "sepono", meaning to put aside, separate, or remove, in reference to the isolated position of the genus in comparison with other members of the "*Taygetis* clade". It should be treated as a feminine noun.

Sepona punctata (Weymer, 1911) **comb. nov.**

Euptychia punctata Weymer, 20 April 1911: 205. **Type Locality**: Brazil, Minas Gerais. **Syntype(s)**, not located.

=*Euptychia griseola* Weymer, 20 July 1911: 211, **n. syn. Type Locality:** Bolivia [La Paz], Mapiri. **Lectotype female** (here designated): 'Original! / nun aber heissen griseola // Mapiri // Collection / v.Rosen // grisea / Weym. // Typus Nr. / *Euptychia griseola* Stgr. i. l. / Weymer / Zoologische / Staatssammlung / München', deposited in ZSM (examined).

=*Taygetis indecisa* Ribeiro, 1931: 33, **n. syn. Type Locality:** Brazil [Rondônia, Rio Jamari]. **Holotype female:** 'Comm.Rondon / No. 43. 19. 6. 14 / Coll. Stolle // HOLOTIPO // N 053/645 // Holótipo *Taygetis / indecisa*/Ribeiro, 1931 / Mielke & Casa-grande det. 1985', deposited in MNRJ (examined).

Taygetis indecisa: May, 1933: 120; *Euptychia griseola*: May, 1933: 120; D'Abrera, 1988: 789; *Pseudodebis griseola*: Forster, 1964: 77; Lamas, 1983: 16; Robbins et al., 1996: 230; Freitas, 2003: 103; *Euptychia punctata*: D'Abrera, 1988: 789; *Taygetis griseola*: D'Abrera, 1988: 756; *Harjesia griseola*: Lamas, 2004: 219; Brévignon, 2008: 68; Brévignon and Benmesbah, 2012: 39; Matos-Maravi et al., 2013: 54; *Yphthimoides punctata*: Lamas, 2004: 223.

Redescription

Male (Figs. 1, 2A-C-D-E, 4A-B-D). Eyes reddish brown, covered with sparse black hairs. Palpus 1.5 times as long as head, brown with light brown hairs (Fig. 2C). Antenna of males 9.0–10.0 mm in length with 36 antennomeres, extending to mid-costa; shaft rust-brown dorsally, orange brown ventrally, sparsely scaled dorsally; club not conspicuously developed, including eleven segments, with apical portion (last five segments) dark brown. Forewing length 23–25 mm ($n = 6$); hindwing length 19–20 mm ($n = 6$). HW outer margin slightly undulate. Male wing venation shown in Fig. 2A. Wings with dorsal ground color dark brown with few markings, restricted to a suffused dark brown outer margin on DFW, and to dark double marginal line, and a submarginal line following contours of marginal line on DHW. Ventral wings light brown; VFW crossed by two thin zigzag dark brown lines, extending from costa to 2A, first line one-third distance from wing base to

Table 2
Comparisons of *Sepona punctata* with exemplar species from related genera in "*Taygetis* clade". For aedeagus and saccus width, the value refers to length/width ratio in the medial portion of each structure; higher numbers therefore represent a narrower structure.

Species	Eyes	Forewing apex	Hind wing margin	Shape of aedeagus	Aedeagus width	Valvae	Uncus shape	Gnathos shape	Tegumen	Saccus width
Sepona punctata[1, 2]	Few sparse hairs	Rounded	Slightly wavy	Strongly curved	23	Bearing a long thin terminal projection	Curved, broad	Elongated, pointed	Pronounced	11
Harjesia blanda[4]	Hairy	Rounded	Wavy	Straight	8	Projection absent	Curved, slender	Elongated, pointed	Not pronounced	4
Posttaygetis penelea[4, 9]	Hairy	Rounded	Wavy	Curved in the distal end	15	Projection absent	Straight, broad	Short, rounded	Not pronounced	4
Pseudodebis valentina[4]	Hairy	Rounded	Slightly wavy	Straight	12	Projection absent	Curved slender	Short, broad	Slightly pronounced	5
Pseudodebis celia[4]	Hairy	Truncate	Wavy	Straight	10	Projection absent	Straight, slender	Short, rounded	Not pronounced	4
Taygetina kerea[5]	Hairy	Acute	Wavy	Straight	13	Projection absent	Straight. Broad	Elongated, pointed	Pronounced	7
Taygetis yphthima[7]	Short sparse hairs in lateral portion	Acute	Wavy	Straight	12	Projection absent	Straight, slender	Elongated, pointed	Pronounced	4
Taygetis laches[3, 6]	Hairy	Truncate	Wavy	Straight	25	Projection absent	Straight. Slender	Elongated, pointed	Slightly pronounced	8
Taygetis mermeria[4]	Hairy	Acute	Wavy	Straight	10	Projection absent	Straight, slender	Elongated, pointed	Not pronounced	6
Taygetis sylvia[4]	Hairy	Acute	Wavy	Straight	6	Projection absent	Straight, broad	Elongated, pointed	Not pronounced	4
Taygetis echo[8]	Few sparse hairs	Rounded	Wavy	Straight	14	Projection absent	Straight, slender	Elongated, pointed	Not pronounced	5

Source of material (all localities in Brazil) 1, Pindamonhangaba, SP; 2, Jaru, RO; 3, Linhares, ES; 4, Marechal Thaumaturgo, AC; 5, Jataí, SP; 6, Campinas, SP; 7, Campos do Jordao, SP; 8, Alta Floresta, MT; 9, Morro do Diabo, SP.

