Description of a new species of *Yphthimoides* Forster, 1964 from Peru (Lepidoptera: Nymphalidae: Satyrinae)

Shinichi Nakahara[1,3*], Eduardo P. Barbosa[2], Ichiro Nakamura[1], Gerardo Lamas[3] and André V. L. Freitas[2]

1. McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA; 2. Departamento de Biologia Animal, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil; 3. Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru. *Correspondence: snakahara@ufl.edu

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Abstract: We here describe and name a new nymphalid butterfly species in the subtribe Euptychiina, *Yphthimoides kinyoni* Lamas, Nakahara & Barbosa, **n. sp.**, based on an integrative taxonomic approach. *Yphthimoides kinyoni* **n. sp.** is currently known solely from the Cosñipata valley (Cuzco, Peru) where it is apparently confined to a narrow elevational zone. We inferred the most comprehensive molecular phylogeny for *Yphthimoides* utilizing a maximum likelihood approach to assess its systematic placement and to support our taxonomy, and further highlight the importance and benefits of a multi-collaborative effort in unravelling the systematics of a problematic group.

Key words: Cosñipata valley, Cuzco, Euptychiina, taxonomy

INTRODUCTION

The Neotropical nymphalid butterfly genus *Yphthimoides* Forster, 1964 (Satyrini: Euptychiina) has been the subject of ongoing systematic revision due to its polyphyletic nature and to it being one of the species-rich euptychiine genera, as well as studies focused on the species complex known as the '*renata* species group' (*sensu* Barbosa *et al.*, 2016, 2017). A comprehensive phylogenetic study was therefore conducted by EPB (Barbosa *et al.*, in press) in order to test a number of formerly proposed taxonomic hypotheses and better understand its species diversity (Freitas *et al*., 2012; Barbosa *et al*., 2015, 2016, 2018). Our research (Barbosa *et al*., in press) suggests that *Yphthimoides* should be restricted to a monophyletic group that includes 19 described species and at least one undescribed species, with the remaining species formerly placed in the genus (Lamas, 2004) requiring reclassification. Like several euptychiine genera, the genus is diverse in the eastern Andes, although somewhat unusually it reaches its highest diversity of species and lineages in southeastern Brazil. This apparent high Brazilian diversity of *Yphthimoides* does not appear to be a sampling artifact, given that over 50 collections have been examined and with intensive fieldwork in several non-Brazilian countries. A number of studies on Euptychiina taxonomy have emphasized the importance of incorporating multiple layers of evidence when generating a taxonomic hypothesis to reduce the likelihood of creating invalid names (e.g., Barbosa *et al.*, in press; Nakahara *et al.*, 2020), and that is the approach that we adopt here.

During the course of field work led by GL, aimed at surveying the butterfly fauna of the Cosñipata Valley in Cuzco and Madre de Dios departments, Peru, a number of unidentified *Yphthimoides* specimens were obtained in 2017-2020. We take this opportunity to describe this *Yphthimoides* species based on an integrative taxonomic approach, including morphological characters and inferring the most comprehensive molecular phylogeny for *Yphthimoides* to assess the systematic placement of the new species, in order to add yet another element not only to this diverse genus but also to the exceedingly rich butterfly fauna of the Cosñipata Valley (Lamas *et al*., 2021).

MATERIALS AND METHODS

We studied the morphology of relevant *Yphthimoides* specimens following standard protocols, namely soaking abdomens for 10 minutes in 10% KOH at 80°C, and performing subsequent genitalic dissection. Genitalic morphology and other external morphological characters were examined using a Leica MZ 16 stereomicroscope at various magnifications up to 100x, with drawings also prepared using a camera lucida attached to this microscope. Genitalia, wing elements and venation terminology largely follow Nakahara *et al.* (2018). Specimens relevant to this study were examined in public and private collections and we use the following acronyms throughout the text: Ichiro Nakamura collection, Williamsville, NY, USA (**ICNA**); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (**MUSM**).

