Harrisinopsis robusta Jordan, 1913 (Zygaenidae: Procridinae, Procridini) from Suriname: description of the female, hostplant and late larval stages, and synonymization of the genus Monalita tremewan, 1973 with Harrisinopsis Jordan, 1913

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HARRISINOPSIS ROBUSTA JORDAN, 1913 (ZYGAENIDAE: PROCRIDINAE, PROCRIDINI) FROM SURINAME: DESCRIPTION OF THE FEMALE, HOSTPLANT AND LATE LARVAL STAGES, AND SYNONYMIZATION OF THE GENUS *MONALITA* TREMEWAN, 1973 WITH *HARRISINOPSIS* JORDAN, 1913

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ABSTRACT. A rearing of *Harrisinopsis robusta* Jordan, 1913 (Zygaenidae: Procridinae) in Suriname is described. A cluster of 30–40 last instar, aposematically colored, larvae was found feeding on *Hirtella paniculata* (Chrysobalanaceae). Three females eclosed in April 2019 and two males in April-May 2020. The phylogeny of the *Monalita-Harrisinopsis* species group is shown, the habitus and genitalia of the species figured and the genus *Monalita* Tremewan, 1973 is synonymized with *Harrisinopsis* Jordan, 1913. Both sexes of *H. robusta* are described as are the last instar larvae and cocoon. The biology of the species is discussed.

Additional key words: *calibana, faurei, laguerrei,* early stages.

The Zygaenidae is a global family with 5 subfamilies and more than 1000 species (Efetov 1997, Efetov 1999, Efetov & Tarmann 2013a, Efetov & Tarmann 2013b, Efetov & Tarmann 2014a, Efetov & Tarmann 2014b, Efetov & Tarmann 2016, Efetov & Tarmann 2017, Efetov et al. 2014a, Efetov et al. 2014b). In the Neotropical Region, however, it is represented by only one subfamily, the Procridinae with one tribe, Procridini. The last review of the Zygaenidae in the Americas was in 1984 and listed 156 species (Tarmann 1984a, 1984b). A new checklist is in preparation (Efetov & Tarmann, in prep.). At the moment, 166 neotropical species are described but many are already known to be new and remain to be described.

The zygaenid fauna for French Guiana was reviewed in 2015 and consisted of 11 species (Tarmann & Drouet 2015). For Suriname, there are no known records. Although several Zygaenidae spp. have been reared in Costa Rica (Janzen & Hallwachs 2009), early stages or hostplants are not known for any species in South America.

The *Harrisinopsis-Monalita* species group (Zygaenidae: Procridinae: Procridini; Fig. 1) consists of four species in South America: *Monalita calibana* (Kaye, 1923) (Fig. 1i), described from Trinidad (Kaye 1923, Tarmann & Cock 2019), *Monalita faurei* (Tarmann & Drouet, 2015) (Fig. 1j), described from French Guiana, *Monalita laguerrei* (Tarmann & Drouet, 2015) (Figs 1k, l), described from French Guiana, and *Harrisinopsis robusta* Jordan, 1913 (Figs 1a–h). *H. robusta* was described from a male from "Amazonas" [Brazil] and has since been recorded from Peru (as *H. tessmanni* Hering, 1928, a junior synonym of *H. robusta*) and French Guiana (Jordan 1913, Hering 1928, Tarmann & Drouet 2015). The male was recently redescribed and the genitalia figured from French Guiana; description of the female was not possible, as the only female available at the time had a partly eaten abdomen (Tarmann & Drouet 2015).

A rearing of *H. robusta* in Suriname in 2019 prompted renewed study of the *Harrisinopsis-Monalita* species group. Here, the phylogeny of the group is re-analyzed, the genera *Harrisinopsis* and *Monalita* are synonymized, both sexes of *H. robusta* are described and the hostplant as well as the late larval stages are figured and described.

Materials and Methods

On 28 March 2019 on the premises of Palulu Camping near Zanderij airport, Para district, Suriname (N 05°25'30", W 055°11'35", 15 m a.s.l), about 40 km south of Paramaribo, the third author found 30–40 small blackish brown-orange larvae feeding on an unidentified plant. A fertile botanical collection of the plant was made and deposited in the herbarium of Naturalis Biodiversity Center (L), Leiden, the Netherlands (voucher Gernaat139). Thirteen larvae were collected and transported to Paramaribo into a

rearing cage with branches of the hostplant in a container with water at ambient temperature. They did not eat, however, soon left the hostplant and most died. On 31 March, the larvae had crept in the small opening between the lid and pot with the hostplant. On 1 April, four whitish cocoons were found on the underside of the lid and out of three of these, two females eclosed on 20 April 2019 and another female on 22 April 2019. To our surprise, on 26 April 2020 a male eclosed and on 25 May 2020 another male from a cocoon not previously found. Immediately after collecting the imagines, a leg was deposited in 100% alcohol for future barcoding. One male and two females (specimens male 7009DB, jvdh-2019-054, 25 May 2020; female 6578DB, RMNH.INS 981140, jvdh-2019-054, 20 April 2019; female 6428DB, jvdh-2019-054, 22 April 2019) were deposited in the collection of Naturalis (RMNH) and one male and one female in the collection of the Sammlungs und Forschungszentrum of the Tiroler Landesmuseen, Hall in Tirol, Austria (specimens male 2019054, 26 April 2020 (Z 4540) and female 2019054B, 20 April 2019 (Z 4434)).

Larval length was measured from the anterior end of the head capsule to the end of the anal plate. Larval setal length was measured from photographs and is reported here relative to the length of the body segment from which the seta originates. As this method is error-prone (segments may contract or extend), the setal lengths

