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Research

Taxonomy

Two New Species of *Taygetina* With a Possible Case of 'Juxta Loss' in Butterflies (Lepidoptera: Nymphalidae: Satyrinae)

Shinichi Nakahara,[1,2,5,6] Pável Matos-Maraví,[3] Eduardo P. Barbosa,[4] Keith R. Willmott,[1] Gerardo Lamas,[5] and André V. L. Freitas[4]

[1]McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, [2]Department of Entomology and Nematology, University of Florida, Gainesville, FL 32611, [3]Biology Centre of the Czech Academy of Sciences, Institute of Entomology, České Budějovice, Czech Republic, [4]Departamento de Biologia Animal and Museu de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil, [5]Departamento de Entomología, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru, and [6]Corresponding author, e-mail: snakahara@ufl.edu

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Abstract

The male genitalic characters of Hexapoda are well known for their great taxonomic and systematic value. Despite insect male genitalia displaying large diversity, variation, and modification across orders, some structures are consistently present, and such characters can serve as the basis for discussion regarding homology. In the order Lepidoptera, a male genitalic structure widely known as the 'juxta' is present in many taxa and absence or modification of this character can be phylogenetically informative at the generic or higher level. We here focus on the systematics of the so-called '*Taygetis* clade' within the nymphalid subtribe Euptychiina, and report an unusual case of 'juxta loss' in a single species, *Taygetina accacioi* Nakahara & Freitas, **n. sp.**, a new species from Brazil named and described herein. Additionally, we describe another west Amazonian *Taygetina* Forster, 1964 species, namely *Taygetina brocki* Lamas & Nakahara, **n. sp.**, in order to better document the species diversity of *Taygetina*. Our most up-to-date comprehensive molecular phylogeny regarding '*Taygetis* clade' recovered these two species as members of a monophyletic *Taygetina*, reinforcing the absence of juxta being a character state change occurring in a single lineage, resulting in an apomorphic condition, which we report here as a rare case in butterflies (Papilionoidea).

Key words: Euptychiina, male genitalia, monophyletic, Papilionoidea, taxonomy

The organs in the genitalia of insects are under strong physiological, reproductive, and evolutionary pressures, and thus these hold a wide range of informative morphological characters for taxa at all levels. This is evidenced in the recognition of the importance of phenotypic and, in particular, genitalic characters in taxonomic and systematic studies, despite the predominance of molecular and genomic data in phylogenetics. The male genitalia display a large diversity of modifications among species and typically provide the majority of taxonomically informative characters in morphological datasets compared with the female genitalia and other insect body parts (e.g., Eberhard 1985, House and Simmons 2005, Song and Bucheli 2010). In this study, we advocate for an integrative taxonomic approach by using genetic distances to identify species and a thorough study of morphological characters, which allowed us to discover the unusual absence of the juxta in butterfly male genitalia and to increase support for species delimitations.

Although the structure of the male genitalia varies across insect orders, the presence of the 'phallus' (i.e., penis) and a pair of 'claspers' for copulation (i.e., valva) are almost universal across insect lineages, reinforcing the view of such organs as homologous with abdominal appendages (e.g., Crampton 1919). Within the order Lepidoptera, the male genitalia consistently possess major homologous structures, such as the 'tegumen' and its modified extension the 'uncus,' which are considered as derivatives of the 9th and 10th abdominal segments, respectively (Klots 1956). In a broad view, the tegumen articulates dorsally with the valvae, comprising the so-called male genitalic capsule. Within the genitalic capsule, the phallus is ventrally supported by the often sclerotized plate-like structure of the juxta, located ventrally on the diaphragma (sensu Pierce 1914). Modifications in juxta morphology, such as sclerotization, projection, reduction, and absence, have aided in the classification and higher-level systematics in various Lepidoptera families

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(e.g., Eyer 1926, Ponoramenko 2007). However, the apparent absence of such a structure is rare (e.g., Wilkinson 1977).

Here, we focus on the taxonomy and systematics of the butterfly genus *Taygetina* Forster, 1964 (Nymphalidae: Satyrinae: Euptychiina). Recent studies using DNA sequence (e.g., Matos-Maraví et al. 2013, Nakahara et al. 2018b) and genomic data (Espeland et al. 2019) have clarified the systematics of the subtribe Euptychiina at the genus level, but have left monophyletic genera without clear synapomorphic morphological characters and a number of polyphyletic genera with signs of convergent evolution of wing patterns (e.g, Nakahara et al. 2016, 2019a; Willmott et al. 2019). Furthermore, molecular data have also suggested that euptychiine species diversity is largely under-estimated, with some genera likely having at least three times more species than those currently described (e.g., Lamas 2004; Freitas et al. 2015, 2018; Nakahara et al. 2019b). These findings urge a synergistic approach between molecular work and careful morphological studies to continue to reveal the species diversity and to clarify the taxonomy and systematics of one of the largest butterfly subtribes in the Neotropics.

With six recognized species, *Taygetina* Forster, 1964, is a relatively small genus in the so-called '*Taygetis* clade' (Lamas 2004, Matos-Maraví et al. 2013). Apart from Matos-Maraví et al.'s (2013) actions in synonymizing the monotypic genus *Coeruleotaygetis* Forster, 1964 with *Taygetina*, and transferring the species *Euptychia oreba* Butler, 1870 and *Taygetis weymeri* Draudt, 1921 to *Taygetina*, the genus has received no attention subsequent to the Lamas (2004) checklist, where the genus was regarded as monobasic. However, during the course of preparing a revision of *Taygetina*, it became overwhelmingly apparent that the taxonomy of this genus is not as straightforward as had previously been thought (Nakahara et al., in preparation). The purpose of this article, therefore, is to contribute towards this revision and our understanding of *Taygetina* diversity by naming and describing two species, based on external morphology, genitalia, and DNA data. We also provide the most comprehensive up-to-date multi-locus molecular phylogeny for '*Taygetis* clade' by incorporating these two new species and several other taxa omitted in Matos-Maraví et al. (2013). The male of one of these two new species apparently lacks a juxta sensu Pierce (1914), which is unusual among butterflies (Papilionoidea).

Materials and Methods

All *Taygetina* specimens relevant to this study were examined in the following collections, and their acronyms as used in the text are as follows:

FLMNH: McGuire Center for Lepidoptera and Biodiversity (MGCL), Florida Museum of Natural History, University of Florida, Gainesville, USA
JPB: James P. Brock collection, Tucson, USA
MIMC: Mike McInnis collection, Floyds Knobs, USA
MUSM: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
QCAZ: Museo de Zoología, Sección Invertebrados, Pontificia Universidad Católica, Quito, Ecuador
ZSM: Zoologische Staatssammlung München, Munich, Germany
ZUEC: Museu de Zoologia da Universidade Estadual de Campinas 'Adão José Cardoso,' Campinas, São Paulo, Brazil

The following acronyms referring to the wings are used throughout the text:

DFW: Dorsal forewing
DHW: Dorsal hindwing
VFW: Ventral forewing
VHW: Ventral hindwing

Morphological Study

External morphology including the genitalia of relevant specimens was examined by appendages being soaked in hot 10% KOH for 10–15 min, dissected, and subsequently stored in glass tubes in glycerine. Morphological characters were examined using a stereomicroscope and drawn using a camera lucida attached to Leica MZ 16 stereomicroscope (Leica, Germany). Images of relevant genitalia were taken by Helicon Focus 6.7.1 using a Canon EOS 6D, subsequently stacked using Helicon Remote (ver. 3.8.7 W) at MGCL; Zeiss Stereo Discovery V20 Stereomicroscope (Zeiss, Germany) at ZUEC. The terminology for those traits associated with wings (area, venation, element, etc.) and genitalia follow Nakahara et al. (2018b).

Molecular Work

DNA extraction and PCR methods largely follow Nakahara et al. (2018a), and relevant primers designed to amplify smaller fragments of the 'barcode' region of the mitochondrial gene cytochrome oxidase I, COI, as in Nakahara et al. (2019b). Sequences generated through this study were uploaded to GenBank and sequence voucher information is provided in Table 1. The dataset (660 bp), including 38 in-group individuals representing virtually all described and undescribed *Taygetina* species, and six individuals as out-groups (see Table 1 for further information), was aligned using MAFFT v7 (Katoh and Standley 2013). We calculated the genetic distances among relevant *Taygetina* species using the Tamura-Nei distance model in Geneious version 11.1.5 (Biomatters Ltd) (Supp Table 1 [online only]).

DNA 'Barcodes'-Based Phylogeny

To have a graphical representation of genetic distances in the genus, we inferred a phylogenetic hypothesis based on the COI barcode. Thereafter, the best-fit substitution model (TIM2+F+I+G4) was obtained by testing 88 models in ModelFinder (Kalyaanamoorthy et al. 2017), and the gene tree with the highest log-likelihood score was estimated by conducting a Nearest Neighbor Interchange search strategy on 20 best initial trees in IQ-TREE v1.6.11 (Nguyen et al. 2015). The gene tree was rooted with *Megeuptychia monopunctata* Willmott and Hall, 1995, based on prior information (Nakahara et al. 2018b). Branch support was calculated using ultrafast bootstrap (UFBoot) with 1,000 replications (-bb 1000), in addition to assessing node support through 1,000 replications of Shimodaira Hasegawa approximate Likelihood Ratio Test (SH-aLRT) (-alrt 1000) (Guindon et al. 2010, Hoang et al. 2018).

