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SYSTEMATICS, MORPHOLOGY AND PHYSIOLOGY

Revision of the "*celia* clade" of *Pseudodebis* Forster, 1964, with Two New Species and Notes on *Papilio phorcys* Fabricius, 1793 (Lepidoptera: Nymphalidae: Satyrinae)

Shinichi Nakahara[1,2] · Daniel H. Janzen[3] · Winnie Hallwachs[3] · Blanca Huertas[4] · Gaurab Nandi Das[5] · Keith R. Willmott[6]

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Abstract

The species-level classification of the "*celia* clade" of the nymphalid butterfly genus *Pseudodebis* Forster, 1964, is revised as part of ongoing revisionary work on this genus. The "*celia* clade" contains three species, of which two, *Pseudodebis darrenthroopi* Nakahara & Willmott, **n. sp.** and *P. tigrillo* Nakahara & Willmott, **n. sp.,** are described and named herein based on morphology and molecular data. Consequently, we increase the described species diversity of *Pseudodebis* to 13, with a remarkable six species occurring in the trans-Andean region. We discuss five specific epithets associated with the clade and designate a neotype for *Papilio celia* Cramer, 1780, and lectotype for *Taygetis keneza* Butler, 1869, based on the same specimen, thus retaining the status of the former name as a senior objective synonym. We also provide a brief historical review for *Papilio phorcys* Fabricius, 1793, an enigmatic name currently synonymized under *Papilio celia*. Nevertheless, we were unable to locate the syntype(s) for this name and the identity of *Papilio phorcys* remains uncertain, so we retain the current synonymy as a parsimonious approach.

Keywords Euptychiina · J. C. Fabricius · taxonomy · William Jones

Introduction

The trans-Andean region (i.e., Mesoamerica + Chocó/Darién/W. Ecuador – *sensu* Myers et al. 2000) is one of the major biogeographical regions on Earth identified as a "biodiversity hotspot." The tropical Andes serve as a barrier to separate this region from the Amazonian region (Brown 1982), with a number of lowland butterfly taxa restricted in their distribution to just one side of the tropical Andes, resulting in the Andean divide separating a number of sister butterfly species. Nevertheless, the eastern side of the Andes harbors higher butterfly diversity in general, although there exist several genera or clades found exclusively in the trans-Andean region. The nymphalid subtribe Euptychiina is a diverse radiation in the lowlands of the Neotropical region with its species richness estimated to exceed 500 species in some 70 genera (Corahua-Espinoza et al. 2022), which follows the aforementioned general distribution pattern, namely with the highest species diversity found in the Amazon basin with few genera and clades restricted to the western side of the Andes, such as members of the so-called "*Cyllopsis* clade" (*sensu* Espeland et al. 2019). The euptychiine genus *Pseudodebis* Forster, 1964, is another group whose known species richness is increasing in the trans-Andean region based on ongoing molecular and morphological work by SN and collaborators.

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✉ Shinichi Nakahara
snakahara@ufl.edu

[1] Entomology and Nematology Dept, Univ of Florida, Gainesville, FL 32611, USA

[2] Depto de Entomología, Museo de Historia Natural, Univ Nacional Mayor de San Marcos, Lima, Peru

[3] Dept of Biology, Univ of Pennsylvania, Philadelphia, PA, USA

[4] Science Department, Natural History Museum, London, UK

[5] Institute of Entomology, Biology Centre CAS, České Budějovice, Czech Republic

[6] McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Univ of Florida, Gainesville, FL, USA

Nakahara et al. (2021a, b) was the first attempt to provide insights into the systematics and species diversity of *Pseudodebis* by formally testing a morphological synapomorphy for the genus and adding three new species from the trans-Andean region to better document its species-level diversity. Despite its monophyly being strongly supported in a number of phylogenetic studies (Matos-Maraví et al. 2013; Nakahara et al. 2019b, 2021a), there exist some taxonomic issues within the genus to be resolved, as indicated in the aforementioned study. One taxonomic problem involving *Pseudodebis* is determining the true species diversity in the "*celia* clade", an issue revealed mainly by "DNA barcode" data. Also, the "*valentina* clade" requires investigation as to the taxonomic status of a few names associated with this group. Due to the limited availability of specimens and insufficient molecular data to satisfactorily resolve species boundaries and assess the taxonomic status of relevant names, we have taken the practical approach of tackling individual species complexes in separate studies. Following Nakahara et al. (2021a, b), we here revise the species-level classification of the "*celia* clade," providing a taxonomic hypothesis for this group based on a combination of molecular data and morphology, particularly wing pattern.

Materials and methods

We largely follow our previous work on *Pseudodebis* for morphological study, using standard techniques to examine the external morphology of euptychiines (Nakahara et al. 2021a, b). Methods used to obtain the DNA barcode region (*sensu* Hebert et al. 2003) are largely in accordance with Nakahara et al. (2015). Information regarding the dataset and maximum likelihood analysis conducted on the University of Florida's Hipergator2 cluster are summarized in Nakahara et al. (2021a, b). The trimmed maximum likelihood tree (Fig. 1) represents the "*celia* clade" collapsed in Nakahara et al. (2021b), and molecular methods are described in that paper. Branch support estimates throughout the text result from a Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT; Guindon et al. 2011), an approximate Bayes branch test (aBayes; Anisimova et al. 2011), and an ultrafast bootstrap test (UFBoot) (Hoang et al. 2018) (SH-aLRT/aBayes/UFBoot). We present branch supports only for major nodes discussed in the present work and removed support values for internal nodes to improve clarity, and we provide the tree file (.tree) with all associated support value information as a Supplement. The following collection acronyms and abbreviations for wings are used throughout the text: AMNH (American Museum of Natural History, New York, USA); BME (Bohart Museum of Entomology, University of California Davis, Davis, USA); DZUP (Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil); FLMNH (McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, USA); ICNA (Ichiro Nakamura Personal Collection, Williamsville, USA); INABIO (Instituto Nacional de Biodiversidad, Quito, Ecuador; former acronym: MECN); MEM (Mississippi Entomological Museum, Mississippi State University, Mississippi, USA); MUSM (Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru); NHMUK (Natural History Museum London, UK); OUMNH (Oxford University Museum of Natural History, Oxford, UK); RMNH (Rijksmuseum van Natuurlijke Historie; currently Netherlands Centre for Biodiversity Naturalis, Leiden, Netherlands); USNM (National Museum of Natural History, Smithsonian Institution, Washington, DC, USA); ZMUC (Zoological Museum, University of Copenhagen, Copenhagen, Denmark); ZSM (Zoologische Staatssammlung München, Munich, Germany); ZUEC (Museu de Zoologia "Adão José Cardoso" da Universidade Estadual de Campinas, Campinas, Brazil); DFW (dorsal forewing); DHW (dorsal hindwing); VFW (ventral forewing); VHW (ventral hindwing).

Results

Figure 1 represents the *Pseudodebis* "*celia* clade" collapsed in Nakahara et al.'s (2021b) maximum likelihood tree based on DNA barcodes (LnL = − 2965.527). This particular clade falls within *Pseudodebis* as a moderately supported sister group to *P. puritana* (Weeks, 1902) + *P. vrazi* (Kheil, 1896) (68.4/0.939/49) (this relationship not shown here), based on 68 sequences representing individuals spanning the range of this clade from Costa Rica to southern Brazil. All individuals from the western Andes (Costa Rica - western Ecuador), except for three samples from western Ecuador (DNA voucher: LEP-37268, 27265, 37266; all currently at FLMNH), form a moderately well-supported clade (Fig. 1; 81.1/0.969/75). This trans-Andean clade is recovered as sister to a clade with the aforementioned three western Ecuadorian specimens and individuals from east of the tropical Andes. Monophyly for the three sequenced west Ecuadorian samples is strongly supported (Fig. 1; 95.5/1/100), whereas the clade with nine individuals from French Guiana, Ecuador, and Brazil is only supported moderately (Fig. 1; 76/0.74/66). These three clades correspond to wing pattern differences discussed below, which, coupled with their range and sympatry, we believe are best regarded as three species. The specific epithet "*celia*" is associated with the clade consisting of specimens from the eastern Andes based mainly on the type locality (see discussion below). We were unable to associate any available names to the two clades from the western Andes, and thus, two new species are named and

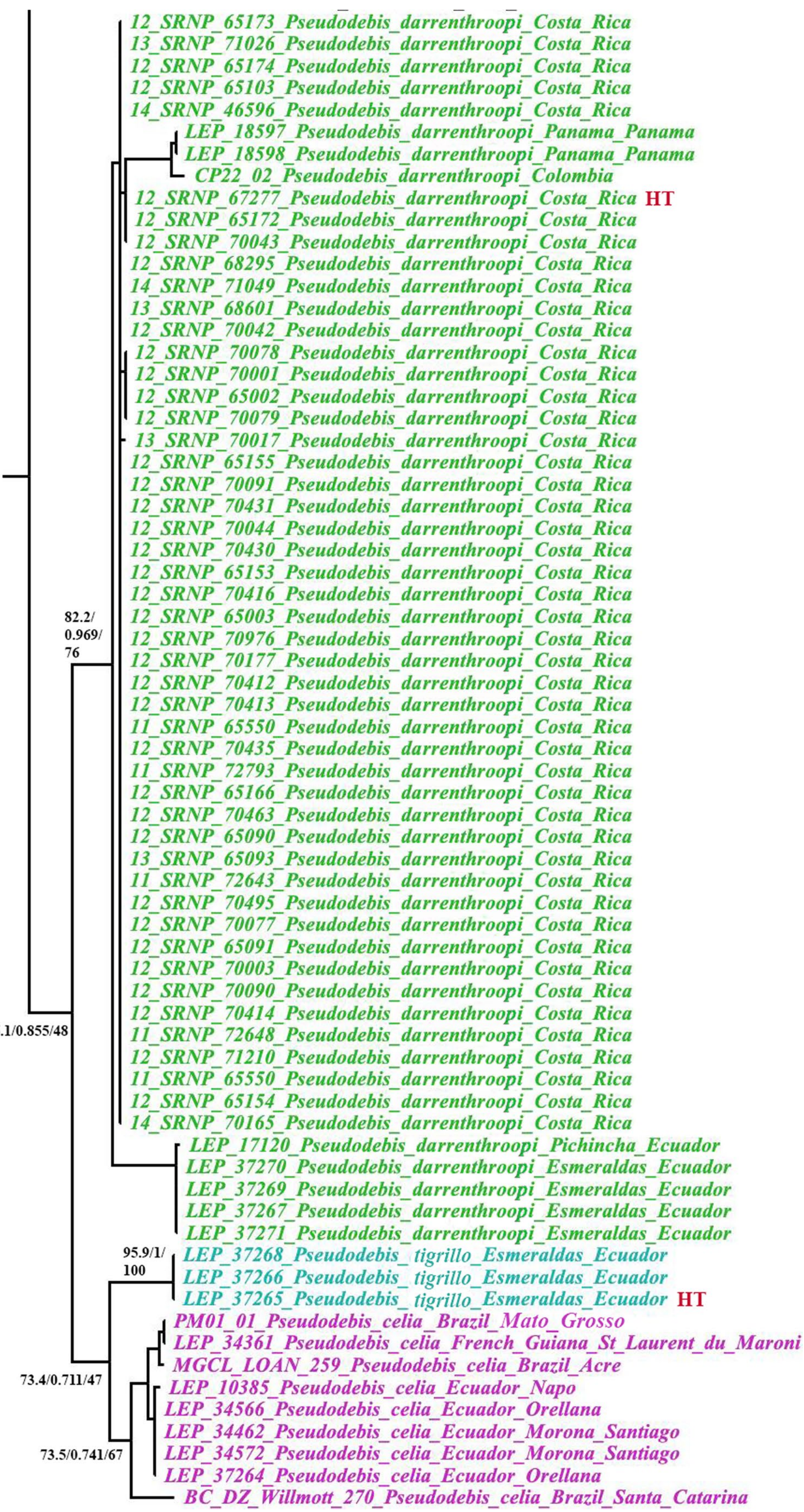

Fig. 1 Maximum likelihood tree showing relationships among the "*celia* clade" of *Pseudodebis*, corresponding to the collapsed relevant clade in Nakahara et al. (2021b: Fig. 1; LnL = − 2965.527). Branch supports are represented by SH-aLRT/aBayes/UFBoot. HT denotes the holotype specimen

described here to recognize these two clades as distinct evolutionary entities.

Pseudodebis Forster, 1964
Type species - *Papilio valentina* Cramer, 1779: 82, pl. 242, fig. A.

Systematic placement and diagnosis. As stated above, all recent molecular phylogenetic studies recovered *Pseudodebis* as a monophyletic group within the so-called *Taygetis* clade (Matos-Maraví et al. 2013; Nakahara et al. 2019b, 2021a, b). The systematic placement of this genus is consistent in these studies, where it is found as sister to the *Taygetis ypthima* group (a study is underway to describe a new genus for this group in order to maintain the monophyly of *Taygetis* Hübner, [1819]) with strong support (Matos-Maraví et al. 2013; Nakahara et al. 2019b, 2021a). In particular, the absence of (or reduced) brachia was identified as a synapomorphic character to diagnose *Pseudodebis* from other closely related genera (Nakahara et al. 2021a).

Pseudodebis celia (Cramer, 1779)
Papilio celia: Cramer 1779: 83, pl. 242, fig. C.
Taygetis celia: Hübner [1819]: 55; Westwood 1851: 357; Butler 1868: 8; Butler [1870]: 10; Kirby 1871: 109; Weymer 1910: 188; D'Almeida 1922: 226; Gaede 1931: 431; Forbes 1953: 98; D'Abrera 1988: 751; Lamas et al. 1991: 10; Murray 2000: 33-34, 57.
Taygetomorpha celia: Lamas 2004: 223; Garwood et al. 2009: 167, fig; Garwood and Lehman 2011: 284, fig [identical individual illustrated in the previous publication]; Mielke et al. 2010: 290; Matos-Maraví et al. 2013: 59-60 [*Pseudodebis celia* n. comb. proposed]
Papilio phorcys: Fabricius: 1793: 80; Donovan 1800-04: pl. 32; Zimsen 1964: 558, 602; Lamas 2004: 223.
Cynthia phorcys: Fabricius 1938: 91.
Nymphales phorcys Latreille 1819: 372; Westwood 1842: 49.
Hyp[anis] ? phorcys: Westwood 1851: 411.
Taygetis keneza: Butler 1869: 19; Godman and Salvin 1881-1882: 99; Weymer 1910: 188, pl. 45b; Lamas 2004: 223
Taygetis celia keneza: Forster 1964: 68, fig. 18.