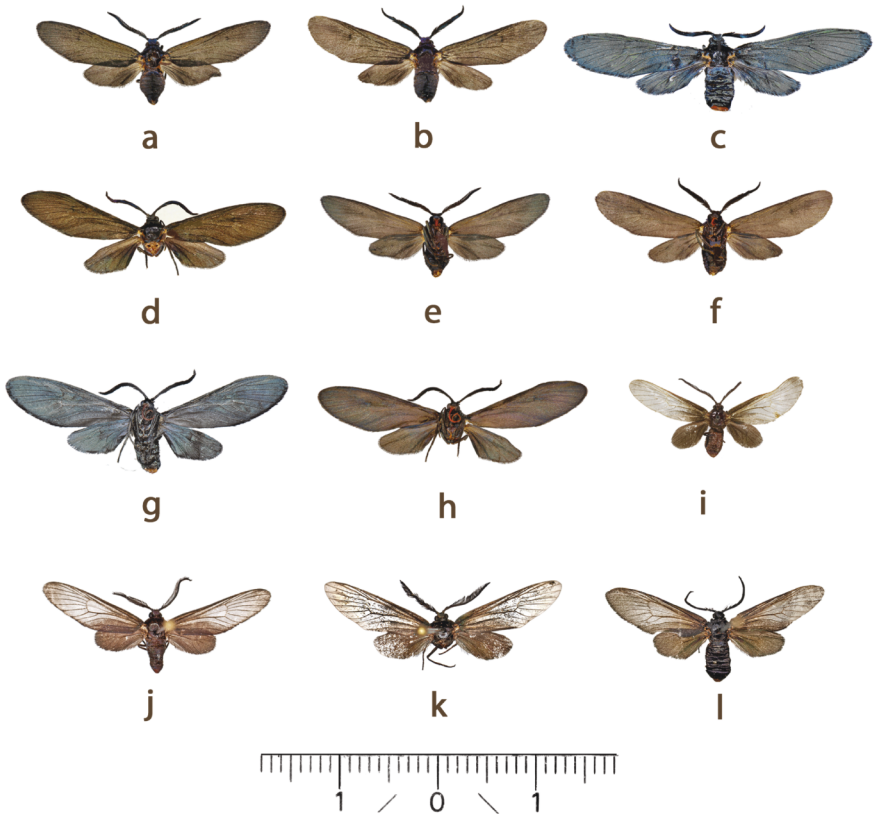

FIG.1. Habitus of members of the *Harrisinopsis-Monalita* species group (Zygaenidae: Procridinae: Procridini). **a**: reared male *Harrisinopsis robusta* Jordan, 1913, Suriname, eclosion 26 April 2020, dorsal view; **b**: reared male *H. robusta*, Suriname, eclosion 25 May 2020, dorsal view; **c**: newly eclosed, reared female *H. robusta,* Suriname, eclosion 22 April 2019, dorsal view; note dark bluish-green sheen; **d**: reared female *H. robusta*, Suriname, eclosion 28 March 2019, ventral view; **e**: specimen a, ventral view; **f**: specimen b, ventral view; **g**: newly eclosed, reared female *H. robusta,* Suriname, eclosion 20 April 2019, ventral view; note dark bluish-green sheen; **h**: specimen d, ventral side; **i**: *Monalita calibana* (Kaye, 1923), Trinidad, holotype, female, dorsal view; **j**: *Monalita faurei* Tarmann & Drouet, 2015, French Guiana, Kaw, pk. 37, 7 July 2000 (D. Faure, leg.), male holotype, dorsal view; **k**: *Monalita laguerrei* Tarmann & Drouet, 2015, French Guiana, piste de Kaw, pk 40+2, 260 m, 24 July - 1 August 2003 (M. Laguerre leg.), male holotype, dorsal view; **l**: *M. laguerrei*, French Guiana, Papinabo, Kourou, 28 July 2003 (D. Faure), female paratype, dorsal view. Scale in mm.

mentioned should be considered as approximations. To avoid lengthy formulations as "2 times the length of a body segment", this is noted as "2 S".

Photographs of the early stages were made with a Nikon D300s camera, an AF Micro Nikkor 105 mm 1:2.8 D lens and a SB-700 flash. The imagines in Leiden were photographed with a Nikon D 800 and an AF-S Micro Nikkor 105 mm 1:2.8 G lens with a standard grey card as background. Photographs were made in NEF-format and with minor adjustments of exposure, contrast and sharpening converted to TIF-files in the same color space. The imagines in Innsbruck were photographed with a Canon EOS 70D mounted on a stand using a SIGMA objective 150mm APO MACRO DG HSM and a specially developed 'photo box' (Black box) with LD illumination with a light grey card as background. The genitalia pictures were made with an OLYMPUS BH2 Microscope and a PANASONIC Lumix DMC-GH4 camera attached to it. The pictures were processed by Helicon Focus Version 7.6.4. (focus stacking) programme.

DNA was extracted from a leg of one reared female imago (voucher RMNH.INS 981140), using the Qiagen DNeasy Blood & Tissue Kit (Qiagen, Venlo, The Netherlands). A 658 fragment of the mitochondrial COI gene was amplified using the primers LepFolF 5`-RKTCAACMAATCATAAAGATATTGG-3` and LepFolR 5`-TAAACTTCWGGRTGWCCAAAAAATCA-3` (Hebert et al. 2004). Bi-directional Sanger sequencing was performed at BaseClear, Leiden, The Netherlands. Sequences were edited and checked for stop-codons in Geneious 8.1.8 (Kearse et al. 2012). Barcode sequence (COI-5P), geographic and ecological data as well as photographs of the specimen were uploaded to the Barcode of Life Data System (BOLD; Ratnasingham & Hebert 2007) and GenBank (GenBank accession number OK502253).

Preliminary analysis of the COI-5P in BOLD showed a 95.70% match with *Harrisinopsis robusta* and a 91.86% match with a *Monalita* sp., both from French Guiana. In order to examine the phylogenetic relationships within the *Monalita-Harrisinopsis* species group, COI-5P sequences were downloaded from Genbank for the following species (species, GenBank accession number, geographical origin): *H. robusta* (MK930683, French Guiana), *M. laguerrei* (MK930778, French Guiana), *M. faurei* (MK930776 and MK930777, both French Guiana) and *Triprocris lustrans* (MK930938, Colorado, USA).

First, comparison of sequences was done by means of the Basic Local Alignment Search Tool (BLAST) algorithm, available in GenBank (Benson et al. 2013). Then, a phylogenetic tree was estimated using the program MEGA 11, available on the internet (Kumar et al. 2018, Stecher et al. 2020, Tamura et al. 2021) according to the methodology as outlined by Hall (2018). Alignment was done with the MUSCLE algorithm in MEGA X (Edgar 2004a, b). A phylogeny was estimated using the Maximum Likelihood method and the Hasegawa-Kishino-Yano model with a discrete Gamma distribution (H-K-Y+G). All positions with less than 95% coverage were eliminated, so fewer than 5% alignment gaps, missing data and ambiguous bases were allowed at any position (partial deletion option). The bootstrap consensus tree, taken to represent the evolutionary history of the taxa, was inferred from 1500 replicates. The tree was rooted with *Triprocris lustrans* (MK930938).

Results

The identification of the reared species in Suriname as *Harrisinopsis robusta* was confirmed by adult morphology and, especially, the male genitalia, which were identical to those of the holotype. Both are described in detail below.

Barcodes and phylogenetic analysis. Comparison of barcodes of *Harrisinopsis* and *Monalita* spp. from Suriname and French Guiana are shown in Table 1. The barcode of *H. robusta* reared in Suriname had a 4.13% base difference compared to *H. robusta* from French Guiana, 7.98% with *Monalita laguerrei* and 9.49-9.95% with *M. faurei*.

The consensus bootstrap tree, rooted with *Triprocris lustrans*, is shown in Fig. 2. Bootstrap support for the various branches was 87–100.

Synonymization of the genera *Harrisinopsis* Jordan, 1913 and *Monalita* Tremewan, 1973.

The genus *Monalita* had been established by Tremewan in 1973 as an objective replacement name for the genus *Lamontia* Kaye, 1923 [Type species *Lamontia calibana* Kaye, 1923: 997, by monotypy] (Kaye 1923, Tremewan 1973). The name *Lamontia* had already been in use as a genus of Spongi, the genus *Lamontia* Kirk, 1895 [Type species *Lamontia zona* Kirk, 1895: 289, by monotypy] (Kirk 1895). *Lamontia* Kirk, 1895 is a valid genus of sponges to date (Borojevic et al. 2000).

Already in 2015, Tarmann & Drouet mentioned: "According to the DNA barcoding results (....) and based on the comparison of male genitalia characters (....) it is doubtful whether the two genera *Harrisinopsis* and *Monalita* can be treated as different genera. Several characters that were so far thought to be characteristic for *Harrisinopsis* (....) are shared with at least one of the

TABLE 1. Comparison of barcodes (% nonidentical bases shown) of *Harrisinopsis* and *Monalita* spp. from Suriname and French Guiana by the Basic Local Alignment Search Tool (BLAST), available in GenBank. Taxa are reported by genus, species, author(s), country and GenBank Accession number.

