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Using DNA barcodes to test the association of sexes and morphs in *Calodesma* spp. (Lepidoptera, Erebidae, Arctiinae, Arctiini, Pericopina) of Trinidad, West Indies, with an overview of the genus, taxonomic changes and a new species

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Abstract

Phalaena militta Stoll, [1781], currently in the combination *Thyrgis militta*, is transferred to the **new combination** *Calodesma militta*. *Phalaena militta* is the type species of *Thyrgis* Walker, 1854, and so *Thyrgis* is a **junior synonym** of *Calodesma* Hübner, [1820]. The **reinstated genus** *Seileria* Dognin, 1923 is the next available name for the genus previously known as *Thyrgis*, and the remaining eight species and their subspecies currently in *Thyrgis* are transferred to **new combinations** as species of *Seileria*: *S. angustifascia* (Hering, 1925), *S. basipunctata* (Hering, 1926), *S. constrictifascia* (Dognin, 1919), *S. flavonigra* (Dognin, 1910), *S. investigatorum* (Toulgoët, 1988), *S. marginata* (Butler, 1875), *S. meres* (Druce, 1911), *S. phlegon* (Druce, 1885), *S. phlegon ruscia* (Druce, 1895), *S. tenuifascia* (Hering, 1930) and *S. tenuifascia daguana* (Hering, 1930). *Eucyanoides* Toulgoët, 1988, currently a synonym of *Thyrgis*, is made a **new subjective synonym** of *Seileria*. Based on DNA barcodes, we recognise three very similar, sexually dimorphic and in two cases polymorphic South American species of *Calodesma* with some phenotypes in common but very similar male genitalia: *C. militta* (BOLD:AAK1660), *C.* sp. cf. *collaris* (BOLD:ABZ2392) and *C. pseudocollaris* **Cock new species** (BOLD:AEI2170). *Calodesma militta* is widespread in South America, with two male morphs (*collaris* and *dioptis*) and two female morphs with variable markings (white and orange morphs). *Centronia plorator* Kaye, [1923] and *Thyrgis lacryma* Dognin, 1919 are variants of the white female morph and are **new synonyms** of *Calodesma militta*. A third female morph with red markings was not sequenced and could not be allocated to a species. *Calodesma* sp. cf. *collaris* (BOLD:ABZ2392) occurs in southern South America with both male morphs but only a white female morph. *Calodesma pseudocollaris* **new species** (BOLD:AEI2170) is only known from Trinidad, with one male morph (*collaris*) and the white female morph. Although more than ten morphs relating to this complex have been described as species, they cannot be synonymised without more data on distribution of the different species or DNA barcodes from the type specimens. Collated life history information indicates species of this group are split between Malpighiaceae feeders and Bromeliaceae feeders, but more work is needed to define these differences. The morphism patterns observed are discussed in terms of Müllerian mimicry and mimicry rings, and we suggest that in Trinidad (and elsewhere) there is a loose mimicry ring of diurnal black species with white spots or transparent patches on the wings which are most conspicuous and frequently observed when feeding on white Asteraceae flowers.

Key words: sexual dimorphism, polymorphism, mimicry, life history, Malpighiaceae, Bromeliaceae, *Seileria*, *Thyrgis*, new combinations

Introduction

Calodesma Hübner, [1820] (in Hübner 1816–[1825]) is a genus of brightly coloured moths in the subtribe Pericopina,

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tribe Arctiini, subfamily Arctiinae of Erebidae (until recently the subfamily Pericopinae of Arctiidae, but see Zahiri *et al*. (2011)). The only comprehensive review is that by Hering (1925) in Seitz' *Macrolepidoptera of the World*, which was done without access to the major collections outside Germany (Lamas 2017). Watson and Goodger's (1986) *Catalogue of the Neotropical Tiger-moths* covered Pericopinae but did not make significant changes, and there have been only a small number of subsequent works dealing with this group, none addressing *Calodesma*. Vincent and Laguerre (2014) included Pericopina in their *Catalogue of the Neotropical Arctiini*, and most recently Lamas (2017) published *An annotated checklist of the Pericopina*, which covered all valid taxa, including 21 species of *Calodesma*, and pointed out that *Thyrgis militta* (Stoll, [1781]), the type species of its genus, appears to be a female of a species of *Calodesma*. Laguerre (2017) treated *Thyrgis*, but was unable to resolve the identity of *T. militta*. Table 1 lists details of all valid taxa of *Calodesma* and the type specimens and/or original illustrations are shown in Figs. 1–3.

collaris Drury LT

albiapex Hering male T

lacryma Dognin HT

collaris Drury plate

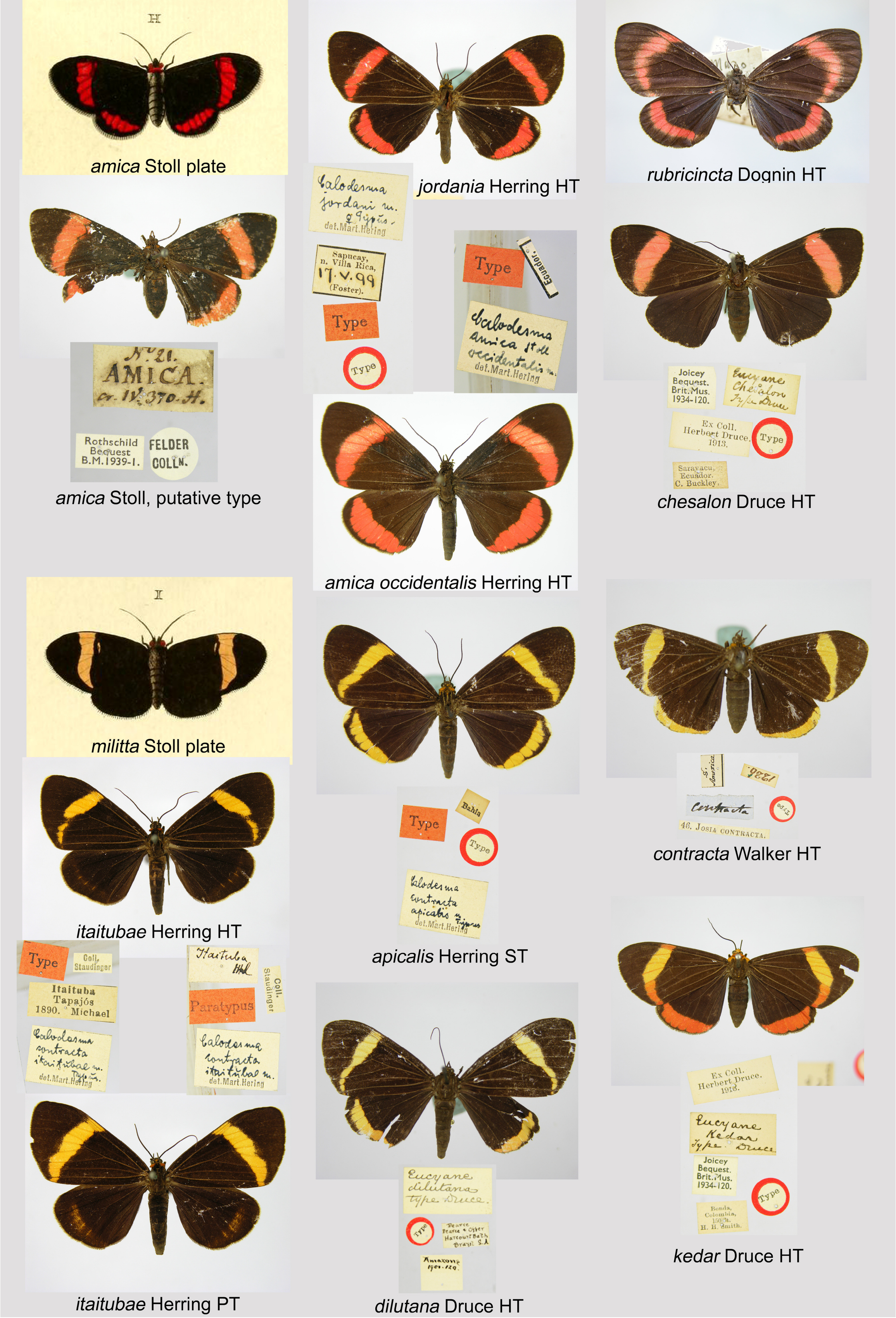
albiapex Hering female T

quadrimaculata Hering,HT

dioptis C. Felder & R. Felder HT

plorator Kaye HT

FIGURE 1. Types of *Calodesma* spp. (1). See Table 1 for details. HT = holotype, LT = lectotype, T = unspecified type. Not to scale. The C. & R. Felder, Kaye, and Walker types are in NHMUK, © The Trustees of the Natural History Museum, London, made available under Creative Commons License 4.0 (https://creativecommons.org/licenses/by/4.0/). The Hering types are in MNHU, the Dognin type is in USNM, and the Drury type is in HMUG, with permission.



amica Stoll plate

amica Stoll, putative type

militta Stoll plate

itaitubae Herring HT

itaitubae Herring PT

jordania Herring HT

amica occidentalis Herring HT

apicalis Herring ST

dilutana Druce HT

rubricincta Dognin HT

chesalon Druce HT

contracta Walker HT

kedar Druce HT

FIGURE 2. Types of *Calodesma* spp. (2). See Table 1 for details. HT = holotype, ST = syntype, PT = paratype, T = unspecified type. Not to scale. The Druce, Stoll and Walker types are in NHMUK, © The Trustees of the Natural History Museum, London, made available under Creative Commons License 4.0 (https://creativecommons.org/licenses/by/4.0/). The Hering types are in MNHU, and the Dognin type is in USNM; with permission.

TABLE 1. Overview of valid species names of *Calodesma* spp., based on Lamas (2017). All are currently placed in *Calodesma*, apart from *Thyrgis militta*, and all are currently treated as full species, apart from *C. amica occidentalis.*

Original combination	Authorship	Published figure	Type Locality	Reported sex	Availability of types[1]
albiapex (*Calodesma*)	Hering 1925	pl. 60h	[Brazil] Bahia, Pernambuco	Not stated	Type series in MNHU
amica (*Phalaena*)	Stoll, [1781] (in Stoll 1780–1782)	pl. 370, fig. H	Suriname	Not stated	No authoritative type material of this species has been located; the putative type in NHMUK is not a type (Lamas 2017)
apicalis (*Calodesma contracta*)	Hering, 1925	None	[Brazil], Bahia	Not stated	Syntype ♀ in NHMUK listed as ♂ in Lamas (2017)
approximata (*Calodesma*)	Hering, 1925	None	[French Guiana], Cayenne	Not stated	Holotype ♂ in MNHU
chesalon (*Eucyane*)	Druce, 1885	None	Ecuador, [Pastaza]	Not stated	Holotype ♀ in NHMUK
collaris (*Phalaena*)	Drury, 1782	pl. 21, fig. 2	Brazil, [Rio de Janeiro]	Not stated	Holotype ♂ in HUMG
contracta (*Josia* (*Thyrgis*))	Walker, 1854	None	‘South America’	Not stated	Holotype ♀ in NHMUK
dilutana (*Eucyane*)	Druce, 1907	None	[Brazil], ‘Amazons’	Not stated	Holotype ♀ in NHMUK
dioptis (*Chamesthema*)	C. Felder & R. Felder, 1874	pl. 103, fig. 13	[Brazil, fl(umen) Amazonas]	Not stated	Holotype ♂ in NHMUK
eucyanoides (*Calodesma*)	Hering, 1925	pl. 61A	[Peru], Pebas; [Brazil] São Paulo de Olivença	Not stated	Syntype ♂♀ in MNHU
exposita (*Stenelopsis*)	Butler, 1877	pl. 8, fig. 13 (venation)	[Brazil], Pará	Not stated	Holotype ♀ in NHMUK
itaitubae (*Calodesma contracta*)	Hering, 1925	None	[Brazil, Pará, Rio Tapajós], Itaituba	Not stated	Syntype ♀ in MNHU
jordani (*Calodesma*)	Hering, 1925	None	Paraguay	Female	Holotype ♀ in NHMUK
kedar (*Eucyane*)	Druce, 1900	None	Colombia, [Magdalena]	Not stated	Holotype ♀ in NHMUK
lacryma (*Thyrgis*)	Dognin, 1919	None	French Guiana, Saint-Laurent du Maroni	Female	Holotype ♀ in USNM
melanchroia (*Cocastra*)	Boisduval, 1870[2]	C. Felder & R. Felder (1874), pl. 103.14	Guatemala	Not stated	Holotype ♀ in NHMUK
maculifrons (*Stenele*)	Walker, [1865]	None	[Honduras]	Male	Holotype ♂ in NHMUK

......*continued on the next page*

TABLE 1. (Continued)

Original combination	Authorship	Published figure	Type Locality	Reported sex	Availability of types[1]
militta (*Phalaena*)	Stoll, [1781] (in Stoll 1780–1782)	pl. 370, fig. I	Suriname	Not stated	No type material located (Lamas 2017)
niepelti (*Calodesma approximata*)	Hering, 1928	None	Colombia, Bella Vista	Not stated	Holotype ♂ in MNHU
occidentalis (*Calodesma amica*)	Hering, 1925	pl. 60h	Ecuador	Not stated	Holotype ♀ in NHMUK
plorator (*Centronia*)	Kaye, 1923	pl. 1, fig. 3	Trinidad, Siparia	Female	Holotype ♀ in NHMUK
quadrimaculata (*Calodesma*)	Hering, 1925	pl 60h	Bolivia, [La Paz]	Not stated	Holotype ♀ in MNHU
rubricincta (*Centronia*)	Dognin, 1923	None	Colombia, Muzo	Female	Holotype ♀ in USNM
tamara (*Calodesma*)	Hering, 1925	pl 61a	[Peru], Pebas; [Brazil] São Paulo de Olivença	Not stated	Two syntype ♀ in MNHU
uraneides (*Esthema*)	Butler, 1871	None	[French Guiana], Cayenne	Not stated	Holotype ♀ in OUNHM

[1] Hunterian Museum and Art Gallery, Glasgow (HUMG), Museum für Naturkunde, Berlin (MNHU), The Natural History Museum, London (NHMUK), Oxford University Natural History Museum (OUNHN), United States National Museum (USNM)

[2] Boisduval (1870) inadvertently used an unpublished name from Felder and Felder (1874), but as he included a description and designated a type, he is the author of the species. In Fig. 3, we include the types of both Boisduval (Guatemala) and Felder and Felder (Mexico). Janzen *et al.* (2009) indicated that *melanchroia* is a synonym of *maculifrons*, and Becker (2013) formally confirmed this.