Fig. 1. Adult male of *Sepona punctata* – Jaru, Rondônia, Brazil. Dorsal above, ventral below.

apex; second line extending from costa to 2A at two-thirds distance from wing base to apex; a conspicuous lighter outer band is adjacent to second line, followed by a darker ocellar region (see next); a thin dark brown zigzag submarginal line with single black dots in vertices and a brown regular marginal line extending from costa to 2A; four dark ocelli in spaces R5–M1 (ocellus 1), M1–M2 (2), M2–M3 (3) and M3–CuA1 (4). VHW crossed by two thin dark brown lines from costa to anal margin, in similar position to those on forewing; a conspicuous lighter outer band is adjacent to second line, followed by a darker ocellar region (see next); a dark brown zigzag submarginal line with single black dots in vertices and a brown regular marginal line extending from costa to 2A; a series of five dark ocelli can be found in cells Rs–M1 (ocellus 1), M1–M2 (2), M2–M3 (3), M3–CuA1 (4) and CuA1–CuA2 (5). Details about ocelli size and shape discussed further below. No conspicuous androconial scales observed.

Male genitalia (Fig. 3A–E). Saccus elongate; tegumen rounded and short; gnathos long and pointed, projecting upwards above uncus; uncus elongated, with lateral expansions in dorsal view, giving an arrowhead appearance; valvae elongated, ending in a bump with a long thin pointed process; aedeagus curved; cornuti absent; juxta sclerotized, linking both valvae together.

Female (Fig. 2B, F, 4C-E-F). Forewing length 24–26 mm ($n = 2$); hindwing length 20–22 mm ($n = 2$). Antenna 11.0 mm in length, with 35 antennomeres, extending to mid-costa. General color and pattern very similar to those of males. Female genitalia as in Fig. 3E, F. Ductus bursae partially sclerotized, corpus bursae rounded; a pair of conspicuous signa present.

Taxonomy and variation

Weymer (1911) described *Euptychia punctata* based on an unstated number of specimens from Minas Gerais, Brazil. Several pages later, he described *Euptychia griseola* based also on an unstated number of specimens from Mapiri, Bolivia. Later, Ribeiro (1931) described a third taxon as *Taygetis indecisa*, based on one female from Brazil, Rio Jamari; this taxon was promptly synonymized with *Euptychia griseola* by May (1933). Descriptions of both *E. punctata* and *E. griseola* were also based on female specimens, and although this cannot be determined unambiguously from their original descriptions, the fact that the types are females in both cases suggests that males were unknown to the authors. No type specimen(s) of *punctata* has been found, but there is a single female in ZSM identified by Forster (1964) as the "Typus" of *griseola*, and we accept that it indeed represents a syntype (which we designate herein as **lectotype**), since this particular specimen (examined) matches precisely the illustration provided subsequently by Weymer (1911: pl. 47g, fig. [7]). The female holotype (examined) of *Taygetis indecisa* Ribeiro is deposited in MNRJ. Although appearing rather different in wing pattern, the names *punctata* and *griseola* apparently represent extremes of geographical variation within a single species. Variation on the dorsal wing surfaces is practically absent and obvious seasonal variations have not been detected. The ventral surface of both wings, however, shows much variation, especially in the number and size of the ocelli. Most individuals from central and southeastern Brazil and eastern Bolivia ("*punctata*" phenotype) have the ocelli reduced to small black dots, sometimes with a tiny white pupil on the VHW; they also present a more homogeneous ventral pattern (Fig. 4E, F). Conversely, individuals from western Amazonia and Guianas (the "*griseola*" phenotype) have more developed ocelli circled by yellowish cream scales and with a white pupil on both wings, and a conspicuous banded pattern on the ventral wings (Fig. 4A, B). Intermediate phenotypes between "*punctata*" and "*griseola*" are known from Acre and Rondônia in Brazil, and from Bolivia, and are usually more similar to the "*griseola*" phenotype (Fig. 4C, D). To our knowledge, no two of these three phenotypes ("*punctata*", "*griseola*" and intermediate) have been recorded in sympatry. The two names were published several months apart, and we thus treat *E. griseola* as a junior subjective synonym of *S. punctata* **n. syn.**