Taxon	OK502253	MK930683	MK930778	MK930776	MK930777	MK930938
Harrisinopsis robusta Jordan, 1913, Suriname, OK502253	-	4.13	7.98	9.49	9.95	12.71
Harrisinopsis robusta Jordan, 1913, French Guiana, MK930683	4.13	-	9.28	10.79	11.25	13.35
Monalita laguerrei Tarmann & Drouet, 2015, French Guiana, MK930778	7.98	9.28	-	9.89	10.20	12.79
Monalita faurei Tarmann & Drouet, 2015, French Guiana, MK930776	9.49	10.79	9.89	-	1.06	12.92
Monalita faurei Tarmann & Drouet, 2015, French Guiana, MK930777	9.95	11.25	10.20	1.06	-	13.53
Triprocris lustrans Beutenmüller, 1894, USA Colorado, MK930938	12.71	13.35	12.79	12.92	13.53	-

known species of *Monalita*. However, at the moment there is simply too little information available for a clear decision (e.g. only one sex known, no information on the early instars, no larval host-plants known). We therefore treat *Harrisinopsis* and *Monalita* here still as two genera following Tarmann (1984)" (Tarmann & Drouet 2015).

Subsequently, examination of the type-species of *Monalita*, *Lamontia calibana* Kaye, 1923 could be done (Tarmann & Cock 2019). Now, the discovery of another population of *Harrisinopsis* in Suriname, enabling examination and description of the female (see below), there are additional reasons to synonymize *Monalita* with *Harrisinopsis*. This decision is also supported by the consensus bootstrap phylogenetic tree of *Harrisinopsis* and *Monalita* spp. (Fig. 2).

We therefore hereby synonymize the genus *Monalita* Tremewan, 1973 with *Harrisinopsis* Jordan, 1913, **new synonym**.

Revised generic diagnosis of *Harrisinopsis*. Forewings long, distally pointed, hindwings short, body short (Fig. 1). The forewings are opaque (e.g. *H. robusta*) or translucent in the male and opaque and at least semitranslucent in the female, the translucent parts weakly covered with very narrow, needle-like scales, the darker parts with broader, more densely arranged scales (e.g. *H. calibana*, *H. faurrei*, *H. laguerrei*). Hindwing with one single spine and forewing with a retinaculum on the base of the subcosta in males (as usual in all Procridinae); hindwing with two bristles (rarely reduced to one) and forewing with a retinaculum consisting of a row of upright scales at the base of CuP in females. In the forewing R3+R4 are stalked, in the hindwing M1 is reduced; a medial stem is present as a vein, at least distally, in both wings. An epiphysis on the foretibia is developed in *H. robusta, H. calibana* and *H faurei*, but absent in *H. laguerrei*. Hindtibia with two apical spurs.

The genitalia of the male (Figs 3a–c) are characterized by a single uncus of variable length that can be reduced to a small structure that consists of a central hook and is accompanied by a pair of strongly sclerotized socii that exceed the length of the uncus in *H. robusta* (Fig. 3a), whereas this structure combination is absent in all the other species where we find a normal single uncus structure (Figs 3b, c); valva with (*H. faurei,* Fig. 3b) or without (all other species, Figs 3a, c) projections, vinculum very broad, without saccus, pulvinus well developed, in one species (*H. laguerrei*, Fig. 3c) transformed into a long process. A striking character is a pair of long, slightly curved, strongly sclerotized, movable projections with pointed apex and with a hairy base, situated on a translucent folded diaphragm on top of the juxta, which is developed in *H. robusta* (Fig. 3a) and *H. laguerrei* (Fig. 3c), but not visible in the other so far known species. Aedeagus slender, straight in *H. faurei* (Fig. 3b) and strongly sclerotized basally, with a sclerotization on vesica in *H. robusta* (Fig. 3a) and *H. laguerrei* (Fig. 3c).

Abdomen of the female short and broad, slightly dorsoventrally compressed in *H. robusta* (Figs 1c, d, g, h) more rounded in the other species. The last segments can be fused to ring-like structures (*H. calibana*, *H. laguerrei*) or only the last two tergites are fused (*H. robusta*). Female genitalia small and partly concealed within the strongly sclerotized last sternites and tergites, like in a shell (Figs 3d–f). Papillae anales very small,

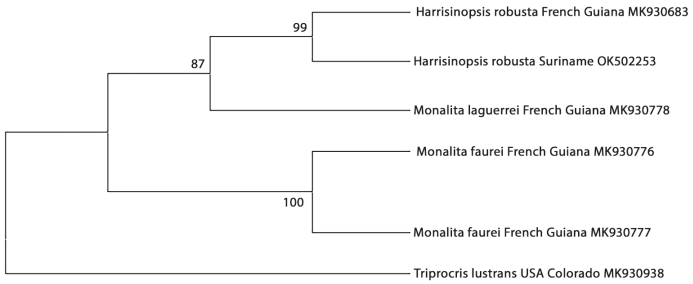

Fig. 2. Consensus bootstrap tree of the barcodes of species of the *Harrisinopsis-Monalita* group in Suriname and French Guiana (labels: taxon, country, GenBank Accession number). In MEGA 11, a phylogeny was estimated using the Maximum Likelihood methodology and the Hasegawa-Kishino-Yano model with a discrete Gamma distribution (H-K-Y+G). All positions with less than 95% coverage were eliminated, so fewer than 5% alignment gaps, missing data and ambiguous bases were allowed at any position (partial deletion option). There were a total of 652 positions in the final dataset. The tree, taken to represent the evolutionary history of the taxa, was inferred from 1500 replicates and rooted with *Triprocris lustrans.* The tree with the highest log likelihood (-1662.04) is shown.

with short setae, apophyses posteriores long and narrow, ostium translucent or sclerotized, rounded. Ductus bursae without (*H. robusta* (Figs 3d, e)) or with tube-like, slightly widened, translucent antrum (all other species) and with a slender, also slightly folded tube-like ductus part until the widening of the corpus bursae; no praebursa present; ductus seminalis slender and translucent.

Revised taxonomic checklist of *Harrisinopsis*. The above-mentioned synonymization of the genera *Harrisinopsis* Jordan, 1913 and *Monalita* Tremewan, 1973 leads to the following revised checklist of *Harrisinopsis* spp. (left column: genus or species; right column: type locality):

***HARRISINOPSIS* Jordan, 1913**
Lamontia Kaye, 1923, preocc. (Kirk, 1895)
Monalita Tremewan, 1973, **new synonym**
H. robusta Jordan, 1913 ..... Amazonas [Brazil]
tessmanni Hering, 1928 ..... Peru
H. calibana (Kaye, 1923) (*Lamontia*),
new combination..... Trinidad
H. faurei (Tarmann & Drouet, 2015) (*Monalita*),
new combination ..... French Guiana
H. laguerrei (Tarmann & Drouet, 2015) (*Monalita*),
new combination ..... French Guiana

Re-description of *Harrisinopsis robusta*, male (Figs 1a, 1b, 1e, f, 3a). Head, thorax and abdomen unicolorous, dark greenish brown, with a brilliant sheen; newly eclosed specimens have a very dark bluish-green sheen. Length of body: 8.0–9.5 mm, length of forewing: 12.0–14.0 mm, breadth of forewing: 4.0 mm (in both males!), length of hindwing: 6.0–7.0 mm, length of antenna: 6.0–7.0 mm. Head, thorax and abdomen densely covered with scales arranged in the form of roofing tiles, scales not bifurcate distally but with a denticulate margin. Head in lateral view with almost flat frons that is slightly projected dorsally; frons 1.5 x broader than compound eye in frontal view; compound eye black, chaetosema triangular, chocolate brown; ocellus small, distance between ocellus and dorsal edge of compound eye approximately 2.0 x broader than diameter of ocellus. Labial palps short, curved upwards, parallel to and almost touching the head capsule. Proboscis orange. Antenna bipectinate, pointed distally, tapering towards apex, with dorsoventrally compressed shaft, length of pectinations ca 3.0 x breadth of shaft at segment 12; sensillae on pectinations (flagellomeres) of medium length, 2.0 x broader than diameter of the shaft of the flagellomeres; number of antennal segments 45–47.