Systematic placement, identification and taxonomy. *Pseudodebis celia* is most easily distinguished from *P. darrenthroopi* **n. sp.** and *P. tigrillo* **n. sp.** by its east Andean distribution, whereas these two closely related species described and named here are trans-Andean taxa. Although lacking strong support, nine sequenced individuals of *P. celia* spanning its range do form a clade (Fig. 1; 73.5/0.741/67), with a sample from Santa Catarina, Brazil (BC-DZ-270) recovered as sister to the remaining eight individuals. Unfortunately, the sister species of *P. celia* has not been confidently resolved based on DNA barcode data, and currently it is weakly supported as sister to *P. tigrillo* **n. sp.** (Fig. 1; 73.4/0.711/47). Despite the rather low support for some relevant nodes, the eastern or western distribution in relation to the Andean divide is clearly reflected in the phylogenetic structure. On the other hand, it must be noted that due to the infra-specific variation of species discussed herein, diagnostic characters provided below are not always applicable to all individuals and thus should be used in combination with geographic distribution. Externally, *P. celia* is readily distinguished from *P. darrenthroopi* n. sp. by the following characters: (1) larger adult size (male forewing length: 31–38 mm ($n = 4$; mean = 35.25 mm) (male forewing length of *P. darrenthroopi* **n. sp.** 31–35 mm ($n = 6$; mean = 32.7 mm); (2) VHW discal band strongly curving inwards in cell 2A and often appearing to terminate at 3A (whereas the VHW discal band is more straight and reaches the inner margin in *P. darrenthroopi* **n. sp.**); (3) posterior half (after passing Cu_1) of the VHW postdiscal band more undulating (posterior half of the VHW postdiscal band less undulating or rather straight in *P. darrenthroopi* **n. sp.**); (4) lamella antevaginalis appearing somewhat like a broadly rounded plate in ventral view with a concavity at the posterior margin (lamella antevaginalis appearing longer vertically and narrow in ventral view compared to lateral plates of the eighth abdominal segment, with somewhat undulating margin in *P. darrenthroopi* **n. sp.**). Characters distinguishing *P. celia* from *P. tigrillo* **n. sp.** are discussed under the latter taxon.

Papilio celia Cramer, 1779 was described in Pieter Cramer's *De Uitlandsche Kapellen* based on an unspecified number of specimens from Suriname (Cramer, 1779). Following the two immediately preceding Neotropical satyrine species (*Papilio valentina* and *Papilio thamyra* Cramer, 1779) described and illustrated on the same plate (pl. 212, Fig. C; see Fig. 2 in the present study), Cramer's "simple" description of *Papilio celia* is written as follows (translation by Hajo Gernaat): "Fig. C. Celia [sic]. Is also an eyed Nymph-Butterfly, which has the upper side of the wings brown, just as the previous [species], without any other pattern [literally, drawing]. This and Fig. B. look a lot like the Pap. Andromeda [sic] and Virgilia [sic], however, show the distinction of the pattern satisfactorily, so that they are distinctive species, different from each other. They live in Suriname." The original illustration in the NHMUK shows the ventral surface of a specimen which has an angled, dark VHW postdiscal line and FW apex protruding at the end of vein M_2, both characters that are distinctive of *P. celia* as recognized here, at least among the butterfly fauna east of the Andes. During the course of compiling pictures of potential types for euptychiine taxa described by Pieter Cramer and Caspar

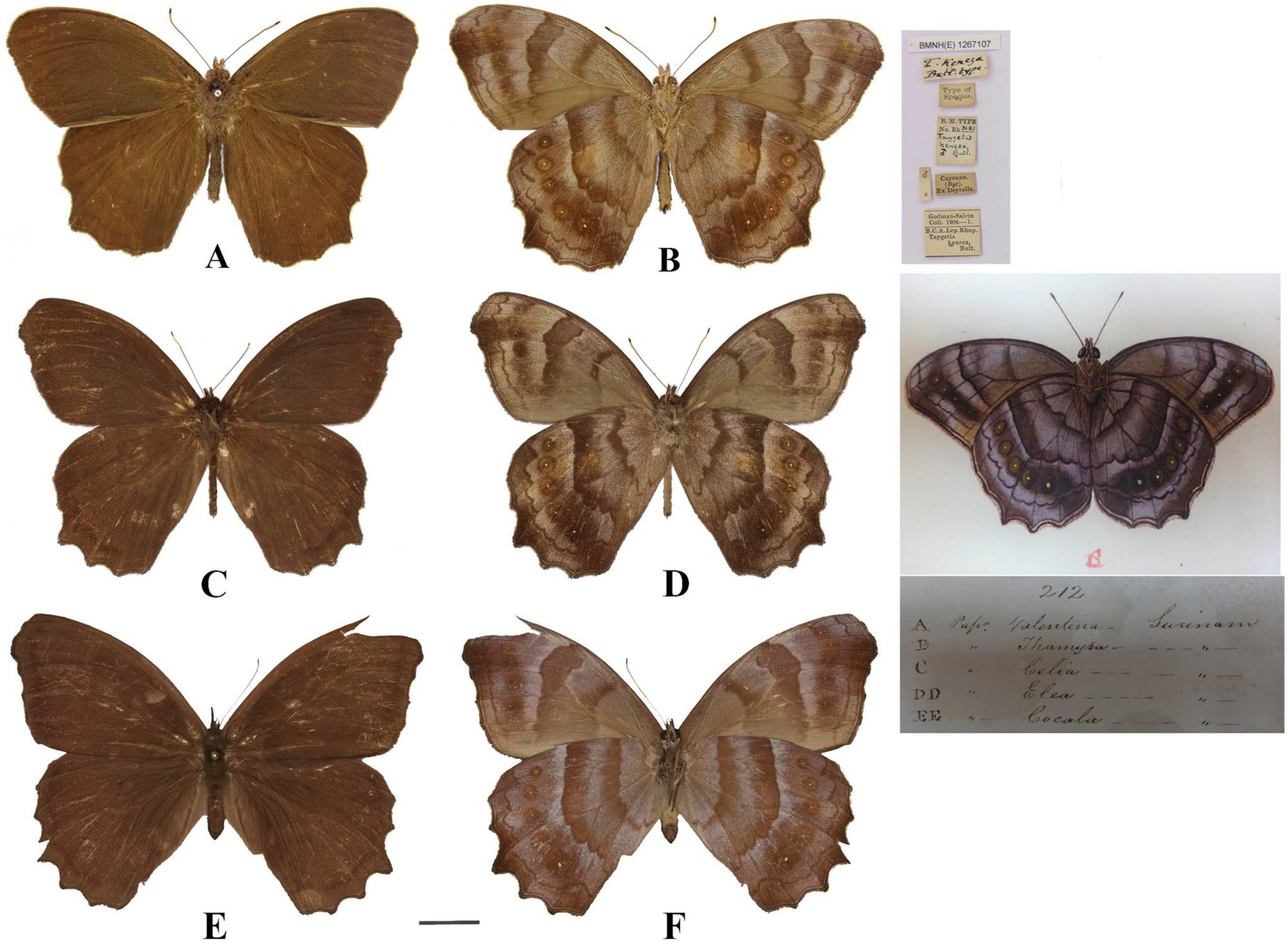

Fig. 2 Adults of species discussed in this study: **A** NEOTYPE of *Papilio celia* (= LECTOTYPE of *Taygetis keneza*), dorsal surface; **B** ventral surface of **A**, with associated labels to the right; **C** *Pseudodebis celia*, male from Orellana, Ecuador, dorsal surface (FLMNH# 209799); **D** ventral surface of **C**; **E** *Pseudodebis celia*, female from Huánuco, Peru, dorsal surface (MUSM# 104311); **F** ventral surface of **E**; **G** *Pseudodebis darrenthroopi* **n. sp.,** HOLOTYPE male from Alajuela, Costa Rica, dorsal surface (12-SRNP-67277); **H** ventral surface of **G**; **I** *Pseudodebis darrenthroopi* **n. sp.,** female from Esmeraldas, Ecuador, dorsal surface (FLMNH# 209806); **J** ventral surface of **I**; **K** *Pseudodebis tigrillo* **n. sp.,** HOLOTYPE male from Esmeraldas, Ecuador, dorsal surface (FLMNH# 209801); **L** ventral surface of **K**; **M** *Pseudodebis tigrillo* **n. sp.,** female from Esmeraldas, Ecuador, dorsal surface (FLMNH# 209803); **L** ventral surface of **N**. Scale bar = 10 mm. Illustration to the right represents the original painting of *Papilio celia* by P. Cramer and associated legends for pl. 212 (credit: Blanca Huertas, © Trustees NHMUK)

Stoll at RMNH (see Nakahara et al. 2019a, for example), we were unable to locate syntype(s) for *Papilio celia*. Further searches in museums such as NHMUK (Cramer types mostly from van Lennep collection, subsequently purchased by Cajetan Felder) and OUMNH, following similarly unsuccessful attempts made to locate type material by Gernaat et al. (2012) and researchers on Jones's work, such as Dick Vane-Wright (pers. comm.). Nevertheless, establishing the identity of the name is important since this is a common, widespread species that has featured in many studies (e.g., D'Abrera 1988; Weymer 1910; Lamas 2004; Lamas et al. 1991; Murray 2000; Mielke et al. 2010). Assuming that the type locality for *Papilio celia* is correct, and we have no reason to think otherwise, our molecular data support the application of this name to the widespread Guianan-Amazonian species that has typically been identified under this name. We therefore designate a neotype for *Papilio celia*, as described further below, to fix this identity.

Papilio phorcys Fabricius, 1793, was described by Johan Christian Fabricius in his *Entomologia systematica* (volume 3.1) based on an unspecified number of specimen(s) from "Indiis" [sic] in William Jones' ([1745]-1818) collection, where [Dru] Drury was cited as a repository for the type material(s) by Jones himself (Fabricius 1793). Nevertheless, Jones' paintings in manuscripts of Lepidoptera (mainly diurnal butterflies – i.e., Papilionoidea) now arranged in six bound volumes, known as "Jones' Icones," were never published (Vane-Wright 2010). The original description of

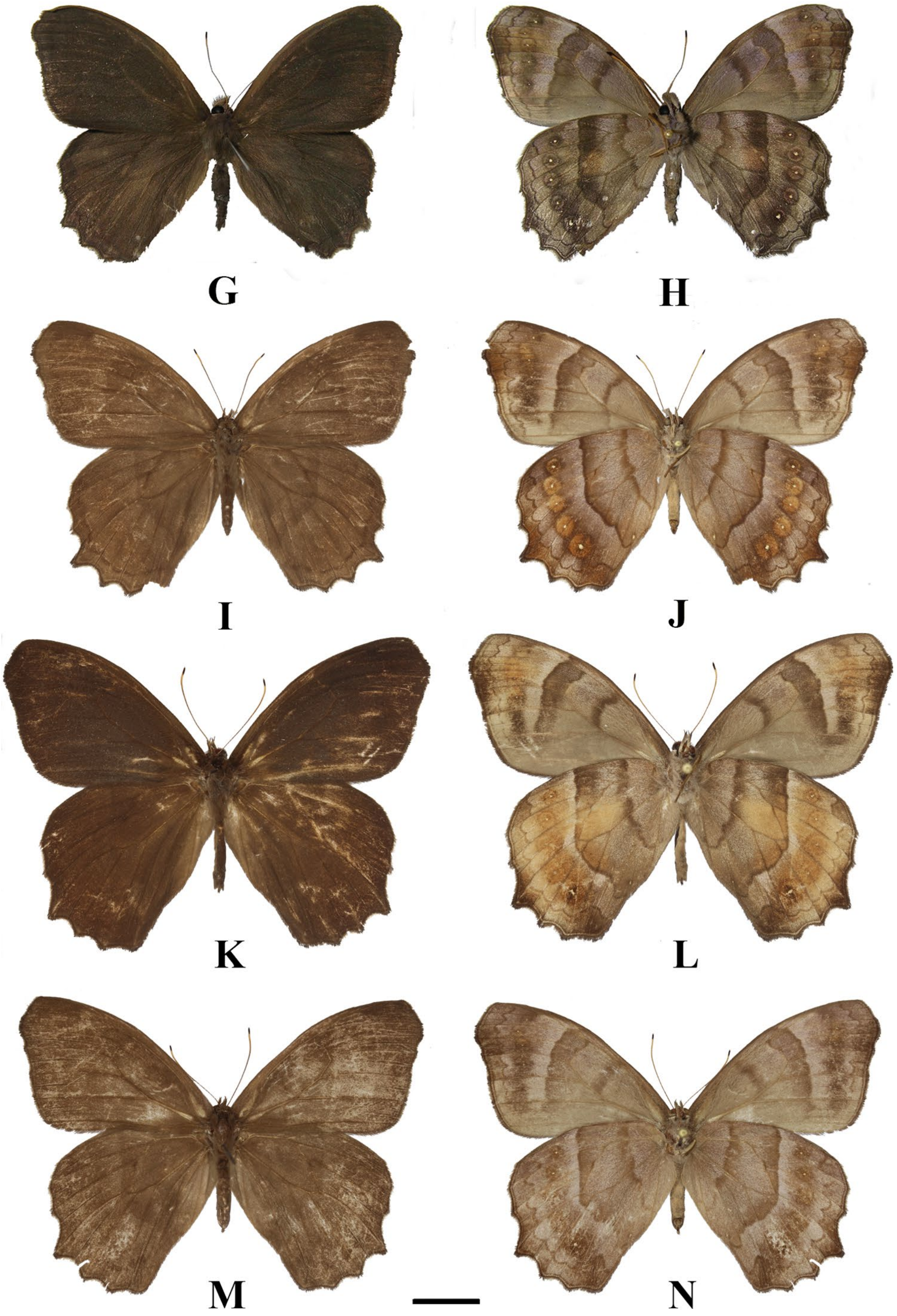

Fig. 2 (continued)

the species in Latin (Fig. 5A) implies that the illustration of the specimen by Jones is in vol. 3, pl. 78, Fig. 1 of his unpublished "Icones." However, the drawing is actually bound in volume 2 (not volume 3 implied in the original description), and it is the first two images on Plate (penciled as) LXXVIII (= 78), which is due to rebinding of the original seven volumes into six volumes, with volumes 2 and 3 being combined into one (Waterhouse 1938). Jones depicted the dorsal surface of a specimen of unknown sex of what he named as *Papilio phorcys* on the left, with uniform pale-brown ground color, and half of the ventral surface on the right (Fig. 5B). Additionally, Jones included the handwritten version of Fabricius' diagnosis of the species just below of his paintings, where he states "caudatis" rather than "subcaudatis." The original description of *Papilio phorcys* by Fabricius is provided in Fig. 5A here followed by the English translation in the paragraph below.