Specimens examined (34 ♂, 27 ♀): **Bolivia. –** *Beni*: Prov. Mamoré, San Ramón, Estancia S/Lorenzo [13°26′9.26″S, 64°36′2.79″W], 13 Oct 2003, T. V. Bosque de Galeria, T17, Yuvinka Gareca leg. (YUGA); *La Paz*: 'Madidi' [14°3′55″S,68°50′49″W] (Aliaga, W.), 4 Oct 2005, 1 ♀ (MUSM), 5 Oct 2005, 1 ♂ (MUSM); Mapiri [15°19′27″S,68°6′50″W], 1 ♂ [LT *griseola*; "Original! / nun aber heissen griseola // Mapiri // Collection / v.Rosen // grisea / Weym. // Typus Nr. / *Euptychia griseola* Stgr. i. l. / Weymer / Zoologische / Staatssammlung / München"] (ZSM); *Santa Cruz*: Buenavista [17°27′S,64°40′W], 750 m (Steinbach, J.), Aug 1907–Apr 1908, 1 ♂ [BMNH-E-1204766] (NHMUK). **Brazil**. – *Acre*: 50 km NW Bujari [9°32′53″S,68°18′9″W], 200 m (Mielke, O., M. Casagrande), 25 Sep 2003, 1 ♀ (DZUP); Assis Brasil, Estação Ecológica do Alto Acre [11°3′S,70°16′W], 300 m (Brown, K. S.), 19 Jul 2005, 1 ♂ [DNA voucher YPH-0346] (ZUEC-AVLF), 21 Aug 2005, 1 ♀ (ZUEC-AVLF), Aug 2005, 1 ♂ [DNA voucher YPH-0502] (ZUEC-AVLF); Marechal Thaumaturgo, Reserva Extrativista do Alto Juruá, Boca do Caipora [9°9′16″S,72°40′21″W] (Brown, K. S. & A. V. L. Freitas), 1 Sep 1997, 1 ♂ [ZUEC LEP-9231], 1 ♀ [ZUEC LEP-9232] (ZUEC); Marechal Thaumaturgo, upper Juruá River, Foz do [Rio] Tejo [8°59′1″S,72°43′W] (Freitas, A.V.L.), 20–27 Aug 1997, 1 ♀ (ZUEC-AVLF); PAD Humaitá, Porto Acre [9°35′29″S,67°32′20″W], 200 m (Mielke, O., M. Casagrande), 8 Oct 2004, 1 ♂ (DZUP); *Espírito Santo:* Colatina [19°31′55″S,40°40′42″W], Aug–Sep 1937, 3 ♂ [24/579, 52/439, 52/438], Sep 1937, 1♀ [24/689] Coll. E. May (MNRJ); Cor.[rego] do