Thorax. Legs concolorous with thorax, foreleg with epiphysis, hindtibia with a pair of very small triangular apical spurs. Wings opaque, densely covered with scales, dark greenish brown, with a brilliant sheen on both wings and on upper- and underside; venation of forewing with R3+R4 stalked, in hindwing all veins free from cell, medial stem developed in both wings. Frenulum developed as a very strong spine, retinaculum very prominent. Fringe dark brown with green sheen, consisting of long slender scales, longer at the anal part of hindwing.

Abdomen. Color and scales as thorax. Anal tuft orange.

Genitalia. See description of male genitalia in the revised generic diagnosis above.

Description of *Harrisinopsis robusta*, female (Figs 1c, 1d, 1g, 1h, 3d, 3e). Characters and size as in male. Length of body: 7.5–8.0 mm, length of forewing: 14.0 mm, breadth of forewing: 4.0 mm, length of hindwing: 7.0 mm, length of antenna: 7.0 mm, length of

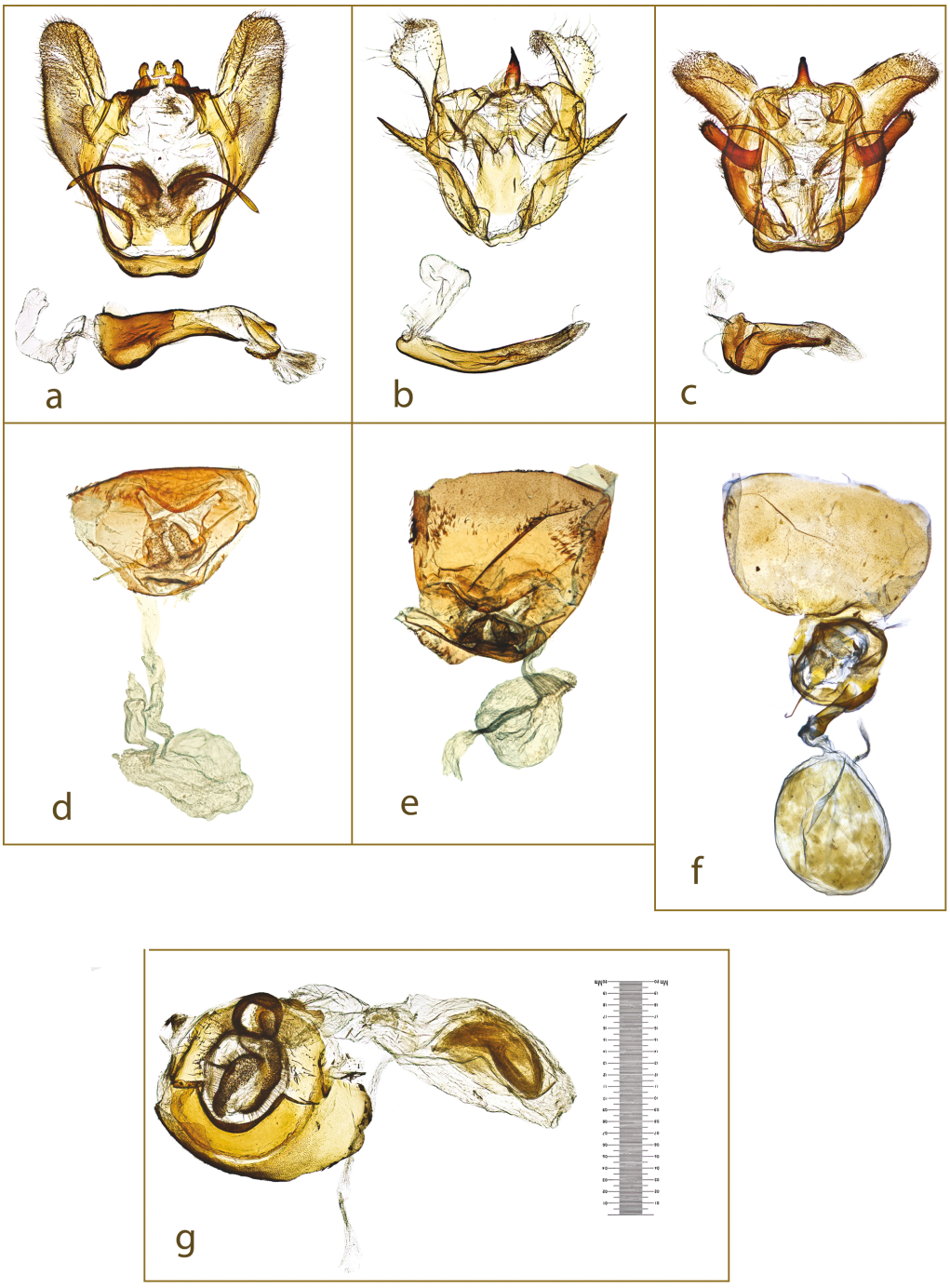

FIG. 3. Genitalia of members of the *Harrisinopsis-Monalita* species group (Zygaenidae: Procridinae). **a-c**: male genitalia (above: uncus, tegumen, valvae; below: aedeagus); **d-g**: female genitalia). **a**: *Harrisinopsis robusta*, male, French Guiana, Kaw, pk 38,5, 8 August 2002 (D. Camus leg.) (ex Coll. J. Cerda) (Gen. prep. GMT Z 3624); **b**: *Monalita faurei* male holotype (for data, see Fig. 1j) (Gen. prep. GMT Z 3625); **c**: *Monalita laguerrei* male holotype (for data, see Fig. 1k) (Gen. prep. GMT Z 3623); **d**: *Harrisinopsis robusta*, female, Suriname (for data, see Fig. 1...) (Gen. prep. GMT Z 4433); **e**: *Harrisinopsis robusta*, female, Suriname (for data, see Fig. 1) (Gen. prep. GMT Z 4434); **f**: *Monalita calibana*, female holotype (for data, see Fig. 1i) (Gen. prep. GMT Z 4367); **f**: *Monalita laguerrei*, female paratype (for data, see Fig. 1l) (Gen. prep. GMT Z 3626). Scale in tenths of mm.

proboscis 4.5–5.0 mm. Head in lateral view with almost flat frons that is slightly projected dorsally; frons as broad as in male, 1.5 x broader than compound eye in frontal view; compound eye black; chaetosema small, triangular, chocolate brown; ocellus small, distance between ocellus and dorsal edge of compound eye approximately 2.0 x broader than diameter of ocellus. Labial palps short, curved upwards, parallel to and almost touching the head capsule. Proboscis orange. Antenna shortly bipectinate, pointed distally, tapering towards apex, with dorsoventrally compressed shaft, length of pectinations ca 2.5 x breadth of shaft at segment 12; sensillae on pectinations (flagellomeres) short, 1.5–2.0 x broader than diameter of the shaft of the flagellomeres; number of antennal segments 45–46.