DNA "barcode" sequences were generated from two

individuals following the methods described in Nakahara *et al.* (2018, 2020). GenBank accession numbers for these newly obtained sequences are as follows: MW715560; MW715561. These sequences were incorporated into the most comprehensive matrix available for the group, compiled by Barbosa *et al*. (in press) for 400 individuals representing 49 taxa and aligned on the CIPRES Science Gateway portal v. 3.1 (Miller *et al*., 2010) using MAFFT v. 7 (Katoh & Standley, 2013). The final concatenated matrix comprised 402 specimens, with a total of 2,799 base pairs from the three genes available for the majority of species: COI, GAPDH and RpS5. *Oressinoma sorata* Salvin & Godman, 1868 was used to root the tree (all voucher information is provided in Barbosa *et al.*, in press). We ran both IQ-TREE (v. 1.6.9) (Nguyen *et al.*, 2015) and IQ-TREE2 (v.2.0.6) (Minh *et al.*, 2020) using different partitioning strategies. For IQ-TREE (v.1.6.9), PartitionFinder v2.1.1 (Lanfear *et al.*, 2017) was used to estimate the best-fit partitioning strategy. The greedy option was used with nine datablocks corresponding to the codon positions of the three gene fragments: the mitochondrial gene COI and two nuclear genes, GAPDH and RpS5. The best scheme found divided the nine datablocks into five subsets and model selections (see Table 1 for details) were done using ModelFinder (Kalyaanamoorthy *et al.* 2017) with edge-linked partition model + FreeRate heterogeneity in IQ-TREE (v. 1.6.9) at the IQ-TREE web server (Trifinopoulos *et al.*, 2016). The systematic placement of the new species was estimated using a maximum likelihood approach, and support was calculated using the ultrafast bootstrap (UFBoot) (Hoang *et al.*, 2018), with 1,000 replications, in addition to assessing node support through 1,000 replications of the Shimodaira-Hasegawa-like approximate Likelihood Ratio Test (SH-aLRT) (alrt 1000) (Guindon *et al*., 2010; Hoang *et al.*, 2018). For IQ-TREE2 (v.2.0.6), the "merge" option was employed in order to find best-fit substitution models and partition subsets through ModelFinder, and the "bnni" option was added to reduce model violation. We ran 10 independent analyses based on the partition and best-fit model of nucleotide evolution provided in Table 1, and the tree associated with the highest likelihood score (LnL=-65066.2669) was rooted as described above. Both UFBoot and SH-aLRT were also used to assess confidence, as described above, but we also employed the approximate Bayes branch test (aBayes; Anisimova *et al.*, 2011) for support value. All analyses related to IQ-TREE2 (v.2.0.6) were conducted on the University of Florida's Hipergator2 cluster.

SPECIES DESCRIPTION

Yphthimoides kinyoni Lamas, Nakahara & Barbosa, **new species**

(Figs. 1-5)

Systematic placement and diagnosis. The maximum likelihood tree estimated in IQ-TREE (v.1.6.9) and IQ-TREE2 (v.2.0.6) resulted in identical topologies and the result of the latter analysis is figured herein (Fig.1). *Yphthimoides kinyoni* **n. sp.** is weakly supported as sister to all *Yphthimoides* except for those in the '*pacta* species group' (*sensu* Barbosa *et al*., in press) (SH-aLRT/aBayes//UFBoot= 82.5/0.795/77).

Table 1. Model of nucleotide evolution selected for maximum likelihood analyses in IQ-TREE (v.1.6.9) and IQ-TREE2 (v.2.0.6).

Partition Subsets for IQ-TREE	Models	Partition Subsets for IQ-TREE2	Models
COI codon1	GTR+F+I+G4	COI codon1	GTR+F+R5
COI codon2	TIM2+F+I+G4	COI codon2	GTR+F+R4
COI codon3, GAPDH codon3, RpS5 codon3	TIM2+F+I+G4	COI codon3	TIM2+F+R3
RpS5 codon1, GAPDH codon1	GTR+F+I+G4	GAPDH codon1, RpS5 codon1	GTR+F+I+G4
RpS5 codon2, GAPDH codon2	GTR+F+I+G4	GAPDH codon2, RpS5 codon2	GTR+F+R3
N/A	N/A	GAPDH codon3, RpS5 codon3	K3Pu+F+R3