FIGURE 3. Types of *Calodesma* spp. (3). See Table 1 for details. HT = holotype, ST = syntype. Not to scale. The Butler, C. & R. Felder, and Walker types are in NHMUK, © The Trustees of the Natural History Museum, London, made available under Creative Commons License 4.0 (https://creativecommons.org/licenses/by/4.0/). The Hering types are in MNHU, with permission.

Kaye and Lamont (1927) recorded *C. collaris* (Drury) (as *Leucopsumis collaris*), *C. plorator* (Kaye) (as *Centronia plorator* Kaye) and *T. militta* from Trinidad. M.J.W. Cock collected Lepidoptera in Trinidad from 1978 to 1982 and on occasional visits thereafter, and accumulated a small number of specimens matching *C. collaris*, *C. dioptis* (C. Felder & R. Felder) and *C. plorator*, together with female specimens resembling *C. plorator* but with reduced markings, two female specimens with yellow/orange markings resembling *C. dilutana* (Bates) and two female specimens with red markings resembling *C. chesalon* (Druce). He noted that *C. collaris* and *C. dioptis* were only known from males in Trinidad, and were almost all attracted to light, whereas the other taxa were only known from females, which were only collected from flowers of *Austroeupatorium inulaefolium* and *Chromolaena odorata* at roadsides in forested areas. Review of the NHMUK collection in the 1980s supported this conclusion, except that variable females similar to *C. plorator* were associated with males resembling *C. collaris*, based on material reared by A. Miles Moss at Belem (= Pará), Brazil. Hering (1925) had made a similar association based on museum material. At the time Cock hypothesised that there were only two species in Trinidad, the two male species being *C. collaris* and *C. dioptis*, with the females with white markings (*C. plorator* and similar) and the females with very similar but yellow/orange markings being the females of *C. collaris*, and the females with red markings being those of *C. dioptis*. This was not taken further, until the development of DNA barcoding based on a defined section of the CO1 mitochondrial gene (Hebert *et al*. 2003), the Barcode of Life Data System (BOLD, http://www.boldsystems.org/) and the use of Barcode Index Numbers (BINs, Ratnasingham and Hebert 2013, Miller *et al*. 2016) provided new tools to address the question, and the stimulus provided by Lamas' (2017) catalogue suggested it would be timely to investigate further. Here we test Cock's hypothesis, and analyse the results from Trinidad in the context of the continental fauna.

Methods

Materials, phenotypes and male genitalia. In addition to material in the research collections of M.J.W. Cock (**MJWC**) and M. Laguerre (**ML**), specimens were located and examined in the Hunterian Museum and Art Gallery, Glasgow (**HUMG**), Museum für Naturkunde, Berlin (**MNHU**), The Natural History Museum, London (**NHMUK**), National Museums of Scotland, Edinburgh (**NMS**), Oxford University Museum of Natural History (**OUMNH**), United States National Museum (**USNM**) and the University of the West Indies Zoology Museum, St. Augustine, Trinidad and Tobago (**UWIZM**). The specimens collected by Cock dated back to before 1982, and those in the other collections were older, and so none were suitable for routine DNA barcoding. In order to obtain DNA barcodes, fresh material was needed, and so S. Alston-Smith and J. Morrall collected *Calodesma* moths in Trinidad when *A. inulaefolium* flowered in September and October and *Chromolaena odorata* flowered in December–January from 2017 to 2020 (Table 2). Selected male specimens were dissected using standard methods (abdomen soaked in 10% KOH for 24h, dissected under a binocular microscope, stained with 1% chlorazol black E, and preserved in glycerol-filled vials pinned with the specimen). In the text below, TL is used as an abbreviation for type locality.

DNA Barcoding and analysis. Fresh samples were barcoded by the CABI molecular laboratory following the protocol described in Cock *et al*. (2017). As the fresh material of orange morphs was very limited, and no fresh material of red morphs was obtained, a separate effort was made to barcode Cock's specimens of these phenotypes from 1978-1982 in the Rougerie laboratory using the protocol described in Cock and Rougerie (2021). Further barcodes for *Calodesma* spp. from the mainland of South America and Central America were obtained from BOLD (https://boldsystems.org/) and from ML.

All 223 available DNA barcodes of more than 458 bp of all *Calodesma* species were compiled, aligned using Muscle (default parameters in MEGA X), and similarity derived using the neighbour-joining model with the default parameters in MEGA X (Kumar *et al*. 2018). The Barcode Index Number (BIN) system (Ratnasingham and Hebert 2013) together with habitus differences were used to categorise clusters. The BIN System is an online framework that clusters DNA barcode sequences algorithmically, and since clusters show high concordance with species, this system can be used to verify species identifications (Ratnasingham and Hebert 2013). Groups were defined with matching BINs as shown in Table 3, and their evolutionary divergence (as % differences) calculated using the maximum composite likelihood model with the default parameters in MEGA X (Kumar *et al*. 2018). To display these results as a neighbour-joining tree of manageable size, a subset of 73 barcodes (Table 4) was selected to eliminate many duplicates while maintaining the diversity of phenotypes.

Early stages and food plants. We report on the rearing of one caterpillar collected in Trinidad. Other information was collected from literature and the internet sources iNaturalist (www.iNaturalist.org) and Janzen and Hallwachs (2022). In the discussion of caterpillars, T1, T2, T3, A1, A2, etc. are used to refer to thoracic segments 1, 2, 3, and abdominal segments 1, 2, etc.

Results

Materials, phenotypes and male genitalia. In addition to the material in MJWC, specimens from Trinidad were located and examined in NHMUK, NMS and UWIZM (Table 2). Alston-Smith and Morrall collected all specimens of *Calodesma* found at flowers of *A. inulaefolium* and *Chromolaena odorata* over 2.5 years as shown in Table 2. Males of both morphs were obtained, together with diverse phenotypes of white-marked females and a small number of orange-marked females, but no red-marked females. Examples are shown in Figs. 4–9 using the taxonomy developed below. Males resembling *collaris* (hereafter '*collaris* morph') are more common than those resembling *dioptis* (hereafter '*dioptis* morph'), female white morphs are considerably more common than female orange morphs, and female red morphs are rare. Further, we were particularly fortunate in the first collecting season of this study (September–October 2017), as on all other occasions *Calodesma* spp. have been rarely encountered (Table 2).

TABLE 2. Museum specimens from Trinidad (pre-1982) and fresh collections of *Calodesma* spp. made in Trinidad for this study.

Phenotypes	Old specimens from collections	Sept–Oct 2017	Dec 2017–Jan 2018	Sept–Oct 2018	Dec 2018–Jan 2019	Sept–Oct 2019	Dec 2019–Jan 2020	Total
Males of *collaris* morph	7	4	0	0	1	1	0	13
Males of *dioptis* morph	1	3	0	1	0	0	0	5
White female morphs	7	26	0	5	0	0	1	39
Orange female morphs	3	2	0	0	1	0	3	9
Red female morphs	2	0	0	0	0	0	0	2

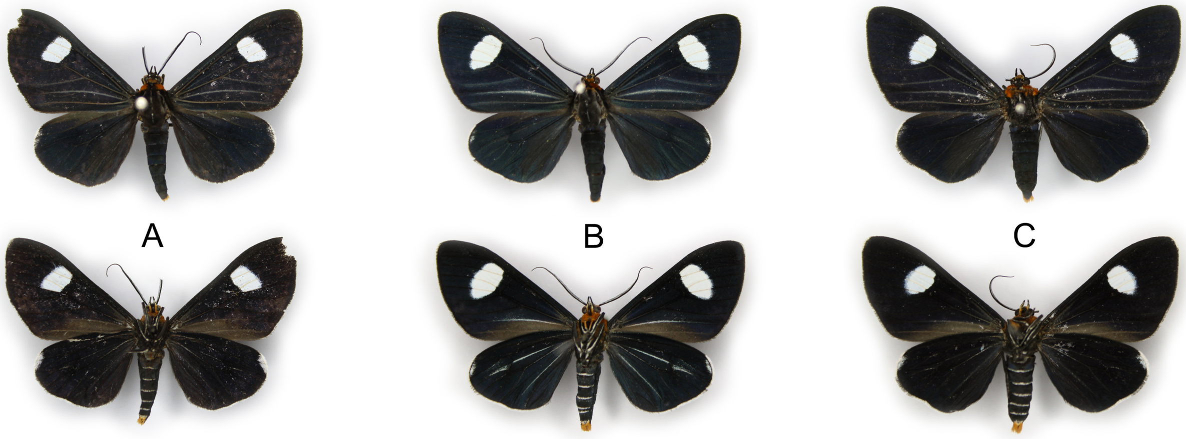


FIGURE 4. Male *Calodesma militta* BOLD:AAK1660 *collaris* morph from Trinidad, W.I., captured at flowers of *Austroeupatorium inulaefolium*; dorsal view above, ventral view below. **A**, Cat's Hill, 24.ix.2017, J. Morrall, DNA 138. **B**, Arima Valley, near Asa Wright Nature Centre, 23.ix.2017, J. Morrall, DNA 139. **C**, Parrylands, x.2017, S. Alston-Smith DNA163. Life size.

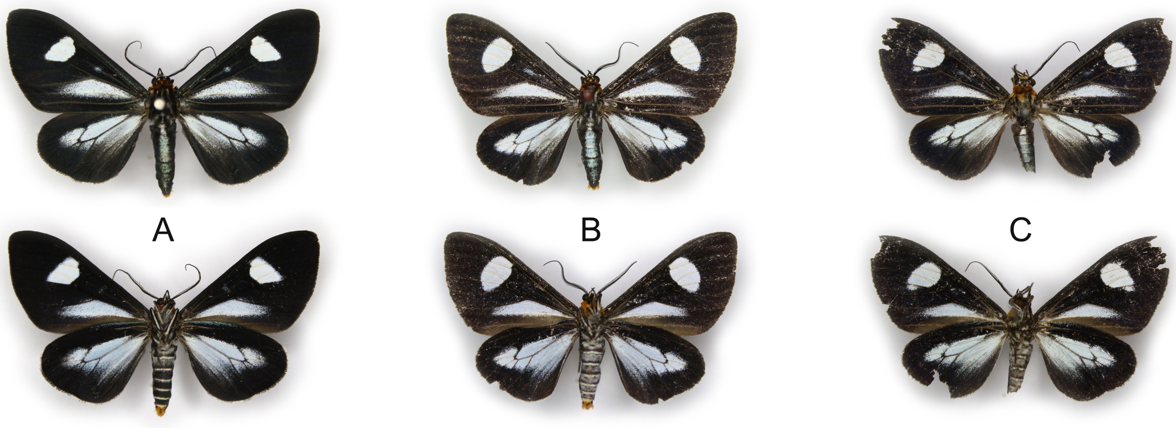


FIGURE 5. Male *Calodesma militta* BOLD:AAK1660 *dioptis* morph from Trinidad, W.I., captured at flowers of *Austroeupatorium inulaefolium*; dorsal view above, ventral view below. **A**, Parrylands, x.2017, S. Alston-Smith, DNA 160. **B**, Parrylands, ix.2018, S. Alston-Smith, DNA 296. **C**, as #A, DNA 161 (dissection 1004). Life size.

