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Research

Vanewrightia gen. nov.—A Highly Variable Taxon of Neotropical Ctenuchina (Lepidoptera: Erebidae: Arctiinae: Arctiini) Revealed by Behavioral Traits

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Abstract

A series of different-looking tiger moths was collected at pyrrolizidine alkaloid baits in the daytime in Peru. They proved to be variants of a new genus, *Vanewrightia* **gen. nov.**, and a new species, *Vanewrightia kiesela* **sp. nov**., both described here. This species presents a striking example of extensive intraspecific variation within a population. Its discovery demonstrates the importance of sampling moths by means other than collecting with light, of studying patterns of wing undersides, and of the value of barcoding. Specimens found in collections considered here potentially to represent further species of the new genus are documented and discussed; *Vanewrightia subflavescens* (Kaye, 1911) **comb. nov**., and *Vanewrightia patawaensis* (Cerda, 2017) **comb. nov.** are established; we propose *Epidesma parva* (Rothschild, 1912) as a junior synonym of *E. aurimacula* (Schaus, 1905). The newly recognized intraspecific variation greatly challenges delimitation of morphospecies and uncovers uncertainties in the taxonomy of *Epidesma* Hübner, [1819]. The occurrence of an oblique forewing band in many Lepidoptera and the stunning similarity in overall appearance of variants of *Vanewrightia* with unrelated taxa, in particular notodontid moths (Josiini) and *Chamaelimnas* C. & R. Felder, [1885] butterflies (Riodinidae), are discussed in the context of mimicry and crypsis, and some perspectives for further research are suggested.

Key words: intraspecific variation, pyrrolizidine alkaloids, pharmacophagy, mimicry, *Epidesma*

Within the Arctiini (Lepidoptera: Erebidae: Arctiinae) many species are di- or polymorphic in wing pattern (including *Euplesia* Felder, 1874 and *Apiconoma* Butler, 1876, Laguerre 2016; *Dysschema* Hübner, 1818, Moraes et al. 2017; *Watsonidia* Toulgoët, 1981, Grados 2019; *Phoenicoprocta* Druce, 1898, M.L. and M.B., in preparation). Within the Arctiina and Callimorphina, there are many that exhibit continuous intraspecific variation for entire pattern (e.g., *Grammia* Rambur, [1866], Schmidt 2009; *Utetheisa* Hübner, [1819], Pease 1968; *Arctia* Schrank, 1802, Cook and Logunov 2016) or certain pattern elements only (*Belemnia* Walker, 1854), notwithstanding that many cryptic species look so similar that separation is impossible without dissection and barcoding (e.g., Espinoza et al. 2017). Here we describe *Vanewrightia* gen. nov. and *V. kiesela* sp. nov., in which individuals vary continuously and to a remarkable extent at a given site, that is within a population. Moreover, variants greatly resemble unrelated taxa of moths and butterflies. That all variants might belong to one species was indicated when a series of specimens from baiting with pyrrolizidine alkaloids (PAs) in the daytime was inspected closely; male genitalia and DNA barcodes eventually confirmed this to be the case. Recognition of the new taxon made it necessary to consider neighboring taxa with the result that another species [*Epidesma parva* (Rothschild, 1912) = *Epidesma aurimacula* (Schaus, 1905)] also turned out to be polymorphic. The study of *Vanewrightia* and *Epidesma*, unfortunately, uncovers a major uncertainty affecting the genus *Epidesma*, which is discussed in detail.

We not only provide the first example of large intraspecific variation within populations of a member of the Ctenuchina but also demonstrate the value of natural history studies and non-light collecting techniques for better understanding moth biodiversity. We also plea to not just study α-taxonomy but rather pay much attention to biological communities.

Materials and Methods

The core set of specimens used for this study was collected at baits in the daytime at the Research Station of the Área de Conservación

Privada at Panguana (9°37′S, 74°56′W, 230 m asl), Dep. Huánuco, Rio Yuyapichis, a tributary of Rio Pachitea, Peru, South America. Baits were either dried plants containing pyrrolizidine alkaloids (PAs; e.g., *Heliotropium indicum* L.) in gauze bags or pure PAs (e.g., monocrotaline, heliotrine) in dishes, displayed openly for collection by hand—sources of PAs attract a variety of insects including many Arctiini ('PA-pharmacophagy'; Boppré 1981, 1984, 2011; Boppré and Monzón 2020). Concurrently, moths were collected with PA-baits and UV-lights at night. Similar-looking specimens from various collections (see below; Tables 1 and 2) were studied in addition; searches for the new taxon by one of us (M.L.) at many other museums, including Washington, Berlin, Geneva, and Paris, were unsuccessful.

Table 1 provides a list of acronyms used for repositories; data of the specimens studied are given in Table 2.

Male genitalia were prepared by boiling abdomens for 15–30 min with a pellet of potash (KOH) in 6 ml water. After being washed with water and then alcohol, genitalia were photographed in natural position and stored in 95% ethanol. A KEYENCE VHX-700FD digital microscope equipped with a VH-Z20R/VH-Z20W zoom lens 20–200×, and a polarization filter OP-87429 was employed for documentation.

For barcoding (Hebert et al. 2003), the COI mitochondrial gene DNA was extracted, amplified, and sequenced at the Canadian Centre for DNA Barcoding (CCDB) in Guelph, Ontario, using legs removed from dry specimens and following standard protocols (Ratnasingham and Hebert 2007). From the project 'Neotropical Arctiidae' within the framework of BOLDSYSTEMS (2020), almost 30,000 sequences of Arctiinae are available, and we used the sequences of all Ctenuchina close to *Vanewrightia* from the general BOLD tree for comparison with barcodes of the species in question.

Clustal X (Jeanmougin et al. 1998) was used initially to compare DNA barcodes obtained from individuals under study. Sequences downloaded from BOLDSYSTEMS (2020) were aligned and analyzed using MEGA7 (Kumar et al. 2016), neighbor-joining (Saitou and Nei 1987), and maximum likelihood estimations (Aldrich 1997). To estimate branch support, Bootstrap values (Felsenstein 1985) were calculated in MEGA7 after 1,000 random replications. Distance calculations were performed using the Kimura 2-parameter (K2P) method in MEGA7 (Kimura 1980) including all sites, with the pairwise deletion option and assuming both a homogeneous pattern of divergence among lineages and a uniform rate of substitutions among sites.

Table 1. Acronyms used for entomological collections

Acronym	Repository
FZE	Collection of Michael Boppré, Professur für Forstzoologie und Entomologie, Albert-Ludwigs-Universität, Freiburg, Germany
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú
NHMUK	Natural History Museum, London, United Kingdom
RvM	Personal collection of Robert Vande Merghel, Brussels, Belgium
SMNK	Landessammlungen für Naturkunde, Karlsruhe, Germany
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany
SNSB	Bavarian State Collection of Zoology, Museum Witt, München, Germany

Nomenclature

This paper and the nomenclatural act(s) it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:ED4BBC9C-819C-4174-B11F-5AB2DC911020.

Results

Several specimens of more or less apparently aposematic arctiine moths with an oblique yellow band running across the middle of the forewings and with more or less additional yellow marking at the forewing bases visited PA-baits during the day (mostly between 4 and 6 pm) in Panguana (Fig. 1). When set, hardly two specimens look identical (Fig. 2, Table 2: PH01–PH24). The yellow markings in addition to the oblique band on the forewings may be missing (Fig. 2O–V), the yellow pattern on the upper sides of the hindwings also varies strikingly and can be very weak or even absent (Fig. 2V). The only common characters were their attraction to PAs and their diurnal activity. However, upon careful inspection, all these specimens share several features (arrows in Fig. 3; description below) which—although several also occur in other species (see below)—in combination are diagnostic and can be used to separate these individuals from very similar-looking arctiine and dioptine moths co-occurring in the same habitat (Fig. 4) but collectable only at night by means of light or PA-baits. The shape of the hindwings and markings on their undersides are the most typical features. From this set of characters, in particular PA-pharmacophagy, we hypothesized that we were dealing with a single but hyper-variable species. The genitalia do exhibit some variation, but the differences are small (see Fig. 6A–K for examples), consistent with the idea that they all belong to one species only.

In trying to find a name for the supposed species in question or for one of its many variants, we did not find an answer, neither in the literature nor in museum collections. In particular, we considered species of *Epidesma* Hübner, [1819] (formerly *Trichodesma* Hampson, 1898 = *Desmotricha* Hampson, 1911), *Napata* Walker, 1854, *Uranophora* Hübner, [1831], *Loxozona* Hampson, 1898 and others which all exhibit an oblique yellow forewing band. *Napata subflavescens* Kaye, 1911 (Fig. 8A) and *Loxozona patawaensis* Cerda, 2017 (Fig. 8B) possess the unusual hindwing underside markings typical for the specimens in question and are considered to be erroneously classified (see below). *Epidesma aurimacula* and *E. parva* turned out to be one variable species (see below).

A comparison of the barcodes of specimens with an oblique yellow forewing band from Panguana revealed that those baited with PAs during the day form a distinct cluster (not shown), and a separate BIN (Ratnasingham and Hebert 2013; see below), nearest to species included in *Epidesma*. Since *Epidesma* is not clearly defined (see below), we establish a new genus, *Vanewrightia*:

Vanewrightia Boppré gen. nov.

(urn:lsid:zoobank.org:act:8BB6BAF9-4CA3-4C6A-B3D6-D6CC461DF4A6)

Type species. *Vanewrightia kiesela* Boppré described below. Other included species: *V.* sp. nov., aff. *kiesela* Boppré, *V. subflavescens* (Kaye, 1911) comb. nov., and *V. patawaensis* (Cerda, 2017) comb. nov.

Table 2. Codes for specimens of *Vanewrightia* s.l. studied (also used in figures), data from their labels, specimen depositories, and cross references to figures