Multi-Locus Phylogenetic Inference

We evaluated the phylogenetic relationships within the genus *Taygetina* using the most comprehensive published multi-locus dataset for the '*Taygetis* clade' (Matos-Maraví et al. 2013). We added to this dataset the COI sequences of one representative of each new described species, *T. brocki* **n. sp.** and *T. accacioi* **n. sp.**, in addition to several other described and undescribed species not included in Matos-Maraví et al. (2013) (Table 1). We ran PartitionFinder v2.1.1 (Lanfear et al. 2017) to estimate the best-fit partitioning strategy. We used the greedy option and 12 datablocks corresponding to the codon positions of the four gene fragments:

Table 1. GenBank accession numbers for DNA sequences used for this study

Code	Genus	Species	COI	EF1a	GAPDH	RpS5	Publication
CP01-18	*Magneuptychia*	*fugitiva*	GU205845	GU205901	GU205958	GU206017	Peña et al. 2010 (Zool. Scr.)
CP06-70	*Megeuptychia*	*monopunctata*	GU205852	GU205908	GU205964	GU206024	Peña et al. 2010 (Zool. Scr.)
CP-Lep-936	*Forsterinaria*	*anophthalma*	GWOTT725-18	X	X	X	Peña et al. 2010 (Zool. Scr.)
CP02-72	*Forsterinaria*	*antje*	JQ392586	JQ392716	JQ392819	JQ392924	Matos-Maraví et al. 2013 (MPE)
CP04-88	*Forsterinaria*	*boliviana*	DQ338799	DQ338943	GQ357435	GQ357564	Peña et al. 2006 (MPE)
CP04-59	*Forsterinaria*	*guaniloi*	JQ392588	JQ392718	JQ392821	JQ392926	Matos-Maraví et al. 2013 (MPE)
DNA99-060	*Forsterinaria*	*inornata*	AY508544	AY509070	X	X	Murray and Prowell 2005 (MPE)
NW126-10	*Forsterinaria*	*necys*	GU205837	GU205893	GU205950	JQ392927	Peña et al. 2010 (Zool. Scr.)
gsm449	*Forsterinaria*	*neonympha*	JQ392590	JQ392720	JQ392823	JQ392929	Matos-Maraví et al. 2013 (MPE)
gsm447	*Forsterinaria*	*pallida*	JQ392587	JQ392717	JQ392820	JQ392925	Matos-Maraví et al. 2013 (MPE)
CP02-60	*Forsterinaria*	*pichita*	JQ392591	JQ392721	JQ392824	JQ392930	Matos-Maraví et al. 2013 (MPE)
UN0264	*Forsterinaria*	*pilosa*	JQ392592	X	JQ392825	X	Matos-Maraví et al. 2013 (MPE)
PM04-03	*Forsterinaria*	*pronophila*	JQ392605	JQ392732	JQ392836	JQ392941	Matos-Maraví et al. 2013 (MPE)
CP04-54	*Forsterinaria*	*proxima*	JQ392593	JQ392722	JQ392826	JQ392931	Matos-Maraví et al. 2013 (MPE)
CP02-57	*Forsterinaria*	*pseudinornata*	JQ392594	JQ392723	JQ392827	JQ392932	Matos-Maraví et al. 2013 (MPE)
gsm488	*Forsterinaria*	*punctata*	JQ392595	JQ392724	JQ392828	JQ392933	Matos-Maraví et al. 2013 (MPE)
PM10-05	*Forsterinaria*	*quantius*	JQ392596	JQ392725	JQ392829	JQ392934	Matos-Maraví et al. 2013 (MPE)
CP02-51	*Forsterinaria*	*rotunda*	JQ392599	JQ392726	JQ392830	JQ392935	Matos-Maraví et al. 2013 (MPE)
CP03-66	*Forsterinaria*	*rustica*	JQ392602	JQ392729	JQ392833	JQ392938	Matos-Maraví et al. 2013 (MPE)
BC-DZ-Willmott-293	*Harjesia*	*argentata*	MH592922	MH592927	MH592944	MH592961	Nakahara et al. 2018b (Insecta Mundi)
CP01-13	*Harjesia*	*blanda*	DQ338800	DQ338945	GQ357436	GQ357565	Peña et al. 2006 (MPE)
CP23-22	*Harjesia*	*obscura*	JQ392610	JQ392737	JQ392839	JQ392946	Matos-Maraví et al. 2013 (MPE)
KW-15-001	*Orotaygetis*	*surui*	MH592920	MH592932	MH592949	MH592966	Nakahara et al. 2018b (Insecta Mundi)
CP04-09	*Parataygetis*	*albinotata*	JQ392615	JQ392741	JQ392843	JQ392950	Matos-Maraví et al. 2013 (MPE)
NN58	*Parataygetis*	*lineata*	JQ392618	JQ392744	JQ392846	JQ392953	Matos-Maraví et al. 2013 (MPE)
NW126-13	*Posttaygetis*	*penelea*	DQ338813	DQ338959	GQ357446	GQ357575	Peña et al. 2006 (MPE)
CP22-02	*Pseudodebis*	*celia*	GU205874	GU205930	GU205988	GU206049	Peña et al. 2010 (Zool. Scr.)
LEP-37349	*Pseudodebis*	*celia_01*	MN271921	X	X	X	Unpublished (Pseudodebis MS)
KW-140716-03	*Pseudodebis*	*celia_02*	MH592911	MH592929	MH592946	MH592963	Nakahara et al. 2018b (Insecta Mundi)
MACN-Bar-Lep-00529	*Pseudodebis*	*euptychidia*	MF545476	X	X	X	Lavinia et al. 2017 (PLOS ONE)
PM01-23	*Pseudodebis*	*marpessa*	JQ392624	JQ392747	JQ392849	JQ392957	Matos-Maraví et al. 2013 (MPE)
CP22-04	*Pseudodebis*	*puritana*	GU205875	GU205931	GU205989	GU206050	Peña et al. 2010 (Zool. Scr.)
PM01-18	*Pseudodebis*	*valentina*	JQ392632	JQ392750	JQ392853	JQ392963	Matos-Maraví et al. 2013 (MPE)
KW-15-003	*Pseudodebis*	*vrazi*	MH592918	X	X	X	Nakahara et al. 2018b (Insecta Mundi)
INB0004265373	*Pseudodebis*	*zimri*	ASARD2530-12	X	X	X	Unpublished (BOLD)
CP23-21	*Sepona*	*punctata*	JQ392607	JQ392734	JQ392838	JQ392943	Matos-Maraví et al. 2013 (MPE)
LEP-00435	*Taygetina*	*banghaasi*	JQ392633	JQ392751	JQ392854	JQ392964	Matos-Maraví et al. 2013 (MPE)
KW-15–077	*Taygetina*	*brocki*	MN099274	X	X	X	This study
PM02-04	*Taygetina*	*kerea*	JQ392645	JQ392763	JQ392866	JQ392976	Matos-Maraví et al. 2013 (MPE)
CP02-13	*Taygetina*	*oreba*	JQ392613	JQ392740	JQ392842	JQ392949	Matos-Maraví et al. 2013 (MPE)
PM02-02	*Taygetina*	*peribaea*	JQ392584	JQ392715	JQ392818	JQ392923	Matos-Maraví et al. 2013 (MPE)
PM03-03	*Taygetina*	*weymeri*	JQ392708	JQ392814	JQ392918	JQ393027	Matos-Maraví et al. 2013 (MPE)
PM04-01	*Taygetis*	*acuta*	JQ392634	JQ392752	JQ392855	JQ392965	Matos-Maraví et al. 2013 (MPE)
PM01-11	*Taygetis*	*angulosa*	JQ392636	JQ392754	JQ392857	JQ392967	Matos-Maraví et al. 2013 (MPE)
BC-DZ-Willmott-015	*Taygetis*	*chiquitana*	MH592921	MH592926	MH592943	MH592960	Nakahara et al. 2018b (Insecta Mundi)
CP02-63	*Taygetis*	*chrysogone*	JQ392637	JQ392755	JQ392858	JQ392968	Matos-Maraví et al. 2013 (MPE)
CP-M110	*Taygetis*	*cleopatra*	KM012983	KM012999	KM013280	KM013176	Matos-Maraví et al. 2013 (MPE)
PM01-02	*Taygetis*	*echo*	JQ392638	JQ392756	JQ392859	JQ392969	Matos-Maraví et al. 2013 (MPE)
PM01-14	*Taygetis*	*oyapock*	JQ392644	JQ392762	JQ392865	JQ392975	Matos-Maraví et al. 2013 (MPE)
PM10-12	*Taygetis*	*laches*	JQ392664	JQ392778	JQ392881	JQ392991	Matos-Maraví et al. 2013 (MPE)
PM14-24	*Taygetis*	*larua*	JQ392669	JQ392782	JQ392885	JQ392995	Matos-Maraví et al. 2013 (MPE)
PM02-01	*Taygetis*	*leuctra*	JQ392670	JQ392783	JQ392886	JQ392996	Matos-Maraví et al. 2013 (MPE)
PM03-01	*Taygetis*	*mermeria*	JQ392675	JQ392788	JQ392891	JQ393001	Matos-Maraví et al. 2013 (MPE)
NW127-28	*'Taygetis'*	*rectifascia*	GU205862	GU205918	GU205976	GU206037	Peña et al. 2010 (Zool. Scr.)
CP09-65	*Taygetis*	*rufomarginata*	JQ392678	JQ392790	JQ392894	JQ393003	Matos-Maraví et al. 2013 (MPE)
MHAAC383-07	*Taygetis*	*salvini*	JQ548414	X	X	X	Unpublished (BOLD)
CP01-49	*Taygetis*	*sosis*	JQ392681	JQ392791	JQ392895	JQ393004	Matos-Maraví et al. 2013 (MPE)