FIGURE 6. *Calodesma militta* BOLD:AAK1660 females white morph from Trinidad, W.I., captured at flowers of *Austroeupatorium inulaefolium*; dorsal view above, ventral view below. **A**, Cat's Hill, 24.ix.2017, J. Morrall, DNA 136. **B**, Parrylands, x.2017, S. Alston-Smith, DNA 166. **C**, as #A, DNA 140. **D**, as #A, DNA 141. **E**, as #B, DNA 174. **F**, as #A, DNA 142. **G**, as #B, DNA 170. **H**, as #B, DNA 167; this specimen is an almost exact match in dorsal view to the type of *Centronia plorator* Kaye. **I**, *Calodesma* sp. unresolved BIN, West Trinity, x.2017, DNA 182 (failed, no barcode available). Life size.

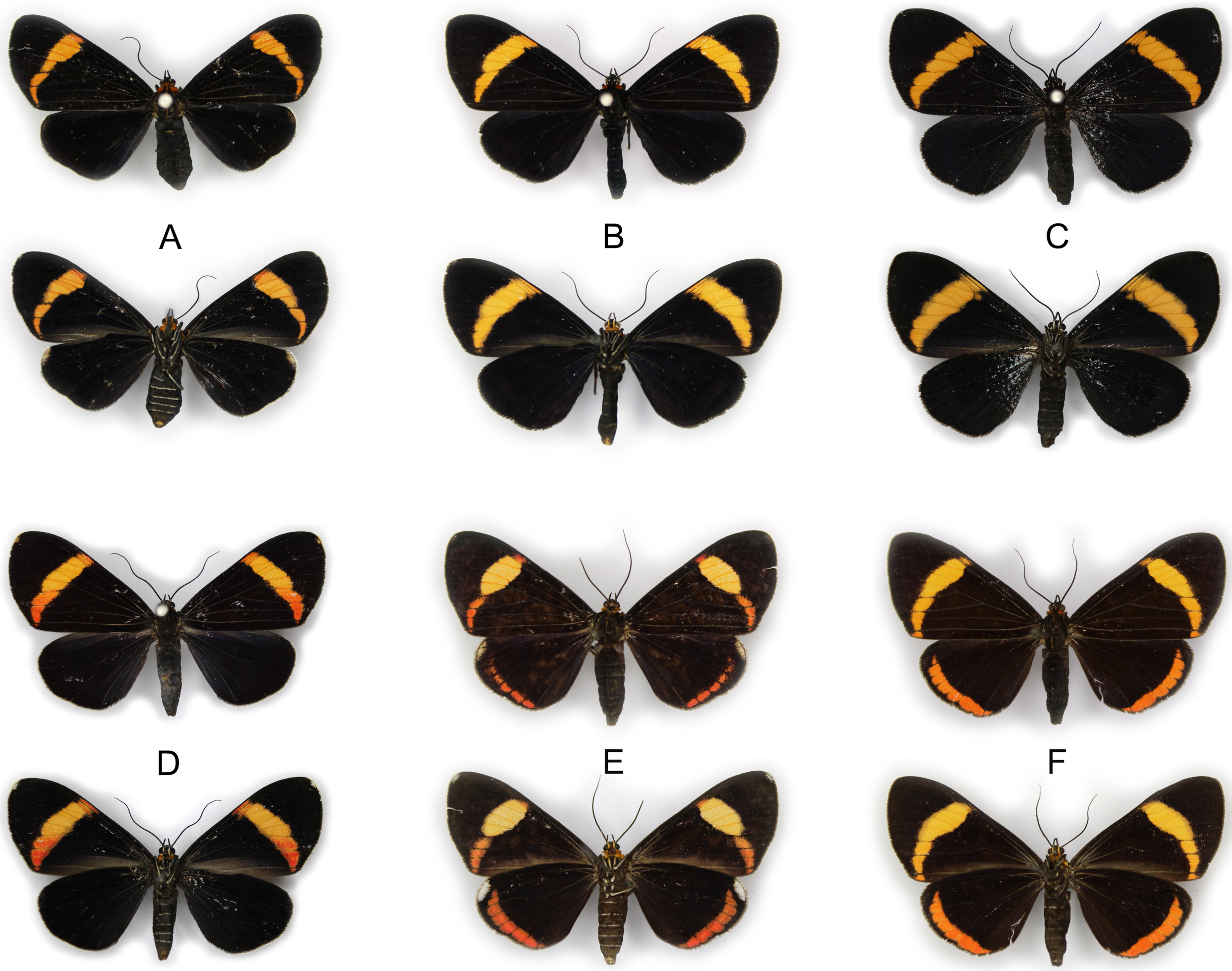


FIGURE 7. *Calodesma militta* BOLD:AAK1660 females orange morph from Trinidad, W.I.; dorsal view above, ventral view below. **A**, Lalaja Ridge, 23.xii.2019 J. Morrall, DNA 377. **B**, Hololo Mountain Road, 3.x.2017 J. Morrall, DNA 145. **C**, Arima valley, Simla, xii.2020, S. Alston-Smith, DNA 475. **D**, Arima valley, Simla, xii.2020, S. Alston-Smith, DNA 474. **E**, East of Point Fortin, 30.ix.1982, M.J.W. Cock, DNA 315. **F**, Rio Claro–Guayaguayare Road, milestones 4–5, 17.ix.1978, M.J.W. Cock, DNA 316. Life size.

FIGURE 8. *Calodesma* sp(p). (unresolved barcodes) females red morph from Trinidad, W.I., captured at flowers of *Austroeupatorium inulaefolium*; dorsal view above, ventral view below. **A**, Rio Claro–Guayaguayare Road, milestones 4–5, 17.ix.1978, M.J.W. Cock. **B**, Arima–Blanchisseuse Road, milestone 9, Textel Road, 11.x.1979, M.J.W. Cock. Life size.

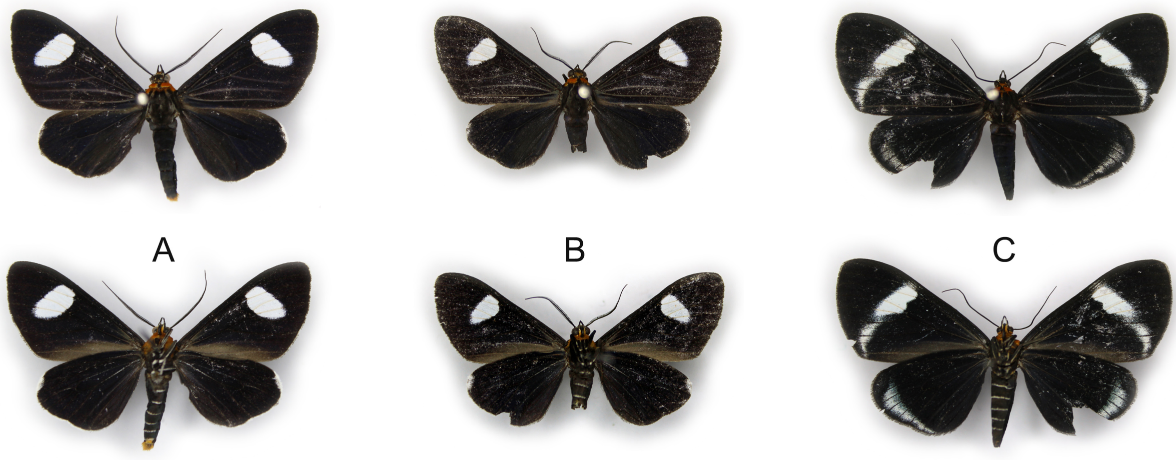


FIGURE 9. Type material *Calodesma pseudocollaris* **new species** Trinidad, W.I., Cat's Hill, at eupatorium flowers, 24.ix.2017, J. Morrall; dorsal view above, ventral view below. **A**, holotype, ♂ DNA 137. **B**, paratype ♂, DNA 135, dissection 1001. **C**, allotype ♀, DNA 143. Life size.

Dissections of the two male morphs from Trinidad (*dioptis* and *collaris*) showed no significant differences in the genitalia (Fig.10). At that point, we expected the DNA barcodes to separate the two phenotypes as species (*C. dioptis* and *C. collaris*), although the possibility that there was only one species present with dimorphic males and trimorphic variable females was also raised.

DNA barcodes and analysis. DNA barcodes were obtained for most of the new material and two of the old specimens. Sequences have been deposited in BOLD and grouped in BOLD dataset DS-CALOD, and details and numbers are listed in Table 4. For analysis we added all sequences of *Calodesma* spp. from BOLD and additional sequences from ML producing results (Fig.12, Table 3) that did not fit Cock's *a priori* hypothesis. The samples from Trinidad appear as two separate BINs, BOLD:AAK1660 with 41 sequences and BOLD:AEI2170 with three, and they are 6.15% different (Table 3). However, the members of these two BINs do not match the phenotypes as expected. Both male morphs (*collaris* and *dioptis*) occur in BOLD:AAK1660, whereas only *collaris* occurs in BOLD:AEI2170. White female morphs including individuals matching *plorator* occur in both BINs, but orange morphs only occur in BOLD:AAK1660, while no red morphs were sequenced. Looking at the members of BOLD: AAK1660, there is only slight variation within the two male morphs apart from the pale veins of the ventral surface of the *collaris* morph which may be present or absent (Fig. 4), whereas the white female morph (Fig. 6) is continuously variable with regard to the thickness and shape of the white forewing spot, the presence of white between the spot and the costa, the presence or absence and strength of a white band from the spot to the tornus, the presence or absence and strength of a white apical spot on the hindwing, the presence or absence and strength of a white submarginal hand on the hindwing, and whether this band is infused with salmon-pink or not. Further there is some variation in female wing shape. Of the 18 sequenced white female morphs examined, no two specimens were identical. There were only seven sequenced specimens of the orange female morph available, but these are variable in similar but less comprehensive ways to the white morph (Fig. 7); in addition, the markings can be a mixture of yellow (forewing spot) and orange (from forewing spot to tornus, hindwing submarginal band).

The small number of sequenced specimens in BOLD:AEI2170, which will be described below as *C. pseudocollaris* **new species,** means that although the two males resemble the *collaris* morph and the single female is a phenotype of the white morph similar to *C. plorator*, we cannot draw any conclusions regarding the absence of any other morphs from this sample. It may be that both male morphs and all female colour morphs occur in both species (BINs), or it may be that only males of the *collaris* morph and white female morphs (of the *plorator* phenotype or variable) occur in BOLD:AEI2170. Dissection of the genitalia of a male from BOLD:AEI2170 showed it to be almost identical to those of the two male morphs (*dioptis* and *collaris*) of BOLD:AAK1660 (Fig. 10). The aedeagus of specimens in BOLD:AAK1660 is slightly more elongate distally, and the distal opening is correspondingly longer, but more dissections of both clusters would be needed to assess individual variability before this character could be considered diagnostic.

