



Phylogeny of the genus *Amerila* (Lepidoptera: Erebidae: Arctiinae: Amerilini), with remarks on male genitalia and descriptions of new species from Africa and Indonesia

NIKOLAI IGNATEV¹ , GYULA M. LÁSZLÓ² , GÜNTER C. MÜLLER³ , HARALD SULAK⁴ ,
ROMAN YAKOVLEV⁵ and ZDENĚK FALTÝNEK FRIC^{6,7}

¹ Senckenberg Research Institute and Natural History Museum, Entomology I Department, Senckenberganlage 25, 60325 Frankfurt am Main, Germany; e-mail: nikolai.ignatev@senckenberg.de

² African Natural History Research Trust, Street Court, Kingsland, Leominster, Herefordshire, HR6 9QA, UK; e-mail: gyulalaszlo@anhrt.org.uk

³ University of Sciences, Techniques and Technology of Bamako, BP 1805, Bamako, Mali; e-mail: guntermuller@hotmail.com

⁴ Museum Witt, Max-Reger-Straße 18, 92637 Weiden in der Oberpfalz, Germany; e-mail: h.sulak@atelier-sulak.de

⁵ Altai State University, Lenina pr. 61, Barnaul, 656049, Russia; Tomsk State University, Lenina pr. 36, 634050, Tomsk, Russia, Western Caspian University, 31, Istiglaliyyat Street, Baku, Azerbaijan; e-mail: yakovlev_asu@mail.ru

⁶ Institute of Entomology, Biology Centre CAS, Branišovská 31, 370 05 České Budějovice, Czech Republic; e-mail: fric@entu.cas.cz

⁷ Czech University of Life Sciences Prague, Kamýcká 129, 165 00 Praha-Suchbát, Czech Republic

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Abstract. The objective of this paper is to reconstruct the phylogeny of the Palaetropical arctiine genus *Amerila* Walker, 1855 through investigations of ancestral distribution and co-evolution of wing patterns linked with mimicry, as well as analyses of genetic and genital morphological traits. We perform analyses of molecular data available from previous studies combined with DNA sequences obtained during this research, a total of 3894 bp for 48 species using one mitochondrial (COI) and six nuclear markers (EF-1 α , GAPDH, RpS5, wingless, arginine kinase, and ATP). We analysed the data using two probabilistic methods: Maximum Likelihood and Bayesian Inference. Among the known species-group taxa, we include for the first time in a phylogenetic analysis the species *A. accra* (Strand), *A. bauri* Möschler, *A. bipartita* (Rothschild), *A. brunnea bipartitoides* Häuser & Boppré, *A. puella carneola* (Hampson), *A. castanea* (Hampson), *A. invidua* (Bethune-Baker), *A. leucoptera* (Hampson), *A. lupia* (Druce), *A. madagascariensis* (Boisduval), *A. nigrivenosa* (Grünberg), *A. puella* (Fabricius), *A. roseomarginata* (Rothschild) and *A. vitrea saalmuelleri* (Rothschild). We describe two new species: *A. florinae* Ignatev, sp. n. from Bacan island (Indonesia) and *A. smithi* László, sp. n. from Zambia, the latter included in the phylogenetic analyses. We raise *A. brunnea bipartitoides*, *A. vitrea saalmuelleri* and *A. puella carneola* to species rank: *A. bipartitoides* stat. rev., *A. saalmuelleri* stat. rev., *A. carneola* stat. rev. We illustrate the habitus and the male and female genitalia of most of the taxa presented in this paper.

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INTRODUCTION

Amerila Walker, 1855, is a diverse Palaetropical genus of Arctiinae comprising some sixty species, with ca. two-thirds of the taxa occurring in the Afrotropics and Madagascar, whilst the remaining third occur in the Indomalayan-Australasian realm from India to New Guinea, the Solomon Islands and north-eastern Australia (Rothschild, 1914; Common, 1990; Häuser, 1993). Species of this genus were formerly attributed to *Rhodogastris* Hübner, 1819 due to a misidentified type species (Häuser & Boppré, 1997). Taxa belonging to *Amerila* are characterised

by their robust body, aposematic colouration and elongate, apically pointed forewing that often possess conspicuous transparent areas of various extent or striking transverse fasciae. These features make them readily distinguishable from other genera of Arctiinae. Many *Amerila* species, however, display a very similar habitus that renders them rather difficult to distinguish, often requiring examination of genital morphology.