Thorax. Legs concolorous with thorax, foreleg with epiphysis, hindtibia with a pair of very small triangular apical spurs. Wings opaque, densely covered with scales, dark greenish brown, with a brilliant sheen on both wings and on upper- and underside; venation of forewing with R3+R4 stalked, in hindwing all veins free from cell, medial stem developed in both wings. Frenulum developed as two narrow spines, retinaculum a small row of hair-like scales on base of CuP. Fringe dark brown with green sheen, consisting of long slender scales, longer at the anal part of hindwing.

Abdomen short and broad, slightly dorsoventrally compressed. When seen from a dorsal view before dissection the fused last two tergites (7 and 8) have a characteristic, downwards bended, lip-shaped distal prolongation. The also fused 7 and 8 sternite ending distally with an edgy structure and with a slightly concave central part. Last sternites and tergites are laterally not fused to a broad complete ring structure like in former *Monalita*. When the abdomen is laterally opened, one can see that the tracheae at the first pleurite starts from the spiracle first with the normal short tube but then form a spherical translucent bulb; all other segments have normal tracheae without such tubes (this character has not been studied comparatively within the Zygaenidae).

Genitalia (Figs 3d, e). Small and partly concealed within the strongly sclerotized last sternites and tergites like in a shell. Papillae anales very small, with short setae, apophyses posteriores long and narrow, three times as long as the length of papillae head, apophyses anteriores absent. Ostium translucent, rounded, situated on the ventral edge of a characteristic, translucent 'window' in form of a mask with 'horns' that is situated between the strongly sclerotized 8th tergite that consists of a prominent helmet-shaped sclerotization and the also strongly sclerotized, smaller and more ring-like ventral sclerotization of the 8th sternite. Ductus bursae with tube-like, slightly widened, translucent antrum and with a slender, also slightly folded, tube-like ductus part until the widening of the disc-like corpus bursae; no praebursa present; ductus seminalis slender and translucent. The strongly folded and almost disc-shaped translucent corpus bursae may be present only in virgin females that have never copulated and never had a spermatophore that is normally widening the corpus and gives it the final shape.

Hostplant and habitat (Fig. 4). The hostplant in Suriname was *Hirtella paniculata* Swartz (Chrysobalanaceae). Description (Van Andel & Ruysschaert 2011; Figs 4b, c): Shrub or small tree, up to 4 m. Young twigs with erect hairs. Leaves alternate, 2.5 - 13.5 x 1.3 - 5.5 cm, base rounded or weakly cordate, apex shortly acuminate, upperside glabrous, shining, underside often with primary vein hairy. Inflorescence terminal or axillary racemes, up to 25 cm, hairy. Receptacle bell-shaped, dark red, hairy, calyx with grey hairs inside, petals white or pink, stamens purple or dark red, long, prominent. Fruit a drupe, club-shaped, first red, later black, ribbed, pulp thin, fleshy. Seed 1. Range: Colombia, Venezuela, Guianas and northern Brazil.

Habitat (Fig. 4a): *Hirtella paniculata* in Suriname is rather common on open areas in savannas, sandy river banks and islets in rivers (Van Andel & Ruysschaert 2011). The individual hostplant of *Harrisinopsis robusta* was in a light gap of late secondary forest on white sand savanna (Fig. 4a).

Last instar larva (Fig. 5). Length 12–18 mm. Overall impression of a rather stout, blackish brown-orange larva with multiple verrucae and long, spatulate, black setae.

Head (Figs 5a, b, e). Mostly concealed beneath fold of prothorax at rest and when feeding. Rather small. Vertices black, smooth. Frontoclypeus dark grey with apical part black. Further details not known.

Thorax (Figs 5a, c-i). Ground color orange, intersegmental membranes light grey. T1: Prothoracic shield oval, black, with a mid-dorsal longitudinal light grey stripe and multiple light grey setae, especially in its rostral half. Anterior to the shield and extending laterally to about midway the shield, there is a large fold, enveloping the head. The part of the fold adjacent to the shield is light grey with some setae, more rostrally the fold has a purplish-grey and somewhat granular appearance and has no setae. Rostrolaterally at the junction of the grey and purplish parts of the fold, there is a transverse row of about seven black pinacula with setae, the caudad end of which is about halfway the