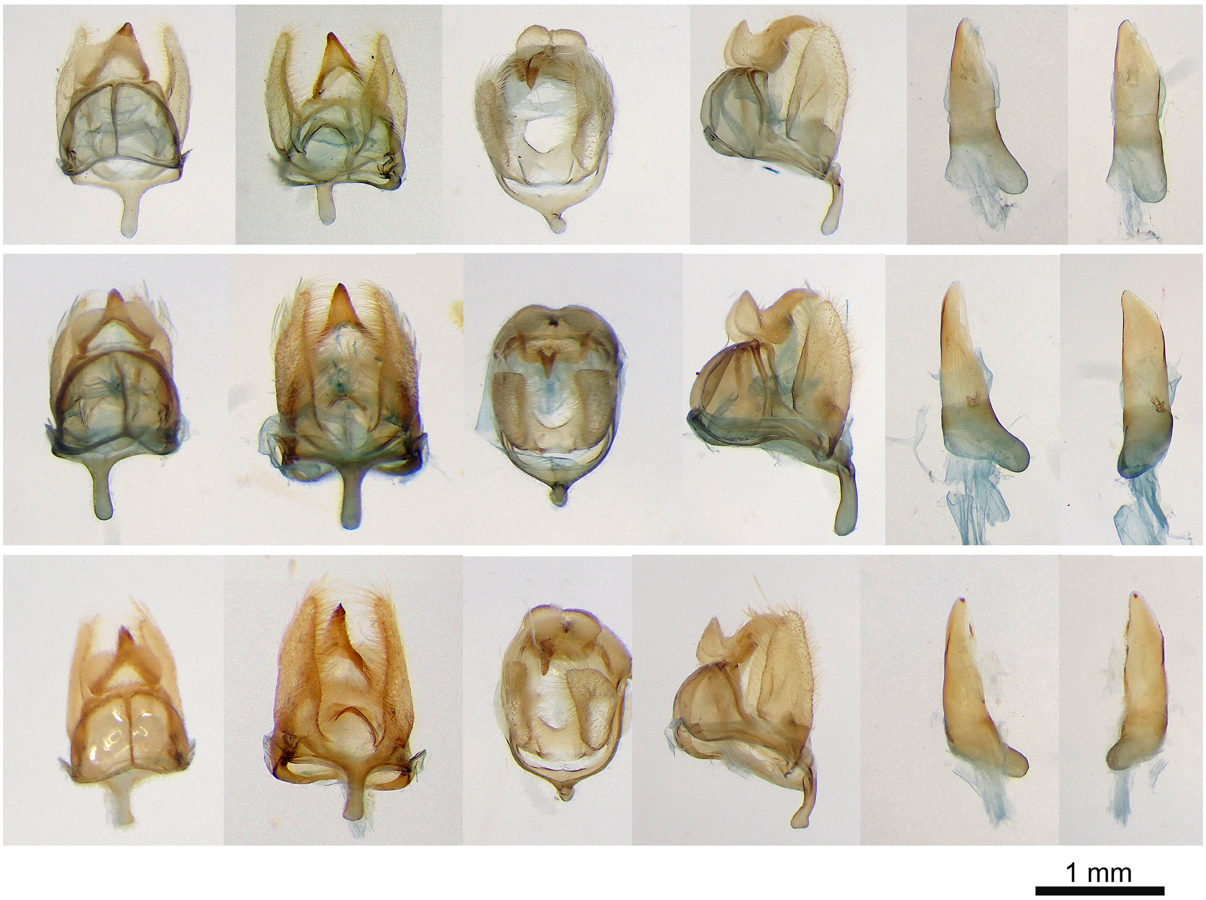


FIGURE 10. Male genitalia of *Calodesma* spp. from Trinidad, W.I. **Top row**, *C. pseudocollaris* **new species**, paratype, Trinidad, W.I., Cat's Hill, eupatorium flowers, 24.ix.2017, John Morrall [MJWC, DNA 135, dissection 1001]. **Middle row**, *C. militta* BOLD:AAK1660 *collaris* morph, Parrylands, eupatorium flowers, x.2017, S. Alston-Smith [MJWC, DNA 162, dissection 1003]. **Bottom row**, *C. militta* BOLD:AAK1660 *dioptis* morph, data as middle row [MJWC, DNA 161, dissection 1004]. Each row from left to right: dorsal view; ventral view; lateral view from left; aedeagus lateral view from left; aedeagus ventral or ventro-lateral view.

When the Trinidad results are considered in combination with mainland DNA barcodes from BOLD and ML's material, the situation becomes more complex (Fig. 12, Table 3). BIN BOLD:AAK1660 occurs in Panama (1 sequence in BOLD), Suriname (2 sequences), French Guiana (2 sequences), Bolivia (1 sequence), Paraguay (3 sequences) and Argentina (3 sequences), and includes public material currently identified as *C. maculifrons* (Walker) (Panama, 1♂), *C. albiapex* (ex Genbank, no locality given, but from eastern Amazon based on our interpretation of Zencker *et al*. (2015)), *C. collaris* (Bolivia) and *C. dioptis* (Bolivia), as well as material identified as *Calodesma* sp. HG01 from Suriname. *Calodesma albiapex* was described from Pernambuco, Bahia State, Brazil (Table 1), within the known range of BOLD:AAK1660; it resembles *C. collaris* (Fig. 4) but has a white spot at the apex of the hindwing (Fig. 1). In appearance, it does not look out of place with members of BOLD:AAK1660 noting that some white females have a trace of an apical spot dorsally and ventrally.

Three males resembling *C. collaris* and one male resembling C. *dioptis* from Bolivia, Paraguay and Argentina appear in a separate BIN (BOLD:ABZ2392), at least 2.43% different from any other group (Table 3).

Calodesma maculifrons was described from Honduras (Table 1). It shows strong female dimorphism, the male and female *maculifrons* morph (Fig. 3) being predominantly orange, and the female *melanchroia* morph mostly black (Fig. 3), as confirmed by rearing and DNA barcodes (Janzen *et al*. 2009). We accept that *C. maculifrons* is correctly applied to material identified as this species from Costa Rica, Panama and western Ecuador in BIN (BOLD: AAA1430), 5.60% different from BOLD:AAK1660 (Table 3). Phenotypically, both morphs of *C. maculifrons* are very different to the various morphs that we have documented from South America, so finding a specimen in BOLD: AAK1660 from Panama resembling the *maculifrons* morph of *C. maculifrons* was unexpected.

FIGURE 11. Male genitalia of *Calodesma* spp. from South and Central America. Top row, *C. militta* BOLD:AAK1660, *collaris* morph, Paraguay (ML, dissection ML2869, DNA MILA1759). Second row, *Calodesma* sp. cf. *collaris* BOLD:ABZ2392, *dioptis* morph, (ML dissection ML2872, DNA MILA.0212). Third row, *C. maculifrons*, Esmeraldas, Ecuador (ML, dissection ML3290. Bottom row, *C. uraneides*, French Guiana, (ML, dissection ML2873)

BOLD:AEI2170 from Trinidad (*C. pseudocollaris* **new species** below) clusters with BOLD:ABZ2392 and *C. maculifrons* from Costa Rica (BOLD:AAA1430) (Fig. 12), but 2.66% different from the former and 0.82% from the latter. As just noted, *C. maculifrons* is very different in appearance to the various morphs that we have documented from Trinidad.

TABLE 3. Estimates of evolutionary divergence over sequence pairs between groups for *Calodesma* spp. The number of base substitutions per site from averaging over all sequence pairs between groups are shown. Analyses were conducted using the Maximum Composite Likelihood model (Tamaru *et al*. 2004). This analysis involved 223 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All positions containing gaps and missing data were eliminated (complete deletion option). There was a total of 387 positions in the final dataset. Evolutionary analyses were conducted in MEGA X (Kumar *et al*. 2018).

Species (BIN)	Number of sequences	1	2	3	4	5	6
1. *Calodesma militta* AAK1660	41	-					
2. *Calodesma uraneoides* AAK1659	8	0.07153	-				
3. *Calodesma* sp. cf. *collaris* ABZ2392	3	0.06497	0.06499	-			
4. *Calodesma maculifrons* AAA1430	166	0.05600	0.05252	0.02428	-		
5. *Calodesma exposita* AAM6367	2	0.08035	0.06826	0.08095	0.07124	-	
6. *Calodesma pseudocollaris* AEI2170	3	0.06152	0.05271	0.02664	0.00820	0.06826	-

Further dissections of material from Central and South America were made to investigate these conclusions (Figs. 10–11). The male genitalia of *C. maculifrons* (Costa Rica), *C. pseudocollaris* **new species** (Trinidad), *C.* cf. *collaris* BOLD:ABZ2392 (Paraguay) and *C. militta* BOLD:AAK1660 (Trinidad and Paraguay) are all very similar. *Calodesma* cf. *collaris* BOLD:ABZ2392 has a more pointed valve, and *C. maculifrons* a narrower valve. The relative size and shape of the tegumen and uncus are easily distorted by the angle at which they are viewed, so it is not justified to attach significance to the small differences that may be discerned. Indeed, it would be inappropriate to use these figures to separate these taxa without knowing more about the range of individual variation that occurs. In contrast, the male genitalia of *C. uraneides* (French Guiana) (Fig. 11) are obviously those of a different species.

Early stages and food plants. Information on caterpillars and food plants from elsewhere offer clues as to how these taxa may be ecologically different. Janzen and Hallwachs (2022) have reared *C. maculifrons* multiple times in Costa Rica, and documented the early stages with photographs. The food plants are several species of Malpighiaceae, particularly *Byrsinomia crassifolia*.

Under the iNaturalist name bellbird20, Gosula (2021) posted images of the early stages of a male *C. militta* (BOLD:AAK1660) *collaris* morph from a caterpillar that he and Aditya Gosula found and reared on *Malpighia glabra* (Malpighiaceae) at Mt. Hope in Trinidad (Fig. 13). The caterpillar was found in the penultimate instar on 24 April 2021, it pupated on 1 May 2021, and the adult emerged on 11 May 2021. The resultant adult was successfully barcoded (BOLD sample ID MJC_546, sequence ID TRIN172-22). In the penultimate instar, the head is brown and smooth with some dark spots in the lower part; T1–T3 are pale brown with dark verrucae with long dark hairs; the abdomen is pale yellow, with long dark hairs and marked as follows; A1, A2, A5, A7 and A9 have a conspicuous reddish-brown dorso-lateral patch surrounding dark subdorsal and dorso-lateral tubercles; a similar reddish-brown patch on the anterior lateral margin of A1, which joins the dorso-lateral patch on A2; a dark dorso-lateral line joins the dorso-lateral marks from A2–A7; an intermittent narrow dark dorsal line, alternating with a chevron shape on A3, A4, A6 and A7; an irregular less dark lateral line A2–A7; legs concolorous; spiracles not distinguishable. In the final instar, the head is pale brown and smooth with some dark spots in the lower part; T1 pale yellow brown with long setae on concolorous verrucae; T2–T3 yellow with long dark and pale setae; body yellow, markings similar to those of penultimate instar, but lateral lines less evident and setae on lateral verrucae pale, and dark on subdorsal and dorso-lateral verrucae; legs concolorous; spiracles not distinguished. Pupation is in a very open loose web of pale silk, and the setae of the last caterpillar instar remain attached to the cast skin. The pupa is transparent, with scattered black spots on the body, and black lines on the wing cases. When newly formed it shows the larval colouring, but then becomes pale brown, before showing the wing colour and markings before eclosion. The early stages of *C. militta* and *C. maculifrons* are very similar.

TABLE 4. Specimen information for the 73 records used in the DNA barcode similarity tree. All records are publicly accessible in BOLD (www.boldsystems.org), the ones generated in this study in BOLD dataset DS-CALOD. (BIN=Barcode Index Number, see Ratnasingham and Hebert (2007)).

Sample ID	BOLD Process ID	GenBank accession number	BIN	*Calodesma* species	Morph	Sex	Barcode length (BP)	Geographical origin
07-SRNP-101841	BLPBE902-07	JQ565325	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste
07-SRNP-103403	BLPBG584-07	JQ566647	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste
07-SRNP-105616	BLPCB071-08	JQ568498	BOLD:AAA1430	*maculifrons*	*maculifrons*	F	658	Costa Rica Alajuela
07-SRNP-111506	BLPCH321-08	JQ563644	BOLD:AAA1430	*maculifrons*	*maculifrons*	F	658	Costa Rica, Guanacaste
07-SRNP-111507	BLPCH322-08	JQ563645	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste
07-SRNP-111508	BLPCH323-08	JQ563646	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste
07-SRNP-111509	BLPCH324-08	JQ563647	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste
07-SRNP-111510	BLPCH325-08	JQ563648	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste
07-SRNP-111511	BLPCH326-08	JQ563649	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste
07-SRNP-111512	BLPCH327-08	JQ563650	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste
07-SRNP-111513	BLPCH328-08	JQ563651	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste
07-SRNP-113500	BLPCJ435-08	JQ555544	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste
07-SRNP-42301	MHMXQ198-08	GU160460	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica Alajuela
07-SRNP-42303	MHMXQ172-08	GU160464	BOLD:AAA1430	*maculifrons*	*melanchroia*	F	658	Costa Rica Alajuela
07-SRNP-42304	MHMXQ197-08	GU160461	BOLD:AAA1430	*maculifrons*	*melanchroia*	F	658	Costa Rica Alajuela
07-SRNP-42305	MHMXQ199-08	GU160462	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica Alajuela
07-SRNP-42306	MHMXQ171-08	GU160463	BOLD:AAA1430	*maculifrons*	*melanchroia*	F	658	Costa Rica Alajuela
08-SRNP-102725	BLPCN188-08	JQ558445	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste
08-SRNP-107306	BLPDC351-09	JQ552547	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica Alajuela
08-SRNP-107501	BLPDC546-09	JQ552723	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica Alajuela
08-SRNP-107787	BLPDC832-09	JQ552985	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica Alajuela
08-SRNP-66118	MHMYC716-09	GU650935	BOLD:AAA1430	*maculifrons*	*melanchroia*	F	658	Costa Rica, Alajuela
08-SRNP-66119	MHMYC696-09	GU650939	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Alajuela
08-SRNP-71674	MHMYC695-09	GU650945	BOLD:AAA1430	*maculifrons*	*maculifrons*	F	658	Costa Rica, Guanacaste
08-SRNP-72359	MHMYC693-09	GU650949	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste
08-SRNP-72360	MHMYC694-09	GU650943	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste

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TABLE 4. (Continued)

Sample ID	BOLD Process ID	GenBank accession number	BIN	***Calodesma*** **species**	Morph	Sex	Barcode length (BP)	Geographical origin
08-SRNP-72361	MHMYC697-09	GU650941	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Costa Rica, Guanacaste
BEVI1178	ARCTC631-10	JF840701	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Panama , Veraguas
BEVI1179	ARCTC632-10	OQ026172	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Ecuador, Imbabura
BEVI1183	ARCTC636-10	JF840703	BOLD:AAA1430	*maculifrons*	*melanchroia*	M	658	Panama
MILA 0639	ARCTA920-07	OQ026170	BOLD:AAA1430	*maculifrons*	*maculifrons*	M	658	Guatemala, Izabal
BEVI1171	ARCTC624-10	OQ026171	BOLD:AAK1659	*uraneides*		M	624	French Guiana
BEVI1184	ARCTC637-10	JN275733	BOLD:AAK1659	*uraneides*		M	658	French Guiana
KLM Lep 09820	LNOUG015-18	OQ075784	BOLD:AAK1659	*uraneides*		M	654	French Guiana
KLM Lep 09932	LNOUG127-18	OQ075785	BOLD:AAK1659	*uraneides*		M	654	French Guiana
KLM Lep 10077	LNOUG272-18	OQ075783	BOLD:AAK1659	*uraneides*		M	652	French Guiana
MILA 0211	ARCTA211-07	OQ026169	BOLD:AAK1659	*approximata*		M	617	French Guiana
NS-RR1347	LNOUF347-11	JN275770	BOLD:AAK1659	*uraneides*		M	658	French Guiana
NS-RR1348	LNOUF348-11	JN275771	BOLD:AAK1659	*uraneides*		M	658	French Guiana
NS-RR1380	LNOUF380-11	JN275772	BOLD:AAK1659	*uraneides*		M	627	French Guiana
BEVI1181	ARCTC634-10	OQ026173	BOLD:AAK1660	*militta s*	*collaris*	M	658	French Guiana
BEVI1182	ARCTC635-10	JF840702	BOLD:AAK1660	*militta*	*collaris*	M	658	Paraguay
BEVI1188	ARCTC641-10	JF840707	BOLD:AAK1660	*militta*	*dioptis*	M	658	Paraguay
MBe0478	ARCMB459-21	Not yet available	BOLD:AAK1660	*militta*	*collaris*	M	658	Peru, Huanuco
MILA 0210	ARCTA210-07	OQ026168	BOLD:AAK1660	*militta*	*collaris*	M	658	Bolivia , La Paz
MILA 1759	ARCTD634-12	OQ026175	BOLD:AAK1660	*militta*	*collaris*	M	658	Paraguay, Canindeyu
MJC_136	TRIN002-21	OP927322	BOLD:AAK1660	*militta*	*collaris*	M	639	Trinidad & Tobago, Trinidad
MJC_145	TRIN010-21	OP927346	BOLD:AAK1660	*militta*	orange	F	642	Trinidad & Tobago, Trinidad
MJC_160	TRIN011-21	OP927335	BOLD:AAK1660	*militta*	*dioptis*	M	643	Trinidad & Tobago, Trinidad
MJC_162	TRIN013-21	OP927340	BOLD:AAK1660	*militta*	*collaris*	M	655	Trinidad & Tobago, Trinidad
MJC_164	TRIN015-21	OP927331	BOLD:AAK1660	*militta*	*collaris*	M	640	Trinidad & Tobago, Trinidad
MJC_169	TRIN020-21	OP927315	BOLD:AAK1660	*militta*	white	F	644	Trinidad & Tobago, Trinidad
MJC_170	TRIN021-21	OP927347	BOLD:AAK1660	*militta*	white	F	653	Trinidad & Tobago, Trinidad

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TABLE 4. (Continued)

Sample ID	BOLD Process ID	GenBank accession number	BIN	*Calodesma* species	Morph	Sex	Barcode length (BP)	Geographical origin
MJC_172	TRIN023-21	OP927310	BOLD:AAK1660	*militta*	white	F	643	Trinidad & Tobago, Trinidad
MJC_295	TRIN025-21	OP927319	BOLD:AAK1660	*militta*	*collaris*	M	647	Trinidad & Tobago, Trinidad
MJC_297	TRIN027-21	OP927323	BOLD:AAK1660	*militta*	white	F	647	Trinidad & Tobago, Trinidad
MJC_298	TRIN028-21	OP927339	BOLD:AAK1660	*militta*	white	F	648	Trinidad & Tobago, Trinidad
MJC_299	TRIN029-21	OP927312	BOLD:AAK1660	*militta*	white	F	648	Trinidad & Tobago, Trinidad
MJC_300	TRIN030-21	OP927334	BOLD:AAK1660	*militta*	white	F	648	Trinidad & Tobago, Trinidad
MJC_416	TRIN033-21	OP927333	BOLD:AAK1660	*militta*	white	F	656	Trinidad & Tobago, Trinidad
MJC_546	TRIN172-22	OP927316	BOLD:AAK1660	*militta*	*collaris*	M	647	Trinidad & Tobago, Trinidad
MJC-291	TTLEP093-19	OP927314	BOLD:AAK1660	*militta*	orange	F	658	Trinidad & Tobago, Trinidad
MJC-292	TTLEP094-19	OP927343	BOLD:AAK1660	*militta*	orange	F	658	Trinidad & Tobago, Trinidad
MJC296	TRIN026-21	OP927342	BOLD:AAK1660	*militta*	*dioptis*	M	648	Trinidad & Tobago, Trinidad
MJC474	TRIN134-22	OP927337	BOLD:AAK1660	*militta*	orange	F	650	Trinidad & Tobago, Trinidad
YB-BCI145251	BCIAR1110-19	MN620737	BOLD:AAK1660	*maculifrons*	*maculifrons*	M	658	Panama
CLV1162	LNOUB105-10	HQ571861	BOLD:AAM6367	*exposita*			658	French Guiana
MILA 2005	ARCTD957-15	OQ026174	BOLD:AAM6367	*exposita*		M	658	French Guiana
BEVI1180	ARCTC633-10	JN275732	BOLD:ABZ2392	sp. cf. *collaris*	*collaris*	M	658	Paraguay, Alto Parana
MILA 0212	ARCTA212-07	OQ413337	BOLD:ABZ2392	sp. cf. *collaris*	*dioptis*	M	619	Bolivia , La Paz
MILA 1760	ARCTD635-12	OQ413338	BOLD:ABZ2392	sp. cf. *collaris*	*collaris*	M	658	Paraguay, Alto Parana
MJC_135	TRIN001-21	OP927326	BOLD:AEI2170	*pseudocollaris* (holotype)	*collaris*	M	643	Trinidad & Tobago, Trinidad
MJC_137	TRIN003-21	OP927330	BOLD:AEI2170	*pseudocollaris* (paratype)	*collaris*	M	641	Trinidad & Tobago, Trinidad
MJC_143	TRIN009-21	OP927321	BOLD:AEI2170	*pseudocollaris* (paratype)	white	F	640	Trinidad & Tobago, Trinidad

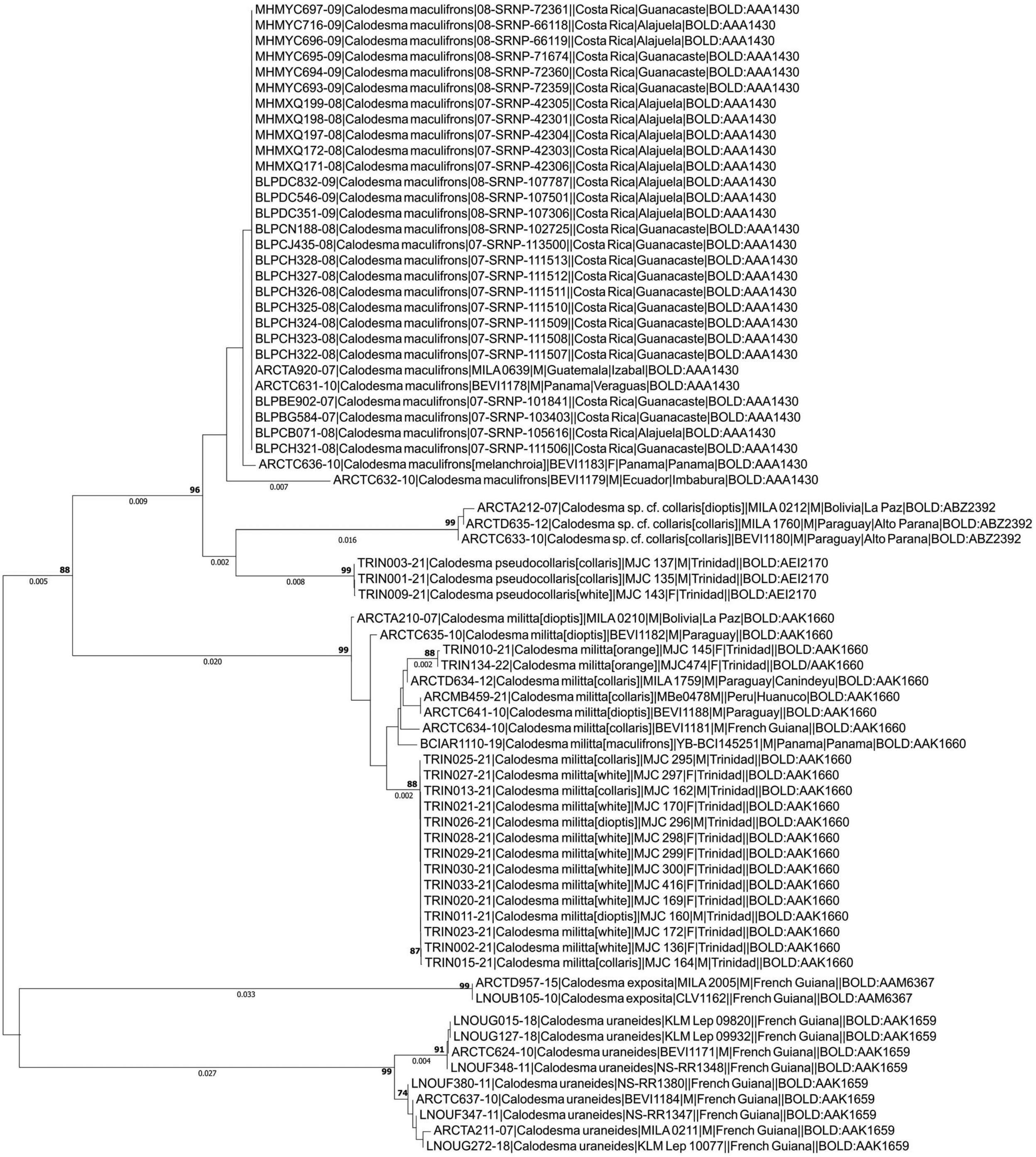

FIGURE 12. Similarity relationships of *Calodesma* spp. based on this work, barcodes from the ML collection, and selected public sequences in BOLD. Many duplicate DNA barcodes available for *C. maculifrons* from Costa Rica and some for *C. militta* from Trinidad are omitted so as to facilitate presentation. The taxonomy used is that developed in this work, and where relevant the names used here for the various morphs are included in parentheses after the scientific name. Bootstrap values are shown only if >70% and distances only if >0.002. The evolutionary history was inferred using the Neighbor-Joining method (Saitou and Nei 1987). The optimal tree with the sum of branch length = 0.15482979 is shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches (Felsenstein 1985). The tree is drawn to scale, with branch lengths (next to the branches) in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Kimura 2-parameter method (Tamura *et al.* 2004) and are in the units of the number of base substitutions per site. The analysis involved 73 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair. There was a total of 689 positions in the final dataset. Evolutionary analyses were conducted in MEGAX (Kumar *et al.* 2018).

FIGURE 13. Life history of *Calodesma militta*, *collaris* morph, collected as penultimate instar on *Malpighia glabra*, Trinidad, Mt. Hope, 10.646 -61.420 (Gosula 2021); penultimate instar found 24.iv.2021; pupated 1.v.2021; adult 11.v.2021. Top row, penultimate instar caterpillar; second row, final instar caterpillar; third row, cast final instar caterpillar skin and pupa; bottom row, adult male.

Hajo Gernaat (pers. comm. 2021) will shortly publish details of the early stages of a *collaris* morph of *C. militta* BOLD:AAK1660, which was reared on *Malpighia glabra* in Suriname. The caterpillar resembles that reared in Trinidad (Fig. 13).