Table 1. Continued

Code	Genus	Species	COI	EF1a	GAPDH	RpS5	Publication
CP-M302	*Taygetis*	*sylvia*	MN433458	MN433460	MN477291	X	Matos-Maraví et al. 2013 (MPE)
CP06-68	*Taygetis*	*thamyra*	JQ392691	JQ392801	JQ392904	JQ393013	Matos-Maraví et al. 2013 (MPE)
PM01-15	*Taygetis*	*tripunctata*	JQ392693	JQ392803	JQ392906	JQ393015	Matos-Maraví et al. 2013 (MPE)
PM03-02	'*Taygetis*'	*uncinata*	JQ392694	JQ392804	JQ392907	JQ393016	Matos-Maraví et al. 2013 (MPE)
INB0004224343	*Taygetis*	*uzza*	ASARD2007-12	X	X	X	Unpublished (BOLD)
PM04-07	*Taygetis*	*virgilia*	JQ392703	JQ392811	JQ392914	JQ393023	Matos-Maraví et al. 2013 (MPE)
PM10-02	*Taygetis*	*ypthima*	JQ392709	JQ392815	JQ392919	JQ393028	Matos-Maraví et al. 2013 (MPE)
LCB 244	*Taygetina*	*oreba*	MN099264	X	X	X	This study
MGCL_LOAN_064	*Taygetina*	*gulnare_01*	MN099265	X	X	X	This study
MGCL_LOAN_287	*Taygetina*	*gulnare_01*	MN099266	X	X	X	This study
LCB 243	*Taygetina*	*gulnare*	MN099267	X	X	X	This study
LCB 245	*Taygetina*	*oreba*	MN099268	X	X	X	This study
BC_DZ_269	'*Taygetis*'	*rectifascia*	MN099269	X	X	X	This study
CP22_01	*Taygetina*	*peribaea*	JQ392583	X	X	X	Matos-Maraví et al. 2013 (MPE)
PM02_05	*Taygetina*	*peribaea*	JQ392585	X	X	X	Matos-Maraví et al. 2013 (MPE)
MGCL_LOAN_022	*Taygetina*	*kerea*	MN099268	X	X	X	This study
UN0402	*Taygetina*	*kerea*	JQ392646	X	X	X	This study
03_SRNP_25200	*Taygetina*	*kerea*	GU334334	X	X	X	Unpublished (BOLD)
03_SRNP_14853	*Taygetina*	*kerea*	GU334336	X	X	X	Unpublished (BOLD)
03_SRNP_25198	*Taygetina*	*kerea*	GU334337	X	X	X	Unpublished (BOLD)
03_SRNP_14849	*Taygetina*	*kerea*	GU334335	X	X	X	Unpublished (BOLD)
05_SRNP_19333	*Taygetina*	*kerea*	GU157557	X	X	X	Unpublished (BOLD)
07_SRNP_57982	*Taygetina*	*kerea*	JQ536337	X	X	X	Unpublished (BOLD)
07_SRNP_58008	*Taygetina*	*kerea*	JQ536339	X	X	X	Unpublished (BOLD)
11_SRNP_21709	*Taygetina*	*kerea*	JQ574510	X	X	X	Unpublished (BOLD)
07_SRNP_59272	*Taygetina*	*kerea*	JQ536905	X	X	X	Unpublished (BOLD)
07_SRNP_57643	*Taygetina*	*kerea*	JQ536338	X	X	X	Unpublished (BOLD)
PM02_04	*Taygetina*	*kerea*	JQ392645	X	X	X	Matos-Maraví et al. 2013 (MPE)
YB_BCI64711	*Taygetina*	*kerea*	KP849365	X	X	X	Basset et al. 2015 (Plos ONE)
YB_BCI64769	*Taygetina*	*kerea*	KP849366	X	X	X	Basset et al. 2015 (Plos ONE)
YB_BCI64799	*Taygetina*	*kerea*	KP849364	X	X	X	Basset et al. 2015 (Plos ONE)
MGCL_LOAN_022	*Taygetina*	*gulnare_01*	MN099270	X	X	X	This study
KW_15_076	*Taygetina*	*brocki*	MN099272	X	X	X	This study
LEP_00435	*Taygetina*	*banghaasi*	MN099273	X	X	X	This study
LEP_10084	*Taygetina*	*banghaasi*	MH592925	X	X	X	Nakahara et al. 2018b (Insecta Mundi)
KW_140719_01	*Taygetina*	*gulnare*	MH592914	X	X	X	Nakahara et al. 2018b (Insecta Mundi)
YPH0238	*Taygetina*	*gulnare*	KU340858	X	X	X	Nakahara et al. 2016 (Neotrop. Entomol.)
KW_15_078	*Taygetina*	*brocki*	MN099275	X	X	X	This study
MGCL_LOAN_003	'*Taygetis*'	*ypthima*	MN099276	X	X	X	This study
NW149_8	'*Taygetis*'	*ypthima*	GU205873	X	X	X	Peña et al. 2010 (Zool. Scr.)
MGCL-LOAN-506	*Taygetina*	*accacioi*	MN099277	X	X	X	This study
MGCL_LOAN_505	*Taygetina*	*accacioi*	MN099271	X	X	X	This study
MGCL_LOAN_507	*Taygetina*	*accacioi*	MN099278	X	X	X	This study

COI and three nuclear genes. We inferred a phylogenetic hypothesis of *Taygetina* species by employing maximum likelihood as an optimality criterion, using the dataset with five partitions in IQ-TREE v1.6.11 with similar parameters as described above, but we left the AUTO function + FreeRate heterogeneity for finding the optimal substitution model for each partition (Table 2). Confidence assessment was done following immediately preceding phylogenetic analysis based only on COI data.

Nomenclature

This paper and the nomenclatural act(s) it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:F19FF91D-BB18-401B-A4F1-D4F32CE4B751

Table 2. Partition schemes and best-fit models selected by IQ-TREE v1.6.11 for multi-locus dataset

Partition Subsets	Models
COI codon1	TPM3u+F+R3
COI codon2	TIM2+F+I+G4
COI codon3, GAPDH codon3, EF1a codon3, RpS5 codon3	K3Pu+F+I+G4
EF1a codon1, RpS5 codon1, GAPDH codon1	TVM+F+R3
EF1a codon2, RpS5 codon2, GAPDH codon2	TN+F+I+G4

Results

The genetic divergence of COI sequences among the three specimens of the new species *T. brocki* **n. sp.** was on average 0.17%

(range from 0.1 to 0.23%), and among these and their closest relative, *T. banghaasi*, was on average 6.15% (range from 5.92 to 6.38%). The genetic divergences among the three specimens of the new species *T. accacioi* **n. sp.** was on average 0.01% (range from 0.005 to 0.014%), and among these and their most closely related species, *T. banghaasi*, *T. brocki* **n. sp.**, and *T. gulnare*, ranged from 4.89 (*T. gulnare*) to 6.1% (*T. brocki* **n. sp.**). Our maximum likelihood tree (LnL = −2,551.7396) based on DNA barcodes recovered *Taygetina* as monophyletic with a high support (Fig. 1A; SH-aLRT/UFBoot = 94.6/95), including the sequences of the generic type species, *T. banghaasi* Weymer 1910. These phylogenetic relationships are congruent with a further phylogenetic analysis using a four-gene published dataset (LnL = −26,315.125), with *Taygetina* strongly supported as monophyletic (Fig. 1B; SH-aLRT/UFBoot = 95.4/99), and sister to *Taygetis* Hübner, [1819] (Fig. 1B; SH-aLRT/UFBoot = 94.5/99). The branch lengths estimated in IQ-TREE for the two species described and named herein are long but nested within the genus, thus reinforcing our decision to describe these species in *Taygetina*.