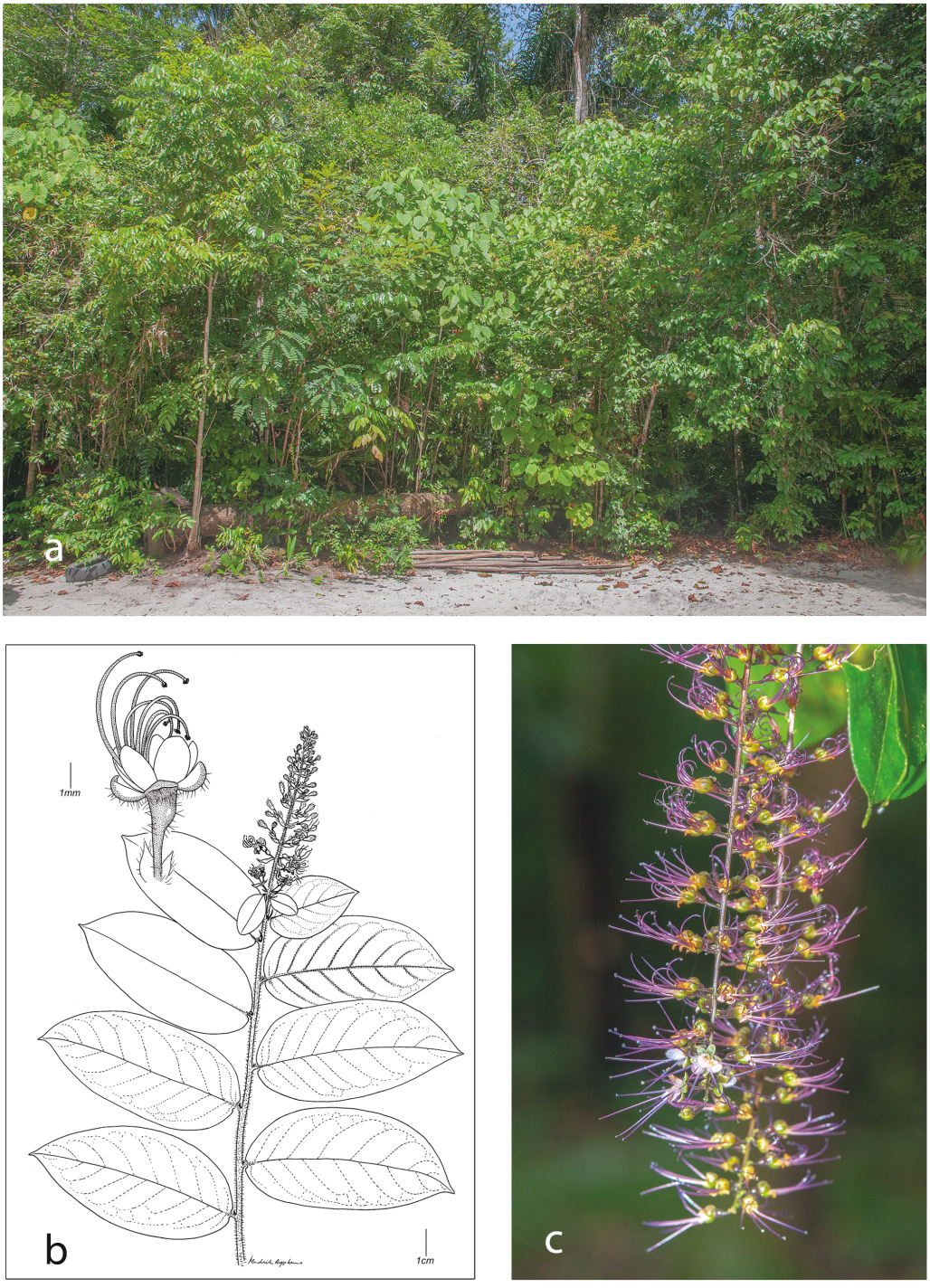

FIG. 4. Habitat of *Harrisinopsis robusta* and its hostplant, *Hirtella paniculata* Swartz (Chrysobalanaceae) in Suriname. **a**: patch of late secondary forest on white sand savanna at Palulu Camping near Zanderij airport (N 05°25'30", W 055°11'35", 15 m asl); the hostplant, on which the larvae were found, is one of the low plants in front of the felled tree; **b**: *Hirtella paniculata*, botanical drawing (H. Rypkema (Naturalis)); **c**: *Hirtella paniculata*, inflorescence; note flowers with pink-purple petals and long, purple stamens. Photographs a and c by third author.

shield, and ventrally there is a small verruca with a tuft of short setae (Fig. 5h). In other individuals, a verruca is present at the location of the transverse row of pinacula (Fig. 5g). The area of T1 caudad to the shield is orange. The beige spiracle is located laterally at the level of the posterior edge of the prothoracic shield. The leg is black with a distinct terminal claw, largely obscured by the subventral purplish area. T2 (Figs 5d, i) with five verrucae (dorsal, subdorsal, upper and lower lateral, subventral). In the middle of the segment and adjacent to the midline there are two, closely apposed, bunches of transversely arranged, small, black setae, 0.1–0.2S long, lying flat on the integument, giving the impression of black spots. The orange-colored dorsal verruca is immediately lateral to these, kidney-shaped, the two poles of which are continuous with the black setal bunches, which possibly originate from them. The dorsal verrucal setae are generally short (0.1–0.3S) and project in all directions, except medially; there are a few long setae (up to 1.2S), one or two of which are spatulate, projecting dorsorostrally. The subdorsal verruca is situated more rostrally than the dorsal one, near the anterior margin of the segment; it is somewhat smaller than the dorsal one, most setae are rather short (0.1–0.3S), some are long (up to 1S), project dorsorostrally and one or two of these are spatulate. The upper lateral verruca is larger, colored orange, located in the middle of the segment, with rather long setae, up to 1.8S, projecting anteriorly as well as laterally; shorter (0.2–0.6S) setae are directed caudad and dorsally. The lower lateral verruca is small, located rostrally in the segment; most setae are of medium length (0.3–0.5S) with a few long ones (1.2S) projecting ventrally and laterorostrally. The subventral verruca is about the size as the upper lateral verruca, setae as the lower lateral verruca. T3 with coloration and verrucae as T2. A few spatulate setae project from the subdorsal and upper lateral verrucae, setae otherwise as T2.

Abdomen (Figs 5a, b, d, j, k). Ground color of A1 and A7–A10 orangish-red, A3–A6 colored black, A2 black with some orangish-red, especially rostrally. Intersegmental membranes grey. Prolegs on A3–A6 and A10, rather short, the base, which has multiple setae, has the segment's color, planta grey, crochets not known. A1–A8 with four verrucae (dorsal, subdorsal, lateral and subventral). The A1 whitish-beige spiracle, the central part of which appears to protrude somewhat, is between the subdorsal and lateral verruca, in the middle of the segment, about at the same position as the T2–T3 upper lateral verruca. Spatulate setae from verrucae absent, otherwise setae as T2–T3. A2–A6: verrucae, setae and spiracle as A1. A7 with the subventral verruca smaller than on A6. A8 as A3–A7, but spiracle larger with the vertical axis tilted backwards about 40°, the lateral verruca with some very long (up to 3.2S), non-spatulate, laterocaudad projecting setae, and the subventral verruca rudimentary. A9 with dorsal and subdorsal verrucae; several very long (up to 8.5S) setae project from the dorsal as well as the subdorsal verrucae, a few of which are spatulate. A10 with rostral part orange, anal plate black with multiple, rather short, setae; further details not known.

Cocoon (Fig. 5l). About 6 x 14 mm, white, flattened, parchment-like, with some spatulate and non-spatulate setae scattered on it, mainly at the margins; pupa not visible; exuvia present on top of the cocoon.

Larval behavior. When found, the larvae were in groups of three to six on the upperside of a leaf of the hostplant, feeding at the leaf margin (Figs 5a, b). Some individuals were on the leaf underside when feeding (Figs 5b, c). The leaf was eaten all through. The larvae were positioned side by side, so that the demarcation of the blackish brown and orange areas on their abdomens was more or less continuous (Fig. 5a). Movement and pupation took place gregariously.

Duration of stages. Last instar at least four days; cocoon-eclosion 20–22 days (three females) or 391–420 days (two males).

Discussion

Harrisinopsis robusta is, to our notion, the first zygaenid to have been reared in South America. The reared imagines provided not only the means for morphological species identification, but, also, the female genitalia allowed filling in the information gap to synonymize the genus *Monalita* Tremewan, 1973 with *Harrisinopsis* Jordan, 1913.

The barcodes from Surinamese and French Guianan *H. robusta* differed by 4.13% (Table 1). For butterflies, typically, barcodes of the same species differ less than 2% (e.g. Zhang et al. 2020). In a large barcoding study of Zygaenidae, comprising about 20% of global species, the mean intraspecies variability was 1.36%, but about 15% of the species studied had an intraspecies divergence of more than 3.00% and most of these were in the subfamily Procridinae. In some cases, a high intraspecies divergence was combined with a low divergence between species in the same (sub)genus, whereas these species were well-separated on morphological grounds (Efetov et al. 2019). A low interspecifc divergence does not occur in *Harrisinopsis*, where we found values of 7.98–9.95% (Table 1). Possibly, the high intraspecific divergence in *H. robusta* is the result of low dispersal rates of individuals with relatively little genetic interchange between subpopulations, allowing a gradual increase of neutral mutations.