Specimen code	Label data	Depository**	Figure(s)
PH01	S-AMERICA / PERU // Huanuco, Rio Yuyapichis // Panguana, ACP // 9°37′ S, 74°56′ W, 230 m // 04.VII.2017 at PA bait // leg. J. Monzón at day // A-9383	FZE	2C, 6H
PH02	S-AMERICA / PERU // Huanuco, Rio Yuyapichis // Panguana, ACP // 9°37′ S, 74°56′ W, 230 m // 30.V.2015 at PA bait // leg. J. Monzón at day // A-3742	FZE	3B, 6A
PH03 PT	S-AMERICA / PERU // Huanuco, Rio Yuyapichis // Panguana, ACP // 9°37′ S, 74°56′ W, 230 m // 29.V.2015 at PA bait // leg. J. Monzón at day // A-3710	FZE	2T, 6K
PH04	S-AMERICA / PERU // Huanuco, Rio Yuyapichis // Panguana, ACP // 9°37′ S, 74°56′ W, 230 m // 27.V.2015 at PA bait // leg. J. Monzón at day // A-3569	FZE	2S, 6B
PH05 PT	S-AMERICA / PERU // Huanuco, Rio Yuyapichis // Panguana, ACP // 9°37′ S, 74°56′ W, 230 m // 20.VII.2017 at light // leg. J. Monzón // A-9560	FZE	2V, 6C
PH06*	PERU, HU, Estación / Biológica Panguana / 9°36′48″/74°56′12″ / 260 m 22.vii.2013 / J. Monzón leg. / PA-plant day	MUSM	2K
PH07	PERU, HU, Estación / Biológica Panguana 9°36′48″/74°56′12″ / 260 m 12.ix.2014 / J. Monzón leg. / PA-plant day	MUSM	2B
PH08*	PERU, HU, Estación / Biológica Panguana / 9°36′48″/74°56′12″ / 260 m 24.ix.2014 / J. Monzón leg. / PA-plant day	MUSM	2E
PH09	PERU, HU, Estación / Biológica Panguana / 9°36′48″/74°56′12″ / 260 m 20.v.2013 / J. Monzón leg. / PA-plant day	MUSM	2H
PH10 PT	PERU, HU, Estación / Biológica Panguana / 9°36′48″/74°56′12″ / 260 m 19.v.2013 / J. Monzón leg. / PA-plant day	MUSM	2I
PH11*	PERU, HU, Estación / Biológica Panguana / 9°36′48″/74°56′12″ / 260 m 17.v.2013 / J. Monzón leg. / PA-plant day	MUSM	2D
PH12	PERU, HU, Estación / Biológica Panguana / 9°36′48″/74°56′12″ / 260 m 19.v.2013 / J. Monzón leg. / PA-plant day	MUSM	2L
PH13	PERU, HU, Estación / Biológica Panguana / 9°37′, S 74°56′ W / 260 m 27.v.2013 / J. Monzón leg. / PA-plant day	MUSM	2A
PH14*	PERU, HU, Estación / Biológica Panguana / 9°37′ S, 74°56′ W / 260 m 21.vii.2013 / J. Monzón leg. / PA-plant day	MUSM	2O
PH15*	Peru – Panguana (Huanuco) / 9°36′50,09′S-74°56′08,29″W / Leg. Vande Merghel V-VI 2015 // *Heliotropium indicum*	RvM	—
PH16*	Peru – Panguana (Huanuco) / 9°36′50,09′S-74°56′ 08,29″W / Leg. Vande Merghel V-VI 2015 // S/*Heliotrop. indicum*	RvM	2F
PH17	Peru, Dep. Huánuco, Pangana / ACP, Rio Yuyapichis / S 09°37′ W 74°56′, 230 mNN / 5.X.2014 / leg. M. Falkenberg& R. Trusch / SMNK E-Lep 302	SMNK	2N, 6D
PH18	PERÚ / Prov. Huánuco, ACP / Panguana / 9°37′S, 74°56′W / L.F., leg. M. Schlemm / 1.X.2016 // ex coll. Michael Schlemm / SMNK; E.Lep 347	SMNK	2G, 6E
PH19	PERU / prov. Huánuco / Yuyapichis Faz. Tropical / S 09°37′ W 74°56′ / June 2013, 210 m / leg. A. Eichinger / MUSEUM WITT	SNSB	2M
PH20	PERU / prov. Huánuco / Yuyapichis Faz. Tropical / S 09°37′ W 74°56′ / June 2013, 210 m / leg. A. Eichinger / MUSEUM WITT	SNSB	2R, 6F
PH21	PERU / prov. Huánuco / Yuyapichis, ACP Panguana / 09°36″S / 74°56″W / June 2013, 220 m / leg. Hubert Thöny / PA-KÖDER: 6 / MUSEUM WITT	SNSB	2U
PH22	PERU / prov. Huánuco / Yuyapichis, ACP Panguana / 09°36″S / 74°56″W / June 2013, 220 m / leg. Hubert Thöny / MUSEUM WITT	SNSB	2P, 6G
PH23 HT	S-AMERICA / PERU // Huanuco, Rio Yuyapichis // Panguana, ACP // 9°37′ S, 74°56′ W, 230 m // 12.VI.2019 at PA bait // leg. J. Monzón at day // B-11533	FZE	3A, 5
PH24 PT	S-AMERICA / PERU // Huanuco, Rio Yuyapichis // Panguana, ACP // 9°37′ S, 74°56′ W, 230 m // 10.VI.2019 at PA bait // leg. J. Monzón at day // B-11471	FZE	2Q, 6I
PL01*	PERU, LO, km 25 / Carr. Iquitos – Nauta / 03°57′13″ / 73°24′28″ / 136 m 18.xii.2015 / J.J. Ramírez	MUSM	9A, 9N
PL02	PERU, LO, Huambe, / km 50 Carr. Iquitos – / Nauta 04°10′05″ / / 73°28′27″ 112 m / 12–13.ix.2017 / J.J. Ramírez	MUSM	9B
PL03*	PERU, LO, Puente / Itaya, km 60 Carr. / Iquitos – Nauta / 04°13′20″ / 73°29′00″ / 99 m 22–23.ix.2017 / J.J. Ramírez	MUSM	—
PL04	PERU, LO, Huambe, / km 50 Carr. Iquitos – / Nauta 04°10′05″ / / 73°28′27″ 112 m / 08-09.xi.2017 / J.J. Ramírez	MUSM	9C
PM01*	PERU, MD, Reserva de Tam- / bopata Explorer′s Inn. 250 m. / 1250/6917 11.XI.97 / C. Häuser & B. Kreusel // Pyrrolizidina bait–day	MUSM	9F
PM02*	PERU, MD, Tambopata / Research Center 300 m / 12°08′/69°36′ 14.ix.2008 / J. Grados // Heliotropium bait–day	MUSM	9D
PM03*	PERU, MD, Albergue / Posada Amazonas / 1247/6914 250 m / 12.V.2002 J. Grados // Heliotropium bait, 4–5 pm	MUSM	9E, 9O
PM04*	PERU, MD, Reserva de Tam- / bopata Explorer′s Inn. 250 m. / 12511//6917 16.XI.97 / C. Häuser & B. Kreusel // Heliotropium bait-day	MUSM	9G
PM05*	PERU, MD, Reserva de / Tambopata. Explorer′s Inn / 1250/6917 14.XI.97 / 250 m. J. Grados // Heliotropium bait-day	MUSM	9K
PM06*	PERU, MD, Albergue / Posada Amazonas / 1247/6914 250 m / 12.V.2002 J. Grados // Heliotropium bait, 3–4 pm	MUSM	9I
PM07*	PERU, MD, Albergue / Posada Amazonas / 1247/6914 250 m / 18.V.2002 J. Grados // Heliotropium bait, 4–5 pm	MUSM	9L
PM08	PERU: Madre de Dios / Reserva de Tambopata / vic. Explorer′s Inn, 200 m, / 16.XI.1997, 12°50′S / / 69°17′W. / C. Häuser & B. Kreusel leg // Gefangen mit Köder: An / Pyrrolizidinalkaloid-Extrakt / (auskristallisiert in Schale)	SMNS	9H, 9P
PM09	PERU: Madre de Dios / Reserva de Tambopata / vic. Explorer′s Inn, 200m, / 15.XI.1997, 12°50′S / / 69°17′W. / C. Häuser & B. Kreusel leg // SMNS—Lep. / 1997 -17 // Gefangen mit Köder: An / trockenem Heliotropium sp. / (Pyrrolizidinalkaloid-haltig)	SMNS	9M, 9R
FG01	French Guyana / Moutouchi / 8 Jan.–25 Feb. 2013 / R. Vande Merghel. Leg.	RvM	10A
FG02	French Guyana / Lodge Moutouchi / 1–30 Sept. 2013 / R. Vande Merghel. Leg.	RvM	10B 10D
FG03	French Guyana / rte Plateau des mines / St Laurent du Maroni / 09/2017 PA Baiting / R. Vande Merghel Leg	RvM	10C
VE01*	La Vuelta, / Caura R., / June 1903 / (S. M. Klages) // Rothschild Bequest / B.M.1939-1 no barcode label	NHMUK	11A
VE02*	La Vuelta / Caura R., / June 1903 / (S. M. Klages) // Rothschild Bequest / B.M.1939-1 // NHMUK 012823279	NHMUK	11B
VE03*	La Vuelta, / Caura R., / May 1903 / (S. M. Klages) // Rothschild Bequest / B.M.1939-1 // NHMUK 012823284	NHMUK	11C

Table 2. Continued

Specimen code	Label data	Depository**	Figure(s)
VE04*	Maripa, / Caura R / (S. M. Klages). // Rothschild / Bequest / B.M.1939-1 no barcode label	NHMUK	11D
VE05*	Maripa. / Caura R. / (S.M. Klages). // Rothschild / Bequest / B.M.1939-I // NHMUK 012823283	NHMUK	11E
BR01*	Para // Adams Bequest. / B.M. P912-399 no barcode label	NHMUK	11F
BR02*	Pará / A. M. Moss / 1 • 38 • 4 // Miles Moss Coll. / B.M. 1947-453 // NHMUK 0128232278	NHMUK	11G
BR03*	Pará / A. M. Moss // Miles Moss Coll. // Dioptidae / Myonia / desmotrichoides / Pará (A. M. Moss.) / Com. on fed. // NHMUK 012823275	NHMUK	11H
BR04*	Pará [illegible] / [illegible] Nov. 6. [19]39? // Miles Moss Coll. / B.M. 1947-453 // NHMUK 012823274	NHMUK	11I
BR05*	Allianca, / below S. Antonio, / Rio Madeira, / Nov. Dec. 1907. / (W. Hoffmanns). // Rothschild / Bequest / B.M. 1939-1 // NHMUK 012823270	NHMUK	11K
BR06*	Teffe (Ega) / Amazones / M. de Mathan / 2° Trimestre 1879 // Ex Oberthür Coll. / Brit. Mus. 1927-3 // NHMUK 012823272	NHMUK	11L

One slash (/) separates lines on a label, two slashes (//) separate labels. (PH) Peru, Huanuco. (PM) Peru, Madre de Dios. (PL) Peru, Loreto. (FG) French Guyana. (VE) Venezuela. (BR) Brazil. (HT) holotype, (PT) paratype. (*) not barcoded or barcode failure. (**) see Table 1.

Fig. 1. Male *Vanewrightia kiesela* sp. nov. gathering pyrrolizidine alkaloids from dry *Heliotropium indicum* plant material put out as bait. Arrow points to uncoiled proboscis.

Diagnosis

Small and very variable black and yellow moths (Figs. 1–3 and 8–11). Features in combination appear to be diagnostic (see arrows in Fig. 3): forewings with pointed apex and with a transverse (oblique) yellow band at the end of the cell which on the underside is often a little wider than on the upperside; hindwing margin distinctly angled between veins CuA_1 and M_3 and then almost straight toward apex; hindwing underside with a basal yellowish or whitish patch that shows a bulge protruding distally on vein M_2 into the wide black border. The hindwing angle as well as the pointed forewing tips are not easily recognizable, depending on the viewing angle. Male genitalia with sclerotized process between tegumen and valvae; prominent coremata.

Description. Male. Small species (forewing length 13–15 mm), with narrow, elongate forewings. Antennae bipectinate. Dorsum of abdomen yellow with black triangles, or black with little yellow; venter white to dark gray. WINGS. General pattern black or dark brown with yellowish or whitish bands and/or patches. Forewing upperside always with an oblique yellow band, sometimes with additional yellow at the base. Hindwing upperside can have yellow or whitish markings, or are black. Specimens often very variable in a single population and at a single collecting site. GENITALIA slightly asymmetrical: the left valva in ventral view always slightly longer than the right. Uncus long, narrow, slightly bent ventrally. Valvae, which extend posteriorly at least as far as the tip of the uncus, slightly curved with a pointed tip. A long translucent, pubescent process reaches posteriorly as far as the tip of uncus. Vinculum evenly rounded, with or without a small saccus. At the junction of the tegumen and the valvae there is a diagnostic, sclerotized process that points dorsally (Fig. 5A–C and E, arrows). Phallus cylindrical, slightly sinuous, with a unique scobinated process. A sclerotized area occurs, shaped as a narrow bar. Coremata present. WING VENATION (Fig. 7) is clearly distinct from *Epidesma ursula* (see Hampson 1898: 452, fig. 241, as *Trichodesma*; Travassos 1938, figs 1, 2, as *Desmotricha*): on the forewing the stalk separating M_1 from the radials in *E. ursula* is missing in *Vanewrightia* where Rs_1, Rs_2, and M_3 are connected; on the hindwing in *E. ursula*, M_2 and M_3 are stalked and M_3 and CuA_1 connected, whereas in *Vanewrightia* M_2 and M_3 are connected at the cell and CuA_1 is separated by a stalk.

Female. Unknown.