Taygetina **Forster, 1964**
Type species—*Taygetis banghaasi* Weymer 1910: 190, pl. 45d

Taygetina brocki Lamas & Nakahara, **n. sp.**
(Figs. 1, 2a–b, 3a–g, 4)
(Zoobank LSID: urn:lsid:zoobank.org:act:F4180E42-6E12-4095-B248-C12E826E58F4)

Systematic placement and diagnosis (Fig. 1). *Taygetina brocki* **n. sp.** is recovered as sister to *T. banghaasi* with a strong to moderate support (Fig. 1A: SH-aLRT/UFBoot = 93.7/95; Fig. 1B: SH-aLRT/UFBoot = 90.1/89). The genetic distances among three barcoded *T. brocki* **n. sp.** individuals (KW-15-076, 077, and 078) range from 0.104 to 0.23%, and the distances between them and its sister species, *T. banghaasi*, range from 5.92 to 6.38% (Supp Table 1 [online only]). These two species can be readily recognized by their differing average adult size, with *T. brocki* **n. sp.** being smaller (male forewing length 25–27 mm [n = 16]; female forewing length 23–26 mm [n = 7]) than *T. banghaasi* (forewing length 31–34 mm [n = 3]; syntype male of *Taygetis banghaasi* in ZSM = 31 mm). *Taygetina brocki* **n. sp.** is also distinguished from *T. banghaasi* by the lack of orange scaling in the discal cell of both VFW and VHW, in addition to its rather whitish/purplish ventral scaling. Furthermore, genitalic characters provide three more diagnostic characters to separate both species, namely: 1) the uncus of *T. banghaasi* being more strongly curved down compared with *T. brocki* **n. sp.**; 2) the sclerotized structure accompanying the plate below the ostium bursae is strongly curved into U-shaped arms with a semicircular plate in the middle of this structure, whereas the sclerotized arms are not curved in and the semicircular plate is reduced in *T. brocki* **n. sp.**; 3) the length of the ductus bursae and corpus bursae are similar in length in *T. banghaasi*, whereas the length of the ductus bursae is twice as great as that of the corpus bursae in *T. brocki* **n. sp.**. The female genitalic modifications in *T. brocki* **n. sp.** seem to be unique in the genus, except for *T. weymeri* (Draudt, 1912), which appears to have the lamella antevaginalis similar when viewed from the ventral side. However, the ostium bursae is located closer to the U-shaped arms in *T. weymeri*, without having a sclerotized plate above as in *T. brocki* **n. sp.**

Description. MALE Forewing length 25–27 mm (n = 16).
Head: Eyes with hair-like setae, white scales at base; first segment of labial palpi short, brownish, adorned with white long hair-like scales and brownish long hair-like scales ventrally, second segment length almost twice as great as eye depth and covered with brownish scales laterally, and with blackish scales along edge of distal two-third of dorsal surface, ventrally adorned with black hair-like scales about 3–4 times as long as segment width, third segment roughly two-fifth of second segment in length and covered with black scales dorsally and ventrally, with brownish-white scales laterally; antennae approximately two-fifth of forewing length, with ca. 37–38 segments (n = 2), distal 13–14 segments composing rather inconspicuous club.

Thorax: Dense long light brown hair-like scales anteriorly, sparse white and light brown long hair-like scales present on meso- and metathorax, with some golden scales, ventrally covered with dirty white long hair-like scales with sparse white scales.

Legs: Foreleg whitish, tarsus and tibia almost same in length, femur slightly shorter; midleg and hindleg with femur whitish ventrally, tibia and tarsus dorsally grayish, ventrally ochre, tarsus and tibia adorned with spines ventrally, pair of tibial spurs present at distal end of tibia.

Abdomen (Fig. 3a): Eighth tergite as sclerotized stripe at base of eighth abdominal segment, in addition to presence of distal broader sclerotized patch; eighth sternite appearing as single broad patch.

Wing venation: Basal half of forewing subcostal vein swollen; base of cubitus swollen; forewing recurrent vein absent; hindwing humeral vein developed; origin of M_2 towards M_1 than M_3.

Wing shape: Forewing subtriangular, costal margin convex, apex appearing somewhat truncated, outer margin convex, inner margin straight, but rounded towards thorax near base; hindwing slightly elongate, rounded, costal margin convex, outer margin sinuate with distal end of M_3 being most pointy, inner margin slightly concave near tornus, anal lobe convex, slightly round.

Dorsal forewing: Ground color brownish, distally appearing darker, black androconial scales present in middle of DFW, roughly mirroring area between VFW discal band and postdiscal band, apparently faded near costa.

Dorsal hindwing: Ground color similar to forewing, distally darker, no visible androconial scales.

Ventral forewing: Ground color grayish chestnut brown, area basal of discal band paler, scattered with whitish scales near discal band; discal band somewhat indistinct, appearing as slightly sinuate brownish band in discal cell and extending below origin of Cu_2 (but see also below); area between discal band and postdiscal band scattered with whitish scales mainly between Radius and Cu_2; postdiscal band sinuate, appearing darker and more defined than previous band, extending from Radius towards inner margin, fading in cell Cu_2 and reaching 2A (but see also below); area between postdiscal band and submarginal band scattered with whitish scales, in addition to band-like streak of dense whitish scales from apex towards tornus, traversing basal of submarginal band and touching some submarginal ocelli; submarginal band undulating, appearing brownish with whitish scaling along distal margin, more sinuate than basal two bands, extending from apex to tornus; marginal band smoothly traversing along outer margin with whitish scaling visible distally; fringe brownish; submarginal ocelli in cells R_5, M_1, M_2, M_3, and Cu_1, all appearing as whitish pupil in somewhat indistinct brownish 'ring' without black central area.

Ventral hindwing: Ground color similar to forewing; area basal of discal band scattered with whitish scales; discal band similar to that of VFW in appearance except for extending from costa towards inner margin and reaching it, curved inwards below 2A (but see also below); area between discal band and postdiscal band scattered with

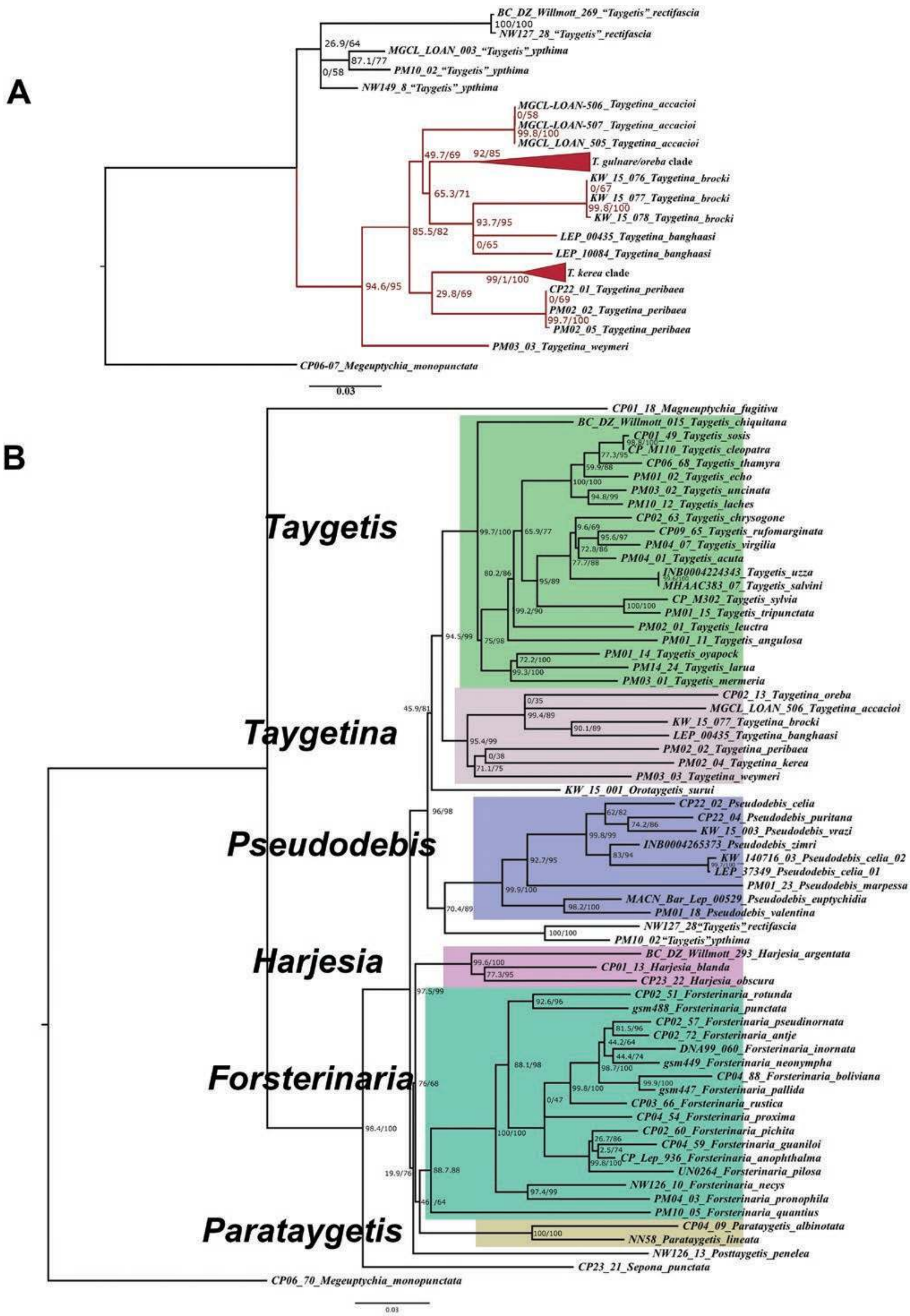

Fig. 1. (A) Maximum likelihood tree of Taygetina (LnL = −2551.7396) based on DNA 'barcodes' data and inferred in IQ-TREE. Support values are represented by SH-aLRT/UFBoot; (B) Maximum likelihood tree of the Taygetis clade (LnL = −26,315.125) based on the 4-gene dataset and inferred in IQ-TREE. Support values are represented by SH-aLRT/UFBoot.