Yphthimoides kinyoni **n. sp.** is unique in the sense that its eighth sternite appears as a narrow band at the base of the abdominal segment (see Fig. 3a, similar to the reduced eighth tergite of many other euptychiines), which distinguishes this taxon from most known euptychiine species. The eighth sternite is often more developed in euptychiines, and may appear as two distinct patches in some taxa. The male genitalia of *Y. kinyoni* **n. sp.** is similar to those of the relatively distantly related species in the so-called '*renata* species group' (as referenced above and indicated in Fig. 1, a clade including *Y. renata* (Stoll, 1780), *Y. blanquita* Barbosa, Marín & Freitas, 2017, *Y. ordinaria* Freitas, Kaminski & Mielke, 2012, *Y. manasses* (C. Felder & R. Felder, 1867), *Y. nareta* Barbosa & Freitas, 2017, and *Y. leguialimai* (Dyar, 1913)) in having serrated, small "teeth" at the inner margin of the apical process of the valva, whereas most other *Yphthimoides* species possess rather prominent projections in this region except for *Y. straminea* (Butler, 1867), which appears to have a single semi-circular hump instead of projections. Nevertheless, the somewhat developed appendices angulares (i.e., appearing wide in lateral view) and short saccus (i.e., shorter than ventral margin of tegumen) distinguish *Y. kinyoni* **n. sp.** from all taxa in the '*renata* species group', since those species have a less-developed (i.e., appearing less wide in lateral view) and longer saccus (i.e. similar, or longer than ventral margin of tegumen). Furthermore, the '*renata* species group' can be characterized by the presence of cornuti, whereas apparently this character is absent in *Y. kinyoni* **n. sp.** Phenotypically, *Y. kinyoni* **n. sp.** is also similar to some species in the '*renata* species group' such as *Y. nareta*, but the male of this new species is distinguished from these taxa by the combination of less reddish ventral ground color and rather prominent VHW ocelli in cells M_2 and M_3, whereas the male of *Y. nareta* overall appears reddish and the VHW ocelli in cells M_2 and M_3 appear reduced. The distally curving VFW postdiscal band below Cu_2 observed in the male of *Y. kinyoni* **n. sp.** may also serve as a diagnostic wing pattern character to distinguish males of these two taxa. We do not know of any females of *Y. nareta*. Nevertheless, the presence of signa distinguishes the female *Y. kinyoni* **n. sp.** from species in the '*renata* species group' since taxa in that group apparently lack signa.

Description. MALE: Forewing length 23.5-24.5 mm (n=7). **Head:** Eyes naked (i.e., without hair-like scales), grayish scales at base; frons dark brownish, with some grayish scales and long grayish hair-like scales visible; first segment of labial palpi similar or slightly narrower than second segment in width, covered with white to brownish scales and elongated scales, whitish or brownish long setiform scales present ventrally, second segment slightly longer than longitudinal eye axis, covered mainly with brownish scales scattered with some whitish scales laterally, elongated whitish hair-like scales along dorsal surface, ventrally with whitish elongated setiform scales and brownish elongated setiform scales, length apparently variable, some as long as third segment of labial palpi, third segment roughly one-fourth to one-third of second segment in

Figure 1. Maximum likelihood tree estimated in IQ-TREE2 (v. 2.0.6) (LnL = -65066.2669), showing the systematic placement of *Y. kinyoni* **n. sp.** and close relatives. Branch supports are represented by SH-aLRT/aBayes//UFBoot.

length, porrect, covered mainly with brownish scales with some whitish scales visible laterally towards base; antennae slightly shorter than half of forewing length, with flagellum ca. 41 antennomeres (n=1), distal 14-15 segments composing rather insignificant club, grayish scales and whitish scales visible on antennomeres (more apparent towards basal segments). **Thorax:** Brownish, dorsally and laterally (above wings) moderately covered with grayish scales and sparse multi-colored long hair-like scales, ventrally (below wings) covered with light grayish scales and long whitish hair-like scales; foreleg reduced, covered with long ochre hair-like scales; femur of pterothoracic legs whitish ventrally and dorsally darker, without spines, tibia and tarsus of pterothoracic legs dark ochre overall, dorsally appearing darker and ventrally lighter, color becomes darker on distal segments of legs, tibia with two longitudinal rows of spines ventrally, in addition to spines present laterally on along sides, tibial spurs present at distal end of tibia, spurs equal in length, tarsus with roughly