Having formerly been poorly studied, the genus received increased attention from taxonomists following publication of the revision of Afrotropical *Amerila* by Häuser &

Boppré (1997). This work formed the basis of subsequent studies on the genus (e.g., Dubatolov, 2009; Przybyłowicz et al., 2019a, c), and it emphasised phylogenetic and morpho-taxonomic aspects that needed to be addressed. Since Häuser & Boppré's revision, two new species have been described from Africa (Przybyłowicz et al., 2019b; Ignatev et al., 2022) and one from Indonesia (Spitsyn & Bolotov, 2020). Furthermore, a mitochondrial COI phylogenetic study of the *Amerila syntomina* complex was also published (Przybyłowicz et al., 2019b). According to systematic studies by Zahiri et al. (2012), Zaspel et al. (2014), and Zenker et al. (2016), *Amerila* forms a lineage distinct from other Arctiinae clades, resulting in the genus being classified as a separate tribe Amerilini as proposed by Dubatolov (2010).

A group of the African species studied by Müller (1980) in his dissertation thesis included the description of several new taxa. Nevertheless, Müller's thesis (1980) has never been published, and thus all the names introduced in his work are not available in nomenclatorial sense (Häuser & Boppré, 1997).

Even though *Amerila* has become popular with researchers and collectors, little is known about its origin, evolutionary past and phylogeny, and the species delimitations and established relationships within the genus are based almost exclusively on male adult morphology.

The present paper examines the phylogenetic relationships of *Amerila* species based on mostly COI-5P sequences combined with the analyses of male genital morphology. We also investigate the potential co-evolution of the habitus of the species with respect to their aposematism (Häuser & Boppré, 1997). Finally, we examined the natural links and evolutionary relationships between Afrotropical and Indomalayan-Australasian *Amerila* species. Our results are based on comprehensive morphological and molecular analyses of large series of *Amerila* specimens deposited in the holdings of numerous European institutional and private research collections. The integrative analyses lead to the recognition of 14 distinct species complexes within the African lineage, and the discovery of two new species that are described in this paper. Additionally, we illustrate the female genitalia structure of 22 species for the first time that were omitted from Häuser & Boppré's (1997) revision.

MATERIAL AND METHODS

Abbreviations of depositories used

ANHRT – African Natural History Research Trust, Leominster, UK; ANIC – Australian National Insect Collection Canberra, Australia; CGM – Collection of Günter Müller, Freising, Germany/Bamako, Mali; CHS – Collection of Harald Sulak, Weiden in der Oberpfalz, Germany; ISEA – Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland; LMK – Landesmuseum Kaernten, Klagenfurt, Austria; MNHN – Museum National d'Histoire Naturelle, Paris, France; MWM/ZSM – Museum Witt, Munich in the collection of the ZSM, Munich, Germany; NECJU – Nature Education Centre of Jagiellonian University, Kraków, Poland; NHMUK – The Natural History Museum, London, UK; NIBGE – National Institute for Biotechnology and Genetic Engineering, Faisalabad, Pakistan; RCRB –

Research Collection of Robert J. Borth, Mequon, USA; SMNS – Staatliche Museum für Naturkunde/State Museum of Natural History, Stuttgart, Germany; UM – University of Maryland, USA; ZFF – Collection of Zdeněk Faltýnek Fric, České Budějovice, Czech Republic; ZSM – Zoologische Staatssammlung München/Bavarian State Collection of Zoology, Munich, Germany.

Other abbreviations

BI – Bayesian Inference; CCDB – Canadian Centre for DNA Barcoding, Biodiversity Institute of Ontario, University of Guelph; DRC – Democratic Republic of the Congo; LG – Genitalia slides prepared by Gyula M. László; ML – Maximum Likelihood; nd – no data; PP – Posterior probability value in Bayesian Inference analysis.

Morphological analysis

Specimens were collected by light trapping and preserved either in 96% alcohol or dried with silica gel immediately upon capture.