DNA Barcodes. All specimens which could be barcoded belong to BIN BOLD:ADO9441 and BIN BOLD:AEA5711 (Fig. 13; see

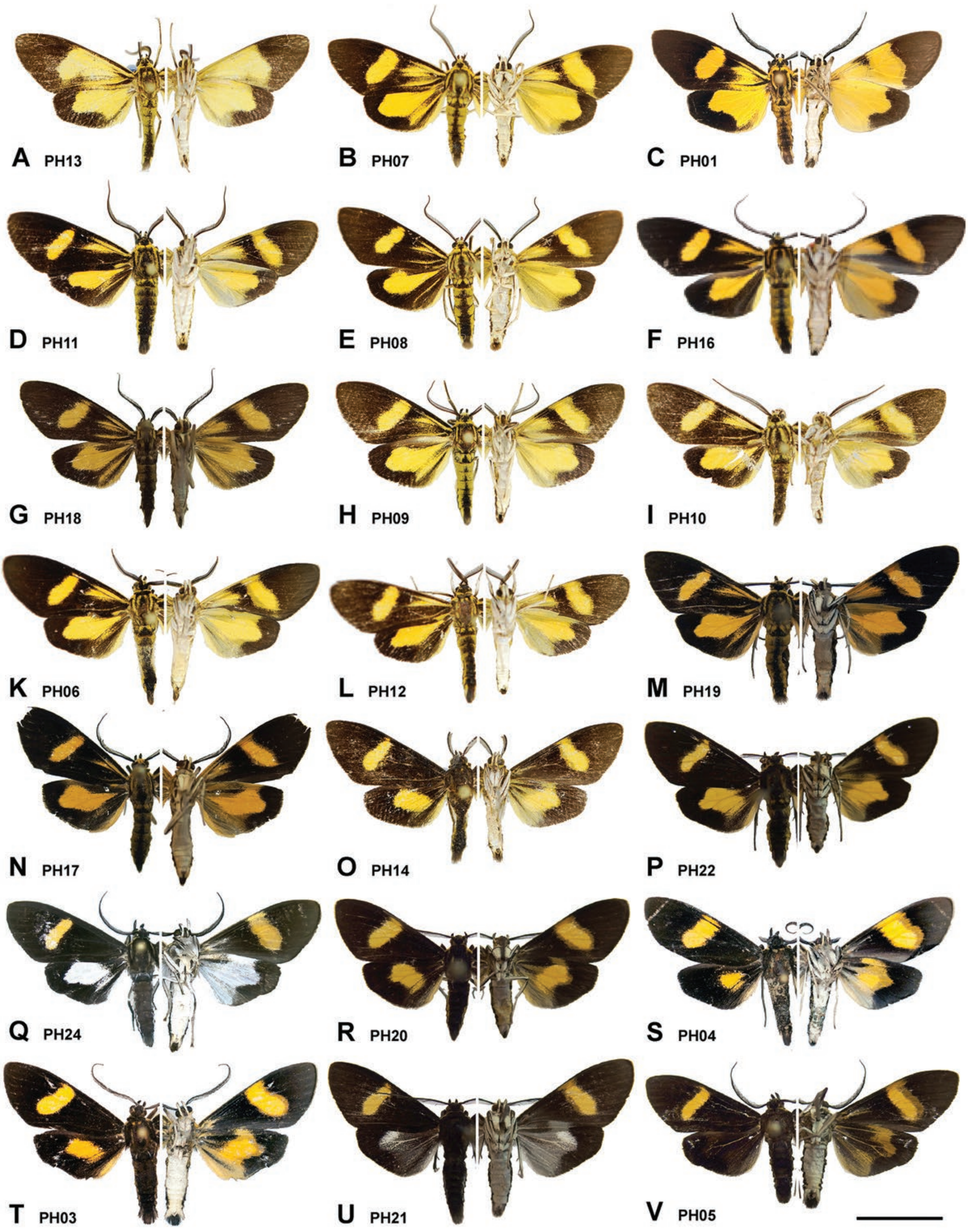

Fig. 2. Examples of variants of male specimens of *Vanewrightia kiesela* sp. nov., collected at pyrrolizidine alkaloid baits during the day in Panguana/Peru (PH), showing the surprisingly large range of variation within a single population, sorted according to the amount of yellow on the upperside wings; left upperside, right underside. Details on specimen codes in Table 2. Scale bar = 1 cm.

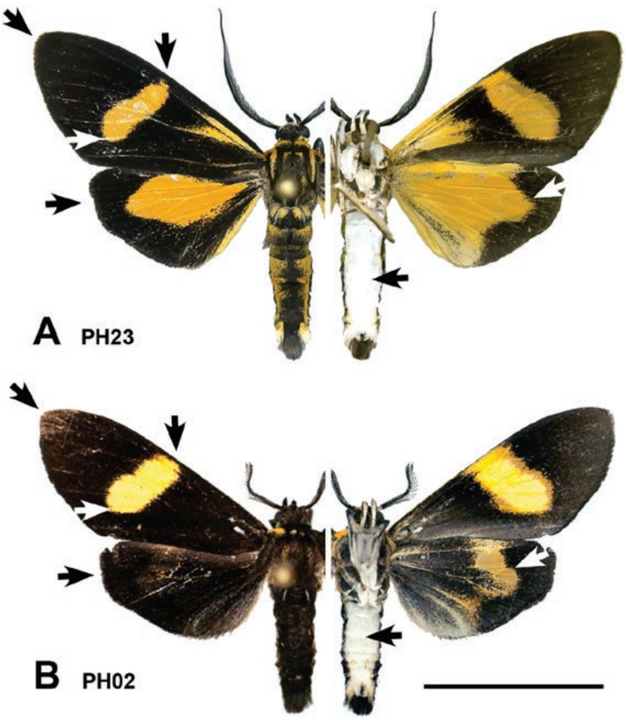

Fig. 3. Extreme variants of *Vanewrightia kiesela* sp. nov., arrows pointing to shared diagnostic characters; see text; left upperside, right underside. Details on specimen codes in Table 2. Scale bar = 1 cm.

below), 7.0 and 7.4%, respectively, distant to *Epidesma aurimacula* (BIN BOLD:AAP4004) treated below.

Variation. Wing pattern highly variable (see below and Discussion).

Biology. Adults are apparently not or only rarely attracted to light but in the daytime males visit sources of PAs (see Discussion).

Distribution. PERU, FRENCH GUIANA, BRITISH GUIANA, most likely also in VENEZUELA, BRAZIL (see below) and other Latin American countries.

Etymology. The new genus is named in honor of Richard I. ('Dick') Vane-Wright to acknowledge his numerous contributions to entomology and thanking him cordially for over 40 yr of friendship with and support of MB. (Dick has mainly published on butterflies—to dedicate to him the name of day-flying moths sharing pattern with several butterflies appears quite appropriate, and the variations between individual moths reflect the diversity of subjects he has treated.) The genus is considered to be feminine.

Vanewrightia kiesela Boppré sp. nov.

Figures 1, 2, 3, 5, and 6A–K

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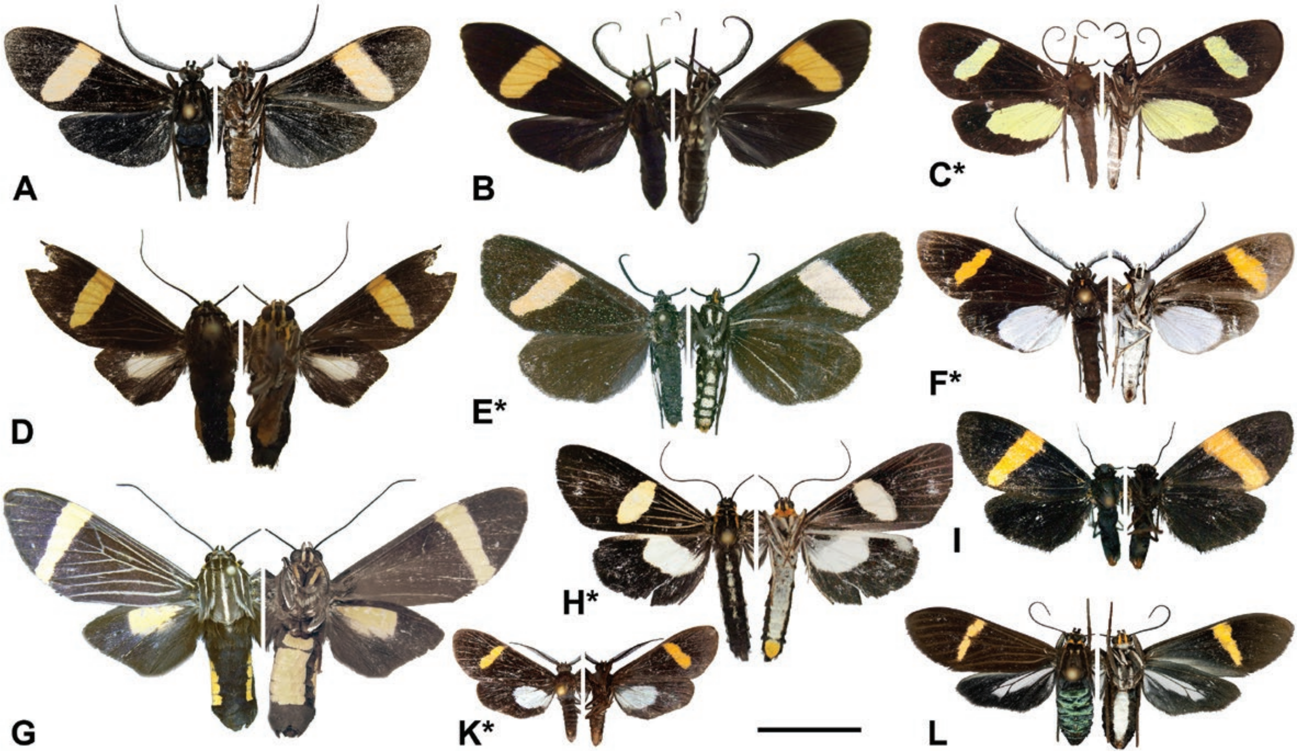

Fig. 4. Examples of arctiine and dioptine (*) species with a forewing oblique band co-occuring with *Vanewrightia kiesela* sp. nov. in Panguana/Peru, collected at PA-baits at night or at light, respectively (see also Fig. 12). They are potentially mistakable for *V. kiesela* but compare with Figs. 2 and 3 for differences in hindwing shape and position of forewing oblique band, missing yellow on hindwing undersides, etc.; left upperside, right underside. (A) *Loxozona lanceolata* (Walker, 1854). (B) *L. nitens* Rothschild, 1912. (C*) *Lyces flavissima* Walker, 1854. (D) *Oridishia klagesi* (Rothschild, 1909). (E*) *Erbessa ursula* (Hering, 1925). (F*) *Proutiella esoterica* Prout, 1918. (G) *O. rutilus* (Stoll, 1782). (H*) *Erbessa* sp. (I) *Antona* sp. (K*) *P. tegyra* Druce, 1899. (L) *Aclytia* sp. Note that all arctiines lack the angled hindwing margin. Scale bar = 1 cm.