Rutz *et al*. (2020) have reared what they refer to as *C. collaris* in Rio Grande do Sul, Brazil, where it is a pest of cultivated Bromeliaceae, particularly the indigenous *Aechmea winkleri* (Bromeliaceae). Only males of the *collaris* morph and females of the white morph were reared. The caterpillar and pupa illustrated are both plain brown. Thus, the caterpillar, pupa and food plant are very different to those of *C. militta* BOLD:AAK1660 reared in Trinidad (Fig. 13), so we suggest that the material of Rutz *et al*. (2020) is *C.* cf. *collaris* BOLD:ABZ2392, although it could also be some other species of this complex of which we are not aware. On this basis, we anticipate that *C. militta* BOLD:AAK1660 and *C.* cf. *collaris* BOLD:ABZ2392 will be clearly distinguished by their early stages. At this stage, there is no clear indication as to the foodplant of *C. pseudocollaris* **new species**, but given that its DNA barcode is clustered with that of *C.* cf. *collaris* BOLD:ABZ2392, it too may prove to be a bromeliad feeder.

Discussion

Our results raise more questions than answers. The Trinidad fauna of *Calodesma* clearly falls into two BINs, 6.15% different, which qualifies them to be treated as two distinct species. However, two (or potentially more) morphs (male *collaris* and white female morph) are common to both barcode species, the two species cannot reliably be separated based on their male genitalia, and adults can feed at the same flowers in the same places at the same time.

The commoner of the two BINs in Trinidad is the variable and widespread BOLD:AAK1660, which we treat as a single species. Alternatively, it might be suggested that DNA barcodes fail to separate the multiple species that make up BOLD:AAK1660. Our results from Trinidad offer support for BOLD:AAK1660 being a single variable species. In particular, the females are continuously variable for multiple factors as mentioned above and shown in Fig. 6, so that of the 18 sequenced white females of BOLD:AAK1660, no two are identical in wing markings. The seven sequenced females with orange markings (Fig. 7) are also all different, giving a strong indication that the orange morph is equally variable. From here it is a small step to accept that males are dimorphic, and that red females will be found to be members of one or both Trinidad species.

The two oldest available names which may be appropriate for BOLD:AAK1660 are *Thyrgis milittta* (Stoll, [1781]) and *C. amica* (Stoll, [1781]). BOLD:AAK1660 females of the orange morph with a forewing band, but no hindwing band (Fig. 7) are similar to Stoll's figure of *T. militta* (Fig. 1). In particular, and matching Stoll's figure, the forewing band can have a sinuous shape, the band narrows towards the tornus, the band may widen at the costa (more so in ventral view), and one specimen shows a small orange spot basal to the band. At this time, we are not aware of specimens of this phenotype from the Guianas (type locality of *T. militta* Suriname), although BOLD:AAK1660 does occur in Suriname and French Guiana. We conclude that *T. militta* is a member of BOLD:AAK1660 and hence it is currently the senior name for this BIN. It follows that it is necessary to transfer *T. militta* to the **new combination** *Calodesma militta.* Furthermore, since *T. militta* is the type species of *Thyrgis* (Lamas 2017), as anticipated by Lamas (2017) and Laguerre (2017), *Thyrgis* Walker, 1854 is therefore a **junior synonym** of *Calodesma* Hübner, [1820]. As Lamas (2017) and Laguerre (2017) further anticipated, the next available name for the genus hitherto known as *Thyrgis*, is the **reinstated genus** *Seileria* Dognin, 1923. The type species of *Seileria* is *S. eucyaniformis* Dognin, 1923 (TL Colombia, Villavicencio), and although Laguerre (2017, p. 98) was only able to discuss this species in a footnote added in press, its habitus and male genitalia (Fig. 14) resemble those of the other species hitherto in *Thyrgis*. Therefore, the remaining eight species and their subspecies currently in *Thyrgis* (Lamas 2017) are transferred to **new combinations** as species of *Seileria*: *S. angustifascia* (Hering, 1925), *S. basipunctata* (Hering, 1926), *S. constrictifascia* (Dognin, 1919), *S. flavonigra* (Dognin, 1910), *S. investigatorum* (Toulgoët, 1988), *S. marginata* (Butler, 1875), *S. meres* (Druce, 1911), *S. phlegon* (Druce, 1885), *S. phlegon ruscia* (Druce, 1895), *S. tenuifascia* (Hering, 1930) and *S. tenuifascia daguana* (Hering, 1930). *Eucyanoides* Toulgoët, 1988, currently a synonym of *Thyrgis*, is now a **new subjective synonym** of *Seileria*.

Based on the variation we have seen within the white female morph of *Calodesma* sp(p). in Trinidad (Fig. 6), it is likely that a red morph of BOLD:AAK1660 that matches Stoll's figure of *amica* is possible, in which case, *C. amica* would be an available name for BOLD:AAK1660. The two names, *militta* and *amica* were published simultaneously (Stoll 1780–1782), and so anticipating that they will be demonstrated to be synonyms in the future, we here stipulate as 'First Reviser' that *militta* should have precedence over *amica* in that eventuality (ICZN article 24.2.2). This will ensure stability for the taxon based on BOLD:AAK1660. However, since we have failed to sequence any red morphs of *Calodesma* and establish their affinities, we have to leave the identity of *C. amica* open and do not treat it as part of BOLD:AAK1660 at this time. If BOLD:AAK1660 is confirmed to include a red female morph, the putative type specimen of *C. amica* in NHMUK is a poor match to Stoll's figure, although it too is likely to be a member of BOLD:AAK1660 (e.g. Fig. 6.I with red substituted for white would resemble the putative type).

The identity of the next oldest name *C. collaris* (Drury, 1782) is ambiguous, as there are differences in the detail between Drury's description, the published plate (Drury 1782, p. 27, Plate 21.2, and p. [77] index) shown here with the putative holotype (Fig. 1) and material currently interpreted as *C. collaris* (Fig. 4). The description does not mention the colour of the collar; it is orange in specimens currently interpreted as *C. collaris* (Fig. 4). The collar is white in at least some plates of Drury's hand-painted published work (e.g. the copies in the Bibliothèque Nationale de France (Paris) and the Smithsonian Institution (Washington); the former available from Gallica, and the latter from the Biodiversity Heritage Library, Fig. 1), but orange in others (e.g. copies in Cornell University Library, University of Alberta and NHMUK; the first two available from Biodiversity Heritage Library). The description states the tongue (i.e. proboscis) is yellow, but it is dark brown in specimens (Fig. 15). The description further states that the palpi are black, whereas only palpi segments 2 and 3 are black and segment 1 is pale orange (Fig. 15). The description also states that the anus (i.e. area around genitalia) is yellow; this area is orange in males but black in females; this is a strong indication that the specimen Drury described was a male, but the antennae in the plate are not bipectinate, rather they are simple, like those of the female.

FIGURE 14. Habitus and male genitalia of *Seileria eucyaniformis* Dognin, type species of the genus *Seileria.* Specimen in MNHU.

Lamas (2017) refers to the holotype in HUMG 'by monotypy'. Drury (1782) does not explicitly state the location of any type material, although some of his types are in HUMG. Our investigation revealed that the specimen thought to be the holotype in HUMG (136410; http://collections.gla.ac.uk/#/details/ecatalogue/137131) differs significantly from Drury's description and plate and is in fact a female *Pheles atricolor* (Butler) (Riodinidae), the identification being confirmed by Jason P.W. Hall (pers. comm. 2020). We conclude that this specimen cannot be the holotype, although it might be a syntype. However, there is a second specimen in HUMG (136411; http://collections.gla.ac.uk/#/details/ecatalogue/137132), which does resemble the description and plate, and we designate this the **lectotype** (Fig. 1). It is a male, with only part of the antennae, which appear bipectinate; the abdomen is missing although at least two legs remain. Drury (1782) described *C. collaris* from Brazil, but Westwood (1837–1842) added more detail based on Drury's records, and clarified that it was sent from Rio de Janeiro by Mr Bonifas in 1775. We have not been able to obtain DNA barcodes for specimens of this appearance from this area, but BOLD:AAK1660 and BOLD: ABZ2392 occur together in Bolivia, Paraguay and north-eastern Argentina, so either or both could occur in the vicinity of Rio de Janeiro and represent Drury's *C. collaris*. As we cannot distinguish BOLD:AAK1660 and BOLD:ABZ2392 on external characters, the true identity of *C. collaris* cannot be resolved without a DNA barcode from the lectotype.

FIGURE 15. Views of the head and anterior thorax of *Calodesma militta*, male *collaris* morph**.**

We do not know what ecological differences there may be between the two Trinidad barcode species, and we can only relate one of the two taxa to the named species from northern South America. To deal with this potential impasse, we treat BOLD:AAK1660 as *Calodesma militta*, describe BOLD:AEI2170 as *C. pseudocollaris* **new species** (below), and refer to BOLD:ABZ2392 as *Calodesma* cf. *collaris* BOLD:ABZ2392. As we do not have any sequences from the Amazon basin, we do not know how far north the range of *Calodesma* cf. *collaris* BOLD: ABZ2392 may extend. This makes it difficult to adjudicate which other available names are synonyms of which of these species. Until we know otherwise, we assume *C. pseudocollaris* is uncommon, restricted to northern South America and absent from the Guianas. We believe that *C. dioptis*, *C. plorator* and *C. lacryma* are more likely to be synonyms of *Calodesma militta* (BOLD:AAK1660), than of *C. pseudocollaris* **new species** or *Calodesma* cf. *collaris* BOLD:ABZ2392, as follows.

Calodesma dioptis was described from a single male from Amazonas (Table 1) which is now in NHMUK (Fig. 1). Males of the *dioptis* morph are known from both *C. militta* and *Calodesma* cf. *collaris* BOLD:ABZ2392 but not from *C. pseudocollaris* **new species** Although there are no sequenced examples of *C. militta* from the Amazon, it occurs north and south of the Amazon Basin, so the type locality of *C. dioptis* is anticipated to be within this range. However, based on current knowledge, this is not true for *Calodesma* cf. *collaris* BOLD:ABZ2392, which at this time has been found only in southern South America. As males of the *dioptis* morph are not known from *C. pseudocollaris* **new species**, and there are no sequences of this latter species from anywhere but Trinidad, it is unlikely that *C. dioptis* will be found to be synonymous. Therefore, we anticipate *C. dioptis* will prove to be a synonym of *C. militta*.

Calodesma lacryma was described from French Guiana (Table 1) and there is a single female type in USNM (Fig. 1). The holotype falls within the range of variation found amongst the white female morph of *C. militta* BOLD: AAK1660 in Trinidad (Fig. 6). *Calodesma militta* (BOLD:AAK1660) is known to occur in French Guiana. There is only one female of *C. pseudocollaris* **new species** so we cannot assess its variability, and there is no indication that the range of this species extends to the Guianas. We therefore consider it appropriate to treat *C. lacryma* as a **new synonym** of *C. militta*.

Calodesma plorator was described from Trinidad (Table 1) and the holotype is in NHMUK (Fig. 1). It is a female of the white morph and fits in the range of variation seen in *C. militta*, but is also close to the single sequenced female of *C. pseudocollaris* **new species** Based on our samples, only one female out of 19 sequenced white female morphs from Trinidad was allocated to *C. pseudocollaris* **new species**, so the odds are strongly in favour of *C. plorator* also being a synonym of *C. militta*. However, without a sequence from the holotype, this cannot be unambiguously confirmed. Nevertheless, as an interim arrangement, we choose to adopt the most likely scenario, and therefore treat *C. plorator* as a **new synonym** of *C. militta*. At some time in the future, sequencing the types of *collaris*, *dioptis*, *lachryma* and *plorator* will enable these conclusions to be tested. At that time. it should be straightforward to link these names to the species concepts used here. In the unlikely event that any of these names prove to apply to *C. pseudocollaris* **new species**, they would then have precedence.

Given these assumptions, and provisional synonyms, BOLD:AEI2170 from Trinidad is undescribed. Given the 0.82% difference between the DNA barcodes of *C. maculifrons* from Costa Rica (BOLD:AAA1430) and BOLD:AEI2170, one option might be to treat it as a subspecies of *C. maculifrons*. However, we note that these two BINs and BOLD:ABZ2392 form one cluster (Fig. 12) and that each group in the cluster has its own BIN. Further, although BOLD:AEI2170 clusters with BOLD:ABZ2392, the latter is more than 2% different from both the other BINs in the group. *Calodesma maculifrons* and BOLD:AEI2170 differ greatly in habitus, but without life history data for the later and/or genomic data, it is difficult to choose between treating BOLD:AEI2170 and BOLD:ABZ2392 as subspecies of *C. maculifrons* or separate species. As a working hypothesis, we opt to treat them as separate species, and we propose the species name *C. pseudocollaris* **new species** below, to facilitate reference to BOLD:AEI2170.