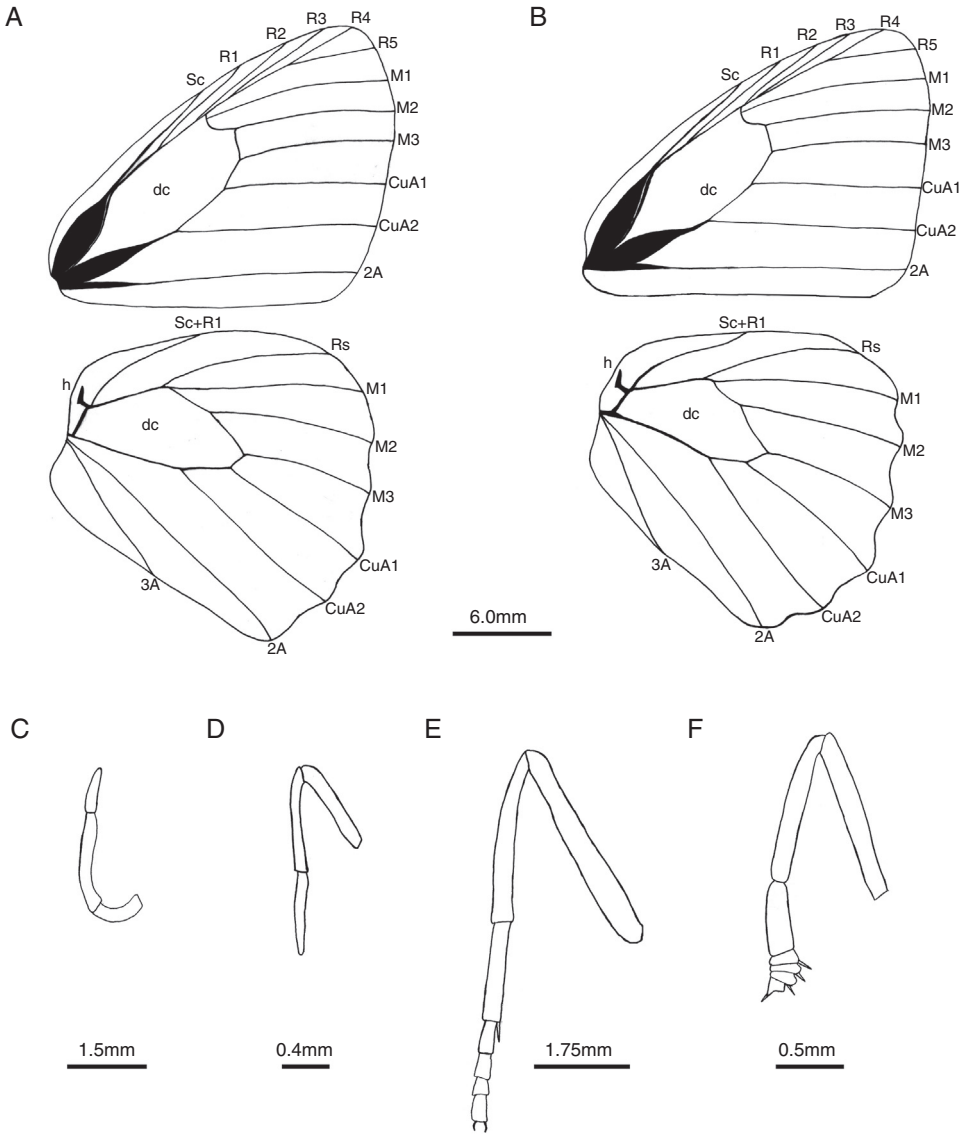

Fig. 2. Morphological characters of *Sepona punctata*. A, male wing venation – forewing above and hind wing below; B, female wing venation – forewing above and hind wing below; C, male palpus; D, male foreleg; E, male midleg; F female foreleg.

Sabiá, Est.[rada] N.[ova] Venecia [19°8′20″S,40°37′8″W], Collatina [sic], Oct 1936, 1♀, E. May leg. [52/336] (MNRJ); *Mato Grosso do Sul*: Bonito [21°7′34″S,56°29′25″W] (Araújo, P. F.), 15 Oct 2014, 1 ♀ [ZUEC LEP-9234; DNA voucher YPH-0507] (ZUEC), 5 Nov 2014, 1 ♂ [ZUEC LEP-9235; DNA voucher YPH-0506] (ZUEC); *Mato Grosso*: 11–18 km N Ribeirão Cascalheira [12°50′47″S,51°46′59″W] (Mielke, O.), 21–23 Aug 1997, 1 ♀ (DZUP); C[oron]el. Rio Branco [15°14′24″S,58°6′49″W], 400 m (Buzzi, Mielke, Elias & Casagrande), 19 Sep 1984, 1 ♂ [DZ-5465; Proj.[eto] Polonoroeste] (DZUP) (Mielke, O., K. S. Brown), 3 Jul 1972, 1 ♂ (DZUP); Diamantino, Rio Arinos, Faz.[enda] S.[ão] João [14°21′18″S,56°9′2″W], 300–400 m (Ebert, H. & H. D.), 5 May 1978, 1 ♂ (DZUP); Chapada dos Guimarães, Buriti [15°23′31″S, 55°53′11″W], 1 Jan 1969, 1 ♂ [ZUEC LEP-9246; Slide no 1762, ♂ genitália, Lee D. Miller] (ZUEC); *Minas Gerais*: Conceição do Mato Dentro [19°2'S,43°25′31″W] (Ramos, G.), 11 Sep 2013, 1 ♀ [ZUEC LEP-9233; DNA voucher YPH-0494] (ZUEC); no specific locality (Boullet), 1913, 2 ♂ (MNHN); *Rio de Janeiro*: Itabapoana [21°8'S,41°41'W], 1 ♀ [BMNH-E-1204794] (NHMUK); *Rondônia*: 67 km S Ariquemes, 5 km S of Cacaulândia on linha C-10 at Rio Pardo off B-65 [10°23′15″S,62°54′53″W] (Austin, G.T.), 14 Oct 1993, 1 ♂ (FLMNH), 8 Oct 1993, 1 ♀ (FLMNH) (Gomes, O.), 15 May 1994, 1 ♀ (FLMNH); 67 km S Ariquemes, 5 km S of Cacaulândia on linha C-10 [10°23′13″S,62°54′12″W], 170 m (Gomes, O.), 1 Aug 1993, 1 ♂ (FLMNH); Jaru [10°27′S,62°30′W] (Brown, K. S.), 30 Sep 1975, 2 ♀ (FLMNH), 5 Oct 1975, 1 ♀ (FLMNH) (Callaghan, C. J.), 10 Aug 1976, 1 ♂ [genitalia vial AVF 7841], 1 ♀ [genitalia vial AVF 7840] (FLMNH); Pôrto Velho [8°45′S,63°53′W], 31 Jan 2010, 1 ♂ [ZUEC LEP-9236; DNA voucher YPH-0511] (ZUEC); Rio Jamari [10°12′S,63°15′W], 1 ♂ [HT *indecisa*; "'Comm.Rondon / No. 43. 19. 6. 14 / Coll. Stolle // HOLOTIPO // N 053/645 // Holótipo *Taygetis* / *indecisa* /Ribeiro, 1931/ Mielke & Casa-grande det. 1985″] (MNRJ); Upper Rio Madeira, Abunã [9°42′S,65°21′W] (Nunes, R. V.), 1 May 2013, 1 ♂ [ZUEC LEP-9230; DNA voucher YPH-0240] (ZUEC); *São Paulo*: Pindamonhangaba, Reserva Natural Municipal do Trabijú [22°50′18″S,45°31′23″W] (Rosa, A. H. B.), 22 Jul 2014, 1 ♂ [ZUEC LEP-9237; DNA voucher YPH-0503] (ZUEC). **Ecuador**. – *Napo*: Río Jatunyacu, Pimpilala [1°4′31″S,77°56′13″W], 800 m (Jasinski, A.), 28 May 1997, 1 ♀ (MZUJ); *Orellana*: [c. 13 km W Coca], Río Payamino [0°26′18″S,77°6′46″W] (Wolhuter, A. & L.), 28 Oct 2009, 1 ♀ (AWLW) (Wolhuter, A. & L., pers. comm. and CD of images); Reserva Biológica