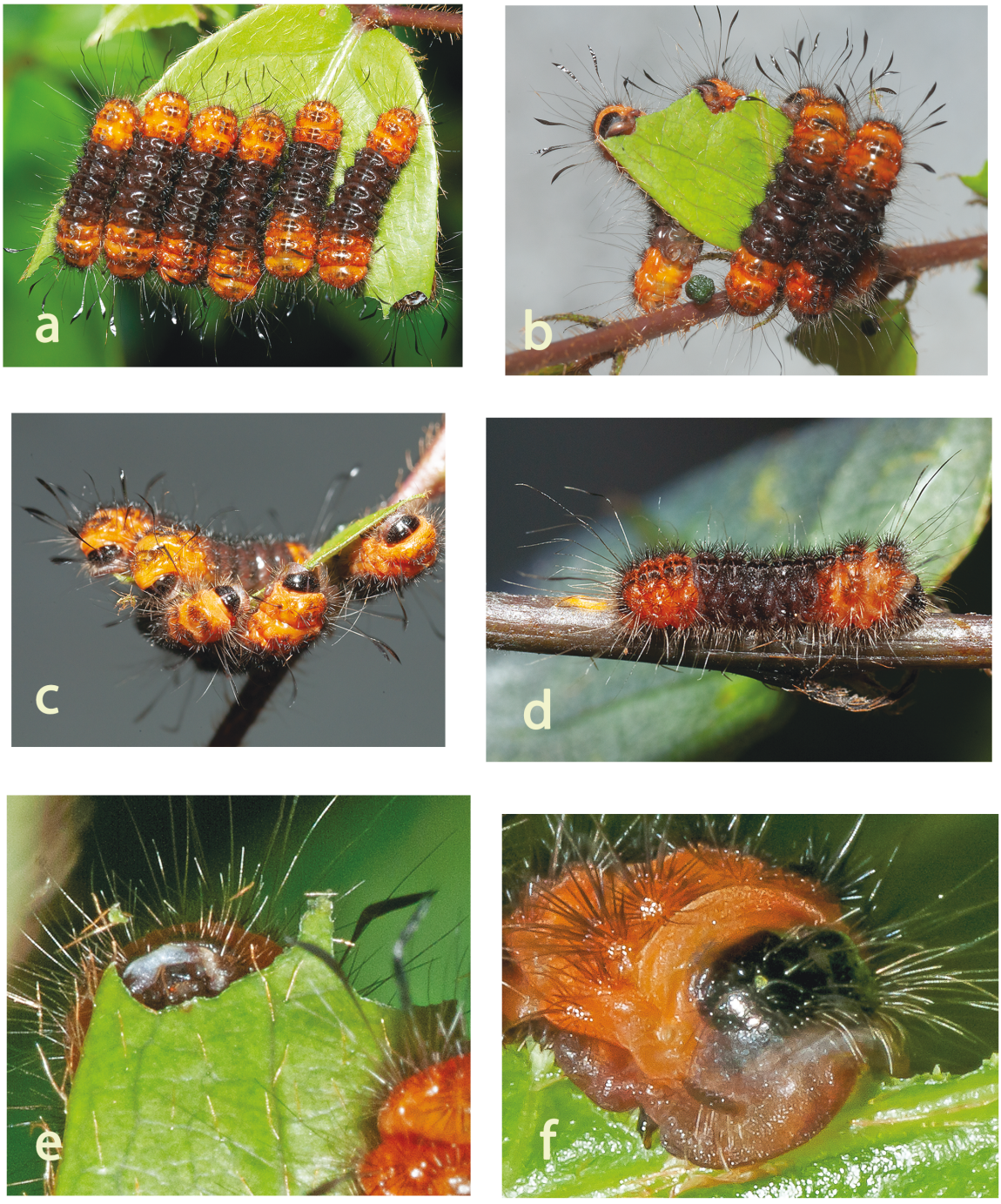

FIG. 5. Last instar larvae of *Harrisinopsis robusta* (Zygaenidae: Procridinae) on *Hirtella paniculata* in Suriname. Date of photographs 28 March 2019, unless stated otherwise. **a**: group of six larvae (dorsal view) feeding on upperside of a leaf and one on the underside; note aposematic coloring and side-by-side positions; **b**: group of five larvae feeding on both sides of a leaf (dorsal and partial ventral view); **c**: group of five larvae feeding on both sides of a leaf (frontodorsolateral view); **d**: lateral view, 3 April 2019; **e**: detail of head, slightly protruding from T1 fold, frontal view; **f**: detail of T1, frontolateral view; note black T1 shield, purple T1 fold with transverse row of black pinacula and T1 leg without spatulate seta.

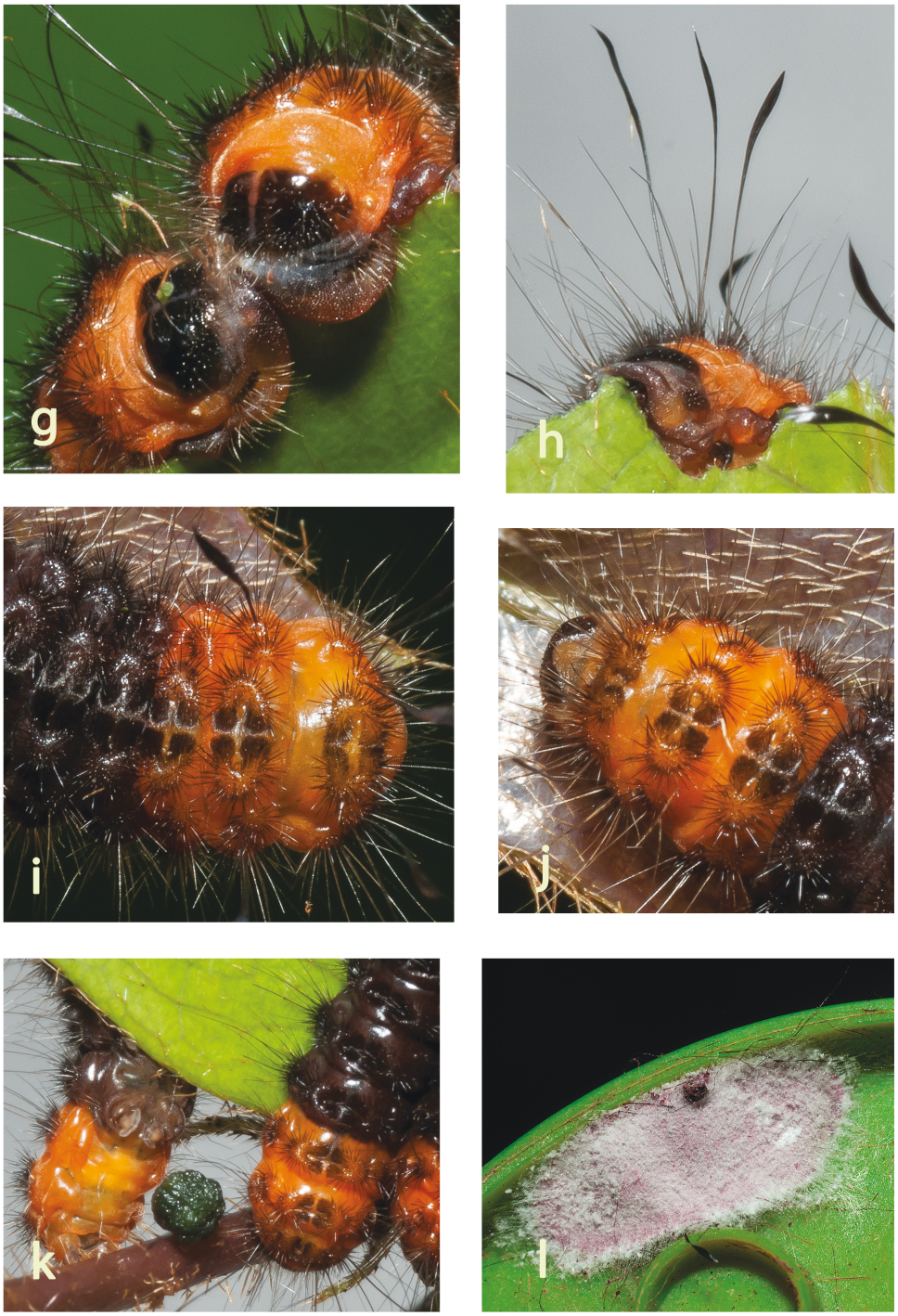

Fig. 5 (continued). Last instar larvae of *Harrisinopsis robusta* (Zygaenidae: Procridinae) on *Hirtella paniculata* in Suriname. Date of photographs 28 March 2019, unless stated otherwise.**g**: detail of T1, frontolateral view; note black T1 shield, purple T1 fold with transverse row of black pinacula; **h**: detail of T1, frontolateral view; note cluster of black pinacula, forming a verruca; **i**: detail of T2-A2, dorsal view; **j**: detail A7-A10, dorsal view; **k**: detail A6-A10, ventral view; **l**: cocoon with some scattered spatulate and non-spatulate setae, 3 April 2019. Photographs by third author.