Calodesma dilutana was described from Amazonas (Table 1), and the holotype was examined in NHMUK (Fig. 2). Lamas (2017) refers to the holotype as male, but it is a female of the orange morph. Lamas (2017, endnote 15) states *C. contracta*, *C. dilutana* and *C. contracta itaitubae* (Fig. 2) are probably conspecific. Given what we now know about the variability of white females of *C. militta*, extrapolating to the orange morph suggests that all three names, as well as *C. kedar* (Fig. 2) are likely to be synonyms referable to *C. militta*. However, as we do not have sequenced specimens exactly matching the types, or from the type localities, we refrain from reaching any firm conclusions.

The two specimens of a red morph from Trinidad (Fig. 8) were not successfully sequenced; they have the forewing band broader and more continuous than seen in the white and orange morphs; further the female with hindwing markings has submarginal spots rather than a submarginal band. Given that these markings are not an exact match to any observed from Trinidad in the white and orange female morphs, we hesitate to draw firm conclusions. However, while it is possible that they represent an additional species, the male for which is currently unknown, we think it more likely that when fresh material can be sequenced they will be found to group with *C. militta*, or possibly *C. pseudocollaris* **new species**, or both.

Taxonomic treatment

Based on these assumptions and conclusions, our taxonomic treatment is as follows. We recognise three very similar South American species with some phenotypes in common: *C. militta* (BOLD:AAK1660), *C.* sp. cf. *collaris* (BOLD:ABZ2392) and *C. pseudocollaris* **new species** (BOLD:AEI2170).

***Calodesma militta* (Stoll, [1781]) BIN: BOLD:AAK1660**
Chamesthema dioptis C. Felder & R. Felder, 1874, TL [Brazil, fl(umen) Amazonas], is probably a synonym.
Thyrgis lacryma Dognin, 1919, TL French Guiana, is made a synonym.
Centronia plorator Kaye, [1923], TL Trinidad, is made a synonym.
Phalaena collaris Drury, 1782, TL Brazil, [Rio de Janeiro], may be a synonym.
Josia (*Thyrgis*) *contracta* Walker, 1854, TL 'South America', may be a synonym.
Eucyane chesalon Druce, 1885, TL Ecuador, [Pastaza], may be a synonym.
Eucyane kedar Druce, 1900, TL Colombia, [Magdalena], may be a synonym.
Eucyane dilutana Druce, 1907, TL [Brazil], 'Amazons', may be a synonym.
Calodesma contracta itaitubae Hering, 1925, TL [Brazil, Pará, Rio Tapajós], Itaituba, may be a synonym.
Calodesma contracta apicalis Hering, 1925, TL [Brazil], Bahia, may be a synonym.
Calodesma jordani Hering, 1925, TL Paraguay, may be a synonym.
Phalaena amica Stoll, [1781], Suriname may be a synonym.

This species is known from Panama, Trinidad, French Guiana, Bolivia, Paraguay and Argentina. Males are mostly dimorphic (*collaris* and *dioptis* morphs), but the single male specimen from Panama resembles the Central American male *C. maculifrons*. Females are dimorphic (white and orange morphs) and highly variable. When more sequences are available, females are expected to be trimorphic (red morph as well). The following sequenced specimens from Trinidad belong to this taxon:

Males *collaris* morph. Arima Valley, nr. Asa Wright, eupatorium flowers: ♂ 23.ix.2017 (John Morrall) [MJWC, DNA 139]. Cat's Hill, eupatorium flowers: ♂ 24.ix.2017 (John Morrall) [MJWC, DNA 138]. Inniss Field, eupatorium flowers: ♂ 6.i.2019 (S. Alston-Smith) [MJWC, DNA 306]. Parrylands, eupatorium flowers: 3♂x.2017 (S. Alston-Smith) [MJWC, DNA 162-164]; ♂ ix.2018 (S. Alston-Smith) [MJWC, DNA 295]

Males *dioptis* morph. Parrylands, eupatorium flowers: 2♂ x.2017 (S. Alston-Smith) [MJWC, DNA 160-161]; ♂ ix.2018 (S. Alston-Smith) [MJWC, DNA 296]

White female morph. Cat's Hill, eupatorium flowers: 4♀ 24.ix.2017 (John Morrall) [MJWC, DNA 136, 140-142]. Parrylands, eupatorium flowers: 10♀ x.2017 (S. Alston-Smith) [MJWC, DNA 165-174]; 4♀ ix.2018 (S. Alston-Smith) [MJWC, DNA 297-300]

Orange female morph. 3♀ Arima Valley, Simla: xii.2020 (S. Alston-Smith) [MJWC, DNA 470, 474, 475]. Hololo Mountain Road, eupatorium flowers: ♀ 3.x.2017 (John Morrall) [MJWC, DNA 145]. Lalaja Ridge, eupatorium flowers: ♀ 23.xii.2019 (J. Morrall) [MJWC, DNA 377]. East of Point Fortin, *Eupatorium* fls: ♀ 30.ix.1982 (M.J.W. Cock) [MJWC, DNA 291]. Rio Claro-Guayaguayare Road, milestone 6.5, *Eupatorium* fls: ♀ 17.ix.1978 (M.J.W. Cock) [MJWC, DNA 292]

Calodesma cf. *collaris* BIN: BOLD:ABZ2392

Phalaena collaris Drury, 1782, TL Brazil, [Rio de Janeiro], may be an available name.

This species is known from Bolivia, Paraguay and Argentine. Males are dimorphic (*collaris* and *dioptis* morphs); sequenced females are white morphs only.

Calodesma pseudocollaris Cock, new species,

BIN: BOLD:AEI2170
urn:lsid:zoobank.org:act:464505E0-2DFE-4146-9C03-0D74A6A5E8AE
(Figs. 9, 10, 16)

Type material. Holotype ♂: Trinidad, W.I., Cat's Hill, eupatorium flowers, 24.ix.2017, John Morrall / DNA sample 135, M.J.W. Cock / M.J.W. Cock dissection 1001 / Holotype *Calodesma pseudocollaris* Cock (to be deposited in NHMUK, ex MJWC).

Allotype ♀: Trinidad, W.I., Cat's Hill, eupatorium flowers, 24.ix.2017, John Morrall / DNA sample 143, M.J.W. Cock / Allotype *Calodesma maculifrons pseudocollaris* Cock (to be deposited in NHMUK, ex MJWC).

Paratype ♂: Trinidad, W.I., Cat's Hill, eupatorium flowers, 24.ix.2017, John Morrall / DNA sample 137, M.J.W. Cock / Paratype *Calodesma maculifrons pseudocollaris* Cock (to be deposited in NHMUK, ex MJWC).

Diagnosis. *Calodesma pseudocollaris* **new species** has males of a *collaris* morph and the only known female is a white morph resembling the type of *C. plorator*. It cannot be distinguished from these morphs of *C. militta* on external morphology or reliably on male genitalia, but can be separated by its DNA barcode. Having said that, the aedeagus of *C. pseudocollaris* **new species** was noted to be less elongate distally, with a shorter distal opening compared to *C. militta*, but individual variation would need to be evaluated on a larger sample before this could be relied upon as a diagnostic feature. Further, the two males are slightly smaller than typical for Trinidad material of *C. militta*, i.e. forewing length 17–19 mm (male), 20 mm (female), compared to male *collaris* morph 19.2 mm (range 18–20, n=6) and white female morphs 21.3 mm (range 20–22 mm, n=18) of *C. militta*, but again we have not seen enough material of *C. pseudocollaris* **new species** to know whether this could be a useful character. Males resembling *C. dioptis* and females with other variants of the white markings or females with orange or red markings as found in *C. militta* are not known for this new species, but the small sample size does not preclude these possibilities.

Description. **Male** as shown in Figs. 9 A-B (full view), 16 A–C (head and anterior thorax), and 10 (male genitalia). **Head**. Lateral and ventral head orange; dorsum dark, with two white dots above the scape; frons dark with some orange setae and a white border; antennae black, with white scaling on pedicel, bipectinate almost to apex;

eyes black; labial palpi segment 1 pale orange; labial palpi segments 2 and 3 black with inner lower margin white. **Thorax**. Collar orange. Dorsally black apart from inner margins of tegulae are white-orange and there is a very short orange dorsal line between the tegulae. Ventrally prothorax and mesothorax orange shading into blackish posteriorly on mesothorax; metathorax black. Forelegs back, with two white-orange lines on the femur, two white lines on the posterior tibia and white scales on the outer margin of the remainder of the leg. Midlegs black, with one (holotype) or two (paratype) white lines the length of posterior tibia, and the remainder of the leg dark (holotype), or with white scales on outer margin (paratype). Hindlegs missing on holotype; as midlegs on paratype. Abdomen black, the posterior margin of the sternites white, and orange scales around the edge of the genitalia. **Wings**. Forewing length 17 mm (holotype), 19 mm (paratype). Dorsal forewing black, with the veins of the dorsal half paler; large white postdiscal spot; fringe black, weakly white at apex. Ventral forewing black; white postdiscal spot as dorsally; fringe white at apex, weakly so in spaces 1B and 2 (CU_2-2A and Cu_1-Cu_2). Dorsal hindwing black, with a narrow, faint white spot at apex; fringe white. Ventral hindwing black, with veins paler in the basal part of the wing; apical spot more clearly marked than in dorsal view; fringe white. **Genitalia**. Small and weakly sclerotised. Tegumen domed and bulbous. Uncus simple, acute, strongly downcurved distally; a broad, bilobed, very weakly sclerotised dorsal project projects posteriorly behind tegumen. Valvae almost membranous, simple. Saccus well developed. Aedeagus short, with a strong bulbous ventral lobe at base; the apex obliquely truncate; no indication of structures associated with the vesica.

Female as shown in Figs 9 C (full view) and 16 D–F (head and anterior thorax). Generally similar to the male apart from the weakly serrate antennae, no orange scales around genital opening, and the larger, broader, less pointed forewings, and more rounded hindwing. Forewing length 20 mm (allotype). The white markings of the wings differ from the male. Dorsal forewing with the white discal spot narrower, extending to the costa and in a narrow arc to the dorsum just basal to tornus; the white markings on the costa and in space 3 (M_3-Cu_1) are suffused with black. Ventral forewing as dorsal; fringe black. Dorsal hindwing with no white apical spot; a weak white marginal-submarginal band, strongly suffused with black and with the veins black; the band starts narrow on the margin in space 1B (Cu_2-2A) and widens and separates from the margin until space 5 (M_1-M_2). Ventral hindwing as dorsal but marginal-submarginal band less suffused with black; fringe black, slightly paler at apex. Genitalia not examined.

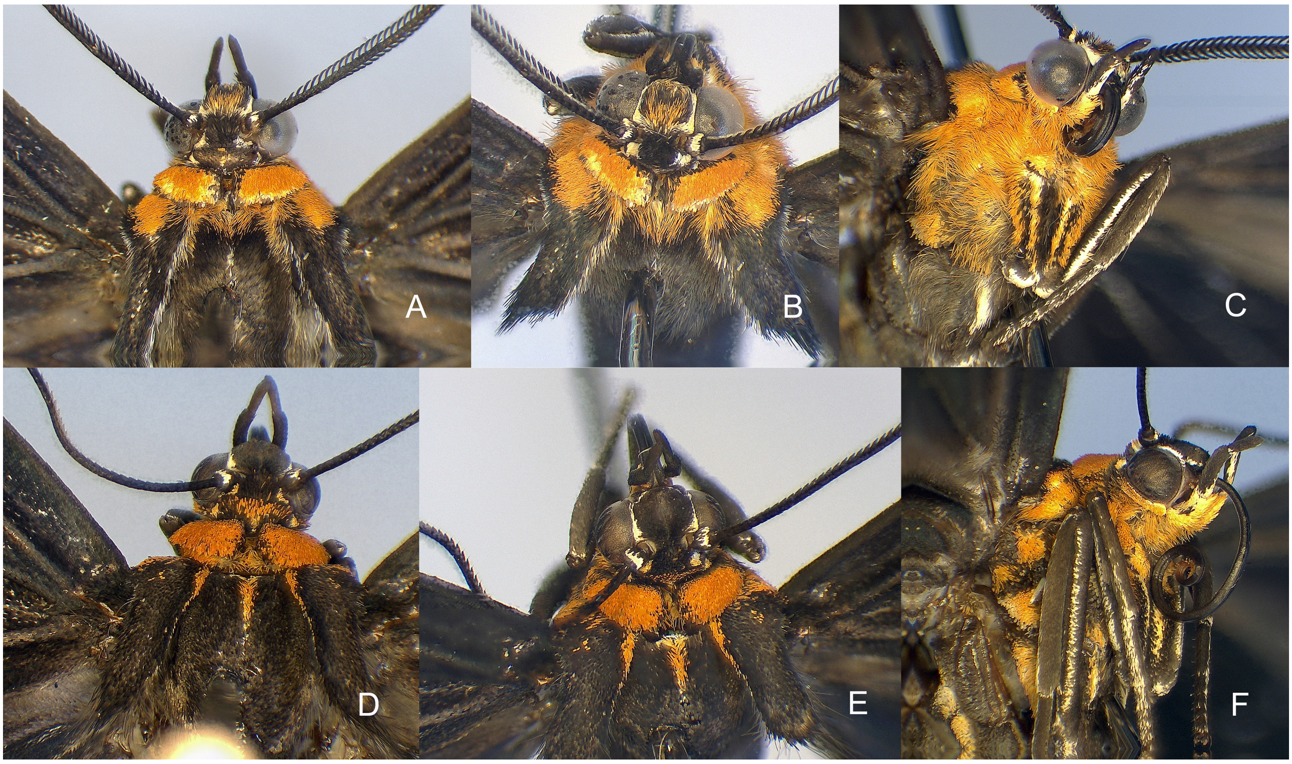

FIGURE 16 Views of the head and anterior thorax of *Calodesma pseudocollaris* **new species.** A–C paratype male. D–F allotype female.