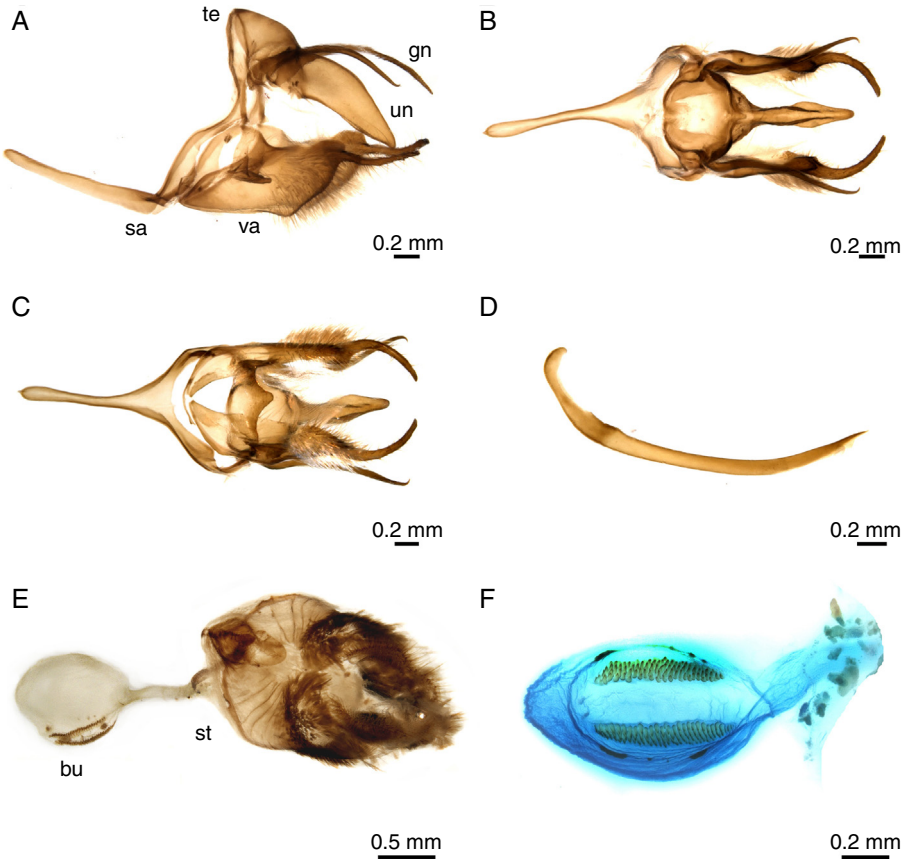

Fig. 3. Male and female genitalia of *Sepona punctata*. A, male genitalia in lateral view; B, male genitalia in dorsal view; C, male genitalia in ventral view; D, male aedeagus (lateral view); E, female genitalia in ventral view; F. female genitalia: detail of the signa in corpus bursae. (sa) saccus, (te) tegumen, (un) uncus, (va) valva, (bu) corpus bursae, (st) sterigma.