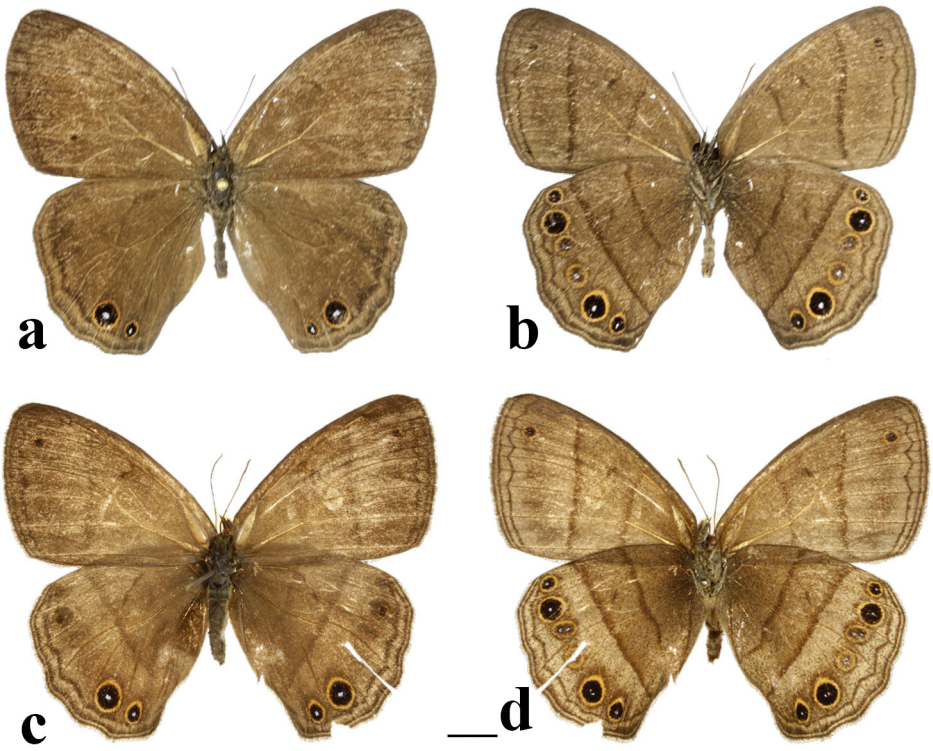

Figure 2. Adults of *Y. kinyoni* **n. sp.**: a) dorsal surface of the holotype male; b) ventral surface of (a); c) dorsal surface of the allotype female; d) ventral surface of (c). Scale bar = 5 mm.