The abdomen was removed and macerated in 10% potassium hydroxide on a heated block for ten minutes. Genitalia were extracted and stained with Chlorazol black and embedded in Euparal on microscope slides according to standard methods of preparation (Lafontaine & Mikkola, 1987). Images of adults were captured using a Nikon D90 SLR camera equipped with a Nikkor AF Micro 60 mm lens. Genitalia were imaged using a Canon EOS 700D or a Leica DFC450 camera mounted on a stereomicroscope.

Forewing length was measured from the base to the apex of the wings, along the costa. Terminology for genital morphology follows Kôda (1987).

Holotype label data are quoted exactly as they appear. A division slash (/) denotes the commencement of a new line, two division slashes (//) data on a further label.

Molecular analyses

For MWM/ZSM samples, total genomic DNA sequences were extracted from leg muscle tissue of dried specimens preserved in 100% ethanol using the Genomic DNA Mini Kit (Tissue), (Geneaid, Taiwan). Seven genes (total = 3,984) from the sampling of Wahlberg & Wheat (2008) were treated for amplification: nuclear EF-1 α (1,071 bp), GAPDH (654 bp), RpS5 (576 bp), wingless (402 bp), AK (600 bp), ATP (440 bp) and the mitochondrial COI (670 bp), the latter providing the basis of BI and ML analyses. The cytochrome c oxidase subunit I gene (COI-5P) was amplified by polymerase chain reaction (PCR) using the primers LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and HCO2198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer et al., 1994). For the nuclear genes, primers were those used by Wahlberg & Wheat (2008). PCR was performed in 11,5 μ l reaction volume using 6,25 μ l, 2 $\times$ Bioline MyTaq HS Red Mix, 4 μ l dH₂O (PCR H₂O), 0,625 μ l of each primer and 2 μ l of the genomic DNA. The PCR profile consisted of an initial denaturation step at 94°C for 5 min, 92°C for 1 min, followed by 40 cycles at 50°C for 1 min, 72°C for 1 min and a final extension step of 5 min at 72°C. Success of amplification was identified using gel electrophoresis on 1% or 2% agarose, followed by GelRed staining and UV visualisation. Successful PCR products (2 μ l each) were purified using a mixture of 135 μ l FastAP + 85 μ l Exo I and sequenced in both directions. Purified PCR products were forward sequenced by Macrogen (Netherlands) applying the T7 sequencing primer or PCR primers. For low-quality samples, reverse sequencing was carried out using either PCR primers or the T3 sequencing primer.

In ANHRT samples, DNA barcodes were obtained by removing tarsal segments from dry specimens and submitted to the CCDB for DNA extraction, amplification and sequencing of cyto-

chrome oxidase subunit I (COI) applying Single Molecule Real-Time sequencing through the Sequel (PacBio) pipeline (Hebert et al., 2018).

COI barcode sequences and nuclear markers (EF-1 α , GAPDH, RpS5, wingless, arginine kinase, and ATP) for other *Amerila* specimens (Table S3) were obtained from the databases BOLD (<http://www.boldsystems.org>) and GenBank (<https://www.ncbi.nlm.nih.gov/>). Sequences of two other Erebidae species, *Miltochrista miniata* (Förster, 1771) (Lithosiini) and *Catocala semirelictata hippolyta* Strecker, 1874 (Catocalini), were used as outgroups. A position of outgroup was left on the software default rooting (Midpoint Rooting). All analysed sequences were trimmed and aligned in Bioedit 7.2. Informer Technologies, Inc. and in Geneious Prime 2021.2.2.

Phylogenetic analyses

ML analyses were performed in IQTree (Nguyen et al., 2015). Bootstrap support was calculated using 1000 replicates. We selected a proper substitution model and partition scheme using PartitionFinder 2.11 (Lanfear et al., 2016). BI Analyses were performed in Mr Bayes 3.2.6 (Ronquist & Huelsenbeck, 2003) with four independent runs, each having three heated and one cold chain. Analyses were conducted for 6 million generations, with a tree sampled every 1000 generations. The first 25% of each run was discarded as burn-in. The values shown in the BI tree (Fig. S1) display the estimated posterior probability, values of 0.70 and above are regarded as good, 0.90 and above as strong. To obtain an ultrametric tree for further analyses, we used BEAST 1.10.4 (Drummond et al., 2012) with BirthDeath model, ML tree as a starting tree, a 50 million chain length, and sampling every 5000 trees. We checked model performances and ESS values by Tracer 1.6. The tree was visualised using Geneious Prime 2021.2.2 and FigTree. The values displayed in the ML tree (Fig. 1) via “?” correspond to ultrafast bootstrap and SH-like approximate likelihood ratio test (Guindon et al., 2010), branch support values of 70 and above are regarded as good; 90 and above as strong. Pairwise sequence divergence was calculated using the Kimura two-parameter distance (K2P) model (Kimura, 1980) in the MEGA version (Kumar et al., 2018).