Río Bigal, 8 de Diciembre [0°32′15″S,77°25′18″W], 975 m (T. & M. García), Oct 2009 (photograph live specimen); *Pastaza*: Puyo, Chifa Restaurant [1°29′13″S,78°0′W], 1000 m (K. Willmott & J. Hall), 25 Aug 1993, 1 ♂ (KWJH); 13 km N Puyo [1°23′26″S,77°58′35″W], 1100 m (Emmel, T. C.), 8 Sep 1969, 1 ♀ (FLMNH). **French Guiana.** – *Saint-Laurent-du-Maroni*: Maroni river, 1 ♀ (FLMNH). **Peru**. – *Cuzco*: Echarate, Alto Manugali [12°27′S,73°02′W], 812 m (Valencia, G.), 5 Apr 2009, 1 ♀ (MUSM); Río Urubamba, Saringabeni [12°11′05″S,72°49′48″W], 442 m (Cerdeña, J., J. Farfán, R. Gutiérrez), 31 Aug 2007, 1 ♀ [fish bait trap] (MUSM); San Martín-3 Camp [11°47′S,72°42′W], 475 m (Valencia, G.), 11 Apr 1997, 1 ♀ (MUSM); *Loreto*: 'Cavallo Cocha' [=Caballococha] [3°55′S,70°31′W], 90 m (Mathan, M. de), May-Jul 1884, 1 ♂ [BMNH-E-786155], 1 ♂ [BMNH-E-786156] (NHMUK); *Madre de Dios*: Boca Río La Torre [12°50′S,69°17′W], 300 m (Covell, C.V.), 22 Oct 1983, 1 ♀ (MUSM) (Lamas, G.), 15 Feb 1982, 1 ♀ (MUSM); Parque Manu, Pakitza [11°56′40″S,71°16′58″W], 340 m (Mielke, O.), 1 Oct 1991, 1 ♂ (DZUP), 24 Sep 1991, 1 ♂ (DZUP), 27 Sep 1991, 1 ♂ (DZUP), 7 Oct 1991, 1 ♂ (DZUP); Parque Manu, Pakitza [11°53′S,70°58′W], 400 m (Lamas, G.), 16 Oct 1990, 1 ♂ (MUSM), 20 Oct 1990, 1 ♂ (MUSM), 7 Oct 1990, 1 ♂ (MUSM) (Rowe, W.), 3 Nov 1990, 1 ♀ (MUSM); Reserva Tambopata [12°50′S,69°17′W], 300 m (Lamas, G.), 31 Oct 1990, 1 ♀ (MUSM); Quebrada Agua Negra [12°53′S,69°17′W], 200 m (Williams, H.), 16 Sep 1995, 1 ♀ (MUSM); Río Madre de Dios, Albergue Amazonia [12°52′S,71°23′W], 500 m (Lamas, G.), 24 Oct 2013, 1 ♀ (MUSM), 28 Sep 2014, 1 ♂ (MUSM), 29 Sep 2014, 1 ♀ (MUSM); Salvación [12°50′S,71°21′W], 500 m (Matthews, M.J.), 6 Aug 1982, 1 ♂ (MUSM); Río Azul [13°3′S,69°55′W], 850 m (Peña, C.), 1 Oct 2010, 1 ♂ [voucher CP24-01] (MUSM), 23 Sep 2010, 1 ♂ (MUSM); Río Azul, Reserva Comunal Amarakaeri [12°49′S,71°6′W], 507 m (Vílchez, M.), 11 Oct 2010, 1 ♀ (MUSM).

Other records: **French Guiana. –** *Cayenne*, Roura, Cacao [4°35′N,52°28′W] (Damico, R.), Feb 1996, 1 ♀ (LBCB) (Brévignon, 2008: 68, pl. 7, fig. 81, 82); *Saint-Laurent-du-Maroni*, Saül [3°37′N,53°12′W], 9 Oct 2011, 1 ♂ (MOBE) (Brévignon & Benmesbah, 2012: 46, pl. 3, fig. 11 [adult wings], 11a [male genitalia]).

Biology and distribution

Sepona punctata is known from eastern Ecuador to southeastern Brazil (Espírito Santo, Rio de Janeiro, Minas Gerais and São Paulo). There are also records from two sites in French Guiana (Brévignon, 2008; Brévignon and Benmesbah, 2012) (Fig. 6). In eastern Ecuador the species is extremely rare, and the few known localities are in the Andean foothills on the types of sandstone soils that frequently support stands of bamboo. Adults are usually scarce and rare in collections, although they were sometimes common in areas with large bamboo patches in the upper Juruá River, in Acre, Brazil (AVLF and K. S. Brown Jr., pers. obs.). The species is usually associated with forested habitats, but some populations in SE Brazil (the "*punctata*" phenotype) are known from riparian forests in the cerrado. The immature stages and hostplants are unknown.

Discussion

The position of *Sepona punctata* as a well-supported sister to the remaining genera in the "*Taygetis* clade", and the polyphyletic