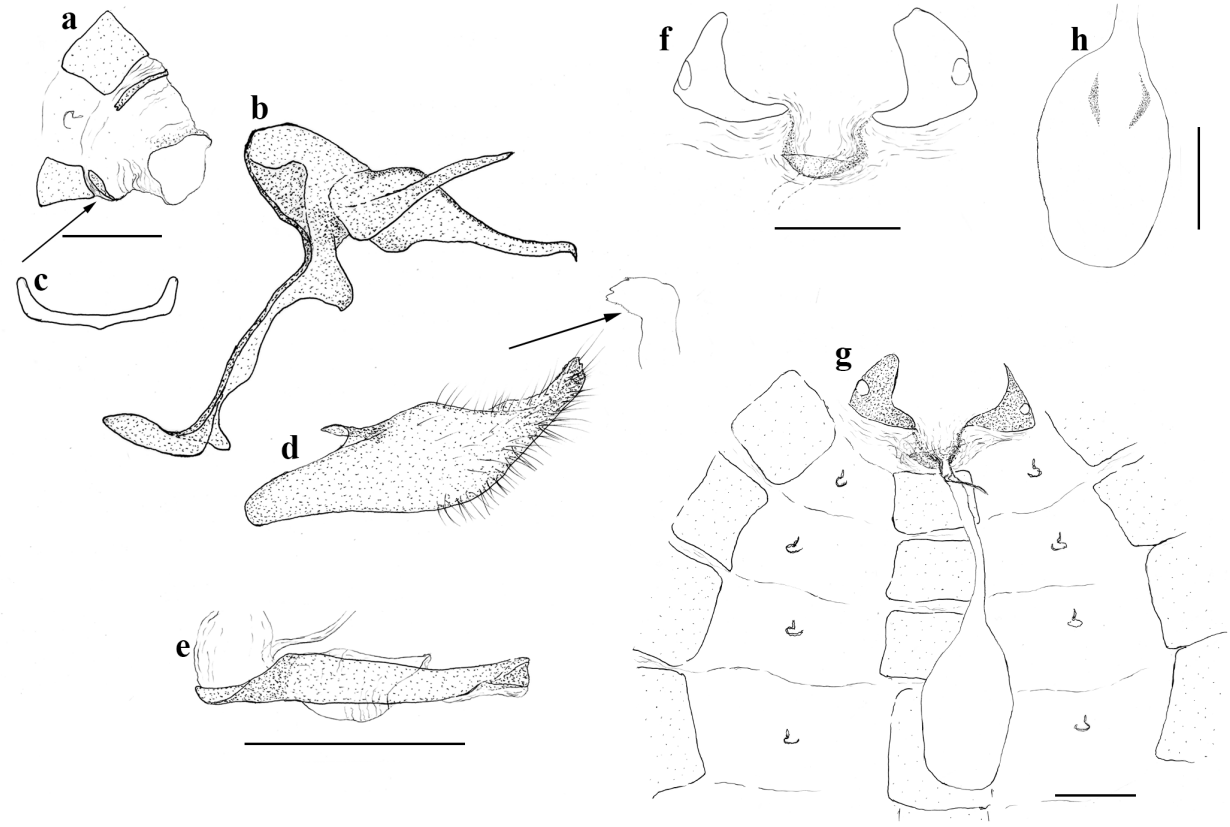

Figure 3. Abdomen and genitalia of *Y. kinyoni* **n. sp.:** a) male terminal abdominal segments showing narrow eighth tergite and sternite; b) lateral view of male genitalia (valvae removed); c) juxta in posterior view; d) valvae in lateral view with a dorsal view of angled apical process showing multiple serrated "teeth"; e) phallus in lateral view; f) female genitalia in ventral view; g) female genitalia in dorsal view; h) signa. Male genitalia based on SN-20-82; female genitalia based on SN-20-83. Scale bar = 1 mm.

Figure 4. Habitat pictures of Chontachaca (Cuzco, Peru) (a & b) and adult of *Y. kinyoni* **n. sp.** in nature (c, at 820-840 m, Chontachaca, Cuzco, Peru; photographed on 10 November 2017). Photo credits for a & b: Ian Segebarth; for c: Andrew Neild.

three longitudinal rows of spines ventrally, rows of spines increase to four from distal end of tarsus and towards distally. **Abdomen:** Eighth tergite and sternite appearing as narrow band along anterior margin of eighth abdominal segment. **Wing venation:** Basal half of forewing subcostal vein swollen; R_2 rising roughly at origin of discocellular vein m_1-m_2; base of cubitus swollen; forewing recurrent vein absent; hindwing humeral vein developed; origin of hindwing M_2 towards M_1 than M_3. **Wing shape and pattern:** *Forewing* subtriangular, apex rounded, costal margin slightly convex, tornus rounded, inner margin almost straight, but rounded towards thorax near base; *Hindwing* slightly elongated vertically, rounded, costal margin slightly convex, outer margin slightly undulating, tornus slightly angular, inner margin slightly concave near tornus, anal lobe convex, slightly round; *Dorsal forewing* no visible androconial scales on DFW, ground color uniformly brown with submarginal band and marginal band appearing darker; *Dorsal hindwing* color similar to DFW, two ocelli present, one in cell Cu_1 and another one in Cu_2, with former ocellus being larger; *Ventral forewing* ground color somewhat chestnut brown, darker discal band and postdiscal band appearing narrow but well-defined; concolorous scaling along discocellular vein; submarginal and marginal band narrower than basal two bands and appearing lighter; small ocellus present in cell M_1, otherwise other elements as illustrated (Fig. 2); *Ventral hindwing* ground color similar to ventral forewing but appearing somewhat two-toned by possessing more "paler" area distal of postdiscal band; general pattern of four VHW bands similar to those of VFW, dark brownish scaling visible just below origin of M_2 extending towards origin of M_3; six submarginal ocelli in cells Rs, M_1, M_2, M_3, Cu_1, and Cu_2, as illustrated; otherwise other elements as illustrated (Fig. 2). **Genitalia:** as illustrated (Fig. 3a-e); hair-like setae only visible at base of uncus (not illustrated); apical process of valva angles in dorsal or ventral view with multiple noticeable serrated small "teeth" present at inner margin; ductus ejaculatorius entering antero-dorsal opening of phallobase posteriorly, vesica exits at posterior tip of aedeagus; no obvious sclerotized cornuti.