Ancestral character state reconstruction of wing colour and body patterns

Given that male adults of *Amerila* have transparent patches on their fore (A) and hind (B) wings, and that their wing basal colouration (C) is either white, brown, or grey, we used the aforementioned characters to infer the evolution of the wing patterns. We reconstructed the ancestral state using fastAnc algorithm for continuous characters (phytools package; Paradis & Schliep, 2019) in R 3.3.1 (R Core Team, 2022) separately for the forewing and the hindwing. We tested the phylogenetic signal of these patterns using Blomberg's K (Blomberg et al., 2003) and Pagel's λ statistics (Pagel, 1999). The K value compares variance-covariance effects of data on phylogeny with a Brownian motion model. Value of λ indicates a transformation of phylogeny, which ensures the best fit of trait data to the Brownian motion model. In both measures, values close to zero represent no phylogenetic signal, the character distribution is random and there is no evolutionary pattern, whereas values close to 1 indicate a strong phylogenetic signal. The values were calculated with R package phytools with the phylosig function with 1,000 simulations).

RESULTS

Species sampled for DNA

We analysed sequences of 256 individuals belonging to 48 species, representing approximately 80% of the spe-

cies of the genus *Amerila*, of which 34 taxa are distributed in Africa or Madagascar, and 14 taxa distributed in the Indomalayan-Australasian region. The best substitution models and partition scheme consisted of six subsets (BIC = 25,588.6, 536 parameters, Table S1). Most nodes in our phylogenetic hypotheses were resolved with moderate to strong support values and were stable regardless of the method we used. The ML and BI display similar topologies (Figs 1, S1) and only the position of the *A. carneola* species complex was recovered differently in the two analyses. In the ML tree, the *A. carneola* lineage was recovered as sister to all the following species groups, but in the BI tree it was found as paraphyletic to *A. lupia* and *A. nigrivenosa*, indicating a conflict in topologies. The *A. magnifica* species group forms a clade that is the ‘basal’ sister group to all other *Amerila*, the latter being subdivided into 13 lineages in ML (Fig. 1) analysis and 14 lineages in BI (Fig. S1) analysis. The species content of each species complex based on the taxa included in the phylogenetic analyses is as follows:

African-Madagascan taxa

A. magnifica species group

A. magnifica (Rothschild, 1910)

A. francesae Ignatev & László, 2022

A. mulleri Häuser & Boppré, 1997

A. bubo species group

A. bubo (Walker, 1855)

A. nigroapicalis species group

A. nigroapicalis (Aurivillius, 1899)

A. luteibarba species group

A. luteibarba (Hampson, 1901)

A. cf. luteibarba (Hampson, 1901) (sample from Gabon)

A. affinis (Rothschild, 1910)

A. bipartita species group

A. bipartita (Rothschild, 1910)

A. brunnea (Hampson, 1901)

A. bipartitoides Häuser & Boppré, 1997 stat. rev.

A. phaedra species group

A. phaedra Weymer, 1892

A. smithi László sp. n.

A. leucoptera (Hampson, 1901)

A. fennia species group

A. fennia (Druce, 1887)

A. carneola species group

A. carneola (Hampson, 1916) stat. rev.

A. castanea (Hampson, 1911)

A. accra (Strand, 1919)

A. femina (Berio, 1935)

A. lupia species group

A. lupia (Druce, 1887)

A. nigrivenosa species group

A. nigrivenosa (Grünberg, 1910)

A. syntomina species group

A. cf. vidua (Cramer, 1780)

A. alexandrae Tarcz & László, 2019

A. syntomina (Butler, 1878)

A. thermochroa (Hampson, 1916)

A. invidua (Bethune-Baker, 1925)

A. rubondoi Häuser & Boppré, 1997

A. puella (Fabricius, 1794)

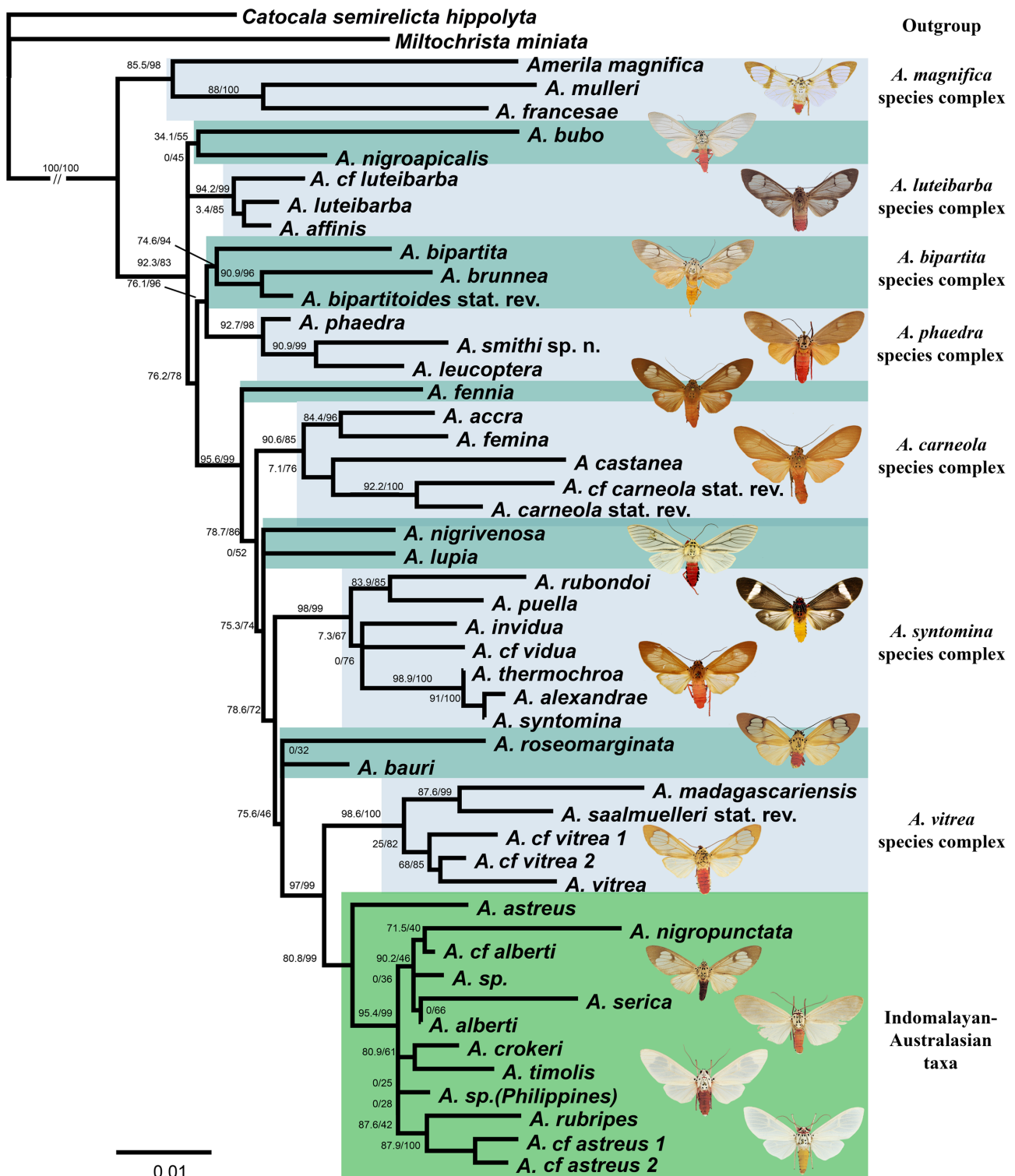


Fig. 1. Phylogenetic tree of the genus *Amerila* Walker, 1855 inferred by Maximum Likelihood analysis. Branch labels display the ultra-fast bootstrap values likelihood testing based on 1000 replicates.