Fabricius's (1793: p. 80, no. 248) description of *Papilio phorcys* consists of four sections: the first paragraph provided the diagnosis of the species (translation by Nick Grishin) "Wings toothed tailed brown: ventral obscurely streaked: hindwings [with] points two gray. ~ Wing[s] all toothed, barely tailed." The second paragraph provided the name "Papilio Phorcys [sic]" and cited "Jones Icones" volume 3, Figure 1 of plate 78. The third paragraph stated its provenance as "Indiis" and that the specimen(s) belonged to Jones collection.

Later, Fabricius (1807: 91) moved the taxon *phorcys* from *Papilio* to *Cynthia* in his book *Systema glossatorum*, where he retained all the information from his original description with its provenance "Indiis". In fact, those specific epithets that appear before and after *phorcys* and were transferred to *Cynthia* in Fabricius (1807) are the same as those in Fabricius (1793), namely *bella* (now in Nymphalinae; a South American taxon), *furcula* (now in Cyrestinae; a South American taxon), *eurocilia* (now in Nymphalinae; an African taxon), *phorcys* and *chelys* (now in Satyrinae; an African taxon), and *lethe* (now in Nymphalinae; a South American taxon). According to Westwood (1842), Fabricius used the term "Indiis" to refer to either West or East Indies, although it is evident that he often employed the terms "India" and "India Orientali" to indicate the East Indian species. However, he also stated that Fabricius expressed his usual vague locality "Indiis" for inhabitants of the West Indies, or South America, and sometimes Africa also (Westwood 1842). Thus, for most of the species he described, Fabricius gave very inaccurate information regarding their actual provenance (Vane-Wright and Gaonkar 2006).

Subsequently, Donovan (1800–1804) included the species *P. phorcys* in his "*Epitome... India*," which supposedly focused on the insect fauna of India and the islands of the Indian seas [Indo-Pacific]. In this work, Edward Donovan illustrated the ventral surface of what he called *Papilio phorcys* on pl. 32 (Fig. 5C), resulting in the only illustration of this taxon besides those associated with the original description. However, Donovans' illustration has some noticeable differences that can be observed compared to Jones' original illustration of this species, such as (1) somewhat developed antennal club (smooth slender club in Jones' drawing); (2) elongated palpi (comparatively shorter in Jones' drawing); (3) hindwing discal cell open (i.e., discal cell and cell M_2 fused; divided in Jones' drawing); (4) lack of the small spot in the VHW cell Cu_2 (present in Jones' drawing); (5) three pairs of legs clearly visible (unusual for nymphalid species). In particular, it is worth mentioning that characters (1) and (3) support the placement of this species in other nymphalid groups as done by subsequent authors. In relation to this, Waterhouse (1938) stated that "Donovan drew most of his illustrations from Jones' Icones and not from the actual specimens." Despite that the basis of this statement by Waterhouse is not clear, it seems reasonable to assume that, at least, the aforementioned wing venation character (3) is accurately illustrated by Jones. This is based on the fact that Jones laid a lot of emphasis on wing venation features when he reviewed the Linnaean classification of butterflies (Jones 1794), thus more likely to have been aware of the importance of wing venation characters in butterfly classification than Donovan. Nevertheless, it is still unclear whether the *P. phorcys* illustration of Donovan was made based on an actual specimen or was a copy based on the original illustration by Jones. Based on Donovans' illustration, Latreille (1819: 372) treated *phorcys* as *Nymphalis phorcys*, with its provenance as "Indes," where he stated that if Donovan's illustration was accurate then the species much be placed in the genus *Nymphalis* (see below for evidence). Subsequently, Westwood (1842: 49) revised Donovans' work by accepting Latreille's notion, where he reissued all Donovan's illustrations and provided the wingspan of the species (2.75 inches). Later, he reassigned the species within the genus "Hypanis" (currently *Byblia* Hübner, [1819]) as *Hyp[anis]? phorcys* in his work on diurnal Lepidoptera (Westwood 1851: 411).

Butler ([1870]) was the next author who studied materials in the Banks and British Museum (NHMUK) collections including "Jones's Icones" (Vane-Wright and Gaonkar 2006). Butler ([1870]) regarded *P. phorcys* as a junior synonym of *Taygetis celia*, without providing justification, and this taxonomic hypothesis has been retained in subsequent works on Neotropical butterfly classification such as the Lamas (2004) checklist. Nevertheless, it must be noted that Butler's ([1870]: 196) catalog did mention an examination of a specimen in the NHMUK registered as *Hipparchia phorcys*, which corresponds to the illustration of *Papilio phorcys* in Donovan (1800–04). Whether Butler really did examine such a specimen is somewhat questionable since later Zimsen (1964: 558, 602) did not report the presence of any type of material(s) in London for *Papilio phorcys*. Furthermore, confusingly, we note that *Papilio* (*Hipparchia*) *phorcys* Freyer, 1836 (a name now associated with the Satyrine genus *Erebia* Dalman, 1816) is clearly a different taxon from *Papilio phorcys* and its Lectotype is housed in the NHMUK (Abadjiev 2002: 34). Another suspicious fact about Butler's ([1870]) note regarding this specific epithet is its generic classification "*Hypanis*" (i.e., *Byblia*), which is a distinctive African taxon classified as a member of Biblidinae, not Satyrinae. Collections at NHMUK have been extensively reviewed and no potential type specimens have been found.

Nevertheless, examination of the illustration of *P. phorcys* by Jones raises some questions as to its true identity. First of all, although the overall appearance of this illustration suggests a species in the genus *Pseudodebis*, the presence of two simple whitish spots on the VHW in cells M_3 and Cu_1 (with a small rather insignificant spot present in Cu_2), coupled with lack of the VHW discal band, somewhat refute the possibility of it corresponding to any known *Pseudodebis* species. In fact, these phenotypic characters do not correspond to any known taxa in the so-called *Taygetis* clade (*sensu* Murray and Prowell 2005) of the nymphalid subtribe Euptychiina, where species with similar wing shape (i.e., somewhat falcate forewing and undulating hindwing outer margin) are concentrated since virtually all species in this clade with this type of wing shape do possess a VHW discal band and/or more than two VHW submarginal ocelli (often five). However, we cannot exclude the possibility of an aberration or damaged specimen. For example, the VHW submarginal ocelli of *Pseudodebis puritana* resemble those two "spots" drawn by Jones, thus if specimen(s) with reduced ocelli in VHW cells Rs, M_1, M_2 exist, they might resemble Jones' illustration, although during the course of examining a number of *Pseudodebis* specimens, such an anomalous individual or anything close was never encountered. We add that OUMNH (2021) also mentioned the identity of *P. phorcys* representing an aberration of *Pseudodebis celia*. Secondly, judging from Jones' illustration of the dorsal surface, the wing venation of *P. phorcys* is in fact unusual for a Satyrinae species from the American continent in not having an inflated basal half of the subcostal vein. A number of euptychiine taxa also possess a swollen base of the Cubitus, including *Pseudodebis celia*, which is apparently also not reflected in Jones' illustrations of *P. phorcys*. Examining his illustrations of *Papilio sosybius* Fabricius, 1793 (an American taxon now placed in the genus *Hermeuptychia* Forster, 1964) which appear in volume 5 (plate LII) of Jones' Icones, it is reasonable to conclude that Jones did pay attention to such venation characters, since his dorsal illustration of *P. sosybius* does show the swollen portion of the subcostal vein, being especially visible on the left forewing.

Most of the original specimens illustrated in the Jones' Icones are lost (Vane-Wright 2010), and some of them were auctioned, especially Drury's collections (Anonymous 1805). Importantly, the catalogs of Drury's collections sales did not have any specimens named *P. phorcys*. As per Cong and Grishin (2014), many sold specimens were not included in the sales catalog. Thus, it would be nearly impossible to discover a syntype of *P. phorcys* by evidence from its label(s). Two studies, Cong and Grishin (2014) and Zilli and Grishin (2018), made an attempt to trace Fabricius type material(s) for a taxon also illustrated in Jones' Icones based on the specimen(s) in Drury's collection, namely *Papilio sosybius* Fabricius, 1793, and *Hesperia busiris* Fabricius, 1793 respectively. Since we are also tracing historical type material(s) of the same provenance, we also consulted with the MacLeay Museum (Sydney, Australia), as a candidate repository for syntype(s) of *Papilio phorcys*. The MacLeay Museum is where Alexander Macleay's entomological collections are currently housed and Alexander Macleay is believed to be one of the main purchasers of Drury's Lepidoptera collection (Zilli and Grishin 2018). On December 21, 2020, SN and Jude Philp from the MacLeay Museum went through images of butterfly drawers at an online meeting, and narrowed down several satyrine specimens which were pinned showing the upper surfaces as potentially representing syntype(s) of *P. phorcys* based on the somewhat falcate forewing. Subsequently, in January 2021, Jude Philp was able to examine the ventral surface of these specimens in person and confirmed that none of them was phenotypically close to the illustration of *Papilio phorcys* in Jones' Icones. As another possible repository of Drury's Lepidoptera collection, we also tried to locate any syntype(s) specimens at the NHMUK, where BH extensively searched the Banks, main and supplementary collections, but no potentially interesting specimens were located. Edward Donovan is another possible purchaser of Drury's Lepidoptera collection, and his collection is now housed at OUMNH (Zilli and Grishin 2018). Nevertheless, our search for syntype(s) of *P. phorcys*, there (OUMNH, via Dick Vane-Wright, pers. comm.) did not yield any results. By following Zimsen (1964) and Vane-Wright and Gaonkar (2006), we also consulted the possibility of ZMUC as a repository by searching their online type catalog (http://www.daim.snm.ku.dk/search-in-types), although with no success. Indeed, *P. phorcys* was not documented in Aurivillius' (1898) catalog of Fabrician Lepidoptera materials housed in Copenhagen; thus, it is unlikely to have been part of the Sehestedt and Tönder-Lund collections.

Over the course of investigating the identity of *P. phorcys*, it became apparent that the illustration associated with the original description also resembles species in the satyrine genus *Melanitis* Fabricius, 1807 (Satyrinae: Melanitini), also reinforced by OUMNH (2021). Members of *Melanitis* are widely distributed in Africa, Asia, and certain parts of Oceania (Larsen 2005). Incidentally, *Melanitis* was established by Fabricius based mainly on the form of antennae and labial palpi in his *Systema glossatorum*, where he simultaneously reclassified *P. phorcys* as a member of the genus *Cynthia*. Clearly, the fact that Fabricius did not transfer *P. phorcys* to *Melanitis* does not necessarily refute the possibility of it actually representing a species of *Melanitis* as now conceived. Despite the wing shape (falcate forewing and undulating hindwing) and overall wing pattern (single VHW band and reduced submarginal ocelli), which are in agreement with some variations of *Melanitis* species (e.g., dry form of *M. leda* (Linnaeus, 1775)), we have not been able to find a specimen of *Melanitis* that closely resembles the illustrations of *Papilio phorcys* as a potential neotype candidate. We further note that there exist some contradictory characters visible in the original illustrations of *Papilio phorcys* which are not usually seen in *Melanitis* species, such as presence of the VHW submarginal band and uniformly brown DFW. In fact, none of the butterfly taxa we considered agrees completely with Jones' illustrations of *Papilio phorcys*, and there might be a possibility that one or more wing element(s) are missing in Jones' original illustration. Considering the high variability of *Melanitis*, there is a possibility to find a specimen of *Melanitis* that reasonably matches the illustrations of *Papilio phorcys* by Jones. It is also worth noting here that two species we have been investigating and that are currently associated with *Melanitis*, namely *Papilio leda* Linnaeus, 1775 and *P. phedima* Cramer, 1780, have names that are older than *Papilio phorcys*; thus, there will be little nomenclatural confusion if the identity of this obscure name is settled based on one of them. Nonetheless, we refrain from drawing a conclusion as to its identity in the present work mainly due to the lack of syntype and the fact that no butterfly species so far appears to match Jones' illustrations of *P. phorcys*. We, therefore, follow and retain the current status as a junior synonym of *Papilio celia* as a parsimonious approach and continue our search for syntype(s). The brief discussion provided above regarding the identity of *Papilio phorcys* is intended to draw attention to this obscure specific epithet and stimulate discussion among Lepidoptera researchers, hoping that one day we will be able to solve the mystery surrounding *Papilio phorcys* based on specimen(s) preserved in natural history collections.

Taygetis keneza Butler, 1869, was described based on an unspecified number of the male specimen(s) from the Salvin collection (Butler 1869). The original description in Latin referred to the type locality as "Cayenne [French Guiana]," and the collector as [Emile] Deyrolle (English translation): "wings above brown: body brown. Wings underneath brown, with less than four bands of diffuse lilac-scaling; two strongly irregular medial bands, an undulating submarginal line and another marginal line, brown; margin itself black; cloudy forewing discal band including five barely distinct ocelli; middle marginal patch black; hindwings with ochreous discocellular patch; cloudy discal band including five distinct ocelli; blackish caudal patch; body grey-brown." The male syntype of this taxon in the NHMUK with the following labels (written verbatim separated by double slashes) is here designated as the lectotype of *Taygetis keneza* (**lectotype designation**): // B.M. TYPE No. Rh 3121 *Taygetis keneza* ♂ Butl.// Godman-Salvin Coll. 1904.-1.// B.C.A.Lep.Rhop. Taygetis keneza Butl.// T. Keneza Butl. type.// Cayenne. (Bar). Ex Deyrolle.// ♂// Type of Species// BMNH(E) 1267107// (NHMUK). This specimen is typical of *Pseudodebis celia* as discussed above, and to permanently establish the name as an objective senior synonym of *Taygetis keneza*, we thus designate the lectotype of the latter name (BMNH(E) 1267107) as the neotype of *Papilio celia* (Fig. 2A, B) (**neotype designation**).