FEMALE: Forewing length 26.5 mm (n=1)
Similar to male, except as follows: five tarsomeres present on foretarsus, with spines ventrally; wing shape overall broader and more rectangular; wing color overall paler. **Female abdomen and genitalia:** as illustrated (Fig. 3f-h); intersegmental membrane of seventh and eighth abdominal segments not expandable, folded only at just below ostium bursae, forming slightly sclerotized semi-circular region, weakly sclerotized region extending towards lateral plate of eighth abdominal segment around ostium bursae, lamella antevaginalis membranous; signa rather short, located ventrally on corpus bursae.

Variation. The sequenced male (LEP-68838) possesses a single pupil in the VHW ocellus in Cu_1, whereas the sequenced female allotype (LEP-68839) exhibits two pupils in this ocellus. Given that these two individuals are supported as conspecific by the DNA data (Fig.1), this observed difference in the pupil number is likely infra-specific variation. Note this discrepancy of pupil number can also be seen between the individuals illustrated in Fig. 4c and Fig. 5b-c.

Types. HOLOTYPE male with the following labels written verbatim: // PERU, CU[zco], Chontachaca 13º02'S, 71º28'W 950m 23.vi.2019 G. Lamas//, deposited in MUSM.

ALLOTYPE female with the following labels written verbatim: //PERU: Cusco Region Rio Cosnipata Valley, Chontachaca-Rio Hospital trail SW of Pillcopata, 811m 13º00'25''S, 71º27'47''W 07.iv.2018 I. Nakamura leg.//DNA voucher LEP-68839// Genitalic vial SN-20-83 S. Nakahara// (ICNA, to be deposited in MUSM).

PARATYPES: Six males with the following labels written verbatim: //PERU: Cusco Region Rio Cosnipata Valley, Chontachaca-Rio Hospital trail SW of Pillcopata, 811m 13º00'25''S, 71º27'47''W 07.iv.2018 I. Nakamura leg.// DNA voucher LEP-68838// Genitalic vial SN-20-82 S. Nakahara// (ICNA, to be deposited in MUSM); //PERU: Cuzco 950m. Chontachaca Cosñipata Valley 5175 12-XI-2017 Kinyon// in MUSM; //PERU, CU[zco], Chontachaca 13º02'S, 71º28'W 950m 27.x.2018 G. Lamas// in MUSM; //PERU, CU[zco], Chontachaca 13º02'S, 71º28'W 950m 18.vi.2019 L. Gibson// in MUSM; same data as holotype, plus //SN-DNA19-56// in MUSM; //PERU, CU[zco], Chontachaca 13º02'S, 71º28'W 950m 25.vi.2019 G. Lamas// in MUSM.

Etymology. This species is named after Steve Kinyon, who collected the first recorded specimen in 2017, as a small recognition for his superb help in surveying the Cosñipata Valley butterfly fauna. The name is to be considered as a Latinized masculine noun in the genitive case.

Distribution and natural history. This species is known to date only from the Cosñipata Valley (Cuzco, Peru), in a narrow band of elevation from 650-950 m (Figs. 4a, b, 5a).

DISCUSSION

Our taxonomic hypothesis for *Yphthimoides kinyoni* **n. sp.** is supported by the most comprehensive multi-locus molecular phylogeny for *Yphthimoides* (Fig. 1) conducted to date. Two sequenced individuals of this new *Yphthimoides* species (LEP-68838; 68839) were recovered as a divergent lineage compared to all known *Yphthimoides* taxa, with its placement as sister to ((*'yphthima* species group') + (*'celmis* species group' + '*renata* species group')) with moderate support (SH-aLRT/aBayes//UFBoot = 82.5/0.795/77), that is, sister to all known *Yphthimoides* except those in the '*pacta* species group' (*sensu* Barbosa *et al*., in press). The monophyly of *Yphthimoides* is also moderately supported (SH-aLRT/aBayes//UFBoot = 85/0.95/74), including both the type species (*Neonympha yphthima* C. Felder & R. Felder, 1867) and *Yphthimoides kinyoni* **n. sp.** as part of the clade, thus we consider this new species to be a member of *Yphthimoides*. Despite the extensive study of the group by EPB and AVLF, no putative synapomorphy for

Figure 5. Habitat picture of Q'eros road (Cuzco, Peru) (a) and adult of *Y. kinyoni* **n. sp.** in nature (b & c, at 650-700 m, road from Pillcopata to Q'eros, Cuzco, Peru; photographed on 25 October 2019). Photo credits for a-c: Andrew Neild.