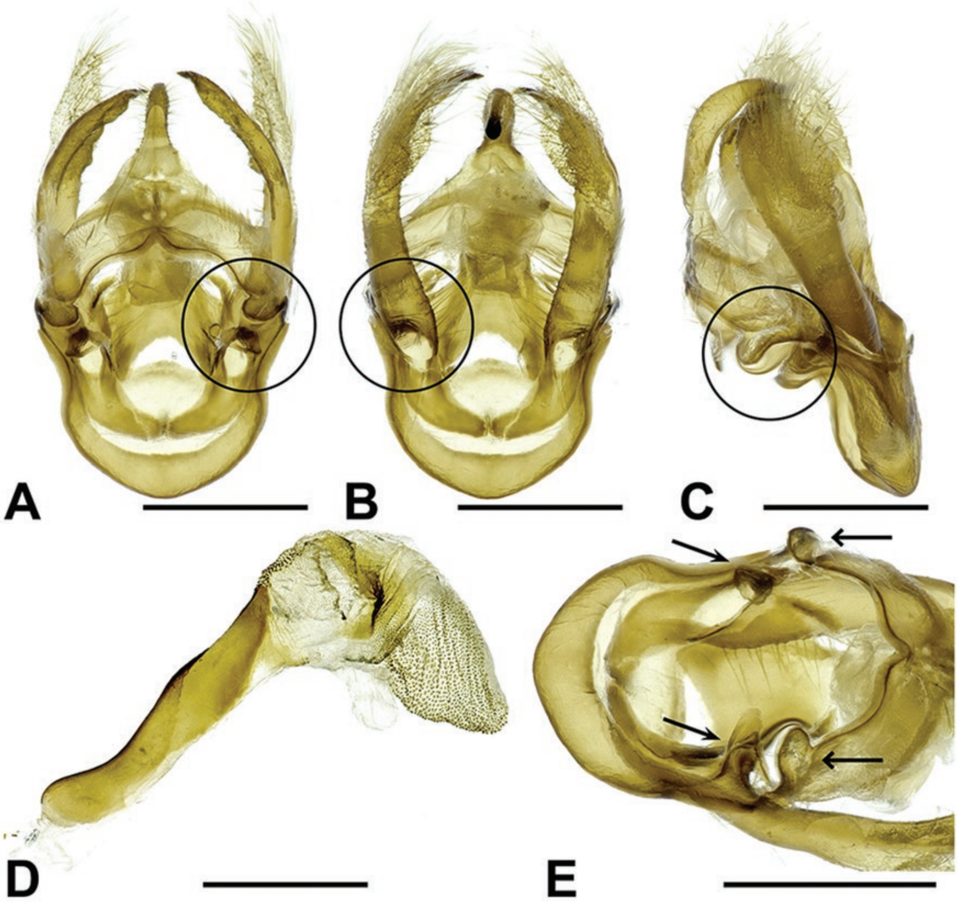

Fig. 5. Genitalia of the male holotype of *Vanewrightia kiesela* sp. nov. (PH23). (A) dorsal, (B) ventral, (C) lateral, (D) phallus, (E) peculiar process on tegumen near junction with valvae (encircled in A–C; arrows in E) enlarged. Scale bars = 1 mm.

Material Examined. PERU, 24 ♂♂ (Figs. 2 and 3; see Table 2: PH01–PH24); see also below.

Type Specimens. Specimen PH23 (Fig. 3A) is designated as the holotype and is, with four paratypes (conservatively selected from one cluster only; PH03, PH05, PH10, PH24), deposited at MUSM. Note that not all characters of the holotype are typical for the species.

Description. *Male*. HEAD AND THORAX. Antennae bipectinate, shaft and rami dark gray, the scape with a white patch frontally. Frons white, vertex black with vivid yellow scales anteriorly and latero-basally. Palpi white with a black lateral line on each side. Patagia yellow or black. Tegulae black, sometimes with a central longitudinal yellow band. Thorax black. LEGS. Coxae pure white. Legs pure white with a dorsal dark gray longitudinal band. ABDOMEN. Above, dirty yellow, irrorated with dark gray scales, a median dark band, the anal tuft gray-bordered on each side with an off-white hair brush. Venter entirely white or gray. FOREWINGS. Upperside deep black with pointed apex and the following pattern: an oblique yellow band at the end of cell starting in the middle of the wing just before costa and abruptly finishing on vein CuA_2, sometimes with an irregular yellow patch occupying the basal third, slightly speckled with black scales. Length: 13.5–15.0 mm (n = 13). Underside generally mirroring the pattern of the upperside but always showing some more yellow. HINDWINGS. Upperside vivid yellow or white, slightly paler on costal and anal area, with a wide black border from apex to tornus, or completely black. The bulge protruding distally from the yellow area into the black border centered on vein M_2, and the angled margin between veins CuA_1 and M_3 are diagnostic. Underside always with some more yellow or white as on upperside and extending to the inner margin. GENITALIA. Uncus long and narrow, slightly narrowed laterally at base and curved downward just before middle where it is larger in lateral view. Valvae moderately curved inwardly, slightly longer than uncus with a pointed and strongly sclerotized tip, slightly asymmetrical: the left one in ventral view slightly longer. A long translucent process covered with long hairs, reaching the tip of valvae. A triangular tooth pointing inside at the last third of valvae length. In lateral view the valvae are abruptly narrowed near extremity. Vinculum evenly rounded without any visible saccus. Juxta elongated, large at base and narrowing on top. Phallus cylindrical, slightly undulated, vesica with a unique scobinated process, a sclerotized thin bar more or less perpendicular to the main axis of the phallus. Variations: the vinculum varies from evenly curved as in the type to slightly angled and with or without a very small saccus (see also below).

Female. Unknown.

DNA Barcodes. In the neighbor-joining distance tree, the barcodes of the 18 specimens sequenced from Panguana form a cluster (BIN BOLD:ADO9441; Fig. 13), with subgroups with sequence divergence of up to 1.8%; the subgroups do not correspond with differences in wing pattern or locality.

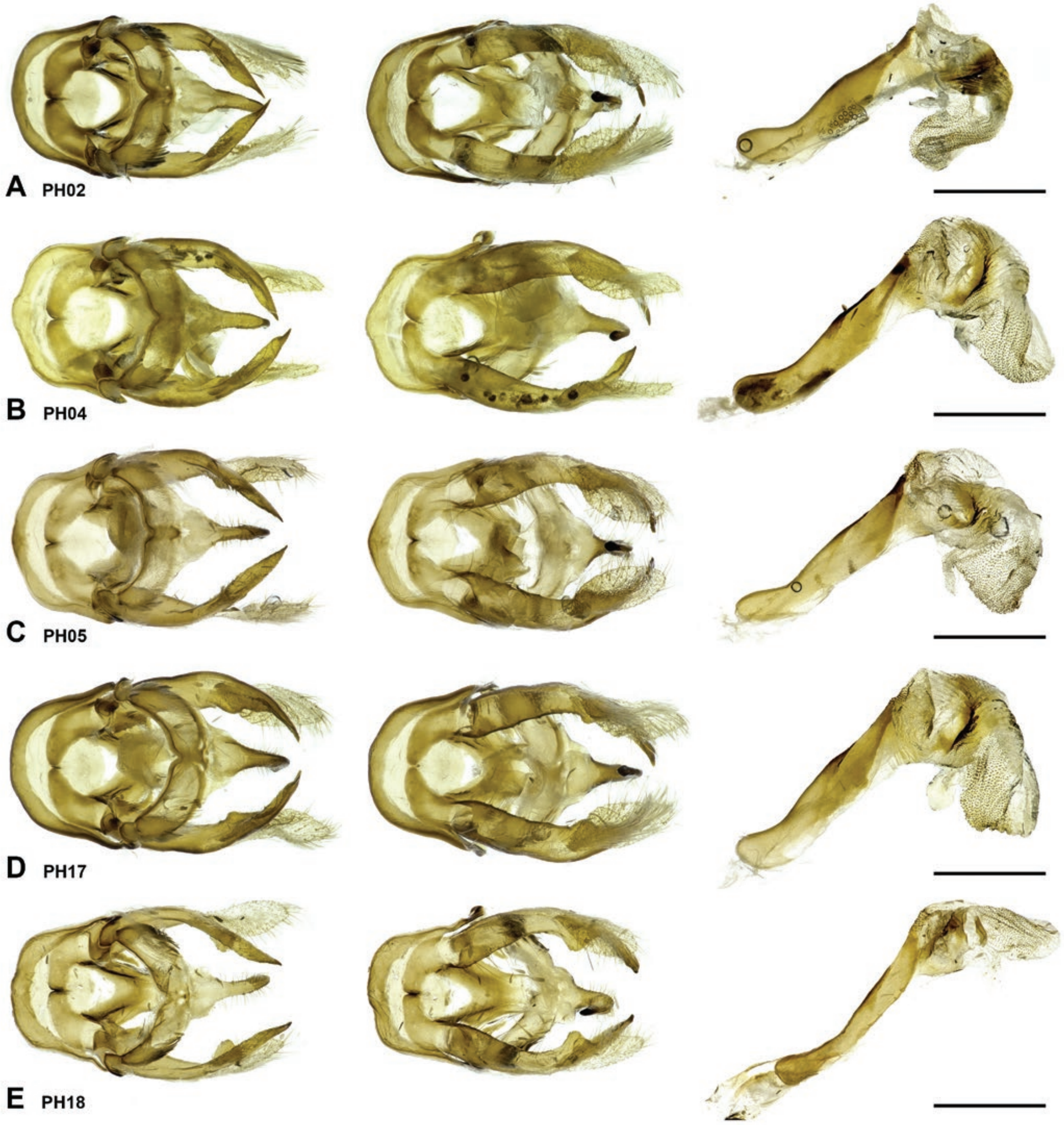

Fig. 6. (A–K) Male genitalia (dorsal, ventral, phallus) of a selection of specimens of *Vanewrightia kiesela* sp. nov. (see Figs. 2 and 3 for habitus). Details on specimen codes in Table 2. Scale bars = 1 mm.

Variation and Differential Diagnosis. The variation in appearance is striking (Figs. 2 and 3); whether or not we have seen all variants remains unknown—we assume that further variants are to be found. This makes a description as well as determination fraught with uncertainty and currently does not permit to give a robust differential diagnosis of *V. kiesela*. The existence of further specimens/species belonging to *Vanewrightia* (see below) increases the problem which is reviewed in Discussion.

Three kinds of variants, each variable, can be recognized: 1) forewings black, basally with some yellow in addition to yellow band, hindwings with some yellow or white within black margin, 2) forewings black with yellow band, hindwings with some yellow or white within black margin, 3) forewings black with yellow band, hindwings entirely black. A fourth kind (forewings with ± yellow in addition to yellow band, hindwings black) might be expected but has not been found. See Discussion for a parallel in *Chamaelimnas* butterflies.

Similar-Looking Species. Not only closely related (see below) but also several *un*related moth and butterfly taxa, which resemble morphs of *V. kiesela* to a more or less high degree are considered in Discussion.

Biology. Largely unknown. Males are diurnal and attracted to sources of pyrrolizidine alkaloids (= PA-pharmacophagous) but not or only very rarely to artificial light.

Distribution. PERU, Huanuco and other regions, most likely also in other Latin American countries (see below).

Etymology. The new species is dedicated to Anita Kiesel who assisted in a more than commendable way in MB's laboratory for over 30 yr; the extra miles she went were always greatly appreciated and her work is acknowledged with cordial thanks.