In *H. robusta*, sexual dimorphism is minor: the female is slightly larger (forewing length 14.0–15.0 mm versus 12.0–14.0 mm in the male), the frenulum consists of two spines (one spine in the male) and the end of the abdomen in the female is more squat. Adult habits may be inferred from existing data. Adults have been collected in April, May and August (Tarmann & Drouet 2015, present study), indicating eclosion of pupae in the long rainy season. The species is probably nocturnal: the two males from French Guiana were collected at a light trap (Tarmann & Drouet 2015) and eclosion of one of our reared females was at about 20:15 h. The proboscis is of normal length (4.5–5.0 mm) for Procridinae spp. and indicates nectar feeding. In contrary to Zygaeninae where the females have their pheromone glands situated at the end of abdomen, Procridinae females attract their males by distributing the pheromone from the intersegmental skins of the 2nd – 5th abdominal tergites (Efetov & Tarmann, 2017: 49, Figs 52–58). It can be postulated that this applies also for *Harrisinopsis*. The female sex pheromones and attractants of Procridini are esters of sec-butanol and fatty acids (Efetov et al. 2011, Efetov et al. 2014b, Efetov et al. 2014c, Efetov et al. 2015, Efetov et al. 2016). In American species the chemical structure of these pheromones and attractants is known for *Acoloithus falsarius* Clemens, 1861, *A. novaricus* Barnes & McDunnough, 1913, *A. rectarius* Dyar, 1898, *Neoilliberis fusca* (H. Edwards, 1885), *Neoalbertia constans* (H. Edwards, 1881), *Neoprocris aversa* (H. Edwards, 1884), *Pyromorpha dyari* (Jordan, 1913), *Triprocris cyanea* Barnes & McDunnough, 1910, *Harrisina metallica* Stretch , 1885, *Harrisina americana* (Guérin-Ménéville, 1844), *Harrisina coracina* (Clemens, 1861), and *Harrisina guatemalena* (Druce, 1884) (Tarmann, pers. obs.; Efetov & Kucherenko 2020). Most probably, *Harrisinopsis* utilizes the same types of molecules as pheromones and attractants.

Several morphological aspects of the larvae were contradictory to expectations or remained unclear. It has been described that the prothoracic legs of Zygaenidae larvae bear an apical pair of spatulate setae, equivalent in size to the claw (Epstein et al. 1999). We did not see them in the *H. robusta* larvae (Figs 5c, f, h). Also, the arrangement of pinacula or verrucae on the T1 fold was not unambiguous. Some larvae showed evidence of a transverse row of black pinacula (Figs 5f, g), but, in others, a verruca was present at this location (Fig. 5h). We could not see whether abdominal prolegs had crochets in a uniordinal mesoseries or whether A2 and/or A7 postspiracular glands (Stehr 1987) were present. Lastly, most larvae of Procridinae have been reported to have a sclerotized comb above the anus (anal comb; Efetov & Tarmann 2017), on which we cannot provide data for *H. robusta*. This would be in agreement with the fact that this character is absent in the American genus *Harrisina*. Resolution by out-of-hand macrophotography of an 18 mm larva was a limiting factor as was the high mortality soon after discovery and, in addition, none of the larvae was vouchered for further study.

H. robusta larvae showed gregariousness (30–40 on the hostplant, moving and pupating as a group) and aposematic coloring, with the aposematic signal for potential predators amplified by their side by side positions (Fig. 5a). This habit has been also observed in larvae of the genus *Harrisina* Packard, 1864, viz. in *H. americana* (Guérin-Ménéville, 1844) and *H. metallica* Stretch, 1885, both feeding on Vitaceae. Generally, larval gregariousness and aposematism are related to unpalatability and chemical protection (Sillén-Tullberg 1988, Greeney 2012).

The combination of black and orangish-red coloring is a well-known aposematic signal, e.g. in palaearctic ladybirds (Coleoptera: Coccinellidae), *Parides* spp. and some *Heraclides* spp. (Papilionidae: Papilioninae), *Heliconius* spp. (Nymphalidae: Heliconiinae) and palaearctic *Zygaena* spp. (Zygaenidae: Zygaeninae) (Naumann et al. 1999, Gernaat et al. 2012). In Suriname, the larvae of several other lepidopteran species show black and orangish red coloring, notably Arctiinae spp. (e.g. *Dysschema tricolora* (Sulzer, 1776), *Pseudalus aurantiacus* Rothschild, 1909 and *Neonerita dorsipuncta* Hampson, 1901), indicating the possibility of a larval black-orangish red mimicry ring in Suriname (Van den Heuvel & Gernaat, to be published).

The mechanism(s) of chemical protection of the *H. robusta* larvae, however, are not clear. Sequestration of host plant allelochemicals is a possibility. Although there are hardly any studies on the phytochemical profile of *Hirtella* spp., Chrysobalanaceae have been shown to contain more than 160 bio-active (cytotoxic, antimicrobial) secondary metabolites, mainly flavonoids and terpenoids, and they are widely used in traditional medicine (Feitosa et al. 2012, Neto et al. 2013). On the other hand, storage of bitter tasting cyanoglucosides by larvae and the ability to release the toxic hydrocyanic acid has been shown in several subfamilies of the Zygaenidae, including the Procridinae (Epstein et al. 1999, Briolat et al. 2019) and may also be the case in *H. robusta*.

During our rearing, three females eclosed in April 2019, whereas two males eclosed in April–May 2020. The long dry season in Suriname is generally from early September till the end of November, with some year-to-year variation (Gernaat et al. 2012), so all eclosions of

H. robusta were well into the rainy season. Therefore, it seems unlikely that the long pupal dormancy was a manifestation of aestivation. Possibly, the species has evolved long pupal dormancy in part of the offspring to increase survival rate, irrespective of sex. However, in Lepidoptera, it is quite common for females to eclose prior to the males, particularly when soon after emergence females commence to produce male-attracting pheromones (e.g. Saturniidae or Arctiinae (Connor 2009)). In these cases, eclosion of the males later than the females is a mechanism to prevent incrossing. Sex-dependent long pupal dormancy could even be a more effective mechanism to prevent incrossing.

Neotropical Zygaenidae are probably much more common than generally thought or observed and represent a wealth of research opportunities. We believe that not only many species await description, the present paper has also indicated that there are many natural history topics to be elucidated.

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