Specimens examined (53 ♂, 15 ♀): Bolivia: *Santa Cruz*: Buenavista, [17°27′34″S, 63°39′40″W], 400 m, 1 ♂ (ZSM). **Brazil**: *Acre*: Assis Brasil, Estação Ecológica do Alto Acre, [11°3′S, 70°16′W], 300 m (Brown, K. S.), 23 Aug 2005, 1 ♂ (ZUEC); *Distrito Federal*: Parque do Gama [16°2′S, 48°8′W], 1000 m (Brown, K. S.), 9 May 1968, 1 ♂ [FLMNH-MGCL-284562; dissection, 2005] (FLMNH); Parque do Gama [16°2′S, 48°8′W], 950–1100 m (Brown, K. S.), 3 May 1968, 1 ♂ [FLMNH-MGCL-284559; dissection, KW-17-081] (FLMNH); *Mato Grosso*: 30 mi. N.E. Cuyabá, Buriti [15°26′S, 55°50′W], 700 m (Brown, K. S.), 11 Mar 1969, 1 ♂ [FLMNH-MGCL-284566; dissection, 2267] (FLMNH), 2 Jan 1969, 1 ♀ [FLMNH-MGCL-284564] (FLMNH), 27 May 1969, 1 ♂ [FLMNH-MGCL-284560; dissection, 2801] (FLMNH); *Minas Gerais*: Paracatu [17°20′S, 46°47′W], (Callaghan, C. J.), 17 May 1973, 1 ♂ [FLMNH-MGCL-284561] (FLMNH); *Pará*: Amazonas, 1 ♂, (ZSM); *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] (Gomes, O.), 11 Sep 1997, 1 ♀ [FLMNH-MGCL-284563; dissection, KW-17-086] (FLMNH); *Santa Catarina*: São Bento do Sul [26°15′S, 49°23′W], 850 m (Rank), Mar 2011, 1 ♀ (DZUP); São Bento do Sul, Rio Vermelho, 850 m (Rank), 29 Mar 2009, 1 ♂ (DZUP); *Not located*: "Brazil" (Callaghan, C. J.), 26 Apr 1971, 1 ♀ [FLMNH-MGCL-284565; Locality "Serve Domini"?] (FLMNH). **Colombia:** *Meta*: Río Ocoa [4°8′N, 73°15′W], 26 Jun 1948, 1 ♂, (AMNH); *Not located*: "Colombia" (Wernicke, R.), 1 ♂ [dissection, SA185], 1 ♀ (ZSM). **Ecuador:** *Morona-Santiago*: jct. Río Mayalico-Río Santiago, Isla de las Conchas [3°2′10″S, 77°58′29″W], 250 m (Hall, J. P. W., Willmott, K. R., J. C. R., J. I. R), 8, 10 Aug 2015, 1 ♀ [FLMNH-MGCL-209538] (FLMNH, INABIO); km 5 Santiago-Méndez rd. [3°1′41″S, 78°2′41″W], 340 m (Willmott, K. R., J. I. R., J. C. R.), 3 Aug 2015, 1 ♂ [FLMNH-MGCL-209647] (FLMNH); *Napo*: Archidona, [0°55′S,77°48′W], 550 m, 1 ♂ [dissection, SA184] (ZSM); km 24 nr. Cotundo, Tena-Baeza rd., 1097–1219 m, (Frania, H. E., Sperling, F. A. H.), 2 May 1982 (USNM); km 49 Tena-Loreto rd. [0°42′51″S, 77°44′26″W], 1300 m (Willmott, K. R., Hall, J. P. W.), 14–15 Mar 1995 (FLMNH); Río Napo, Puerto Napo-Ahuano rd., Jatun Sacha [1°3′S, 77°35′9″W], 400–450 m (Gallice, G.), 28 Aug 2010, 1 ♂ [JS342] (FLMNH); *Orellana*: km 16.5 Loreto-Ávila Viejo rd. [0°37′35″S, 77°24′15″W], 720 m (Hall, J. P. W., Willmott, K. R., J. C. R., J. I. R), 25, 26 Jul 2016, 1 ♂ [FLMNH-MGCL-209799] (FLMNH) (INABIO); km 35 Pompeya-Estación Científica Yasuní rd. [0°37′50″S, 76°27′39″W], 260 m (Hall, J. P. W., Willmott, K. R., J. C. R., J. I. R), 29 Jul 2015, 1 ♂ [FLMNH-MGCL-209641] (FLMNH); *Pastaza*: Río Capahuari, Kapawi Lodge, [2°32′30″S, 76°51′32″W], 250 m (Willmott, K. R., Hall, J. P. W.), 21, 22, 27 Jul 2009, 1 ♂ [FLMNH-MGCL-149552] (FLMNH); *Sucumbíos*:

km 10.5 Lumbaqui-Baeza rd. [0°0′15″S, 77°25′W], 700 m (Willmott, K. R.), 16 Jul 2016 (INABIO); Río Napo, Limoncocha [0°24′S, 76°37′W], 300 m (Drummond, B. A.), 22 May 1974, 1 ♂ [FLMNH-MGCL-284547; dissection, 3456, Lee D. Miller] (FLMNH); km 12 Lumbaqui-Baeza rd. ["0°0′15″S, 77°25′W]], 850 m (Hall, J. P. W., Solis, M. A.), 17 Aug 2002, 1 ♂ (USNM); *Zamora-Chinchipe*: 5 km S Zurmi, Sumak Yaku mine rd., [4°8′38″S, 78°38′57″W], 1000 m (Hall, J. P. W., Willmott, K. R., J. C. R., J. I. R.), 26, 28, 29 Jul 2018 (INABIO); km 10 Los Encuentros-El Panguí, ridge E San Roque [3°42′11″S, 78°35′36″W], 1050 m (Hall, J. P. W., Willmott, K. R., J. I. R.), 18, 19, 23 Jul 2018 [FLMNH-MGCL-297494] (FLMNH). **French Guiana:** *Cayenne*: Dégrad Stoupan [4°45′N, 52°20′W] (Harvey, D. J.), 9 Nov 1988, 1 ♂ (USNM); Roura-Kaw road [4°34′8″N,52°13′9″W] (Russell, W. H.), 18 Dec 1997, 1 ♂ [FLMNH-MGCL-284500; 6–16 km E Roura] (FLMNH); *St-Laurent du Maroni*: Saül, [3°51′30″N, 53°18′14″W], 200–450 m, 2011 (LBCB) (Nakahara, S.), 5 Aug 2014, 1 ♀ [FLMNH-MGCL-209438; on light; dissection SN-20-73] (FLMNH). 22 Nov 1993, 1 ♂ (USNM). **Guyana:** *Bartica*: Kartabo, 4 Aug 1920, 1 ♂ (AMNH), 31 Dec 1920, 1 ♀ (AMNH), 3 May 1924, 1 ♂ (AMNH); *East Berbice-Corentyne*: New River Triangle, Camp Jaguar, 152 m (Steinhauser, S. R.), 10 Nov 1980, 1 ♂ [FLMNH-MGCL-284506; SN-17-73] (FLMNH), 14 Nov 1980, 1 ♂ [FLMNH-MGCL-284502] (FLMNH), 15 Nov 1980, 1 ♂ [FLMNH-MGCL-284507; dissection SN-17-225] (FLMNH), 16 Nov 1980, 1 ♂ [FLMNH-MGCL-284503] (FLMNH), 18 Nov 1980, 1 ♂ [FLMNH-MGCL-284504; dissection SN-17-72], 1 ♂ [FLMNH-MGCL-284505] (FLMNH); Acarai Mts. Sipu R. [1°23.2′N, 58°56.8′W] (Fratello, S.), 29 Oct–12 Nov 2000, 1 ♂ [USNM ENT 00233729] (USNM); Two Hat Mt, E. Kanukus, S. Rupununi, S. Slope [3°8.8′30″N, 59°6.9′W] (Fratello, S., et al.), 23-28 Sep 2000, 1 ♂, USNM). **Paraguay:** *Canindeyú*: Reserva Mbaracayu, cabin area [24°8′3″S, 55°31′44″W], 273 m (Nakamura, I), 5 Dec 2017, 1 ♂ [in fish trap] (ICNA); **Peru:** *Amazonas*: Cordillera del Cóndor, Quebrada Kegkem [3°38′S, 78°18′W], 700 m (Grados, J.), 19 Nov 2003, 1 ♂ [MUSM-LEP-104301], 1 ♂ [MUSM-LEP-104302] (MUSM); *Cuzco*: Quincemil [13°14′S, 70°46′W], 686 m (Alarcón, V.), 18 set 2010, 1 ♂ [MUSM-LEP-104304] (MUSM); Río Urubamba, Timpia, [12°5′31″S, 72°49′12″W], 408 m (Cerdeña, J.), 25 agos 2007, 1 ♂ [MUSM-LEP-104303] (MUSM); *Huánuco*: 25 km S. Tingo María, Puente Chinchavito [9°30′46″S,75°56′37″W], 880 m, (Covell, C. V.), 21 Jun 1983, 1 ♂ [FLMNH-MGCL-284551] (FLMNH), (Olson, E. C.), 21 Jun 1983, 1 ♂ [FLMNH-MGCL-284550] (FLMNH); Río Monzón, 3 km SW Tingo María [9°19′S, 76°2′W], 850 m (Grados, J.), 27 Sep 1996, 1 ♀ [MUSM-LEP-104311] (MUSM); Tingo María, [9°18′S, 76°0′W], 750 m, Jul 1963, 1 ♂ (ZSM); Tingo María [9°18′S,76°0′W], 800 m (Douglass, J. F.), 7 Aug 1979, 1 ♀ [FLMNH-MGCL-284553] (FLMNH); *Madre de Dios*: Amazonia Lodge, [12°31′N, 68°56′W], 491 m (Kinyoni, S.), 11 Nov 2012, 1 ♂ (USNM); Parque Manu, Pakitza, [11°55′48″S,71°15′18″W], 340 m (Casagrande, M.), 17 Oct 1991, 1 ♂ [MUSM-LEP-104310], (MUSM) (Clarke, N. L.), 20 abr 1991, 1 ♂ [MUSM-LEP-104308; dissection, CP-30] (MUSM), (Harvey, D. J.), 4 May 1991, 1 ♀ [MUSM-LEP-104312; dissection, CP-23] (MUSM); Parque Manu, Pakitza [11°55′48″S, 71°15′18″W], 400 m (Lamas, G.), 8–14 Sep 1989, 1 ♂ [MUSM-LEP-104307; dissection, CP-60] (MUSM) (Robbins, R. K.), 6 Oct 1990, 1 ♀ [MUSM-LEP-104313] (MUSM) (Rowe, W.), 3 Nov 1990, 1 ♂ [MUSM-LEP-104309] (MUSM), 4 Nov 1990, 1 ♀ [MUSM-LEP-104314; dissection, CP-88] (MUSM); Parque Nacional Manu, Cocha Cashu, [11°53′S, 71°25′W], 350 m (Lilleengen, P.) (collection unknown) (Lilleengen, P., pers. comm. (email to KRW 29 Sep 2016)); Reserva Tambopata, La Colpa [13°9′S, 69°37′W], 250 m (Aibar, P.), 7 May 2000, 1 ♂ [MUSM-LEP-104306; dissection, CP-90] (MUSM); Río Alto Madre de Dios, 9–15 km downstream Shintuya, left bank [12°36′21″S, 71°13′31″W], 420 m (Douglass, J. F.), 21 Jul 1980, 1 ♂ [FLMNH-MGCL-284552; dissection, KW-17-080] (FLMNH); Río Madre de Dios, Albergue Amazonia [12°52′S, 71°23′W], 500 m (Brock, J.), 1 Oct 2011, 1 ♀ [MUSM-LEP-104316] (MUSM), 26 set 2011, 1 ♀ [MUSM-LEP-104315] (MUSM); *Puno*: Río Tambopata, Z. R. Tambopata-Candamo [13°22′S, 69°34′W], 230 m (Bohórquez, I.), 31 Aug 1992, 1 ♂ [MUSM-LEP-104305] (MUSM). **Suriname:** *Sipaliwini*: Alalapadu, 350 m (Simon, M. J.), Mar 2002, 1 ♂ [FLMNH-MGCL-284501] (FLMNH). **Venezuela:** *Amazonas*: Cerro de la Neblina, Base Camp [0°50′N, 66°10′W], 140 m (Spangler, P. M., P. J., Faitoute, R. A., Steiner, W. E.), 23 Feb 1985, 1 ♂ (AMNH); *Aragua*: Parque Nacional Henri Pittier, Rancho Grande [10°20′58″N, 67°41′3″W], 1125 m (Sullivan, J. B.), 20 Jul 1979, 1 ♂ [FLMNH-MGCL-284497], 1 ♂ [FLMNH-MGCL-284499; dissection, KW-17-051] (FLMNH); *Carabobo*: nr. Puerto Cabello, San Esteban [10°26′N, 68°1′W] (Sullivan, J. B.), 25 Sep 1938, 1 ♂ [FLMNH-MGCL-284498] (FLMNH).

Other records: Brazil: *Mato Grosso*: Rio Paranaita (ZUEC) (data from Genbank, http://www.nymphalidae.net/db.php or other sources). **Ecuador:** *Napo*: Río Napo, Puerto Napo, [1°3′S, 77°47′W], 500 m (Piñas, F.), 28 May 2004, 1 ♂/♀ [FDPR-16988] (FRPI) (Darwin Andean Butterfly Database of FRPI); Tena [1°3′59″S, 77°37′5″W], (Horton, T.), 1 Dec 2019 (photograph live specimen) (https://www.inaturalist.org/observations/36599022); *Orellana*: Loreto [0°25′59″S, 77°20′2″W] (Horton, T.), 13 Nov 2017 (photograph live specimen) (https://www.inaturalist.org/observations/26989148); *Zamora-Chinchipe*: km 7 Zamora-Loja old rd., Quebrada de Chorillos [4°2′31″S, 78°59′27″W], 1200 m (Willmott, K. R., Hall, J. P. W.), Nov (Willmott & Hall (unpublished data)).