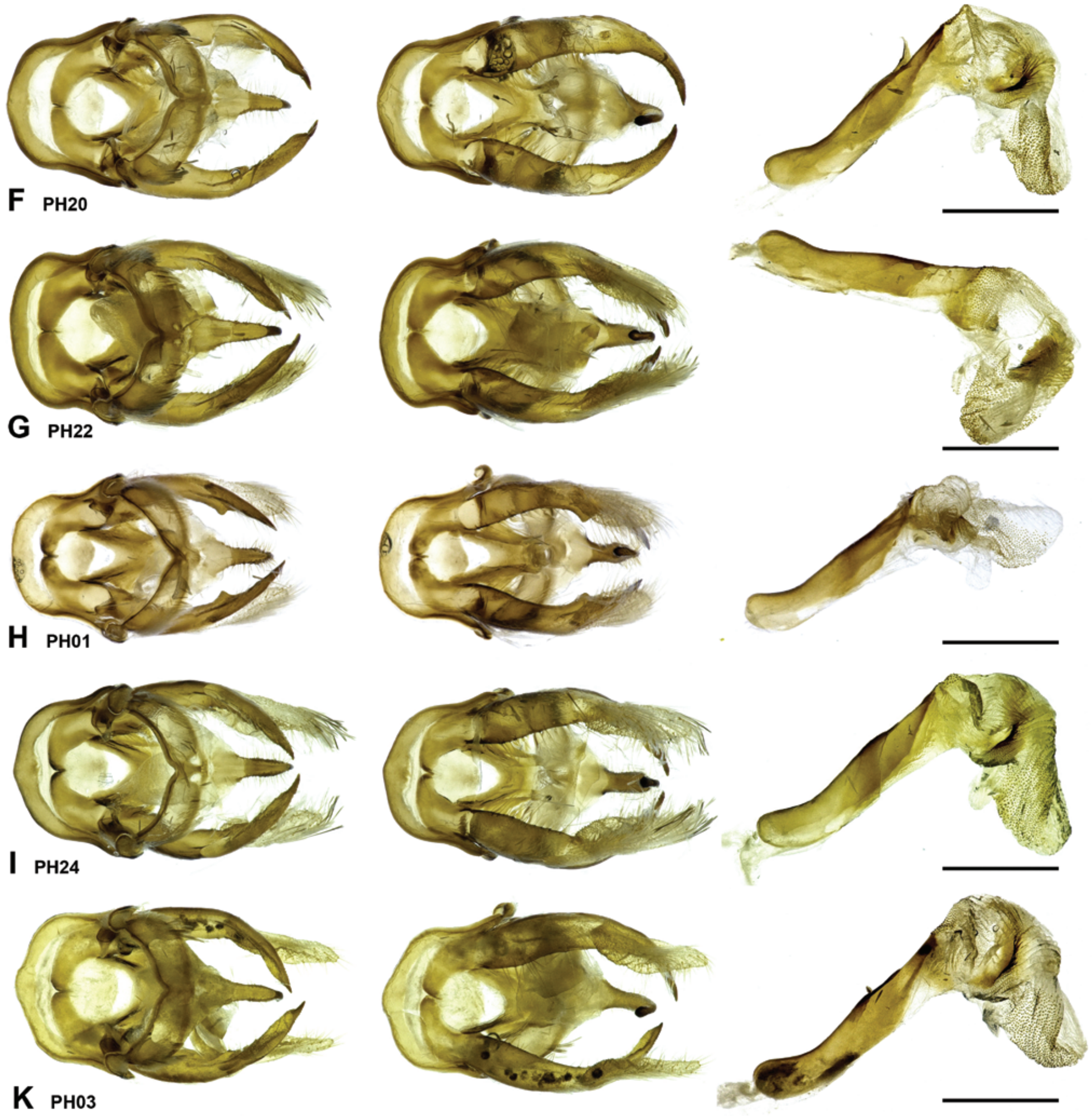

Fig. 6. Continued.

Vanewrightia sp. nov., aff. *kiesela* Boppré

Barcoding has revealed two specimens 3.8% distant from *V. kiesela*—but almost identical in appearance—which have received BIN BOLD:AEA5711 (Fig. 13). For reasons given above, we postpone to formally name this operational taxonomic unit until more specimens are available for an adequate description.

Vanewrightia subflavescens (Kaye, 1911) comb. nov.

Figure 8A

Napata subflavescens Kaye, 1911: 143 (1 ♂). **Type locality:** BRITISH GUIANA. **Type depository:** McGuire Centre for Lepidoptera & Biodiversity, Gainesville, FL.

Napata subflavescens—Hampson (1914: 261, pl. XIV, f. 19); Draudt (1915: 140, pl. 29c); Cerda (2017: 153).

Uranophora subflavescens—Beccaloni et al. (2003). Following Grados (1999: 11–12), some authors have included species formerly placed in *Napata* Walker, 1854, in the genus *Uranophora* Hübner, [1831]. However, formal justification of this synonymy is wanting, and the type species differ considerably. Cerda (2017: 134) has separated the two genera on the basis of male genitalia.

Comments. *Napata subflavescens* is a small dark moth with a yellowish oblique band on the forewing. This band, clearly enlarged in the center, goes from costa where it is wide to tornus where it is narrow. The hindwing is angled, and the underside of the hindwing has the characteristic pattern of *Vanewrightia*, i.e., a basal yellowish patch with a bulge protruding into the wide dark border on the wing. In contrast to *V. kiesela*, the basal patch is restricted to the costal half of the wing, being extensively sullied with dark scales on the anal half. It is not known if there is intraspecific variation.

Potentially, *V. subflavescens* is a variant of *V. kiesela*. However, there is nothing to support this idea because the only available specimen exhibits a unique pattern not seen in *V. kiesela* (see also Discussion). Definitely it does not belong to *Napata* or *Uranophora*

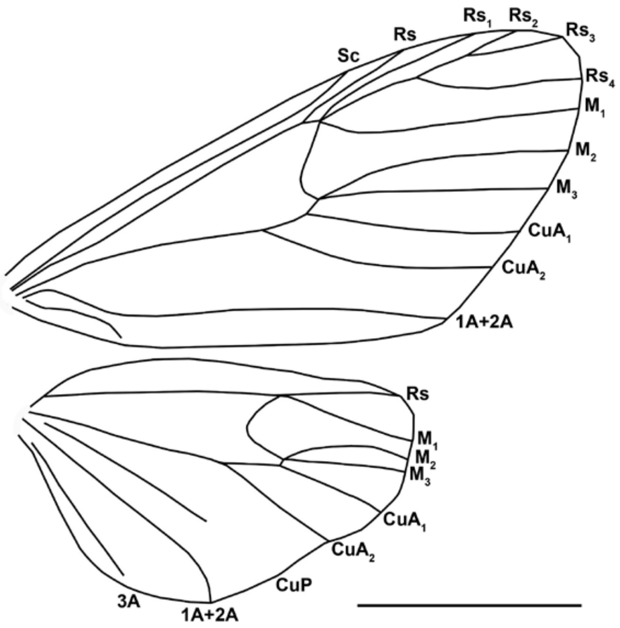

Fig. 7. Wing venation of *Vanewrightia* gen. nov. Scale bar = 1 cm.

but to *Vanewrightia* because the male genitalia differ extensively from both *Uranophora* and *Napata* (see Cerda 2017: 133, 143).

Vanewrightia patawaensis (Cerda, 2017) comb. nov.

Figure 8B and C

Loxozona patawaensis Cerda, 2017: 152, Pl. 4, fig. 14 (1 ♂). **Type locality:** FRENCH GUIANA. **Type depository:** private collection of J.-A. Cerda, French Guiana.

Comments. Described from a unique male collected by day at flowers near Camp Patawa in French Guiana. The species is clearly similar to the holotype of *V. kiesela* (Fig. 3A) especially on the underside; it is not known if there is intraspecific variation. The oblique yellow band on the forewing is slightly longer, reaching vein 1A+2A instead of CuA$_2$, there is no basal patch but only some very faint yellowish lines along the veins. On the hindwings, the only visible pattern is a complex network of faint yellowish lines and scales in and around the cell; hindwing uppersides greatly resemble a specimen from Venezuela (VE03; cf. Figs. 8B and 11C; see Discussion). The head, patagia, tegulae, and thorax are largely dark with only faint yellow lines; the abdomen is dark gray with some yellowish hairs. Beneath, the palpi are orange-yellow not white. The white abdomen is bordered by a row of yellow hairs on each side. On the forewings, the basal patch is reduced to some whitish and yellow streaks, and on the hindwings, the yellow basal area is crossed by four narrow, blackish bands: one at the anal border, one anterior to vein 1A+2A, one in the cell and one just posterior to the costa. The yellow area is scattered with blackish scales. In the male genitalia (Fig. 8C), the valvae are longer, clearly extending beyond the tip of the uncus, their extremities abruptly narrowed in the last third and the tip acutely pointed. In lateral view, the extremity has a dorsally bent spoon-shape, and the uncus is evenly curved without any widening. The vinculum is angled with a small saccus. The process of the vesica has a clear, sclerotized bar more or less in continuous with the phallus.

Potentially, *V. patawaensis* is a variant of *V. subflavescens* and/or *V. kiesela*; however, currently, there is no objective reason for any such assumption (see Discussion). Definitely, it does not belong to *Loxozona* but to *Vanewrightia* because the male genitalia are similar to *V. kiesela* and very different from *Loxozona*, and the pointed forewing apex differs from the rounded forewing in *Loxozona* which in turn always displays a completely unmarked hindwing underside.

Supplementary Specimens of *Vanewrightia* gen. nov.

In four collections, we have found further specimens that originate from habitats outside Panguana and are definitely *Vanewrightia*. Here, we document and briefly characterize them without a formal attribution of specific names (see Discussion).

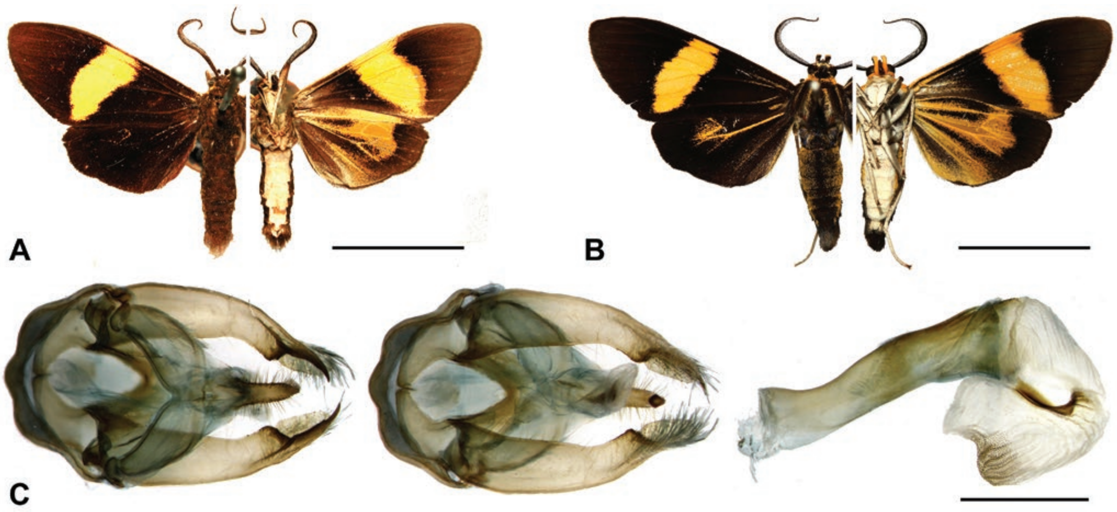

Fig. 8. Holotypes of (A) *Napata subflavescens* Kaye, 1911 and (B) *Loxozona patawaensis* Cerda, 2017, both here transferred to *Vanewrightia* gen. nov.; left upperside, right underside. (C) Genitalia (dorsal, ventral, phallus) of *V. patawaensis*. Courtesy of B. Hermier (A) and J.-A. Cerda (B); (B, C) from Cerda (2017). Scale bars = (A, B) 1 cm, (C) 1 mm.