***A. roseomarginata* species group**

A. roseomarginata (Rothschild, 1910)

***A. bauri* species group**

A. bauri Möschler, 1884

***A. vitrea* species group**

A. vitrea Plötz, 1880

A. cf. vitrea (Pakistan)

A. madagascariensis (Boisduval in Delegorgue, 1847)

A. saalmuelleri (Rothschild, 1911) stat. rev.

Indomalayan-Australasian taxa

A. cf. astreus (Drury, 1773)

A. nigropunctata (Bethune-Baker, 1908)

A. alberti (Rothschild, 1910)

A. serica Meyrick, 1886

A. crokeri (MacLeay, 1826)

A. timolis (Rothschild, 1914)

A. rubripes (Walker, 1865)

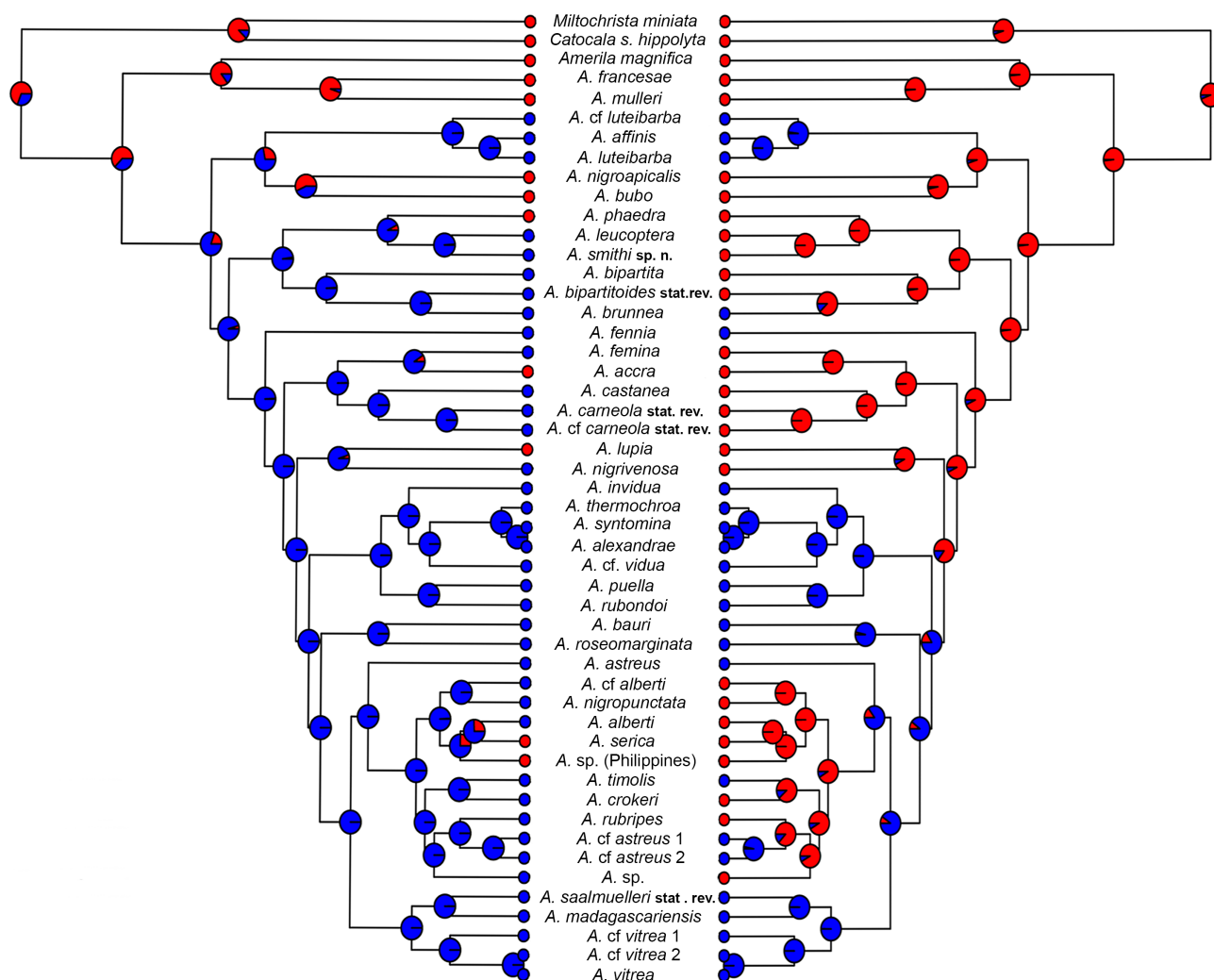


Fig. 2. Reconstruction of ancestral wing pattern. Presence (blue) or absence (red) of translucent patches on forewings (left tree) and hindwings (right tree) in male adults.