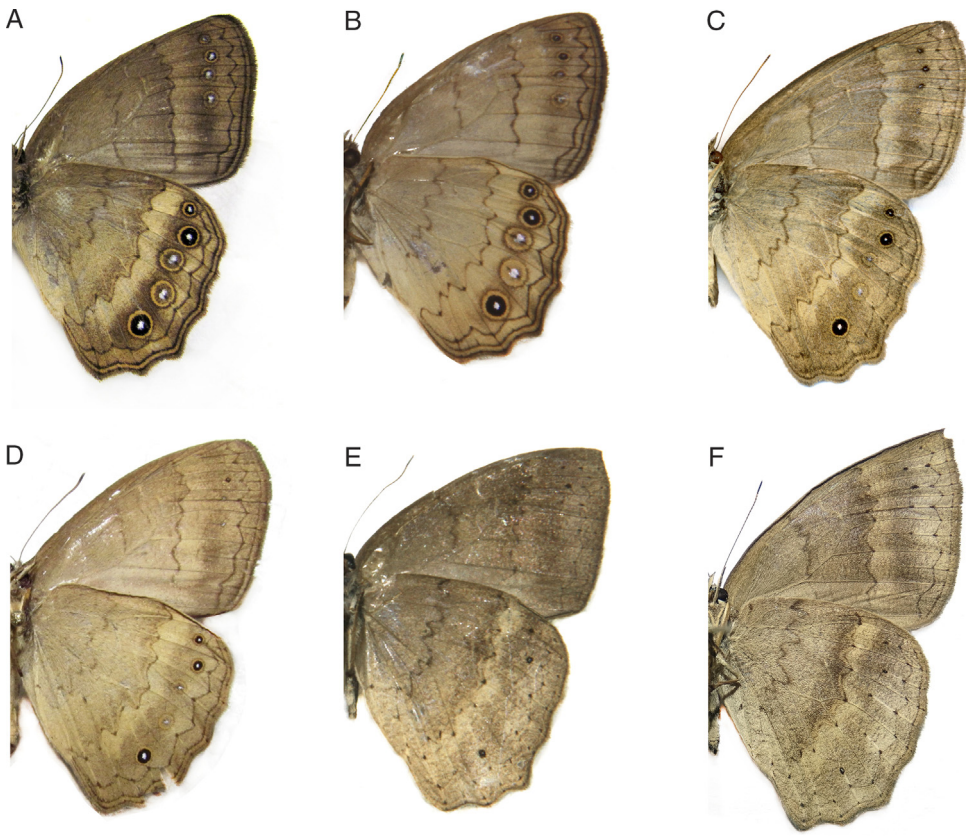

Fig. 4. Variation in wing pattern of *Sepona punctata* (all from Brazil). A, Abunã, Rio Madeira, Rondônia; B, Porto Velho, Rondônia; C, Estação Ecológica do Alto Acre, Acre; D, Porto Acre, PAD Humaitá, Acre; E, Conceição do Mato dentro, Minas Gerais; F, Parque Municipal do Trabijú, Pindamonhangaba, São Paulo (A, B, D – males; C, E, F – females).

nature of *Harjesia* as illustrated by Matos-Maravi et al. (2013) and in the present paper (Fig. 5), clearly shows that this species is not part of *Harjesia* (which has as its type species *Taygetis blanda* Möschler, 1877). The reasons for erecting a new genus for this taxon are therefore clear: unless all species in the "*Taygetis* clade" are lumped into a single genus, an undesirable option given the morphological variation and taxonomic diversity within the clade, there is no way to circumscribe monophyletic genera in the clade without making this taxon a monobasic genus. In addition to its phylogenetic position, the male genitalia of *S. punctata* is quite distinct from all known species of *Harjesia* (Forster, 1964 and unpublished results of the authors), presenting several unique characters, including the extremely thin and curved aedeagus and the unique shape of the valvae (see Fig. 3A and Table 2).

The known wing patterns of *S. punctata* are highly variable, but although specimens from western Amazonia and Guianas are quite

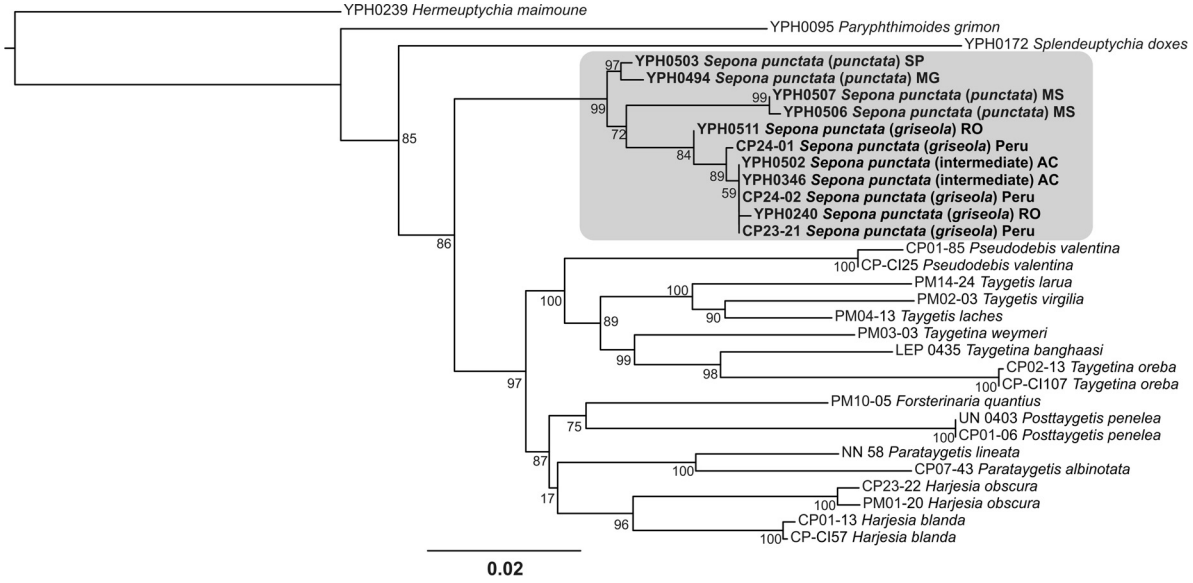

Fig. 5. Relationships among *Sepona punctata* and selected species in the "*Taygetis* clade" and several outgroups inferred with maximum likelihood. Numbers near branch nodes are bootstrap branch support. Names in parentheses for *Sepona punctata* refer to the phenotype of the voucher specimens (see text).