Distribution and Biology. This species is known from east of the tropical Andes, mainly from the lowlands of Guianas, Colombia, Ecuador, Peru, Bolivia, Brazil, and Paraguay. We have so far not examined any materials from southern Venezuela.

Pseudodebis darrenthroopi Nakahara & Willmott, **new species**

Taygetis celia keneza [misidentification]: DeVries 1987: 267, pl. 47, fig. 17.

Pseudodebis celia [misidentification]: Glassberg 2007: 157, fig.

Systematic placement and diagnosis. *Pseudodebis darrenthroopi* **n. sp.** is recovered as sister to *P. tigrillo* **n. sp.** + *P. celia*, although the support for this relationship is relatively low (76.1/0.855/57; Fig. 1). Nevertheless, this new species is recovered as a clade with stronger support (81.1/0.969/75; Fig. 1). See our discussion below regarding the inclusion of five Ecuadorian individuals in *P. darrenthroopi* **n. sp.** despite them being genetically somewhat divergent from individuals from Costa Rica, Panama, and Colombia. See relevant sections of *P. celia* and *P. tigrillo* **n. sp.** for diagnosis. As mentioned in Nakahara et al. (2021b) (as "undescribed species from Panama"), *P. darrenthroopi* **n. sp.** is broadly sympatric with *P. hartmanni* Nakahara & MacDonald, 2021, in Costa Rica and Panama, and these two taxa may be somewhat similar, especially worn specimens. Nevertheless, these two species can be readily distinguished by their adult size, with *P. darrenthroopi* **n. sp.** (see forewing length below) being smaller than *P. hartmanni* (male forewing length of *P. hartmanni*: 35–40 mm (mean 37 mm; *n* = 5)), as well as the much broader apical process of the valva in *P. darrenthroopi* **n. sp.** (apical process of valva narrow in *P. hartmanni*) and the anterior margin of the tegumen being more pronounced in lateral view in *P. darrenthroopi* **n. sp.** (appearing more flattened in *P. hartmanni*). These diagnostic characters are also applicable in terms of distinguishing *P. darrenthroopi* **n. sp.** from *P. pieti* Nakahara and Willmott, 2021, a taxon phenotypically resembling *P. darrenthroopi* **n. sp.** which occurs in western Ecuador (consult discussion for first instar larval character to distinguish these two taxa).

Description. MALE: Forewing length: 31–35 mm (*n* = 6; mean = 32.7 mm)

Head: Eyes with hair-like scales, with whitish scales at base; frons with creamy white scales and somewhat darker long seti-form scales; first segment of labial palpi short, with whitish scales laterally, whitish or brownish long seti-form scales present ventrally, second segment of labial palpi roughly similar to longitudinal eye axis in length, dorsally with dirty-white seti-form scales, laterally with concolorous scales, ventrally with long hair-like scales either whitish or brownish, these hair-like scales variable in length, some longer than the third segment of labial palpi in length, third segment roughly one-third of the second segment in length, covered with brownish scales with a stripe of whitish scales present laterally extending from base to distal end; antennae slightly shorter than half of the forewing length, with flagellum *ca.* 34–38 antennomeres (*n* = 2), distal 11–13 segments composing rather insignificant club with distal several segments appearing darker. **Thorax:** Dorsally and laterally (above wings) brownish, rather densely covered with grayish-brown long hair-like scales, ventrally (below wings) covered with long whitish hair-like scales; foreleg reduced, covered with whitish hair-like scales, femur, foretibia and foretarsus roughly similar in length, small subsegment present at the distal end of tarsus; pterothoracic leg femur appearing grayish dorsally and whitish ventrally, tarsus and tibia yellowish-brown, dorsally appearing darker than ventrally, distal tarsal segments appearing darker, tibial spurs present at the distal end of the tibia (two spurs equal in length), tibia with two longitudinal rows of spines ventrally, in addition to spines present laterally on along sides, tibial spurs present at the distal end of tibia, spurs equal in length, tarsus with roughly three longitudinal rows of spines ventrally, rows of spines increase to four from the distal end of tarsus and towards distally. **Abdomen:** Eighth tergite reduced, present along the anterior margin of the eighth abdominal segment as a sclerotized stripe. **Wing venation:** Basal half of forewing subcostal vein swollen; R_2 rising roughly above the origin of discocellular vein m_1-m_2; discocellular vein m_1-m_2 curving inwards (compared to rather straight m_2-m_3); base of cubitus swollen; forewing recurrent vein absent; hindwing humeral vein developed; origin of M_2 nearer M_1 than M_3. **Wing shape:** as illustrated (Fig. 2E, F). **Wing pattern:** as illustrated (Fig. 2E, F), black androconial scales occupying roughly middle of DFW, roughly mirroring area between VFW discal band and postdiscal band, but extending basally beyond the discal band and distally beyond postdiscal band (both on ventral side), faded near costa; black androconial scales sparsely present in DHW discal cell and adjacent area; orangish shading in VHW discal cell variable, ranging from lacking in some specimens to visible and shading extending into adjacent distal cells. **Genitalia:** as illustrated (Fig. 3B); anterior margin of tegumen developed and convex; hair-like setae visible at base of uncus; brachium reduced; apical process of valva short and broad with rather straight distal margin; ductus ejaculatorius entering the antero-dorsal opening of phallobase posteriorly, vesica exits at the posterior tip of aedeagus; no obvious sclerotized cornuti (i.e., cornuti apparently absent).

FEMALE: Forewing length: 30–34 mm (*n* = 2; mean = 32 mm)

Similar to male except as follows: Foreleg with five tarsomeres with spines present ventrally; forewing somewhat broader; DFW and DHW without androconial scales.

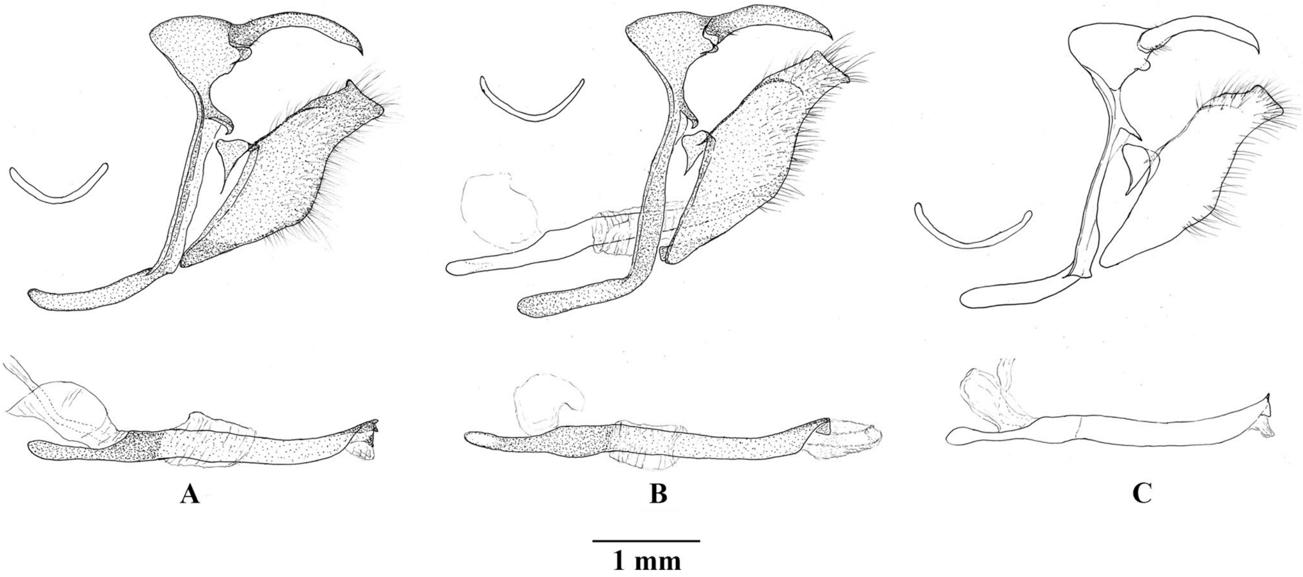

Fig. 3 Male genitalia of species discussed in this study: **A** *Pseudodebis celia*, genital capsule in lateral view with juxta in frontal view to the right; phallus in lateral view (bottom) (based on genitalic vial SN-17-220); **B** *Pseudodebis darrenthroopi* **n. sp.,** genital capsule in lateral view with juxta in frontal view to the right; phallus in lateral view (bottom) (based on genitalic vial KW-17-50); **C** *Pseudodebis tigrillo* **n. sp.**, genital capsule in lateral view with juxta in frontal view to the right; phallus in lateral view (bottom)

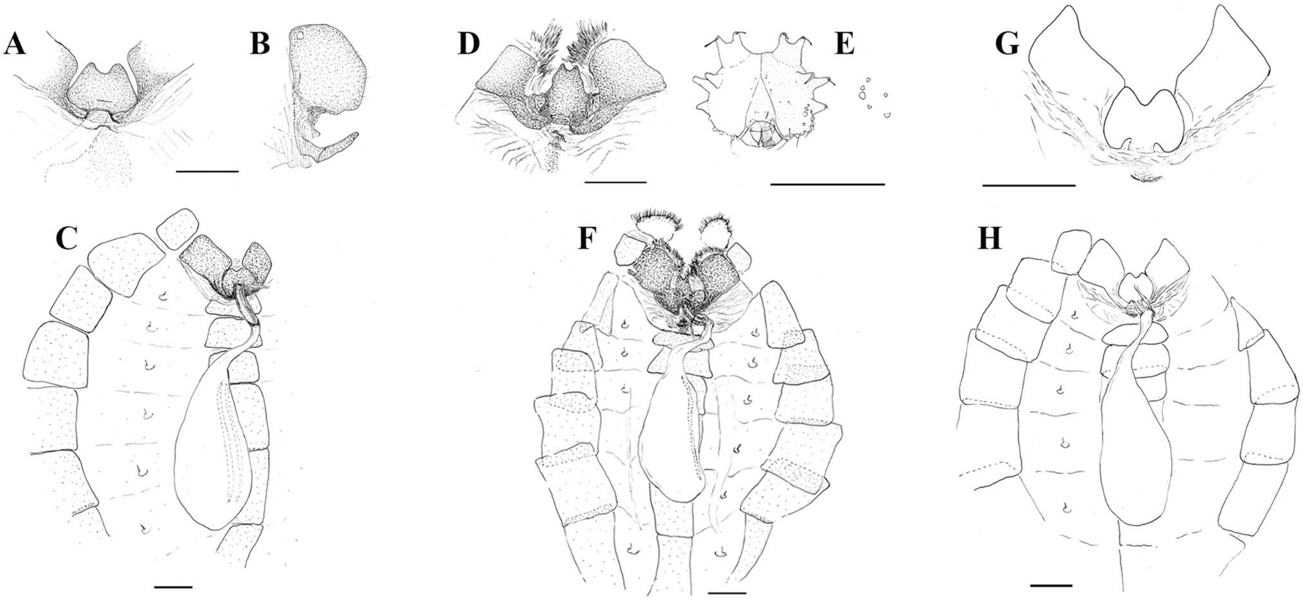

Fig. 4 Female genitalia of species discussed in this study: **A** *Pseudodebis celia*, lamella antevaginalis in ventral view; **B** lamella antevaginalis and a lateral plate of the eighth abdominal segment; **C** female genitalia in dorsal view (based on genitalic vial SN-20-73). **D** *Pseudodebis darrenthroopi* **n. sp.,** lamella antevaginalis in ventral view; **E** head capsule of the first instar with stemmata arrangement to the right; **F** female genitalia in dorsal view (based on genitalic vial SN-20-77). **G** *Pseudodebis tigrillo* **n. sp.,** lamella antevaginalis in ventral view; H) female genitalia in dorsal view (based on genitalic vial KW-17-97). Scale bars represent 1 mm

Abdomen and genitalia: as illustrated (Fig. 4D, F); intersegmental membrane of seventh and eighth abdominal segment ventrally folded, pleated and expandable, with weakly sclerotized region present; lateral margin of lamella antevaginalis not overlapping with a lateral plate of the eighth abdominal segment; ductus seminalis delineates basal sclerotized region and posterior membranous region of ductus bursae; corpus bursae large, reaching the basal portion of the abdomen.

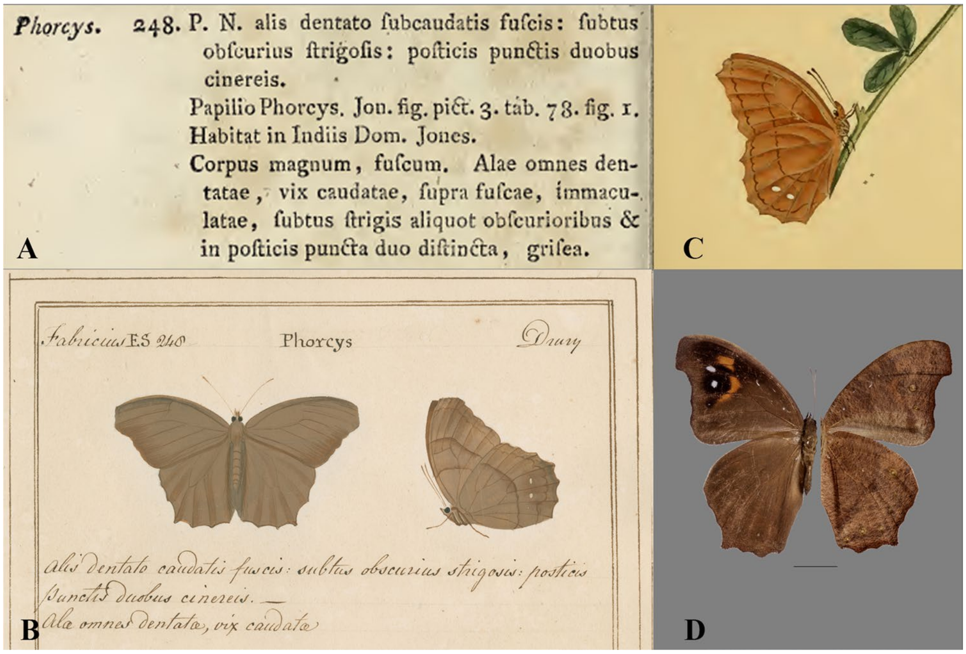

Fig. 5 Historical illustrations of *Papilio phorcys*, its original description and subsequent illustration. **A** original description of *Papilio phorcys* in Latin, by J. C. Fabricius in his *Entomologia systematica* (Fabricius 1793)); **B** illustrations of *Papilio phorcys* by William Jones from an unpublished manuscript known as Jones' "Icones" (credit: OUMNH); **C** subsequent illustration of *Papilio phorcys* by Edward Donovan in his *Epitome... India* (Donovan 1800); D) exemplar specimen of *Melanitis* from eastern Himalaya. Scale bar = 10 mm

Phorcys. 248. P. N. alis dentato ſubcaudatis fuſcis: ſubtus obſcurius ſtrigoſis: poſticis punctis duobus cinereis.