Yphthimoides has been identified to morphologically support its placement.

Despite Cosñipata Valley being a relatively well-surveyed region visited by a number of Lepidoptera researchers, starting with Claude Gay in the mid-1800s (e.g., Lamas 1989; Ignatov *et al.*, 2011; Lamas *et al*., 2021), and including recent sampling by IN as well as a number of other lepidopterists, *Yphthimoides kinyoni* **n. sp.** remained unnoticed until recently with no known museum specimens in over 50 public and private collections examined during the course of a collaborative research project on euptychiine systematics (see below for further information). The entire type series was, in fact, collected between November 2017 and June 2019, and it remains a mystery why this species was not sampled prior to 2017. Some rare nymphalid butterflies are apparently confined to a narrow elevational band along the slopes of the tropical Andes (e.g., *Memphis falcata* (Hopffer, 1874)) (pers. obs.), and this might apply to *Y. kinyoni* **n. sp.** as well. The recently photographed individuals (photographer: Andrew Neild) are also from Cosñipata Valley from 650-840 m, indicating that their provenance is virtually the same as the type series. We hope this article will raise awareness of this poorly known butterfly species to increase our knowledge of its distribution by revealing additional specimens from new localities that could improve assessment of its geographic range and conservation status.

We note that a number of recent descriptions of new euptychiine taxa based on an integrative taxonomic approach, including this present study, were made possible through a multi-collaborative effort by a number of researchers from different institutions (see https://www.floridamuseum.ufl.edu/museum-voices/euptychiina/). Despite molecular data being used extensively in various biodiversity-related research in this era, it is still common to see taxonomic hypotheses among butterflies based solely on comparative morphology (e.g., Henao, 2019). This can be problematic because observation of morphological traits may result in interpreting homoplasious characters as putative synapomorphies, as evidenced by Forster (1964). Nevertheless, compiling information on relevant specimens and genetic data generated by multiple researchers has enabled us to delimit likely generic level clades containing the type species for all described euptychiine genera, and thus assess placement of new species by ensuring that they form a clade with the respective type species. The significance of this multi-collaborative study can be seen by a statement made in the description of another *Yphthimoides* species named less than a decade ago, *Y. ordinaria* in Freitas *et al*. (2012): "*Additionally, because most of the above [euptychiine] genera were erected without a clear diagnosis, the correct assignment of a new species in a valid genus is usually tentative, and for the moment is best done by comparison [of morphology] with the type species of each genus*". The fact that most new euptychiine species can now be described by incorporating multiple layers of evidence to help maintain monophyly of existing genera would not have been possible without broad international collaboration.

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LITERATURE CITED

Anisimova, M., Gil, M., Dufayard, J. F., Dessimoz, C., Gascuel, O. 2011. Survey of branch support methods demonstrates accuracy, power, and robustness of fast likelihood-based approximation schemes. *Systematic Biology* 60(5): 685-699.

Barbosa, E. P., Marín, M. A., Giraldo, C. E., Uribe, S. I., Freitas, A. V. L. 2016. Description of two new species of the Neotropical genus *Yphthimoides* Forster, 1964 (Lepidoptera: Nymphalidae: Satyrinae) from the "*renata* clade". *Neotropical Biodiversity* 2(1): 87-98.

Barbosa, E. P., Marín, M. A., Giraldo, C. E., Uribe, S. I., Freitas, A. V. L. 2017. Corrigendum. *Neotropical Biodiversity* 3(1): ii.

Barbosa, E. P., Seraphim, N., Valencia, G., Azeredo-Espin, A. M., Freitas, A. V. L. 2021. Systematics of the Neotropical genus *Yphthimoides* Forster, 1964 and the clade composed by the genera *Moneuptychia* Forster, 1964, *Pharneuptychia* Forster, 1964 and the species *Euptychoides castrensis* (Schaus, 1902) (Nymphalidae: Satyrinae) with notes on the biogeographic history of *Yphthimoides*. *Molecular Phylogenetics and Evolution* (in press).