DNA barcodes. Three identical barcodes were obtained, which form BIN BOLD:AEI2170, most similar to *C.* sp. cf. *collaris* BOLD:ABZ2392 and *C. maculifrons* BOLD:AAA1430 (Fig. 12).

Variability. Only two males of the *collaris* morph and one white female morph have been sequenced. Given these small numbers and the relative frequency of the different morphs in *C. militta*, our sample is too small to comment on the probability of this subspecies occurring in other morphs and colours.

Distribution. Trinidad and Tobago, Trinidad: Cat's Hill (type series). This is an area of disturbed lowland forest with scattered on-going oil extraction using pumpjacks.

Etymology. The name refers to the resemblance of the males to *C. collaris*, but that they are a different species, i.e. false *collaris*. The original name, *collaris*, is adjectival in the genitive case, unchanging for gender agreement; it refers to the orange collar.

An overview of the genus *Calodesma*. Finally, we revisit the list of valid taxa in the genus *Calodesma*, and summarize in Table 5, the implications of what we report here. For convenience, we refer to the *militta* group, which comprises *C. macularis*, and the three species that include males of the *collaris* morph: *C. militta* (BOLD: AAK1660), *Calodesma* sp. cf. *collaris* (BOLD: ABZ2392), and *C. pseudocollaris* **new species** (BOLD:AEI2170).

TABLE 5. Comments on the valid species names of *Calodesma* in light of our findings.

Valid name	Sex of type(s)	Type locality	Comments
albiapex Hering 1925	♀	Brazil, Bahia	Synonym in *militta* group
amica Stoll, [1781]	♀	Suriname	Probably synonym in *militta* group
apicalis Hering, 1925	♂, ♀	Brazil, Bahia	Synonym in *militta* group
approximata Hering, 1925	♂	French Guiana	♂ synonym of *C. uraneides*
chesalon Druce, 1885	♀	East Ecuador	Synonym in *militta* group
collaris Drury, 1782	♂	Brazil, Rio de Janeiro	Synonym in *militta* group
contracta Walker, 1854	♀	'South America'	Synonym in *militta* group
dilutana Druce, 1907	♀	Brazil, 'Amazons'	Synonym in *militta* group
dioptis C. Felder & R. Felder, 1874	♂	Brazil, 'Amazons'	Synonym in *militta* group
eucyanoides Hering, 1925	♂, ♀	Amazons (Peru, Brazil)	Valid species
exposita Butler, 1877	♀	Brazil, Pará	Valid sexually dimorphic species[1]
itaitubae Hering, 1925	♀	Brazil, Pará	Synonym in *militta* group
jordani Hering, 1925	♀	Paraguay	Synonym in *militta* group
kedar Druce, 1900	♀	Colombia	Synonym in *militta* group
lacryma Dognin, 1919	♀	French Guiana	Synonym of *C. militta*
maculifrons Walker, [1865] (=*C. melanchroia*)	♂	Honduras	Valid species in *militta* group
militta Stoll, [1781]	♀	Suriname	Valid species in *militta* group
niepelti Hering, 1925	♂	Colombia	Subspecies or synonym of *C. uraneides*. Only known from ♂.
occidentalis Hering, 1925	♀	Ecuador	Synonym in *militta* group
plorator Kaye, [1923]	♀	Trinidad	Synonym of *C. militta* (or possibly senior synonym of *C. pseudocollaris*)
quadrimaculata Hering, 1925	♀	Bolivia	Probably synonym in *militta* group
rubricincta Dognin, 1923	♀	Colombia	Perhaps synonym in *militta* group
tamara Hering, 1925	♀	Amazons (Peru, Brazil)	Valid species; Only known from ♀.
uraneides Butler, 1871	♀	French Guiana	Valid species

[1] The male can be seen here: http://v3.boldsystems.org/index.php/Taxbrowser_Taxonpage?taxid=450899

Our similarity tree (Fig. 12) indicates six species of *Calodesma*, a relatively small proportion of the 21 named species. However, of the valid species recognised in our overview (Table 5) only *C. tamara* and *C. eucyanoides* are not included in Fig. 12; all the others are expected to fall within the *C. militta* group, except perhaps C. *quadrimaculata* and C. *rubricincta*. Progress with the allocation of which of these names are synonyms of which of the species recognised here will now depend on sequencing the original type material, or strong evidence based on distribution of morphs and species. This is well beyond our scope, but we hope our work will encourage others to address this challenge.

Concluding discussion

This study has shown that there are two species of *Calodesma* in Trinidad. One, *C. militta* (BOLD:AAK1660), is common in Trinidad, very widespread in South America, sexually dimorphic and extremely variable in the female (Figs. 6). The other, *C. pseudocollaris* **new species** (BOLD:AEI2170, Fig. 9) is relatively uncommonly collected, so far only known from Trinidad, and the male and female each closely resemble the corresponding commonest morph for that sex of *C. militta*.

At the risk of indulging in speculation, we offer a possible interpretation of the patterns involved based on Müllerian mimicry and mimicry rings. A mimicry ring is a group of species with similar conspicuous aposematic or warning markings that is usually based on Müllerian mimicry, but may also include Batesian mimicry and stages in between, such as moderately distasteful species, or species that are sometimes distasteful and sometimes not. The distasteful species may have sequestered poisonous chemicals from their food plants or have synthesised poisonous chemicals. The mimicry ring provides protection to the participants from visually-hunting predators, particularly insect-eating birds, on the basis that birds will learn from first or early encounters that Lepidoptera of this form are distasteful, and so avoid them thereafter.

Noting that in Panama the only sequenced specimen of *C. militta* resembles the male of *C. maculifrons*, we suggest this is a local case of Müllerian mimicry, causing *C. militta* to diverge from the typical morphs found in South America and converge on a Central American model in areas where the two species overlap. Noting that *C. militta* and *C. maculifrons* are closely related, it is possible that a common ancestor had these different patterns incorporated into its genome, from where they could be rapidly switched on or off through natural selection (Fujiwara and Nishikawa 2016, McMillan *et al*. 2020).

In Trinidad, there are no obvious mimicry groups for the orange or red female morphs, but the two male morphs and the white female morph of *C. militta* and both sexes of *C. pseudocollaris* **new species** may well form part of a loose mimicry ring of diurnal black species with white spots or transparent patches on the wings which are most conspicuous and frequently observed when feeding on the white flowers of *Austroeupatorium inulaefolia* or the very pale pink flowers of *Chromolaena odorata*. In this situation, species with white spots and species with transparent spots will look similar because of the underlying white or pale flowers. In Trinidad, in addition to white morphs of the two *Calodesma* spp., species which appear to belong to this mimicry ring include *Ctenucha andrei* Rothschild (Erebidae, Arctiinae, Arctiini, Ctenuchina), *Autochloris almon* (Cramer), *Calonotus craneae* Fleming, *C. tripunctatus* Druce (Erebidae, Arctiinae, Arctiini, Euchromiina), and *Melanchroia atera* (Stoll) (Geometridae, Ennominae) (Fig. 17), but only the last named is sometimes common. Alston-Smith and Morrall occasionally collected all these species on flowers of *A. inulaefolium* and *Chromolaena odorata* when collecting *Calodesma* spp. for this study (authors' unpublished data). We therefore suggest that there is natural selection within *Calodesma* spp. in Trinidad favouring the white morphs that fit this mimicry ring rather than the orange or red female morphs which do not fit another mimicry ring. There are several uncommon species of Riodinidae with similar orange markings, suggesting that this would not be a strong mimicry ring in Trinidad. The nearest models for the red morph are the much larger *Heliconius erato adana* Turner and *H. melpomene flagrans* Stichel (Cock 2020), which are perhaps too different in size to form an effective mimicry ring with red *Calodesma* morphs. The fact that orange morph of *C. militta* and the red morph expected to be part of *C. militta* persist in Trinidad suggests that they may be involved in stronger mimicry rings on the mainland. We have not been able to assess this, but casual observations in museum collections suggest that in other areas of South America orange and red morphs are more common than the white morph. Obviously, there is still much to consider and some interesting hypotheses to explore.

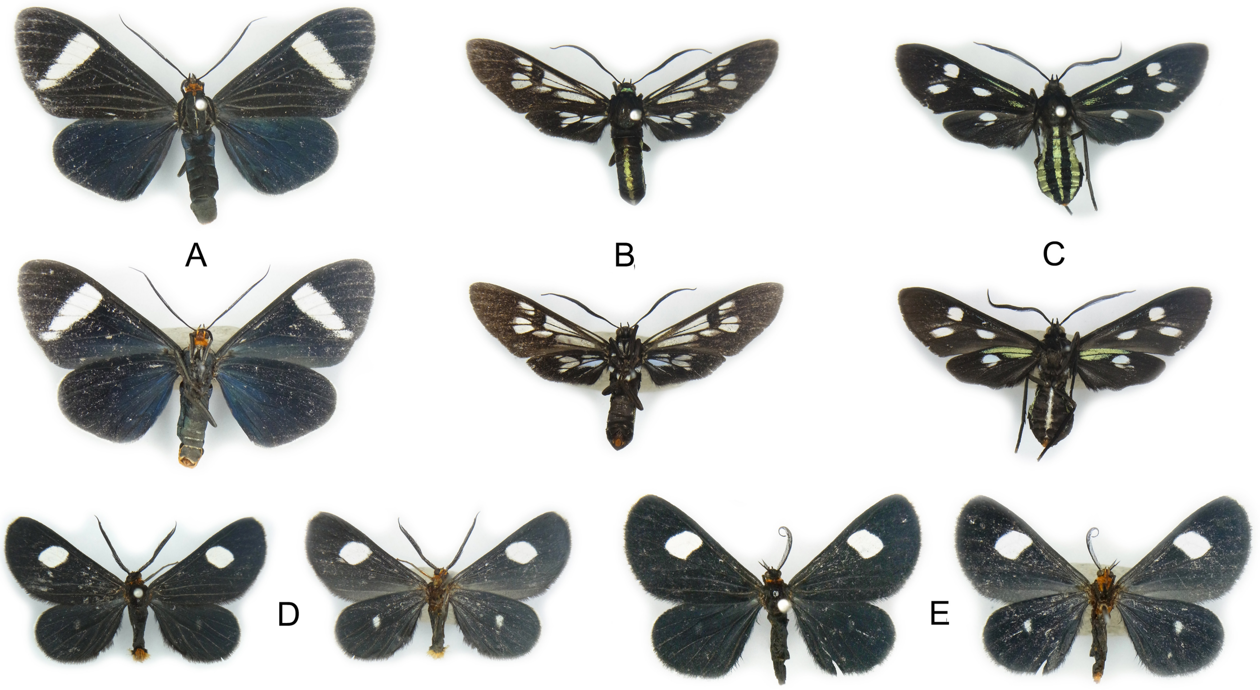

FIGURE 17. Mimicry ring of diurnal black moths with white or transparent spots in Trinidad, W.I. in which the white morphs of the two *Calodesma* spp. in Trinidad fit; all captured at flowers of *Austroeupatorium inulaefolium*; A-C, dorsal view above, ventral view below; D–E, dorsal view left, ventral view right. **A**, *Ctenucha andrei* Rothschild ♀ Cat's Hill, 24.ix.2017 (J. Morrall). **B**, *Autochloris almon* (Cramer) ♀, data as #A. **C**, *Calonotus tripunctatus* Druce ♀, data as #A. **D**, *Melanchroia atera* (Stoll) ♂, Parrylands, x.2017 (S. Alston-Smith). **F**, *M. atera* ♀, data as #A. Life size.

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