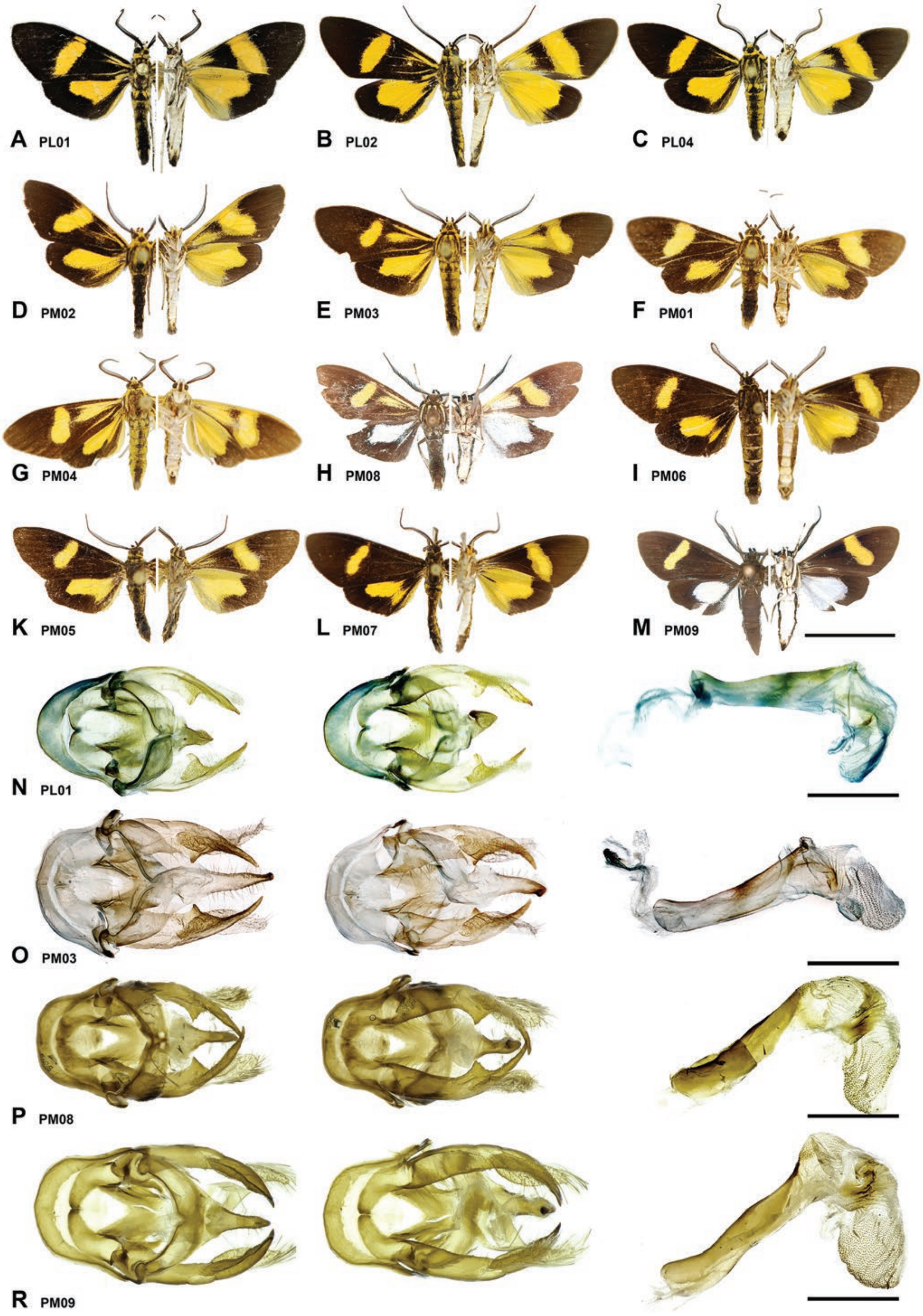

Fig. 9. (A–M) Male specimens of *Vanewrightia* gen. nov., collected at pyrrolizidine alkaloid baits in the daytime in Peru but in habitats other than Panguana (see Fig. 2); left upperside, right underside. (N–R) Male genitalia of selected specimens; dorsal, ventral, phallus from left to right. Details on specimen codes in Table 2. Scale bars = (A–M) 1 cm, (N–R) 1 mm.

Specimens from Peru

Thirteen specimens collected in Loreto and Madre de Dios, respectively, deposited in MUSM and SNSB (Fig. 9A–M, Table 2: PL01–PL04, PM01–PM09), share basic characters with *V. kiesela* from Panguana and add to their diversity in appearance. PM08 and PM09 have a white (not yellow) hindwing pattern, PM09 does not clearly show the typical bulge on the underside of the hindwing, and the genitalia show some variation. In the specimens from Loreto (PL01–PL04), the forewing oblique band extends to vein 1A+2A and their genitalia vary slightly: the saccus is rounded, the anterior part of the tegumen is narrower, and the leaflets are more arched, while in *V. kiesela*, the saccus is somewhat truncated, the tegumen is wider, and the valves less arched. Nevertheless, all were caught at PA-baits and DNA barcodes of selected specimens fit with *V. kiesela* (Fig. 13). The branching within BIN BOLD:ADO9441 does not reflect the origins of the specimens, rather those from Panguana and Madre de Dios are interspersed; the specimens from Loreto are separated by 1.3% from the main *V. kiesela* cluster.

Specimens from French Guiana

From French Guiana we have seen three specimens (Fig. 10; Table 2: FG01–FG03), also collected in the daytime at PA-baits, which are very similar to the holotype of *V. kiesela* but do not show variation. In comparison with *V. kiesela*, on the forewings the oblique yellow band ends at vein 1A+2A not at CuA_2. The basal yellow patch is almost absent, reduced to a small elongated patch at the base of anal border and a blurred elongated triangle below costa, this triangle is fused with the oblique band which is sharply bent at right angle near tornus. On the hindwings, the basal yellow area is reduced due to the presence of a blackish band along the costa and along the anal border which is narrowly yellow on margin. The head, patagia, tegulae, and thorax are markedly darker. The venter is not pure white but interspersed with yellow hairs. On the underside of the forewings the anal border is blackish, compared with yellowish white in *kiesela*. On the underside of the hindwings, the basal area is not pure yellow, but there are two streaks of blackish scales, one along the anal border and one below the costa, near the base. Forewing length ca. 14 mm. Female unknown.

The genitalia of FG02 (Fig. 10D) exhibit small differenes to *V. kiesela*: in ventral view, the valvae appear narrower and smoother. In lateral view the uncus is widened after the middle not before. The juxta is wider at base, shorter, and much more constricted in the middle. In lateral view, the last third of the valvae seems different, the phallus is more sinuate, and the sclerotized area has a different shape. DNA barcodes of FG01–FG03 form a subcluster of *Vanewrightia* (BIN BOLD:ADO9441), with a barcode gap of 1.0–1.1% to the main *V. kiesela* cluster and 1.8% to specimens from LO (Fig. 13).

Specimens from the NHMUK

In the NHMUK, several individuals (for examples see Fig. 11, Table 2: VE01–VE05, BR01–BR06) resembling one or the other variants of *V. kiesela* from Peru were found; they either carry no name label or are treated as *Epidesma obliqua* (Schaus, 1898). Without dissection or sequencing eleven specimens can be allocated to *Vanewrightia* and divided into three groups: group A contains five specimens (Fig. 11A–E, Table 2: VE01–VE05) from Venezuela (Caura Valley), group B contains five specimens (see Fig. 11F–K, Table 2: BR01–BR05) from Brazil (Pará and Rondonia), and group C with one specimen (Fig. 11L, Table 2: BR06), also from Brazil (Amazonas).

Group A is characterized by a deep oblique yellow band on the forewing upperside and a yellow central patch on hindwings displaying the characteristic bulge around vein M2. On the forewing underside, the oblique band is slightly longer and wider and there is a whitish streak basally, whereas in one variant on the hindwing the basal area is large, milky-white, with the characteristic bulge. The species is variable and on the hindwing underside the basal area can be white only in the anal half or the milky-white area is largely suffused with dark scales. On the hindwing upperside, the yellow basal area can be reduced to a small patch or totally absent.

Group B is more similar to the French Guiana entity with a longer and wider oblique yellow band and a basal area with yellowish lines on veins. The yellow patch on the hindwing is largely bordered by black but displays the characteristic bulge. On the underside, on forewings, the basal area is yellow separated from the oblique yellow band by a large black band, and on hindwings, there is a large yellow

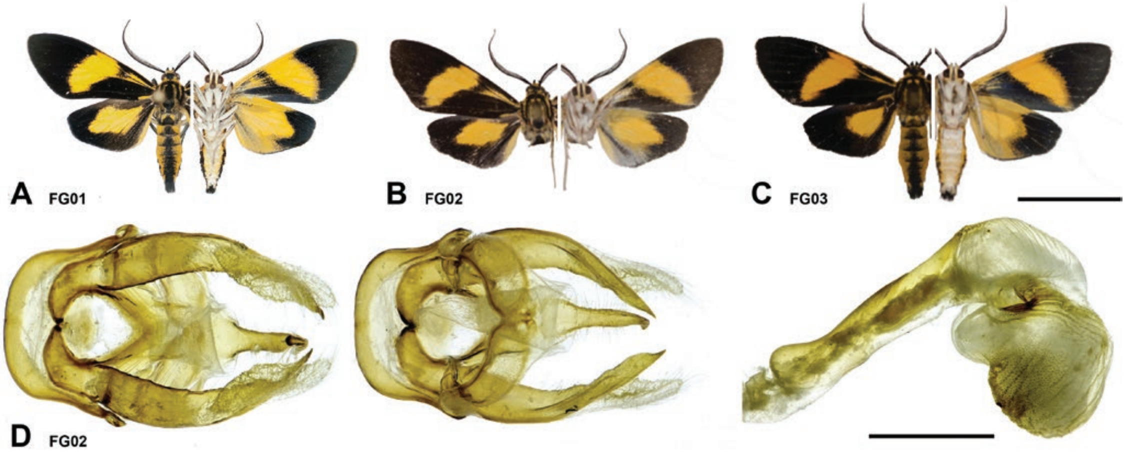

Fig. 10. (A–C) Male specimens of *Vanewrightia* gen. nov., collected at pyrrolizidine alkaloid baits in the daytime in French Guiana (courtesy of Robert Vande Merghel); left upperside, right underside. (D) Male genitalia of FG02; dorsal, ventral, phallus from left to right. Details on specimen codes in Table 2. Scale bars = (A–C) 1 cm, (D) 1 mm.

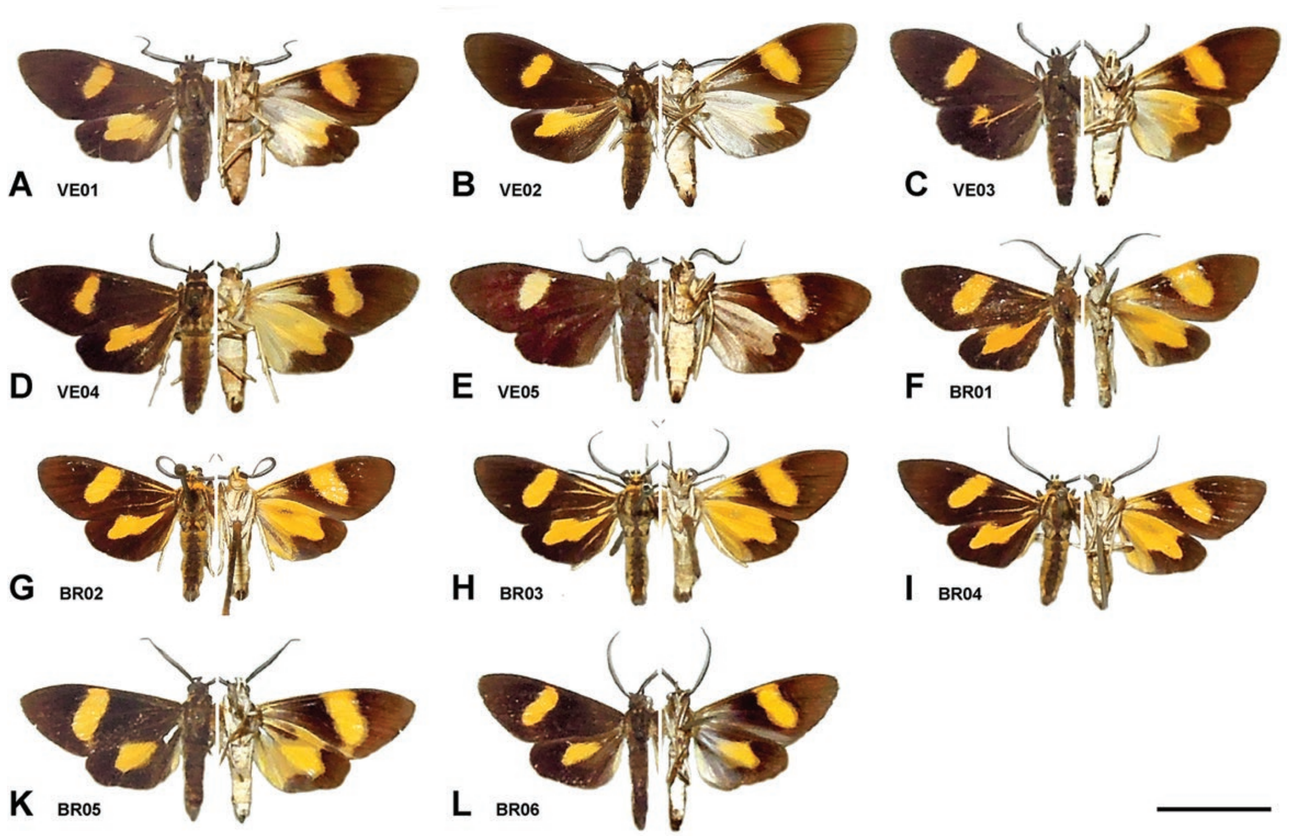

Fig. 11. Examples of unnamed moths housed in the NHMUK and showing characters typical for *Vanewrightia* gen. nov.; see text; left upperside, right underside. (A–E) Group A (D is mirrored because the specimen misses the left forewing). (F–K) Group B. (L) Group C. Details on specimen codes in Table 2. Photographs by Trustees of the Natural History Museum, London. Scale bar = 1 cm.

area bordered by black from apex to near tornus, sometimes with faint blackish streaks.