whitish scales, basally more dense; postdiscal band similar to that of VFW in appearance except for passing origin of M_3, crossing 2A and apparently reaching inner margin where it terminates (but see also below); area between postdiscal band and submarginal band scattered with whitish scales, especially area near postdiscal band and area close to submarginal band; submarginal band similar to

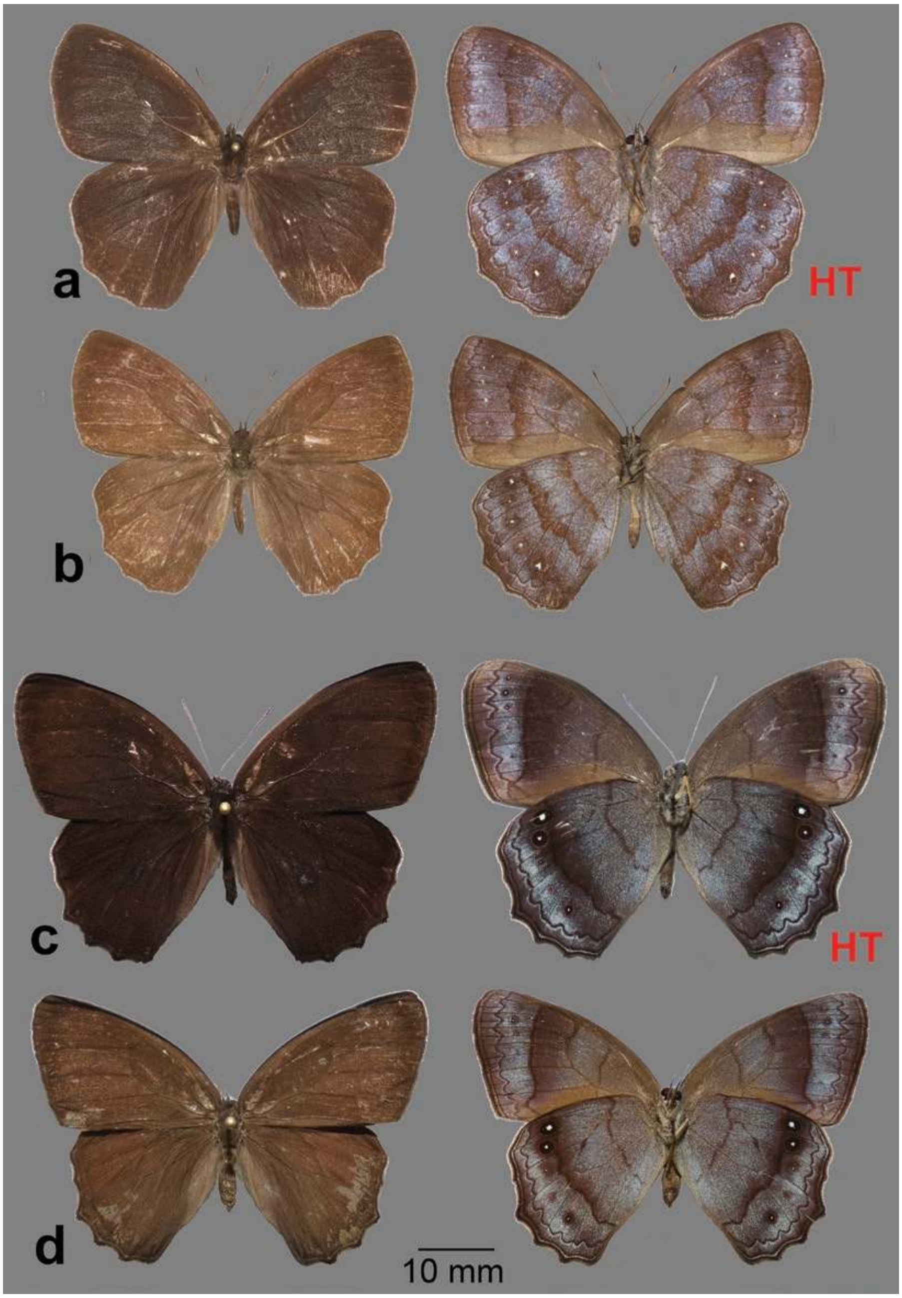

Fig. 2. *Taygetina* type specimens: (a) *T. brocki* **n. sp.**, holotype male, dorsal on left, ventral on right (MUSM-LEP 105430); (b) *T. brocki* **n. sp.**, paratype female, dorsal on left, ventral on right (MUSM-LEP 105433); (c) *T. accacioi* **n. sp.**, holotype male, dorsal on left, ventral on right (ZUEC LEP 11039); (d) *T. accacioi* **n. sp.**, paratype female, dorsal on left, ventral on right (ZUEC LEP 11040).

that of VFW in appearance except for bent inwards when crossing Cu_2; marginal band similar to that of VFW in appearance; fringe brownish; submarginal ocelli in cells Rs, M_1, M_2, M_3, and Cu_1, similar to those of VFW in appearance except for ocellus in Cu_1 being most prominent and occasionally black central area present.

Genitalia (Fig. 3a–d): Tegumen semicircular in lateral view, dorsal margin convex and ventral margin straight; uncus broad in lateral view, appearing robust (in contrast with many other euptychiines), slightly curved and posteriorly terminating in single point in lateral view, no visible hair-like setae; brachium tapering towards apex, similar to uncus in length, apical point positioned above uncus in lateral view, parallel to uncus with apical edge curving inwards in dorsal view; combination of ventral arms from tegumen and dorsal arms from saccus rather straight, slightly broadening near saccus; appendices angulares present, curving inwards; saccus straight, anteriorly somewhat angular, similar to tegumen plus uncus in length; juxta present as shallow 'U-shaped' plate with apical point rounded (Fig. 3c); valva appearing roughly parallelogram in lateral view and distally setose, ventral margin convex, in addition to presence of concavity distally, dorsal margin distal of costa accompanying 'hump' at base of apical process, height of hump similar to width of apical process, apical process about one-third of entire valva length, terminating in rather round blunt end; phallus roughly straight, similar in length to tegumen plus uncus, phallobase occupying about