Following the results of the molecular and morphological analyses, we raise *A. brunnea bipartitoides* Häuser & Boppré, 1997, *A. puella carneola* (Hampson, 1916), and *A. vitrea saalmuelleri* (Rothschild, 1911) to species rank and establish here – *A. bipartitoides* stat. rev., *A. carneola* stat. rev., and *A. saalmuelleri* stat. rev. The female of *A. bipartitoides* stat. rev. remains unknown.

Reconstruction of ancestral wing pattern

Reconstruction of ancestral wing pattern shows that the translucent forewing patches are predominant (Fig. 2). This reconstruction indicates that the patches developed either once in the ancestor of the genus and disappeared in *A. bubo*, *A. accra*, *A. lupia*, *A. serica* and an unidentified sample from the Philippines, or they appeared independently in the *A. luteibarba* species group and a common ancestor of the majority of the other species, followed by disappearance in *A. accra*, *A. lupia*, *A. serica*, and the Philippines species (Fig. 2). Translucent patches in the hindwing appear to have separately originated in the *A. luteibarba*, *A. brunnea*, *A. carneola*, *A. puella* species complexes, in the species *A. roseomarginata*, *A. astreus* and *A. timolis* (as a narrow stripe), and in the *A. vitrea* species group (Fig.

2). The original wing colour in male adults was probably brown, since the phylogenetic distribution of dark brown is similar to the pattern of translucent patches of the forewing (Fig. 3). The presence of a forewing translucent patch shows a clear phylogenetic signal, i.e., a correlation between the occurrence of the character and the evolution of the species, ($K = 1.337$, $p = 0.001$; $\lambda = 0.999$, $p < 0.001$). Less developed, but still visible, is the phylogenetic signal for the presence of translucent patches in hindwing ($K = 0.442$, $p = 0.016$; $\lambda = 0.782$, $p < 0.001$) and in the basal colouration of the non-translucent part of the wings ($K = 0.585$, $p = 0.01$; $\lambda = 0.758$, $p = 0.012$).

Taxonomy

Amerila florinae Ignatev, sp. n.

(Figs 70, 111)

ZooBank taxon LSID:

B67EC842-4894-448F-ACA3-89A63FB17830

Diagnosis. The habitus of the new species is reminiscent of the other taxa and *Amerila timolis* (Rotschild, 1914) (Fig. 69) based on the similar wing pattern where both taxa have a semitransparent area in the postdiscal area of