Group C seems divergent with respect to the anal border area of the hindwing underside, which is largely suffused with white.

Epidesma aurimacula (Schaus, 1905)

Figure 12A–F

Trichodesma aurimacula Schaus, 1905: 190. **Type locality:** VENEZUELA, Caura Valley. **Type depository:** holotype in National Museum of Natural History, Washington, DC; type number 8504.

Desmotricha aurimacula—Hampson (1914: 279); Zerny (1912: 129, 1931: 20); Draudt (1915: 155); Travassos (1938: 43).

Epidesma aurimacula—Cerda (2017: 165).

Trichodesma parva Rothschild, 1912: 158. **Type locality:** (VENEZUELA) Maripa, Caura River. **Type depository:** Holotype in NHMUK. **syn. nov.**

Desmotricha parva—Hampson (1914: 278); Draudt (1915: 155); Travassos (1938: 44).

Epidesma parva—Cerda (2017: 167).

Comments. *Epidesma aurimacula* (Fig. 12A and D–F) and *E. parva* (Fig. 12B and C) differ in the expression of the oblique yellow forewing band and, in particular, in their hindwing pattern which is completely black in *E. parva* but exhibits a white or yellow central patch of variable size on both upper- and underside in *E. aurimacula*. Fine white or yellow crosslines on the upperside of the abdomen separate the segments clearly. Their genitalia are identical (Fig. 12A and B) and sequences of specimens with either pattern from Peru, French Guiana, Columbia, and Brazil form BIN BOLD:AAP4004 (Fig. 13). Therefore, we propose *E. parva* to be a junior synonym of *E. aurimacula*.

Epidesma aurimacula thus is another polymorphic species that visits PA-baits (personal observation). As in *V. kiesela*, its delimitation cannot finally be given because the full range of variation remains unknown. Perhaps, further species, e.g., *E. albicincta* (Hampson, 1905) and *E. josioides* (Zerny, 1931) are synonyms for *E. aurimacula* (their hindwing shapes might be an indication), but this can only be clarified by barcoding.

One might argue, *E. aurimacula* should be treated as *Vanewrightia*, or *V. kiesela* and *V.* sp. nov., aff. *kiesela* as *Epidesma*; this issue is discussed below.

Vanewrightia gen. nov. versus *Epidesma* Hübner, [1819]

Establishing *Vanewrightia* does not resolve *Epidesma* appearing as a polyphyletic genus like many other genera in the current taxonomy of Arctiinae; *Epidesma* is in need of a thorough revision.

A common denominator of all *Epidesma* is an oblique forewing band, a character that *Epidesma* shares with many other moths and butterflies (see Discussion). Having found highly variable taxa (see above) and realizing that the currently recognized species of *Epidesma* are very similar in appearance renders their status doubtful. Because the full range of pattern variation is not yet known (in *V. kiesela* and *E. aurimacula* and, perhaps, further

Fig. 12. Selection of species of *Epidesma* to demonstrate their variation and similarity with respect to wing pattern versus male genitalia. (A–F) *Epidesma aurimacula* syn. nov. from Panguana/Peru (A, B), from French Guiana (C, D), from Bolivia (E), from Venezuela (F). (G) *E. klagesi*. (H) *E. ursula* from French Guiana. (I) *E.* sp. nr *ursula* from Costa Rica. (K) *E.* sp. nr *klagesi* from Costa Rica. (L) *E.* nr *crameri* from Peru. (M) Recently transferred from *Epidesma* (Laguerre 2019): *Aphymolis similis*; left upperside, right underside; genitalia dorsal, ventral, phallus from left to right. Scale bars = 1 cm for moths, 1 mm for genitalia. See also Fig. 4.

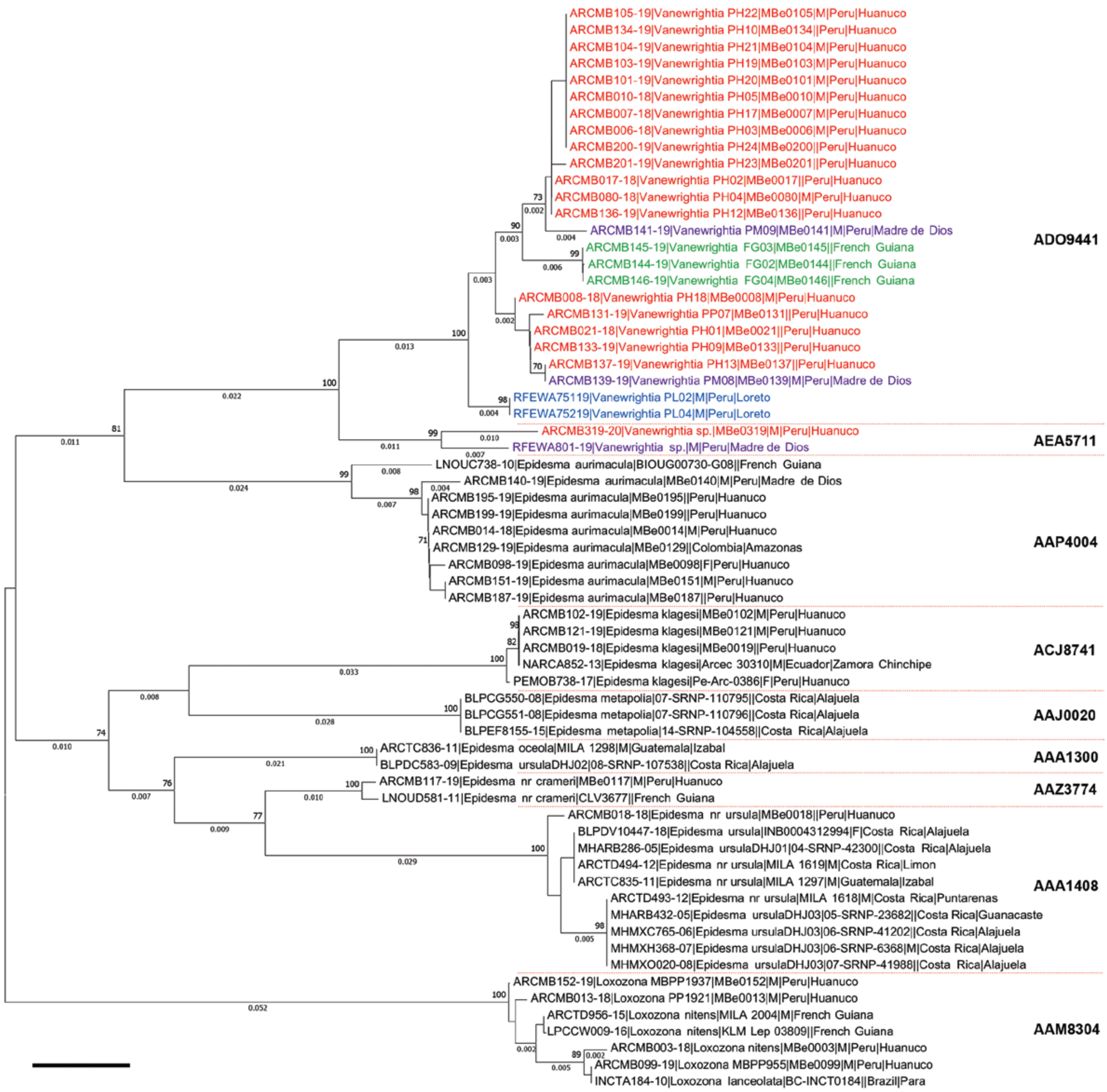

Fig. 13. Neighbor-joining distance tree of 27 COI sequences of *Vanewrightia* gen. nov. and 38 of its neighbors from BOLDSYSTEMS (2019) with BIN BOLD codes. Distances (normalized to 1) are given below each branch (omitted if <0.002) and bootstrap supports above each branch (in bold, only if >70%) obtained with MEGA7 (Kumar et al. 2016). For *Vanewrightia*, the collection sites are highlighted by colors. Scale bar = 1%.

Epidesma), only with large series of specimens, of which genitalia and DNA sequences are available, can the long-outstanding revision of *Epidesma* be achieved.

The BOLD database (BOLDSYSTEMS 2020) currently houses sequences of 230 specimens (167 from Costa Rica) of *Epidesma* given 42 names; only six BINs are public which include seven names. FUNET (Savela 2020) currently recognizes 15 species of which two have to be omitted (*E. similis* is now in *Aphymolis* (Laguerre, 2019) and *parva* = *albimacula*, see above). The name of the type species, *Epidesma ursula* (Stoll, [1781]), appears in three BINs, but likely none represents *E. ursula* s.str. Notably, there is no new species description in this genus for the past 90 yr. The old descriptions were made quite superficially, all species greatly resemble each other, and only Travassos (1938) and Cerda (2017) provided drawings of genitalia (of *E. ursula*, *E. klagesi*, *E. aurimacula*, and *E. crameri* only). Figure 12 documents the variation and similarity with respect to wing pattern versus male genitalia for some species of *Epidesma* available to us.

In conclusion, the polyphyly of *Epidesma* cannot be resolved at present. In particular, the knowledge on variation in *Vanewrightia* and *E. aurimacula* documented here makes it likely that there are further species with more or less intraspecific variation and questions if all currently recognized species are valid. To provide meaningful characters to delimit species morphologically (and eventually for characterizing genera), genitalia and barcodes of many specimens from many localities are required for both *Vanewrightia* and all *Epidesma*. While this is a demanding prospect, it is now clear that the 'ctenuchines with an oblique forewing band' are not only taxonomically challenging but also very interesting, even more so when considering ecological aspects (see below).

Discussion and Perspectives

Our documentation of striking intraspecific variation in these Neotropical moths sheds new light on a long-standing taxonomic problem. While we recognize, (re-)describe and include three species in *Vanewrightia* gen. nov., and document further specimens that belong to this genus, in particular from Venezuela (VZ01–VZ05) and Brazil (BR01–BR06; Fig. 11; Table 2), which are very similar to *V. kiesela* but perhaps not identical, several issues remain uncertain or open. Because of the limited material and missing details, DNA barcodes in particular, robust species delimitations cannot be given at this point, and we conservatively refrain from formally naming all currently available specimens, even though some almost certainly do belong to this species. Also, without a robust idea of the geographical distribution of *Vanewrightia* and frequencies of its variants, it would be idle speculation to consider subspecies or other concepts. For a final statement on variation in male genitalia, more specimens are also required.

Specimen VE03 (Fig. 11C; Table 2) is a good example of the taxonomic problem: does it belong to *V. patawaensis* (Fig. 8B) or is it instead a member of *Vanewrightia* group A, or do they both represent variants of a single species? It definitely belongs to *Vanewrightia* but to which species remains open until more information on members of *Vanewrightia* and the range(s) of their intraspecific variation becomes available. The study of further specimens very likely will entail a modification of the characterization of the genus *Vanewrightia* and its currently recognized species. For the time being, objective reasons to differentiate the specimens under discussion further, or to lump them, are lacking. Actually, it cannot be ruled out that *V. kiesela* represents variants of *V. subflavescens* and/or *V. patawaensis*. Since both of these previously named species are based on poor descriptions and only a single individual each—which we are currently unable to study further—are known and also quite few specimens of *Vanewrightia* are available altogether, we have no arguments to lump them. While it could be the case that all the names and specimens represent variation within a single species, currently no facts (diagnostic characters) exist to justify synonymizing *V. patawaensis* with *V. subflavescens*, and placing all the specimens considered in our study under *V. patawaensis* does not seem a helpful option. Therefore, in our view, the only way to resolve this issue of intraspecific variation is to retain existing nominal taxa, and add a new species even if this may eventually prove to be a junior synonym. This dilemma will persist until a thorough revision of *Epidesma* becomes possible (see above).