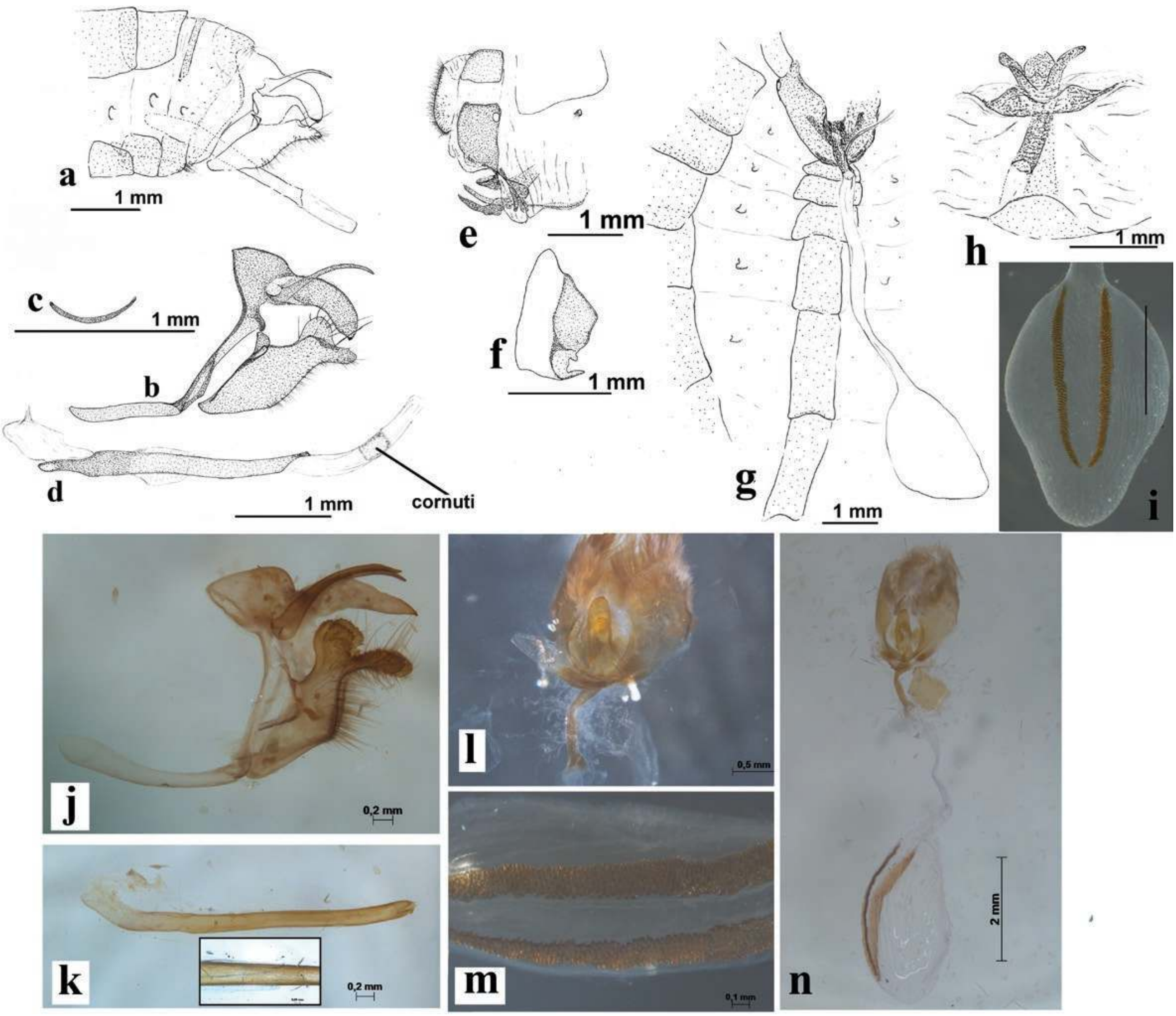

Fig. 3. *Taygetina* genitalia: (a) Terminal abdominal segments of male *T. brocki* **n. sp.** in lateral view; (b) male genitalic capsule of *T. brocki* **n. sp.** in lateral view; (c) juxta in posterior view; (d) phallus of *T. brocki* **n. sp.** in lateral view (vesica everted to better visualize cornuti); (e) Terminal abdominal segments of female *T. brocki* **n. sp.** in lateral view; (f) papillae analis (hair-like setae omitted); (g) female abdomen and genitalia of *T. brocki* **n. sp.** in dorsal view (inter-segmental membrane folded); (h) female genitalia of *T. brocki* **n. sp.** in ventral view (inter-segmental membrane expanded); (i) signa; (j) male genitalic capsule of *T. accacioi* **n. sp.** in lateral view; (k) phallus of *T. accacioi* **n. sp.** in lateral view (cornuti emphasized in black square); (l) female genitalia of *T. accacioi* **n. sp.** in ventral view; (m) signa; (n) female genitalic capsule of *T. brocki* **n. sp.** in postero-ventral view. (a–d) based on SN-19–108; (e–f) based on SN-19–115; (g–i) based on SN-19-12; (j–k) based on ZUEC LEP 11039 (holotype); (l–n) based on ZUEC LEP 11040.

one-fourth of phallus, ductus ejaculatorius visible as illustrated, posterior portion of aedeagus somewhat curved upwards, manica covering less than half of aedeagus, weakly sclerotized region of vesica apparently present as cornuti (Fig. 3d).

FEMALE Forewing length 23–26mm (n = 7).

Similar to male except as follows: Female foretarsus divided into five distinct segments; androconial scales absent in DFW. **Female abdomen and genitalia** (Fig. 3e–i): Eighth tergite developed, uniformly sclerotized; papillae anales without posterior apophysis; intersegmental membrane of seventh and eighth abdominal segment pleated and expandable, weakly sclerotized region present; lamella antevaginalis sclerotized, forming rectangular plate just below ostium bursae accompanied by 'U' shaped sclerotized structure, which is connected to anterior margin of sclerotized plate at lateral side of eighth abdominal segment, spiracle visible at top right corner of this plate (see Fig. 3e); ductus bursae approximately basal one-sixth sclerotized, remaining portion membranous; ductus seminalis exits at juncture of this sclerotized region and membranous region; corpus bursae roughly 'pear-shaped,' less than half in length compared with ductus bursae, extending across entire abdomen, with two signa parallel to each other.

Variation. The VFW and VHW discal and postdiscal bands are variable in appearance, less sinuate in some specimens (e.g., FLMNH-MGCL 281600; MUSM-LEP 105419), and some appear rather straight and broad due to fading basally (e.g., FLMNH-MGCL 281599).

Types. *Holotype:* male with the following labels: PERU, MD, Albergue Amazonia 1252/7123 [= 12°52′S, 71°23′W], 500 m 29.ix.2014 G. Lamas// MUSM Loan KW-15–077// MUSM-LEP 105430// (MUSM).

Fig. 4. *Taygetina accacioi* **n. sp.** male genitalia posterior view (left, based on ZUEC LEP 11040); ventral view (right, based on ZUEC LEP 11039), both showing absence of juxta.

Paratypes (17 males, 9 females): 17 males with the following labels PERU, MD, Albergue Amazonia, 1252/7123 500 m 29.ix.2014 G. Lamas // MUSM-LEP 105428// (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 29.ix.2014 G. Lamas // MUSM Loan KW-15–076// MUSM-LEP 105429// (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 10.ix.2012 L. Gibson// MUSM-LEP 105425// (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 26.x.2013 G. Lamas// MUSM-LEP 105426// (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 28.x.2013 G. Lamas// MUSM-LEP 105427// (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 29.ix.2011 J. Brock// MUSM-LEP 105422// (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 15.v.2012 J. Brock// MUSM-LEP 105423// (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 15.v.2012 J. Brock// MUSM-LEP 105424// (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 29.ix.2011 J. Brock// MUSM-LEP 105419// (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 29.ix.2011 J. Brock// MUSM-LEP 105420// (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 29.ix.2011 J. Brock// MUSM-LEP 105421// (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 28.ix.2011 J. Brock// MUSM-LEP 105417// (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 2.x.2011 G. Lamas// MUSM-LEP 105418// Genitalia vial SN-16–79 S. Nakahara// (MUSM); PERU, MD Albergue Amazonia, 1252/7123 500 m 28.ix.2011 G. Lamas// MUSM-LEP 105416// [genitalia in vial, without associated label] (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 28.ix.2014 G. Lamas// MUSM-LEP 105415// (MUSM); PERU: Madre de Dios: Rio Alto Madre de Dios, Atalaya Amazonia Lodge 491 m, 27 × 2013 leg. J.P. Brock// DNA sample ID: 11-BOA-13383C02 c/o Nick V. Grishin// SN-19–108 Genitalic vial// (JPB); Ecuador Orellana Estación Científica Yasuní 0°39′ LS, 76°22′ LW 17-5-2018 275 m S. Mena & F. Checa Ex:red// QCAZ I 25942// 622// (QCAZ); nine females with the following labels: PERU, MD, Albergue Amazonia, 1252/7123 500 m 29.ix.2011 J. Brock// MUSM Loan KW-15–078// MUSM-LEP 105433// (MUSM); PERU, MD, Albergue Amazonia, 1252/7123 500 m 29.ix.2011 J. Brock// MUSM-LEP 105431// Genitalia vial SN-16–69 S. Nakahara// (MUSM); PERU, MD, Albergue Amazonia 1252/7123 500 m 29.ix.2011 J. Brock// MUSM-LEP 105432// (MUSM); PERU: Madre de Dios: Rio Alto Madre de Dios, Atalaya Amazonia Lodge 491 m, 28 × 2013 leg. J. P. Brock// DNA sample ID: 11-BOA-13383C03 c/o Nick V. Grishin// (JPB); Ecuador, Napo Cotundo [c. 0°50′09.13″ S, 77°48′10.37″ W] 4–6 October 1988 700 m [750–800 m] McInnis// (MIMC); Ecuador Orellana Estación Científica Yasuní 0°39′' LS, 76°22′ LW 29-7-2018 275 m S. Mena & F. Checa Ex:red// QCAZ I 259420// 694// (QCAZ); JUNE 1973 MISAHUALLI, NAPO, 650 m ECUADOR R. de Lafebre// Genitalic vial SN-19-12// FSCA Florida State Collection of Arthropods// FLMNH-MGCL Specimen 281599// (FLMNH); ECUADOR: NAPO Rio Coca, 300 m. vii.1971 R. de Lafebre// Genitalic vial SN-19-11// A. C. Allyn Acc. 1971-41// FLMNH-MGCL Specimen 281600// (FLMNH); ECUADOR: NAPO Rio Coca, 300 m. vii.1971 R. de Lafebre// Allyn Museum photo No. 070675-10// A. C. Allyn Acc. 1971-41// Genitalic vial SN-19–115// FLMNH-MGCL Specimen 284908// (FLMNH).