Papilio Phorcys. Jon. fig. pict. 3. tab. 78. fig. 1.

Habitat in Indiis Dom. Jones.

Corpus magnum, fuſcum. Alae omnes dentatae, vix caudatae, ſupra fuſcae, immaculatae, ſubtus ſtrigis aliquot obſcurioribus & in poſticis puncta duo diſtincta, griſea.

Fabricius E.S 248 Phorcys Drury

alis dentato caudatis fuscis: subtus obscurius strigosis: posticis punctis duobus cinereis. —

Alæ omnes dentatæ, vix caudatæ

DNA barcode sequence of the holotype (BOLD sequence ID: MHMYS775-12): AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAGTAGGTACTTCTCTTAGTTTAATTATTCGAATAGAATTAGGAAACCCAGGATATTTAATTGGTGATGATCAAATTTATAATACAATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGTAATTGATTAGTACCTTTAATATTAGGAGCTCCTGATATAGCATTTCCCCGTATAAATAATATAAGATTTTGATTACTTCCCCCTTCTTTAATTTTATTAATTTCTAGTAGTATTGTTGAAAATGGTGCTGGAACAGGATGAACAGTTTACCCCCCCCTTTCATCTAATATTGCCCATAGAGGAGCCTCTGTTGATTTAGCTATTTTTTCACTTCATTTAGCTGGAATTTCATCAATCTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAATAATATATCTTATGATCAAATACCATTATTTGTATGAGCTGTTGGAATTACAGCTCTTCTTTTACTTCTTTCTTTACCAGTTTTAGCAGGAGCAATTACTATACTTTTAACTGACCGAAATTTAAATACATCATTTTTTGATCCTGCAGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Etymology. *Pseudodebis darrenthroopi* **n. sp.** is named in honor of Mr. Darren Throop of Canada in recognition of his major 2022 financial support for the new BioAlfa process to facilitate Costa Rican bioliteracy through the construction of the national DNA barcode library for its wild biodiversity (https://ibol.org/barcodebulletin/features/how-a-tropical-country-can-dna-barcode-itself/). The species-group name is considered to be a Latinized masculine noun in the genitive case.

Types. HOLOTYPE, male: COSTA RICA: Area de Conservación Guanacaste (sector: Rincon Rain Forest, Palomo), *Alajuela* province: [10.96187, − 85.28045], 96 m, Mar 11 2012 [collected as a penultimate instar caterpillar on Feb 16 2012], 1 ♂ [12-SRNP-67277, BIN BOLD: AEG1787], (USNM).

PARATYPES (93 ♂, 18 ♀): Colombia: *Risaralda*: Itaburi [5°16′14″N, 76°3′39″W], 1000 m, Jan 1946, 1 ♂ [FLMNH-MGCL-284494; dissection, 2803] (FLMNH); *Valle del Cauca*: Anchicayá [3°34′27″N, 76°46′W], 600 m, (Sullivan, J. B.), 20–24 Jan 1992, 1 ♂ [FLMNH-MGCL-284496] (FLMNH). *Valle del Cauca*: Río Dagua, (Rosenberg, W.), 1 ♂ [NHMUK014172535], 1 ♂ [NHMUK014172533] (NHMUK); Juntas (Mathan, M. de), 1897–1898, 1 ♀ [NHMUK014172612], 1 ♀ [NHMUK014172613] (NHMUK; *Not located*: "Colombia," 1 ♂ (USNM). **Costa Rica** (Note: all data for—SRNP—specimen codes can be individually downloaded from http://janzen.sas.upenn.edu): Área de Conservación Guanacaste: Gallinazo [11°1′5″N, 85°22′19″W], 360 m, 24 Jul 2011, 1 ♂ [11-SRNP-65550] (BOLD (www.boldsystems.org, 12 Mar 2018)); Medrano [11°0′58″N, 85°22′52″W], 380 m, 21 Jan 2012, 1 ♂ [11-SRNP-72648] (BOLD (www.boldsystems.org, 12 Mar 2018)), 25 Jan 2012, 1 ♂ [11-SRNP-72793] (BOLD (www.boldsystems.org, 12 Mar 2018)), 5 Jan 2012, 1 ♂ [11-SRNP-72643] (BOLD (www.boldsystems.org, 12 Mar 2018)); **Costa Rica:** *Área de Conservación Guanacaste*, 1 ♂ [12-SRNP-70090] (BOLD (www.boldsystems.org, 12 Mar 2018)), 13 Feb 2013, 1 ♂ [13-SRNP-70017] (BOLD (www.boldsystems.org, 12 Mar 2018)), 13 Sep 2014, 1 ♂ [14-SRNP-46596], 16 Feb 2012, 1 ♂ [12-SRNP-70079] (BOLD (www.boldsystems.org, 12 Mar 2018)), 19 Jul 2014, 1 ♂ [14-SRNP-71049] (BOLD (www.boldsystems.org, 12 Mar 2018)), 22 Jul 2014, 1 ♂ [14-SRNP-70165] (BOLD (www.

boldsystems.org, 12 Mar 2018)), 23 Feb 2012, 1 ♂ [12-SRNP-70177] (BOLD (www.boldsystems.org, 12 Mar 2018)), 26 Jan 2012, 1 ♂ [12-SRNP-70003] (BOLD (www.boldsystems.org, 12 Mar 2018)), 26 Mar 2012, 1 ♂ [12-SRNP-70413] (BOLD (www.boldsystems.org, 12 Mar 2018)), 28 Mar 2012, 1 ♂ [12-SRNP-70412] (BOLD (www.boldsystems.org, 12 Mar 2018)), 3 Jul 2014, 1 ♂ [12-SRNP-65002], 1 ♂ [12-SRNP-65003], 1 ♂ [12-SRNP-65090], 1 ♂ [12-SRNP-65091], 1 ♂ [12-SRNP-65103], 1 ♂ [12-SRNP-65153], 1 ♂ [12-SRNP-65154], 1 ♂ [12-SRNP-65155], 1 ♂ [12-SRNP-65166], 1 ♂ [12-SRNP-65172], 1 ♂ [12-SRNP-65173], 1 ♂ [12-SRNP-65174], 1 ♂ [12-SRNP-70044], 1 ♂ [12-SRNP-70091], 1 ♂ [12-SRNP-70414], 1 ♂ [12-SRNP-70416], 1 ♂ [12-SRNP-70430], 1 ♂ [12-SRNP-70431], 1 ♂ [12-SRNP-70463], 1 ♂ [12-SRNP-70495], 1 ♂ [12-SRNP-70976], 1 ♂ [13-SRNP-68601], 1 ♂ [13-SRNP-71026] (BOLD (www.boldsystems.org, 12 Mar 2018)), 30 Sep 2012, 1 ♂ [12-SRNP-68295] (BOLD (www.boldsystems.org, 12 Mar 2018)), 31 Jan 2012, 1 ♂ [12-SRNP-70042] (BOLD (www.boldsystems.org, 12 Mar 2018)), 31 Mar 2012, 1 ♂ [12-SRNP-70435] (BOLD (www.boldsystems.org, 12 Mar 2018)), 5 Feb 2012, 1 ♂ [12-SRNP-70001], 1 ♂ [12-SRNP-70043], 1 ♂ [12-SRNP-70078] (BOLD (www.boldsystems.org, 12 Mar 2018)), 6 Feb 2012, 1 ♂ [12-SRNP-70077] (BOLD (www.boldsystems.org, 12 Mar 2018)), 9 Jul 2012, 1 ♂ [12-SRNP-71210] (BOLD (www.boldsystems.org, 12 Mar 2018)), 9 Mar 2013, 1 ♂ [13-SRNP-65093] (BOLD (www.boldsystems.org, 12 Mar 2018)); *Limón*: Hitoy Cerere Reserve [11.016 -85.3805], 1–4 Jul 2008, 1 ♂ (USNM); *San José*: Bajo La Hondura [10°4′N, 83°59′W], 1150–1450 m (Nakamura, I.), 22 Jul 2010, 1 ♂ (ICNA). **Ecuador:** *Esmeraldas*: km 18.5 San Lorenzo-Lita rd. [1°9′7″N, 78°44′43″W], 50 m (Hall, J. P. W., Willmott, K. R., Aldaz, R.), 7 Aug 2016, 1 ♂ [FLMNH-MGCL-209802; dissection SN-17-221] (FLMNH); Río Santiago, Reserva de Tigrillo, Peñon del Santo trail [0°51′3″N, 78°46′40″W], 80 m (Willmott, K. R., J. I. R., J. C. R.), 10, 13 Jul 2016, 1 ♂ [FLMNH-MGCL-209804; dissection SN-17-203], 1 ♀ [FLMNH-MGCL-209806] (FLMNH); [0°51′N, 78°46′37″W], 100 m (Willmott, K. R., J. I. R., J. C. R.), 11, 13 Jul 2016 [FLMNH-MGCL-209805; dissection SN-17-204] (FLMNH); *Manabí*: Palmar, [0°10′S, 79°28′W], 300 m (Laddey, D. B.), 2 Apr 1941, 1 ♂ [FLMNH-MGCL-284519] (FLMNH); *Pichincha*: [12 km E] Santo Domingo [de los Colorados], [Hotel] Tinalandia [0°18′S, 79°4′W] (Smith, M. J.), 13–15 Jul 1983, 1 ♂ (BME); [12 km E] Santo Domingo [de los Colorados], [Hotel] Tinalandia [0°18′S, 79°4′W], 549 m (Smith, J. A.), 6–14 May 1994, 1 ♂ (BME); 12 km E Santo Domingo de los Colorados, [Hotel] Tinalandia, [0°18′S, 79°4′W] (Harris, L. & C.), 25 Apr–1 May 1988, 1 ♂ [FLMNH-MGCL-284527] (FLMNH); 12 km E Santo Domingo de los Colorados, [Hotel] Tinalandia [0°18′S, 79°4′W], 700 m (Covell, C. V.), 22 Apr 1983, 1 ♂ [FLMNH-MGCL-284530] (FLMNH); 12 km E Santo Domingo de los Colorados, [Hotel] Tinalandia [0°18′S, 79°4′W], 750–850 m (Austin, G. & A.), 8 May 1988, 1 ♂ [FLMNH-MGCL-284531] (FLMNH); 12 km E Santo Domingo de los Colorados, [Hotel] Tinalandia, [0°18′S,79°4′W], 848 m (Milner, P. F.), 5–10 May 2002, 1 ♂ [FLMNH-MGCL-284529; dissection, KW-19-035], 1 ♂ [FLMNH-MGCL-284536; dissection, KW-19-036] (FLMNH); Hotel Tinalandia [0°18′S, 79°4′W] (Smith, J. A.), 6–11 May 1990, 1 ♂ (BME); Reserva Mangaloma [0°7′15″N, 78°59′37″W], 700–815 m (Willmott, K. R., J. I. R., J. C. R.), 11 Jul 2015, 1 ♀ [FLMNH-MGCL-209364; dissection, KW-17-114] (FLMNH), 13 Aug 1976, 1 ♀ [FLMNH-MGCL-284544] (FLMNH) (Drummond, B. A.), 22 Mar 1977, 1 ♂ [FLMNH-MGCL-284542] (FLMNH); Taguaza [0°18′S, 79°2′W], 1750 m (Lafebre, R. de), Jun 1975, 1 ♂ [FLMNH-MGCL-284510] (FLMNH). **Nicaragua:** *Atlántico Sur*: Nueva Guinea [11°40′N, 84°27′W] (Anderson, R. A.), 26 Oct 1976, 1 ♂ [FLMNH-MGCL-284475] (FLMNH), 27 Oct 1976, 1 ♂ [FLMNH-MGCL-284468; dissection, KW-17-50] (FLMNH), 28 Oct 1976, 1 ♂ [FLMNH-MGCL-284466], 1 ♂ [FLMNH-MGCL-284467] (FLMNH); Volaina, [11°45′N, 84°5′W] (Anderson, R. A.), 27 Aug 1976, 1 ♂ [FLMNH-MGCL-284465] (FLMNH). **Panama:** *Bocas del Toro*: Fortuna cabins (Pablo Seco Forest Preserve) [8°46′40.86″N, 82°25.02″W], 910 m (MacDonald, J. R.), 3 Aug 2019, 1 ♂ (MEM); *Coclé*: 5 miles W Panama City (Douglas, M. G.), 16–17 Aug 2007, 1 ♂ [FLMNH-MGCL-284476; dissection SN-20-76], (FLMNH); *Colón*: Corundú (Anderson, R. A.), 24 Nov 1978, 1 ♂ [FLMNH-MGCL-284482] (FLMNH); Ft. Sherman (Black Tank Rd) (MacDonald, S. L.), 10 Aug 1978, 1 ♀ (MEM); Gatun (Ridge Road) (MacDonald, J. R.), 11 Aug 1978, 1 ♂, 5 Aug 1978, 1 ♂ (MEM); Gamboa, [9°7′13″N, 79°41′59″W], 50 m (Dickel, T. S), 25 Nov 1969, 1 ♂ [FLMNH-MGCL-284485] (FLMNH); Gamboa (Pipeline Road) [9°7′37.8″N, 79°42′53″W], 70 m, (MacDonald, J. R.) 12 Aug 2012, 1 ♀ (MEM); Madden Forest [9°12′45″N, 79°36′57″W], 80 m (Anderson, R. A.), 2 Oct 1975, 1 ♀ [FLMNH-MGCL-284478] (FLMNH) (Dickel, S.), 24 Aug 1969, 1 ♂ [FLMNH-MGCL-284481] (FLMNH), 28 Aug 1976, 1 ♂ [FLMNH-MGCL-284483] (FLMNH) (Jae, R.), 20 Aug 1969, 1 ♂ [FLMNH-MGCL-284477; dissection, 3904] (FLMNH), 5 Oct 1971, 1 ♂ [FLMNH-MGCL-284474] (FLMNH); *Panamá*: Albrook (Field) [8°59′N, 79°33′W], (Dickel, T. S), Sep 1975, 1 ♂ [FLMNH-MGCL-284486] (FLMNH); Bayano [9°3′N, 78°40′W] (Nicolay, S. S.), 5 Jan 1975, 1 ♂ (USNM); c. 12 km E Lake Bayano Bridge, [9°9′9″N, 78°41′20″W], 80 m (Nakamura, I.), 11 Sep 2013, 1 ♀ (ICNA), 9 Aug 2011, 1 ♀ (ICNA); Canal Zone, Farfán