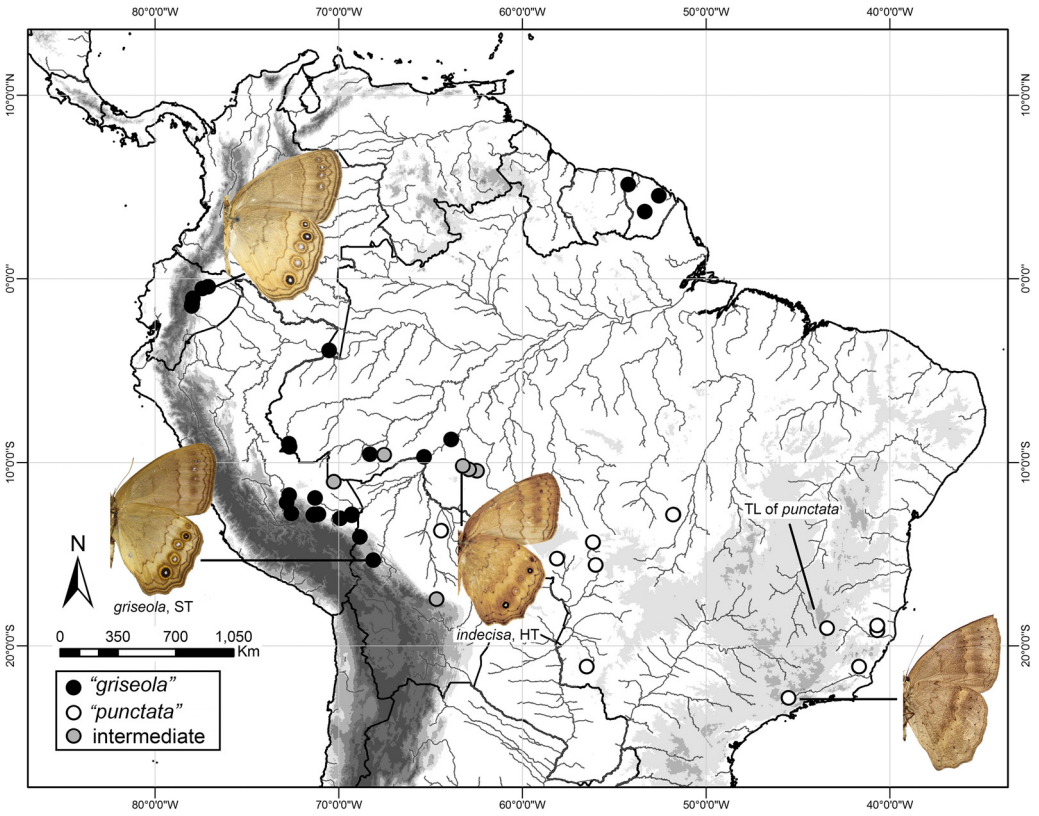

Fig. 6. Recorded localities of *Sepona punctata* (based on all examined material; see text for details). Black dots = "*griseola*" phenotype; white dots = "*punctata*" phenotype; gray dots = intermediate phenotypes.

divergent from those from southeastern Brazil, individuals with intermediate wing pattern are known from eastern Bolivia, and Acre and Rondônia, Brazil. In addition, these differences are not related to seasonal forms and, based on the few known individuals, there is low variation within populations, including in the sites where intermediate populations are known. These reasons were considered sufficient to not recognize subspecific taxa within this species.

The above-described variation in wing patterns throughout the distribution of *S. punctata* easily explains why this taxon was described as three different species, twice by the same author (Weymer, 1911), in three different genera (see the synonymic list above). This situation is a perfect example of how complex is the taxonomy of Euptychiina, where most of the large genera are non-monophyletic, with species spread in two or more different clades (as is the case of *Splendeuptychia* Forster, 1964, *Cissia* Doubleday, 1848, and *Paryphthimoides* Forster, 1964, see Peña et al., 2010).

Hopefully, forthcoming studies combining morphological and molecular data will help to disentangle the complex and species-rich clade which constitutes the subtribe Euptychiina, providing a well resolved phylogeny that will serve as a framework for future studies focusing on diversification patterns of Neotropical butterflies.

Conflicts of interest

The authors declare no conflicts of interest.

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