Etymology. The specific epithet is dedicated to James Phillip Brock, who collected most specimens of the type series. Jim kindly provided information on the habitat, in addition to loaning specimens for study. It is a masculine noun in the genitive case.

Distribution (Fig. 5). This species is known from middle to low elevations in the eastern slope of the Andes, in the department of Madre de Dios, Peru, in addition to six specimens from Napo and Orellana provinces, Ecuador.

Remarks. This taxon is evidently extremely local, as evidenced by it being known from only a single site in Peru and very few sites in Ecuador, despite intensive collecting in both countries over the last few decades by a number of researchers.

James Brock (personal communication), who collected more than half of the existing specimens of *T. brocki* **n. sp.** in the Amazonia lodge area in Peru, did not notice any bamboo or unusual grasses in the vicinity. The forest where the holotype and paratypes were found is a mature second growth in a seasonally flooded area that was formerly a tea plantation, and specimens were collected inside the forest as far as 40 feet from the trail. In Ecuador, Sebastián Mena and María F. Checa (personal communication) collected a male and female of *T. brocki* **n. sp.** in the 50-hectare research plot in Yasuní National Park, an area of primary lowland rain forest on gently rolling terrain. Both specimens were collected by hand-net on cloudy days resting 1 m above the ground, the male at 14:00 h on top of a leaf and the female at 10:40 h under a leaf. Despite intensive surveys of butterflies within the same 50 hectare plot using both fruit and carrion traps since 2002 (e.g., Checa et al. 2009), *T. brocki* **n. sp.** has not otherwise been collected there. Mike McInnis (personal communication) collected a female specimen near Cotundo on a gradual hillside in secondary forest with trails.

Taygetina accacioi Nakahara & Freitas, **n. sp.**
(Figs. 1, 2c–d, 3h–l, 4)
(Zoobank LSID: urn:lsid:zoobank.org:act:F327CF82-35C3-4461-A0D4-F5CF3BB4369B)

Systematic placement and diagnosis (Fig. 1). *Taygetina accacioi* **n. sp.** is likely a member of the monophyletic *Taygetina* based on morphological and molecular data, although its systematic placement within the genus cannot be confidently assessed based on the DNA ‘barcode’ data (Fig. 1). The genetic divergence is >5% between *T. accacioi* **n. sp.** and any other of the 35 examined *Taygetina* taxa, whereas the genetic distance among the three barcoded individuals of *T. accacioi* **n. sp.** (MGCL-LOAN-505, 506, and 507) range from 0.005 to 0.014% (Supp Table 1 [online only]). *Taygetina accacioi* **n. sp.** is readily distinguishable from other members of the genus by its pronounced ocellus in the VHW cell Rs with a large white pupil; this ocellus is reduced and/or incomplete in *T. brocki* **n. sp.**, *T. banghaasi*, *T. weymeri*,

Fig. 5. Distribution map for the two *Taygetina* species described and named herein.

and *T. peribaea* (Godman and Salvin, 1880). *Taygetina kerea* (Butler, 1869), *T. oreba* (Butler, 1870), and *T. gulnare* (Butler, 1870), on the other hand, all possess a complete ocellus in the VHW cell Rs, but this is much smaller than the one in the VHW cell M1, whereas these two ocelli are similar in size or the ocellus in Rs is larger in *T. accacioi* **n. sp.** The male genitalia of *T. accacioi* **n. sp.** can be readily distinguished from other *Taygetina* species by lacking the juxta, a structure that is usually present in butterflies, and also by a 'thumb-like' apical process of the valva with a serrated dorsal margin.

Description. MALE Forewing length 29 mm (*n* = 2).

Head: Eyes with hair-like setae, white scales at base; first segment of labial palpi short, brownish, adorned with cream short hair-like scales dorsally and white and dark brownish long hair-like scales ventrally, second segment length almost twice as great as eye depth and covered with brownish scales laterally, and with blackish scales along edge of distal two-third of dorsal surface, ventrally adorned with black hair-like scales about 3–4 times as long as segment width, third segment roughly two-fifths of second segment in length and covered with black scales dorsally and ventrally, with brownish-white scales laterally; antennae approximately two-fifths of forewing length, with ca. 42 segments (*n* = 2), distal 13–14 segments composing rather inconspicuous club.

Thorax: Dorsally covered with dense long light brown hair-like scales, with some light brownish cream scales, ventrally covered with dirty white long hair-like scales with sparse white scales.

Legs: Foreleg covered with short white and long cream hair-like scales, tarsus and tibia almost same in length, femur slightly shorter; midleg and hindleg covered with short and long hair-like whitish cream scales, tarsus and tibia adorned with spines ventrally, pair of tibial spurs present at distal end of tibia.

Abdomen: Eighth tergite as sclerotized stripe at base of eighth abdominal segment, in addition to presence of distal broader sclerotized patch; eighth sternite appearing as single broad sclerotized patch.

Wing venation: Basal half of forewing subcostal vein swollen; base of cubitus swollen; forewing recurrent vein absent; hindwing humeral vein developed; origin of M_2 towards M_1 than M_3.

Wing shape: Forewing subtriangular, costal margin convex, apex appearing not truncated (in comparison with immediately preceding species) and appearing rather rounded, outer margin convex, inner margin straight, but rounded towards thorax near base; hindwing slightly elongate, rounded, costal margin convex, outer margin sinuate with distal end of M_3 being most pronounced, inner margin slightly concave near tornus, anal lobe convex, slightly round.

Dorsal forewing: Ground color brownish, distally appearing darker, black androconial scales present in middle of DFW, roughly mirroring area between VFW discal and postdiscal band, apparently faded near costa.

Dorsal hindwing: Ground color similar to forewing, darker around tornus and distal end of M_2 and of M_3, Cu_1, and Cu_2, no visible androconial scales.

Ventral forewing: Ground color light chestnut brown; discal band somewhat indistinct, appearing as slightly sinuate brownish band in discal cell and extending below Cubitus; area between discal band and postdiscal band sparsely scattered with whitish scales; postdiscal band rather straight, appearing darker and somewhat more defined than previous band, extending from Radius towards inner margin, bent distally in cell Cu_2 and touching submarginal band, and terminating around 2A; area between postdiscal band and submarginal band scattered with whitish scales, more dense in cells Cu_1 and Cu_2 than cells above; submarginal band undulating, appearing brownish with whitish scaling along distal margin, more sinuate and defined than basal two bands, extending from apex to tornus; marginal band smoothly traversing along outer margin with whitish scaling visible distally; fringe dark brownish; submarginal ocelli in cells R_5, M_1, M_2, M_3, and Cu_1, ocellus in cell M_1 appearing as whitish pupil in somewhat indistinct brownish 'ring' with black central area, remaining ocelli smaller and appearing as more reduced ocelli (but see below).

Ventral hindwing: Ground color darker than forewing; area basal of discal band scattered with whitish scales; discal band similar to that of VFW in appearance except for more defined and curving outwards in discal cell, extending from costa towards inner margin and reaching 3A; area between discal band and postdiscal band scattered with whitish scales except for distal one-third where revealing dark ground color; postdiscal band similar to that of VFW in appearance except for not strongly bent distally in cell Cu_2 and crossing 2A where it is apparently fused with submarignal band near inner margin; area between postdiscal band and submarginal band scattered with whitish scales, especially near submarginal band in cells M_1, M_2, M_3, and Cu_1; submarginal band similar to that of VFW in appearance except for apparently fused to postdiscal band near inner margin; marginal band similar to that of VFW in appearance except for being more sinuate reflecting undulating hindwing margin; fringe dark brownish; submarginal ocelli in cells Rs, M_1, M_2, M_3, and Cu_1, ocellus in Rs being most pronounced with white prominent pupil in indistinct brownish 'ring' filled with black, ocellus in M_1 second largest (but see also below) with white pupil similar but smaller than ocellus in Rs, ocellus in Cu_1 similar but smaller than ocellus in cell M_1, ocelli in cells M_2 and M_3 reduced (but see also below).

Genitalia (Fig. 3j–k): Tegumen appearing semi-circular, somewhat skewed left in lateral view, dorsal margin convex and ventral margin straight; uncus broad in lateral view, 1.5 times longer than tegumen, appearing robust (in contrast with many other euptychiines), slightly curved and posteriorly terminating in single point in lateral view, no visible hair-like setae; brachium broad at base, tapering towards apex, similar to uncus in length, apical point positioned above uncus in lateral view, parallel to uncus with apical edge curving inwards in dorsal view; combination of ventral arms from tegumen and dorsal arms from saccus straight, slightly broadening near saccus; appendices angulares present, curving inwards; saccus long and rather straight, rounded anteriorly, similar to tegumen plus uncus in length; juxta absent (Fig. 4); valva basal two-thirds appearing roughly as a parallelogram in lateral view, distally setose including apical process, ventral margin convex, in addition to presence of concavity distally, dorsal margin distal of costa, apical process 'thumb-like,' lateral projection with rounded posterior end starting slightly narrow near base and dorsally serrated, accompanied with rounded large semicircular plate, with serrated dorsal margin, located at base of dorsal margin of projecting upwards; phallus roughly straight, similar in length to tegumen plus uncus, phallobase occupying about one-fourth of phallus, ductus ejaculatorius visible as illustrated, posterior portion of aedeagus somewhat curved upwards, manica covering about half of aedeagus, cornuti very small and visible as weakly sclerotized region of vesica (Fig. 3k).