[8°56′24″N, 79°34′20″W], 50 m (Anderson, R. A.), 16 Dec 1969, 1 ♀ [FLMNH-MGCL-284479] (FLMNH) (Jae, R.), 2 Oct 1971, 1 ♂ [FLMNH-MGCL-284473] (FLMNH), 3 mi N. Summit [9°6′20″N, 79°37′5″W], (Michner, C. D.), 8 Apr 1945, 2 ♂ (AMNH); Cerro Campana [8°41′N, 79°55′W], 750–792 m, (King, H. L.), 12 Jan 1973, 1 ♂ [FLMNH-MGCL-284487] (FLMNH) (Miller, L. D.), 2 Dec 1972, 1 ♂ [FLMNH-MGCL-284480] (FLMNH); Cerro Campana [8°40′55.7″N,79°55′43.7″W], 800–830 m (MacDonald, J. R.), 13 Feb 2013, 1 ♂, 17 Aug 1978, 1 ♂ (Riley, T.), 30 Aug 2021, (MacDonald, J. R.), 1 ♀, 30 Aug 2021, 1 ♀ (MEM); Cerro Cedro, 3 Oct 1977, 2 ♂ [USNM ENT 00945368] [USNM ENT 00945367] (USNM); Cerro Jefe [9°12′14″N, 79°23′8.9″W], 850 m (MacDonald, J. R.), 11 Aug 2011, 1 ♂ (MEM); Cocoli (MacDonald, S. L.), 13 Jan 1986, 1 ♂ (MEM); Howard Air Force Base, [8°54′54″N, 79°35′58″W] (Anderson, R. A.), 6 Oct 1984, 1 ♂ [FLMNH-MGCL-284484] (FLMNH). **Neotropical country unknown:** *Not located*: no data, 1 ♀ [FLMNH-MGCL-284554; dissection, 4520], 1 ♀ [FLMNH-MGCL-284555; dissection, 4511], 1 ♀ [FLMNH-MGCL-284556; dissection, 4519], 1 ♀ [FLMNH-MGCL-284557; dissection, 4505], 1 ♀ [FLMNH-MGCL-284558; dissection, 4512] (FLMNH).

Distribution and Natural History. *Pseudodebis darrenthroopi* **n. sp.** ranges from Nicaragua to western Ecuador. The only known natural food plant of this species is *Rhipidocladum racemiflorum* (Steud.) McClure (Poaceae: Bambusoideae: Bambuseae), based on the ongoing Lepidoptera biodiversity inventory of Área de Conservación Guanacaste (Janzen and Hallwachs 2016). In Costa Rica, the butterfly is relatively abundant in mid- to low- elevation rain forest on the lower slopes of Cordillera of Área de Conservación Guanacaste, where 59 larvae have been found feeding only on the leaf blades of this native woody bamboo, in habitats occupied by at least 35 species of other Poaceae that are fed on by the caterpillars of many species of satyrine caterpillars. In central-western Ecuador, this species is locally not uncommon in the lowland rain forest from sea level to 700 m, where it typically occurs in close association with *Guadua* Kunth (Poaceae: Bambusoideae: Bambuseae) bamboo groves. Both sexes were found attracted to rotting banana bait in the understory and midstory.

Immature Stages. The first instar head capsule found inside the female abdomen during the dissection of SN-20-77 (illustrated in Fig. 4E) shows the following notable features: scoli developed and bifurcated, two thread-like (unlike typical spatula-like (i.e., flattened and fanned) setae of "*Taygetis* clade" species) setae on each scoli; chalazae developed, each with setae (P3, L1, A3); primary setae AF1, AF2, F1, A1, S1, S2, S3 noticeable, stemma 3 largest, closer to stemma 2 than 4.

Antepenultimate instar (Fig. 7A, B; based on 12-SRNP-70413): Head light olive green with pitted sculpturing, vertex rather flattened with bifurcating scolius, epicranial notch insignificant, epicranial suture extending roughly two-fifths of frontal area, seven developed chalazae visible on one side, stemmata 1, 2, 4-6 roughly equal in size, stemma 3 largest and close to stemma 2 than 4. Body chartreuse, two-toned band extending along the sub-dorsal area; creamy white rather insignificant band traversing lateral area above spiracles; spiracles visible as light brownish spots, prominent on T1 and A8; ventral prolegs present on A3 to A6, caudal prolegs present on A10; bifid caudal filaments elongate (longer than A8 in dorsal view), separated. Body length: 13 mm.

Penultimate instar (Fig. 7C, D; based on 11-SRNP-72643): Head lime green with pitted sculpturing, vertex rather flattened with bifurcating scolius appearing orangish distally, epicranial notch minute, epicranial suture extending roughly two-fifths of frontal area, seven developed chalazae visible on one side, two setae (C1 and C2) on one side of clypeus noticeable, labrum apparently setose but number not discernable, stemmata 1, 2, 4-6 roughly equal in size, stemma 3 largest and close to stemma 2 than 4. Body bright lime green, two creamy white bands extending along the sub-dorsal area from T2 to A9; creamy white band traversing lateral area above spiracles; spiracles visible as whitish spots, prominent on T1 and A8; ventral prolegs present on A3 to A6, caudal prolegs present on A10; bifid caudal filaments elongate (longer than A8 in dorsal view), separated. Body length: 24 mm (Figs. 5 and 6).

Ultimate instar (Fig. 7E, F; based on 12-SRNP-65090): Head light ocher with apparently bumpy sculpturing, vertex rather flattened and marked with dark green, with stubby scolius appearing darker laterally and distally, epicranial notch minute, epicranial suture extending roughly two-fifths of frontal area, frons appearing narrower (compared to the previous instar), three rounded chalazae visible on one side, one seta on one side of clypeus noticeable, setae on labrum not discernable, stemmata 1,2, 4-6 roughly equal in size, stemma 3 largest and close to stemma 2 than 4. Body ocher, two dark green spots visible dorsally on T1, T2, and T3 with dark "v-shaped" markings dorsally, pink and white bands extending along subdorsal area, prominent from A3 to A6; creamy white band traversing lateral area above spiracles; spiracles visible as whitish spots, prominent on T1 and A8; ventral prolegs present on A3 to A6, caudal prolegs present on A10; bifid caudal filaments elongate, curled inwards and touching to each other at apex (longer than A8 in dorsal view). Body length: 32 mm.

Remarks. As discussed under the taxonomy of *Pseudodebis celia*, none of the existing available names related to *P. celia* represents the trans-Andean clade. In the "Discussion" section, we justify why we regard the clade composed of five individuals from western Ecuador as representing *P darrenthroopi* **n. sp.** rather than a distinct species.

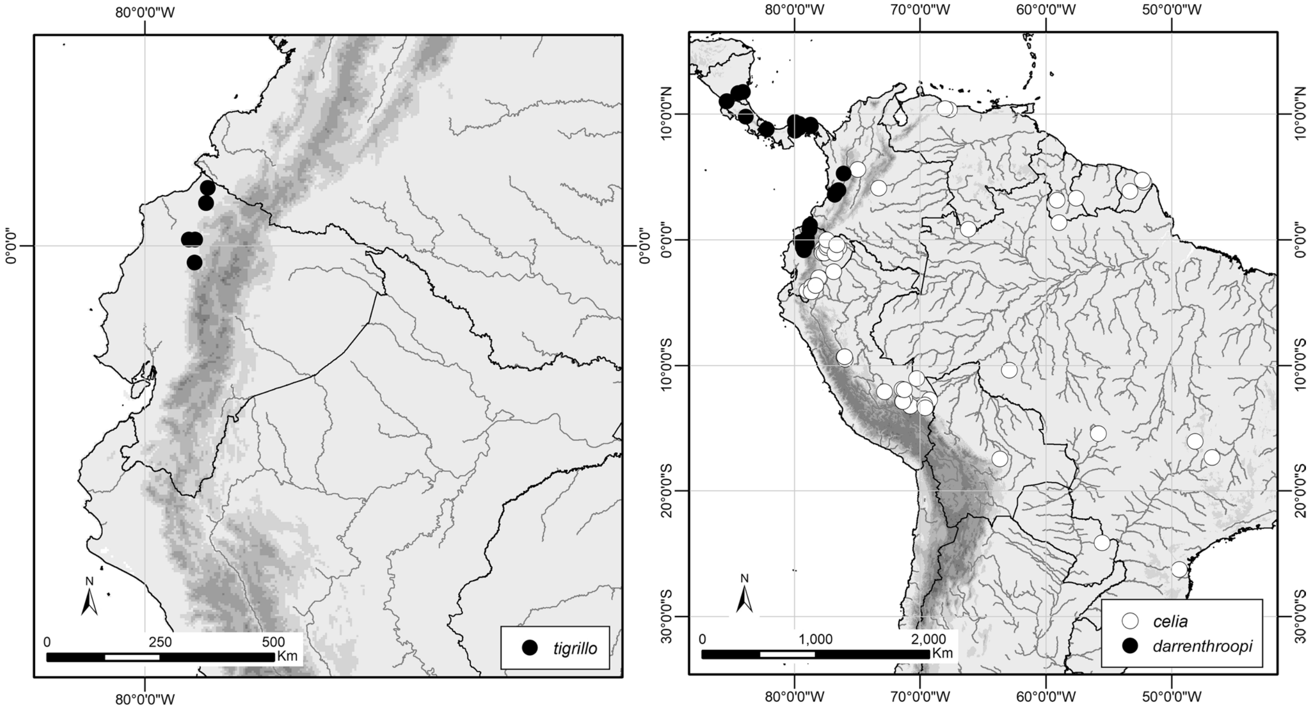

Fig. 6 Distribution map for *Pseudodebis* taxa discussed herein

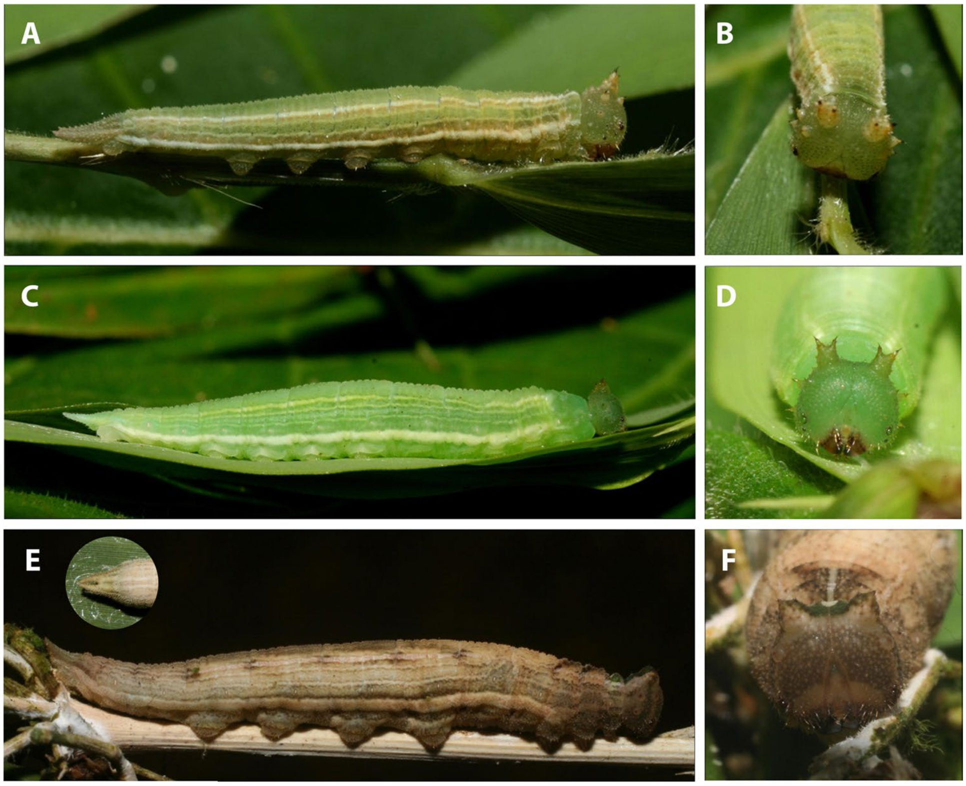

Fig. 7 Immature stages of *Pseudodebis darrenthroopi* **n. sp.: A** antepenultimate instar (based on 12-SRNP-70413), lateral view; **B** dorso-frontal view; **C** penultimate instar (based on 11-SRNP-72643), lateral view; **D** frontal view; **E** ultimate instar (based on 12-SRNP-65090), lateral view with dorsal view of caudal filaments above; **F** frontal view. Scale bar not provided, see description for measurements

Pseudodebis tigrillo Nakahara & Willmott, **new species**

Systematic placement and diagnosis. Based on the DNA barcode data, *Pseudodebis tigrillo* **n. sp.** is sister to *P. celia*, although with weak support (Fig. 1; 73.4/0.741/67). *Pseudodebis tigrillo* **n. sp.** is distinguished from *P. darrenthroopi* **n. sp.,** with which it is sympatric in western Ecuador, by the combination of following characters: (1) outwardly curving (straighter in *P. darrenthroopi* **n. sp.**) VHW postdiscal band in cell 2A; (2) overall somewhat dull color ventrally, with yellowish-brown scales covering VHW discal cell and extending into adjacent cells (no or much reduced ventral yellowish-brown scaling in *P. darrenthroopi* **n. sp.**); (3) VHW submarginal ocelli, especially those in cells M_2 and M_3, somewhat obscured by yellowish-brown scales; (4) rounded broad plate-like lamella antevaginalis in ventral view. Characters (1), (2), and (3) can also be used to distinguish *Pseudodebis tigrillo* **n. sp.** from *P. celia*, in addition to (1) smaller adult size (male forewing length of *P. tigrillo* **n. sp.:** 30–31 mm (*n* = 3; mean = 30.3 mm)) (male forewing length of *P. celia*: 31–38 mm (*n* = 4; mean = 35.25 mm)); (2) posterior half (after passing Cu_1) of the VHW postdiscal band straighter in *P. tigrillo* **n. sp.** (posterior half of VHW postdiscal band undulating in *P. celia*). *Pseudodebis tigrillo* **n. sp.** is also broadly sympatric with *P. nakamurai* Nakahara & Willmott, 2021, in western Ecuador, and they may appear similar in terms of adult size and overall ventral wing coloration and pattern. However, the same genitalic characters used to distinguish *P. darrenthroopi* **n. sp.** and *P. hartmanni* can also be used to diagnose *P. tigrillo* **n. sp.** from *P. nakamurai*.