Barbosa, E. P., Siewert, R. R., Mielke, O. H. H., Lamas, G., Willmott, K. R., Freitas, A. V. L. 2018. Redescription of *Yphthimoides patricia* (Hayward, 1957), with taxonomic notes on the names *Euptychia saltuensis* Hayward, 1962 and *Yphthimoides manasses* (C. Felder & R. Felder, 1867) (Nymphalidae: Satyrinae). *Zootaxa* 4422(4): 537-557.

Barbosa, E. P., Silva, A. K., Paluch, M., Espin, A. A., Freitas, A. V. L. 2015. Uncovering the hidden diversity of the Neotropical butterfly genus *Yphthimoides* Forster (Nymphalidae: Satyrinae): description of three new species based on morphological and molecular data. *Organisms Diversity & Evolution* 15(3): 577-589.

Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high 820 throughput. *Nucleic Acids Research* 32(5): 1792-1797.

Forster, W. 1964. Beiträge zur Kenntnis der Insektenfauna Boliviens XIX. Lepidoptera III. Satyridae. *Veröffentlichungen der Zoologischen Staatssammlung München* 8: 51-188.

Freitas, A. V. L., Kaminski, L. A., Mielke, O. H. H., Barbosa, E. P., Silva-Brandão, K. 2012. A new species of *Yphthimoides* (Lepidoptera: Nymphalidae: Satyrinae) from the southern Atlantic forest region. *Zootaxa* 3526: 31-44.

Guindon, S., Dufayard, J. F., Lefort, V., Anisimova, M., Hordijk, W., Gascuel, O. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology* 59(3): 307-321.

Henao, E. R. 2019. Dos nuevas especies de mariposas (Nymphalidae: Satyrinae) de la región amazónica colombiana. *Boletín científico. Museo de Historia natural. Universidad de Caldas* 23(2): 193-207.

Hoang, D. T., Chernomor, O., von Haeseler, A., Minh, B. Q.,Vinh, L. S. 2018. UFBoot2: 859 Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35(2): 518-522.

Ignatov, I. I., Centeno, P., Janovec, J. P., Tobler, M. W., Grados, J., Lamas, G. 2011. Patterns of diversity, composition, and distribution of sphingid moths along an elevational gradient in the Andes-Amazon region of southeastern Peru. *Annals of the Entomological Society of America* 104(1): 68-76.

Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K. F., von Haeseler, A., Jermiin, L. S. 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14(6): 587-589.

Katoh, K., Standley, D. M. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30(4): 772-780.

Lamas, G. 1989. "Viaje al Cuzco", de Claude Gay. *Boletín de Lima* 11(63): 23-28.

Lamas, G., McInnis, M. L., Busby, R. C., Robbins, R. K. 2021. The lycaenid butterfly fauna (Lepidoptera) of Cosñipata, Peru: checklist, elevational patterns, and rarity. *Insecta Mundi* 0861: 1-34.

Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., Calcott, B. 2017. PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* 34(3): 772-773.

Miller, M. A., Pfeiffer, W., Schwarts, T. 2010. *Creating the CIPRES Science Gateway for inference of large phylogenetic trees*, pp. 1-8. *In*: *Proceedings of the Gateway Computing Environments Workshop (GCE)*. New Orleans, Louisiana.

Minh, B. Q., Schmidt, H. A., Chernomor, O., Schrempf, D., Woodhams, M. D., von Haeseler, A., Lanfear, R. 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 37(5): 1530-1534.

Nakahara, S., Lamas, G., Willmott, K. R., Espeland, M. 2020. Description of a new genus and species for a common and widespread Amazonian satyrine butterfly (Lepidoptera: Nymphalidae: Satyrinae: Satyrini). *Peer J* 8(e10324): 1-25.

Nakahara, S., Willmott, K. R., Mielke, O. H. H., Schwartz, J., Zacca, T., Espeland, M., Lamas, G. 2018. Seven new taxa from the butterfly subtribe Euptychiina (Lepidoptera: Nymphalidae: Satyrinae) with revisional notes on *Harjesia* Forster, 1964 and *Pseudeuptychia* Forster, 1964. *Insecta Mundi* 0639: 1-38.

Trifinopoulos, J., Nguyen, L.-T., von Haeseler, A., Minh, B. Q. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44(W1): W232-W235. https://doi.org/10.1093/nar/gkw256.