While day-activity and attraction to PAs initially helped to recognize *V. kiesela* and seem to be a diagnostic character of *Vanewrightia*, we do not know anything regarding the biology of the specimens found at the NHMUK. Unfortunately, most of their labels do not provide information on the circumstances of their collection. From our experience, we assume all were collected in the daytime. Of the SMNK and SNSB material, the respective collectors told us that they employed PA-baits as well as light, but, most unfortunately, the specimens were not labeled, respectively, and thus it can only be said that most likely they were collected during the day and at PA-baits. According to their labels PH05 and PH18 were collected at light but we assume that these are a mix-ups since PA-baits were also used during the collection period. To have found them at light would be very surprising; if *Vanewrightia* would be attracted by light, then more specimens would be available in collections.

Specimens of *Vanewrightia* seem to be very rare in collections, likely because they escaped collectors by their diurnal activity and nonvisitation to artificial light; some may escape detection in collections due to previous sorting according to similarity and disassociation. We have to mention that we have specifically searched for *V. kiesela* in Panguana for several months but did not find many specimens; it seems to be a rare species in Panguana at least. A label on a *Vanewrightia* from Pará says 'com. on fed' (BR03: Table 2); if that means common on fedegoso (= vernacular name for *Heliotropium*), then it would mean that it was collected at *Heliotropium* and also that there was a large population. Remarkably, this and some additional specimens at the NHMUK (BR02–BR04) were collected by A. Miles Moss, an entomologist who published on *Heliotropium* as an attractant (Moss 1947) but without knowing about PAs.

Similarity of *Vanewrightia* with Unrelated Taxa

Identifying *Vanewrightia* species based on their appearance is doubly challenging: on the one hand, because of the great intraspecific variation a demarcation of the species has much uncertainty, on the other hand, because they can easily be confused with very similar-looking species in the same moth community (see Figs. 2, 4, and 12). Examining a large collection such as the NHMUK greatly increases the challenge and the confusion: not only are there many Arctiinae but also Notodontidae (Dioptinae) and others with the same general wing pattern; several *Erbessa* (Dioptini) species exhibit an angled hindwing margin (see Miller 2009: plate 4), a main diagnostic character of *Vanewrightia*. Specimen BR03 (Fig. 11H) was misidentified by Moss as *Myonia desmotrichoides* Hering, 1925, a species later put into *Erbessa* and for a long time considered likely to be an arctiine (Miller 2009: 149).

Even more striking is the similarity of some *Vanewrightia* variants (Figs. 2Q and 9M) with *Erbessa tegyroides* Miller, 2009: 169, plate 4, a peculiar notodontid (Dioptini) that is also day-active, in which the males have yellow hindwings and the females white hindwings. According to Miller (2009: 869), it forms a mimicry ring with *Proutiella tegyra* Druce, 1899 (Fig. 4K), E*phialtias abrupta* Hübner, [1809] (Josiini), *Ordishia klagesi* (Rothschild, 1909; Fig. 4D; Arctiinae), and a diurnal pyralid, *Nachaba* sp. (Chrysauginae); *P. esoterica* (Prout, 1918; Fig. 4F) would also fit (Miller 2009: 684).

Chamaelimnas briola Bates, 1868 (Riodinidae: Riodininae: Riodinini) requires particular consideration. This butterfly occurs in a variety of forms (Fig. 14), is discussed as a mimic of some moths (Seitz 1916), and demonstrates a striking parallel to *Vanewrightia*. However, it is not that the similarity is particularly accurate, rather *Vanewrightia* and *Chamaelimnas* appear to show variation in the very same pattern elements (see above) although instead of a yellow forewing band *Chamaelimnas* has a more or less yellow dot. In Panguana, a habitat of *Vanewrightia* where no specific search for *Chamaelimnas* has yet been undertaken, four variants of *C. briola* have been collected. Seitz (1924: 655) commented on the genus: 'The shape of the yellow spots differs at every habitat and is so characteristic that one can exactly see from it, whether a specimen of the genus has been captured on the Corcovado near Rio, or in the Serra do Mar near Santos, in Espiritu Santo or in Blumenau'. This means that *C. briola* has different patterns in different populations and is comparable with the many cases of geographic variation within a species. However, Stichel (1928) has heavily (and sarcastically) opposed this statement. If Stichel (1928) is right, *Chamaelimnas* would—just like

Vanewrightia—show high variation *within* a population. This issue, unfortunately, has not been properly addressed in the past 90 yr and *Chamaelimnas* remains an understudied taxon, too. However, from Ecuador there is evidence that different forms do co-occur (Fig. 14).

Other, equally understudied taxa also fit into the discussion: species of *Seirocastnia* (Agaristinae) and *Cyllopoda* (Geometridae) show a similar pattern to some variants of *Vanewrightia* and to *Chamaelimnas*, perhaps also exhibiting intraspecific variation but not yet studied.

Pattern-forming processes and intraspecific differences in wing pattern are gaining considerable interest in Lepidoptera (see, e.g., Nijhout 2003a,b; Joron et al. 2006; Nadeau 2016; Gawne and Nijhout 2019). Both *Vanewrightia* and *Chamaelimnas* appear to be potentially interesting taxa for the study of evolutionary developmental biology.

'Mimetic' Relationships

Here is not the place to discuss mimicry in Arctiinae in any detail. However, a few remarks need to be made. Without a doubt, some Arctiinae are obviously and quite plausibly involved in mimicry, including *Chetone* (Pericopina) and Heliconiinae (Elias and Joron 2015) or wasp-like Ctenuchina and Hymenoptera (Vespidae; Simmons 2009; Boppré et al. 2017 and references therein); these examples to not permit or suggest much generalization. For most species with similarities to unrelated taxa, plausibility can be challenged; where mimicry has been suggested for Arctiinae, it is usually unknown which is profitable or unprofitable prey, respectively, and who or what is the selecting agent. Neither has it been adequately demonstrated that putative models and (co-)mimics live together, or which characters are relevant for antagonists. In an ecological context, all can be very different to those aspects that taxonomists perceive or consider.

For many species assumed to form mimicry rings, one also has to consider if they simply protect themselves *via* crypsis or masquerade (see Boppré et al. 2017: table 2). Perhaps, an oblique yellow band, which has convergently evolved in many moths and butterflies worldwide, is a cryptic or disruptive pattern, making both day- as well as night-active Lepidoptera difficult to detect when at rest. Note that while many of the taxonomically diverse species discussed here on close inspection exhibit some differentiating characters or not, when the moths sit at rest, most are invisible. Note that to a predator the only visible pattern element is a yellow band on a dark brown background (Fig. 15). Similarities observed in moths differ from classical cases of mimicry and seem more complex than the famous textbook examples on butterflies. In either case, the great similarities of taxa often mislead taxonomist and are an issue in need for investigation by ecologists dealing with prey–predator relationships. Polymorphism and variation, particularly in aposematic species, add to the complexity (see Briolat et al. 2019).

Conclusions

In view of the striking variation within *V. kiesela* and a limited number of specimens, the message of our paper, unfortunately, is not and cannot be to clarify fully the systematics of this taxon and its relatives but to make field-collectors as well as museum curators aware of the phenomenon and interesting questions behind it. This also holds true for all *Epidesma*.

Baiting with PAs in Latin America is not only rewarding with respect to *Vanewrightia* and *Epidesma*—with this method we are finding several other new species in the Neotropics (Grados 2004; M.L. and M.B., unpublished data) as we did previously in the Old World (e.g., Häuser and Boppré 1997; Scherer and Boppré 1997; see Boppré and Monzón 2020).

Fig. 14. Variants of *Chamaelimnas briola* Bates, 1868 (Riodinidae: Riodininae: Riodinini) from Sangay National Park, Ecuador, sorted according to the amount of yellow on the upperside wings (reproduced with permission from Petit 2019; re-arranged). Compare the variation in pattern elements of this butterfly with those of *Vanewrightia* (Figs. 2, 9, 10, and 11). Natural size 29–33 mm.

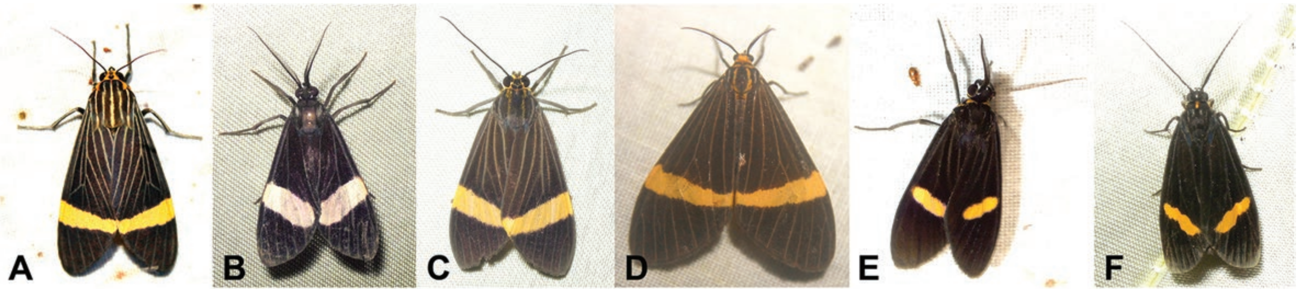

Fig. 15. Small selection of moths from Panguana with an oblique forewing band (see Fig. 4), photographed in resting position; sizes not adjusted. (A) *Ordishia rutilus*. (B) *Loxozona lanceolata*. (C) *Epidesma crameri*. (D) *Euchlaenidia ockendeni* Rothschild, 1910. (E) *E. aurimacula*. (F) *Proutiella esoterica*.

Seeking rare moths of uncertain identity and changing the status of species of which only a single specimen is available may seem a bit insane in times of global biodiversity loss on an immense scale. However, the little we know about both *Vanewrightia* and *Epidesma* s.l. teaches us not only a lesson on intraspecific wing pattern variation but also on 1) the need and importance of natural history studies (cf. Ricklefs 2012), although currently not popular (Ríos-Saldaña et al. 2018); 2) the need for more (amateur) entomologists in Latin America, in particular those who look for early instars and rear and breed moths and who employ not only lights for collecting (Grados et al. 2015; Boppré and Monzón 2020); 3) the need to investigate entire moth communities and their biologies instead of concentrating on α-taxonomy; 4) morphospecies should not be described on the basis of single specimens (see Dayrat 2005; Lim et al. 2012); 5) specimen labels should include the circumstances of collection (at light, at bait, at flower, during the day/night, etc.; see Ferro and Summerlin 2019) to foster and facilitate integrative taxonomy (Schlick-Steiner et al. 2010); 6) characters on the underside can be important for identification; unfortunately, many books and internet resources only illustrate uppersides of moths; and 7) variation in male genitalia is a subject that requires much more attention. Male genitalia in insects are generally considered to show no or low within-species variability (due to the lock-and-key hypothesis; see Shapiro and Porter 1989). If at all, most often genitalia preparations for descriptions are made from a single specimen only. There are, however, reports of great intraspecific variation in lepidopteran genitalia (Mutanen et al. 2006; Gilligan and Wenzel 2008, and references therein), suggesting the need to study a series of specimens; for Arctiinae, genitalic variation is as yet uninvestigated.

Hopefully, this report will stimulate researchers in Latin America to look out for *Vanewrightia* (and on *Chamaelimnas* and others); quite possibly, there are areas and/or times when their abundance is high. We believe that there are some more specimens hidden in collections, and more will be found when baiting with PAs in late afternoons. Any additional specimen of *Vanewrightia* s.l. will be important for better understanding the striking intraspecific variation of this taxon. We are also most curious to see females of *Vanewrightia*—are they as variable as the males? Or do they have a completely different appearance?

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