Description of male. 30–31 mm (*n* = 3; mean = 30.3 mm)

Similar to immediately preceding species except as follows: VFW and VHW ground color appearing more ocher-like, thus consequently resulting in a few wing elements appearing more "yellowish"; VHW ocher-like shading in discal cell extending into adjacent cells, thus obscuring some VHW submarginal ocelli; VHW postdiscal band curving outwards in cell 2A; Genitalia illustrated in Fig. 3C. **Female.** 31 mm (*n* = 1). Ventral surface appearing somewhat violet compared to male; apparently lacking marking in VHW discal cell (*n* = 1); Genitalia illustrated in Fig. 4E–F.

DNA barcode sequence of the holotype male (GenBank Accession: MN271936): TTTGAGCAGGTATAGTAGGTACCTCTCTTAGTTTAATTATTCGAATAGAATTAGGAAATCCAGGATATTTAATTGGTGATGATCAAATTTATAATACAATTGTCACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGTAATTGATTAGTACCTTTAATATTAGGAGCTCCTGATATAGCATTTCCACGTATAAACAATATAAGATTTTGATTACTCCCCCCCTCTTTAATCTTATTAATTTCTAGTAGTATTGTTGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCCCTTTCATCTAATATCGCTCATAGAGGAGCCTCTGTTGATTTAGCTATTTTTTCACTTCATTTAGCTGGAATTTCTTCAATCTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAATAATATATCTTATGATCAAATACCATTATTTGTATGAGCTGTTGGAATTACAGCTCTTCTCTTACTTCTCTCATTACCAGTTTTAGCAGGAGCAATTACTATACTTTTAACTGATCGAAATTTAAATACATCATTTTTTGATCCTGCAGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Etymology. The specific epithet is based on the Spanish word "tigrillo," part of the name of the Reserva de Tigrillo, a reserve protecting some of the last undisturbed wet lowland forest in northwestern Ecuador and its associated fauna, including this new species. "Tigrillo" is a common name for Oncilla (*Leopardus tigrinus* (Schreber, 1775) (Felidae, Mammalia)) and other similar mottled black, cream, and orange Neotropical cats, and the name thus also refers to the similar colors of this new butterfly species, and in particular the distinctive orange ventral coloration. This specific epithet is considered to be a masculine Latinized noun in apposition.

Types. HOLOTYPE, male: ECUADOR: *Esmeraldas* province km 18.5 San Lorenzo-Lita rd., [1°9′7″N, 78°44′43″W], 50 m (Hall, J. P. W., Willmott, K. R., Aldaz, R.), 7 Aug 2016, 1 ♂ [FLMNH-MGCL-209800; dissection SN-17-202] [DNA voucher LEP-37265] (FLMNH, to be deposited in INABIO).

Paratypes (8 ♂ 3 ♀): Colombia: *Valle del Cauca:* Juntas [Río Dagua], [3°46′27″N, 76°44′41″W], (Mathan, M. de), 1897 I-1898, 1 ♂ [NHMUK014172614] (NHMUK); Río Dagua (W. Rosenberg), 1 ♀ [NHMUK-014172537] (NHMUK); Popayán, 1897, 1 ♂ [NHMUK014172534] (NHMUK). **Ecuador:** *Santo Domingo de los Tsáchilas*: Río Palenque, [0°36′12″S,79°18′36″W], 400 m, 10 Aug 1976, 1 ♂ [FLMNH-MGCL-284541; dissection, KW-17-085] (FLMNH); *Esmeraldas*: Río Santiago, Reserva de Tigrillo, lodge [0°51′N,78°46′37″W], 100 m (Willmott, K. R., J. I. R., J. C. R.), 11, 13 Jul 2016, 2 ♂ (INABIO); Río Santiago, Reserva de Tigrillo, Peñon del Santo trail, [0°51′3″N, 78°46′40″W], 80 m (Willmott, K. R., J. I. R., J. C. R.), 10, 13 Jul 2016, 1 ♂ [FLMNH-MGCL-209801], 1 ♀ [FLMNH-MGCL-209803; dissection KW-17-97] (FLMNH), 2 ♂ (INABIO); *Pichincha*: Hotel Tinalandia, Río Tanti, [0°20′S,79°0′30″W], 750–800 m (Willmott, K. R., Hall, J. P. W.), 1 Jul 1993, 1 ♂ (FLMNH), Jul 1991, 1 ♂ (FLMNH); Hotel Tinalandia, Río Tanti [0°20′S, 79°0′30″W], 750–800 m (Hall, J. P. W., Willmott, K. R.), 29 Jun 1993, 1 ♂ [FLMNH-MGCL-284520; dissection SN-17-201] (FLMNH); Reserva Mangaloma [0°7′15″N, 78°59′37″W], 700–815 m (Willmott, K. R., J. I. R., J. C. R.), 11 Jul 2015, 1 ♀ (INABIO).

Other records: Ecuador: *Pichincha*: Hotel Tinalandia, Río Tanti [0°20′S,79°0′30″W], 750–800 m (Willmott, K. R., Hall, J. P. W.), 29 Jun 1993 (sight record); Pedro Vicente Maldonado-Puerto Quito rd., Finca de Goulaine [0°7′17″N, 79°7′24″W], 450 m (Goulaine, M.) (sight record) (Goulaine, M. (7 Jan 2020, pers. comm. by email to KRW)).

Distribution and Natural History. This species is known from western Ecuador, namely from the three provinces of Esmeraldas, Pichincha, and Santo Domingo de los Tsáchilas, in addition specimens recorded from western Colombia in Valle del Cauca.

Discussion

We revised the "*celia* clade" of *Pseudodebis* based on morphology and molecular data, and as a result, we described and named two new species of *Pseudodebis* from the trans-Andean region, increasing the described species diversity of *Pseudodebis* to 13 (Nakahara et al. 2021a, b). It must be noted that all of the recently described *Pseudodebis* species (*P. nakamurai*, *P. pieti*, *P. hartmanni*, *P. darrenthroopi* **n. sp.,** and *P. tigrillo* **n. sp.**) are elements of the trans-Andean region, and taking into account the existing Central American species, *P. zimri* (Butler, 1869), approximately half of the species richness of *Pseudodebis* is concentrated in the trans-Andean region. We further note that the number of known trans-Andean *Pseudodebis* is likely an underestimate, with several additional undescribed *Pseudodebis* species awaiting description (Nakahara et al., in prep). Thus, as mentioned above, this article is part of an ongoing study aimed at revising *Pseudodebis* as a whole, and additional publications are in preparation by SN and collaborators. Further discussion of the species diversity and distribution of the genus is therefore best left to a future paper. On the other hand, several points arising from the present study do merit further discussion.

First, we must note that the decision to regard as conspecific the various populations of *P. darrenthroopi* **n. sp.** sampled here is somewhat subjective. The five sequenced west Ecuadorian samples (LEP-17120, LEP-37270, LEP-37269, LEP-37267, and LEP-37271) are genetically divergent from other sequenced specimens from Costa Rica, Panama, and Colombia. Nevertheless, the independent 10 likelihood searches we performed in IQ-TREE2 while preparing data for Nakahara et al. (2021b) (see this article for details) recovered at least once the Ecuadorian clade as nested inside the clade containing individuals from Costa Rica, Panama, and Colombia. Furthermore, the sole sequenced individual from Antioquia, Colombia (CP22-02), an area biogeographically part of the trans-Andean region, grouped with two specimens from Panama (LEP-18597 and LEP-18598), and this clade is also somewhat genetically divergent compared to sequenced individuals from Costa Rica. It therefore seems likely that the divergence we observed in Fig. 1 for Ecuadorian specimens is an artifact due to the lack of samples from western Colombia. Additionally, the phenotypes of specimens we examined from western Ecuador and western Colombia do appear to be somewhat consistent with individuals from Central America (Nicaragua – Panama), and the diagnostic characters discussed above are also applicable to them. However, the orangish scales in the VHW discal cell more often appear to be absent or reduced in specimens from western Ecuador and western Colombia in comparison with individuals from Central America (Nicaragua – Panama). A similar wing pattern gradient (presence/absence of wing element) has also been observed in other euptychiines from the trans-Andean region, for instance, *Amiga arnaca* (Fabricius, 1776) (see Nakahara et al. 2019a). Thus, it seems plausible that the wing pattern differences we observed in *P. darrenthroopi* **n. sp.** represent a broadly clinal phenotype within a single species. *Pseudodebis darrenthroopi* **n. sp.** occurs in sympatry with *P. tigrillo* **n. sp.** in western Ecuador and we consider that the morphological differences and molecular data provided herein support their species-level status. We do not regard either of these two species as a trans-Andean population of *P. celia* since both possess phenotypic characters that can be used to distinguish them from *P. celia* (see above). *Pseudodebis tigrillo* **n. sp.** in particular, is recovered as a strongly supported clade (95.9/1/100; Fig. 1), whereas its sister relationship to *P. celia* is only weakly supported, thus not providing strong evidence in favor of treating it as a subspecies of *P. celia*. We, however, admit that deciding on the taxonomic status of distinctive, allopatric populations involves some subjective judgement, especially without more comprehensive geographic and genomic sampling, and our decision was based on the two independent lines of evidence currently available to us, morphology and DNA barcode data.

We also note that the thread-like primary setae of the first instar head capsule of *P. darrenthroopi* **n. sp.** reported and illustrated herein is a unique character as a member of the "*Taygetis* clade." Based on available published literature regarding immature stages of species in the "*Taygetis* clade" where information on the first instar primary setae was made available, many species possess spatula-like setae (e.g., *Taygetis ypthima* (Hübner, [1821]) - Müller 1886; *T. mermeria* (Cramer, 1776), *T. cleopatra* C. Felder & R. Felder, 1867, *T. laches* Fabricius 1793, *T. thamyra* (Cramer, 1779) - Murray 2001a; *Forsterinaria pronophila* (Butler, 1867) - Freitas and Peña 2006; *Forsterinaria quantius* (Godart, [1824]) and *F. necys* (Godart, [1824]) - Freitas et al. 2016; *Taygetis rufomarginata* Staudinger, 1888 - Baine et al. 2019; *Pseudodebis marpessa* (Hewitson, 1862) - Murray 2001b; *Pseudodebis nakamurai* and *P. pieti* - Nakahara et al. 2021a). It must be noted that Debra Murray's unpublished dissertation shows rather thread-like setae for the first instar head capsule of *Pseudodebis celia* (as *Taygetis celia*), *Pseudodebis valentina*, and *Posttaygetis penelea* (Cramer, 1777) (Murray 2001b: Figs. 2.5, 2.7), described as "lobe-like" with some modifications. Nevertheless, Murray (2001b) describes primary setae of the first instar head capsules for *Taygetis* taxa as "lobe-like" as well, and further study is needed to clarify the character states of these taxa. Given that we only know information regarding the first instar head capsule for less than 20 species (out of 86 described species) in the "*Taygetis* clade," it is premature to draw any conclusion as to its status as a putative synapomorphy for the "*Taygetis* clade," especially considering the existence of species with contradicting character state regarding the primary setae of the first instar head capsules (e.g., *Taygetis virgilia* (Cramer, 1776); Murray 2001a). On the other hand, the developed bifurcating scoli of the first instar head capsule of *P. darrenthroopi* **n. sp.** are consistent with those aforementioned species in the "*Taygetis* clade" with a known first instar, except for two species in *Pseudodebis* (references cited above). Thus, *P. darrenthroopi* **n. sp.** is in fact readily distinguishable from two closely related species in the genus, namely *P. nakamurai* and *P. pieti*, on the basis of two characters of first instar head morphology. These morphological differences are congruent with genitalic differences between the "*celia* clade" and clade composed of (*P. nakamurai* + *P. pieti* + *P. hartmanni*). Nevertheless, the genitalic characters appear to be somewhat homogeneous within these two clades, which is consistent with other euptychiine groups (e.g., *Zischkaia* Forster, 1964; Nakahara et al. 2019c).

In summary, this revision contributes towards a better understanding of *Pseudodebis* species diversity, highlighting the importance of incorporating information from both morphology and molecular data, as has been repeatedly discussed in recent euptychiine studies (e.g., Nakahara et al. 2020; Espeland et al. 2019). In fact, documentation of the two new species described herein might not have been possible based solely on morphological data given the rather subtle wing pattern differences and homogeneous genitalia within the "*celia* clade" of *Pseudodebis*. Clearly, genetic data have contributed greatly towards discovering hidden *Pseudodebis* diversity. On the contrary, we were unable to settle the nomenclature for *Papilio phorcys* in the present study. We hope the brief historical discussion provided above will shed some light on this obscure name and stimulate some discussion among Lepidoptera researchers and further contribute towards clarifying the status of this enigmatic taxon in the future.

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Nomenclature **ZooBank registration:** urn:lsid:zoobank.org:pub:EACF1D2A-B8E0-4D46-A72F-2C6323B831CC

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Declarations

Conflict of Interest The authors declare no competing interests.

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