FEMALE Forewing length 28mm (n = 1).

Similar to male except as follows: Female foretarsus divided into five distinct segments; androconial scales absent in DFW; wing color pattern paler. **Female abdomen and genitalia** (Fig. 3l–n): Eighth tergite developed, uniformly sclerotized; papillae anales without posterior apophysis; intersegmental membrane of seventh and eighth abdominal segment pleated and expandable, weakly sclerotized region present; lamella antevaginalis sclerotized, forming somewhat oval-shaped plate just below ostium bursae accompanied by 'U' shaped sclerotized structure, which is connected to anterior margin of sclerotized plate at lateral side of eighth abdominal segment, with spiracle visible at the top right corner of this plate; ductus bursae approximately basal one-third sclerotized, remaining portion membranous; ductus seminalis exits at juncture of this sclerotized region and membranous region; corpus bursae elongated, approximately half in length compared with ductus bursae, extending across entire abdomen, with two signa parallel to each other and extending through the entire length of corpus bursae.

Variation. The VFW ocelli in cells R_5, M_2, and Cu_1 appear more as complete ocelli in one male (ZUEC LEP 11041), whereas more reduced and pupil and black central area are not visible in the other male (ZUEC LEP 11039). The ocellus in the VHW cell Rs is similar in size to ocellus in the VHW cell M_1 in ZUEC LEP 11039, whereas the former ocellus is larger than the latter in ZUEC LEP 11041.

Types. *Holotype:* male with the following labels (labels separated by double transverse bars): HOLOTYPUS// BRAZIL, Bahia, Ilhéus, Cachoeira Lisa, 15°0′15″S, 39°8′10″W, 15–31.I.2000, Accacio, G. M. leg., MGCL-507 / ind. 1480 IFR21// MGCL-LOAN-507// ZUEC LEP 11039//. Deposited in the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC).

Paratypes (1 male, 1 female)*:* female with the following labels (labels separated by double transverse bars): PARATYPUS// BRAZIL, Bahia, Ilhéus, 14°59′9″S, 39°6′4″W, 15–31.I.2000, Accacio, G. M. leg., MGCL-506 / ind. 1457 IFR12// MGCL-LOAN-506// ZUEC LEP 11040//. Other paratype, male with the following labels: PARATYPUS// BRAZIL, Bahia, Una Biological Reserve, Una, 15°7′54″S, 39°10′31″W, 15–30.XI.1999, Accacio, G. M. leg., MGCL-505 / ind. 0517 IIFR11// MGCL-LOAN-505// ZUEC LEP 11041//. Both deposited in the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC).

Etymology. This specific epithet honors Gustavo de Mattos Accacio, a Brazilian independent biologist who conceived and performed an extensive trap study in the state of Bahia that resulted in the collecting and subsequent discovery of this new species. The specific epithet is a masculine noun in the genitive case.

Distribution (Fig. 5). This species is known to date only from the south of Bahia State, Brazil. Specifically, the species was collected from the region of Ilhéus and Una municipalities.

Remarks. The three known specimens of this new species have been barcoded, and the low genetic distances among them supports their conspecificity (see Fig. 1). Besides the three specimens that compose the type series, two additional individuals were captured and released in two other sites in the same region in south Bahia, including: 1) a forest fragment near Cachoeira Lisa, Ilhéus, 15°1′15″S, 39°9′18″W (January 2000) and 2) a second site inside the Una Biological Reserve, Una, 15°10′36″S, 39°1′53″W (May 2000) (see Accacio (2002) for information regarding these two individuals), which is a large conservation unit that provides an effective opportunity for the long-term conservation of *Taygetina accacioi* **n. sp.** The biology and habits of this species remain largely unknown and it can be considered a rare species within its known distributional region. For example, in the large bait trap study in south Bahia, only five specimens of this species were captured (out of 3,706 captured butterflies in 132 traps over three sampling periods) (Accacio 2002). Based on these five records, the species is associated with tableland forest, a lowland rainforest locally known as 'tabuleiro forest.' These forest formations, also known as 'Hiléia Bahiana' (Andrade-Lima 1966), extend from Espírito Santo north of the mouth of Rio Doce river, to south Bahia, with warm annual temperatures with little fluctuation and deciduousness in some tree species (Peixoto et al. 2008). All five specimens were captured inside well-preserved forests away from cocoa plantations and forest edges, which might suggest that the species is associated with undisturbed habitats.

Discussion

We describe two species of *Taygetina* using an integrative approach consisting of an analysis of morphological and molecular characters. This study increases the number of described species in the genus to eight. However, the actual diversity of *Taygetina* is likely higher as ongoing morphological and molecular studies to revise the genus are finding highly divergent lineages within the known species *T. kerea*, *T. oreba*, and *T. gulnare* (Nakahara et al., in preparation). The most comprehensive multi-locus phylogeny for the '*Taygetis* clade' to date (Fig. 1B) recovered *Taygetina* as sister to *Taygetis* with a strong support (Fig. 1B; SH-aLRT/UFBoot = 94.5/99), a relationship in accordance with previously inferred molecular phylogenetic hypothesis (Matos-Maraví et al. 2013, Nakahara et al. 2018b, Espeland et al. 2019).

The molecular phylogenetic relationships can be supported by the appearance of *Taygetina* adults being phenotypically similar but smaller than members of the genus *Taygetis*. Despite the fact that the monophyly of most genera in the '*Taygetis* clade' being supported by molecular data, identifying morphological characters to diagnose these genera is somewhat more challenging. For example, Nakahara et al. (2018b) suggested the absence of brachia as being a definitive synapomorphy for *Pseudodebis* Forster, 1964. However, the presence or absence of this character can be highly variable within other related genera, such as *Harjesia* Forster, 1964 and *Taygetina* (discussed earlier). In this study, we found that the heavily sclerotized ductus bursae posterior to the origin of the ductus seminalis appears to be characteristic of many *Taygetina* species, while this structure in its closely related genus *Taygetis* is either membranous (e.g., *T. laches* (Fabricius, 1793); *T. sylvia* Bates, 1866) or weakly sclerotized (e.g., *T. mermeria* (Cramer, 1776); *T. chrysogone* Doubleday, [1849]). Evaluating such potential synapomorphies to diagnose and circumscribe genera in the *Taygetis* clade in broader taxonomic studies would be extremely valuable in refining the classification of this group (Nakahara et al., in preparation).

The absence of the juxta in *T. accacioi* **n. sp.** is an unusual condition not only for the subtribe Euptychiina, but also for butterflies (Fig. 4). A few euptychiine species have been described as having the juxta as 'membranous,' such as *Moneuptychia vitellina* Freitas & Barbosa, 2015 (Freitas et al. 2015), but nevertheless, the juxta is still visible as a weakly sclerotized band under the phallus in *M. vitellina*, unlike *T. accacioi* **n. sp.**. Some other Satyrinae taxa (e.g., *Lymanopoda nivea* Staudinger, 1887) also possess a weakly sclerotized (or membranous) juxta, but, again, the complete absence of juxta has never been reported, to our knowledge, in any other Satyrinae species. Even in the entire family Nymphalidae, there exist few records of reduced or membranous juxta. For example, Willmott and Freitas (2006) coded the juxta of *Ithomia drymo* Hübner, 1816 (Nymphalidae: Ithomiini) as 'absent (unsclerotized),' although a weakly sclerotized plate is visible in this species and thus the juxta is not strictly absent. The African nymphalid genus *Antanartia* Rothschild & Jordan, 1903, includes species without a juxta, although the base of the valva forms an arm-like structure ventrally supporting the phallus. With the exception of *Antanartia*, we do not know of any butterfly taxa where the juxta is reported as absent. Although the juxta is described as 'absent' in some Lepidoptera (e.g., certain genera of Psychidae [Roh et al. 2018], Gelechiidae [Ponoramenko 2007]), this character state, as reviewed here, is atypical of butterflies (Papilionoidea) and thus we consider this observation to be extremely valuable to report. We advocate for an increasing interest in morphological studies that could be coupled with the findings of molecular and genomic work. Even in well-studied insect groups, such as butterflies of the Neotropics, highly unusual character states can be discovered with a thorough study of existing museum specimens and new collections, which will improve confidence in species delineations and higher-level systematics efforts that otherwise rely heavily on molecular data.

Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

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