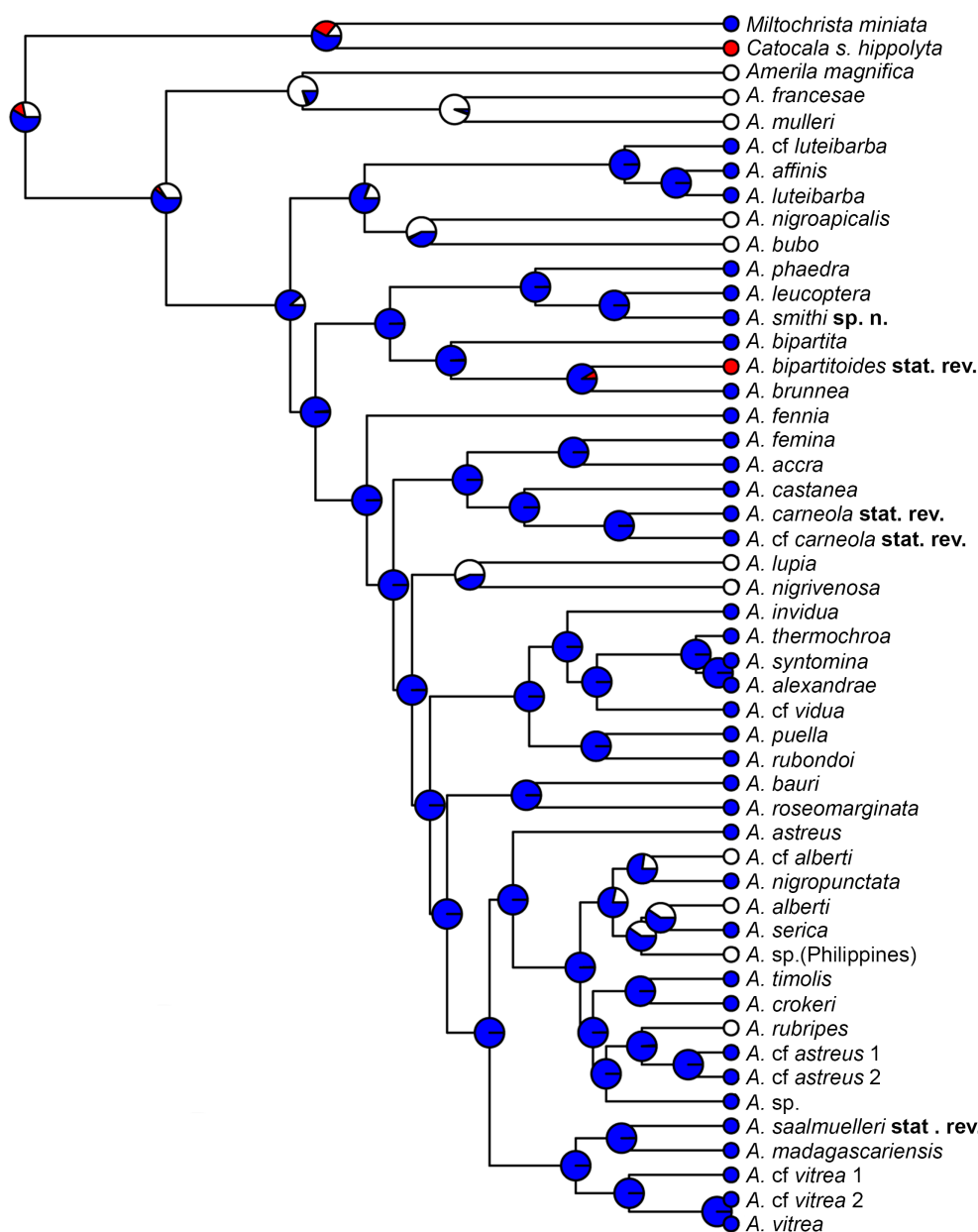


Fig. 3. Basal colouration of wings in male adults. Red, blue, and white indicate gray, brown, and white basal colouration of wings, respectively.

forewing and a stripe of pale yellow scales near the costal margin of the hindwing. However, the new species clearly differs from *A. timolis* in its darker colouration, and in the shape of the forewing where the apex is more pointed. Moreover, the male genitalia structures of the new species are slightly different from those of *A. timolis*, where the latter has a narrower tegumen and a noticeably shorter valva (Figs 111, 112).

Description. Male (Fig. 70). Forewing length: 23–24 mm. **Head.** Antenna filiform, brown; scapus and pedicellus barrel-shaped, red; flagellum with very thin and short ciliation, first 5–7 segments of flagellum covered in brownish-red scales dorsally. Frons slightly bulged, light brown, with rounded spot of dark brown scales posteriorly; vertex thickly covered by light brown scales, with large dark brown sub-quadrate central mark posteriorly. Compound

eye very large, globular; ocellus distinct; proboscis well developed. Labial palp upcurved, rounded apically, covered by red and dark brown scales, distally bearing a blotch of dark brown scales; first segment approximately same in length as second, red with dark-brown rounded spot laterally, second segment red, dark brown laterodistally, third segment ca. half as long as second, red, with dark-brown apex. **Thorax.** Patagium, tegula, mesoscutum, mesoscutellum light brown; patagium with large, dark brown basolateral, and postero-lateral dot, tegula with lateral dot, and with large triangular medial spot. Mesoscutum with two dark brown dots basally, and with one large dark brown spot medially; mesoscutellum with two dark brown dots distally. Metascutum covered in long reddish hairs. Foreleg with coxa reddish, with brown blotch basally; femur pale red; epiphysis reddish with stripe of brown scales

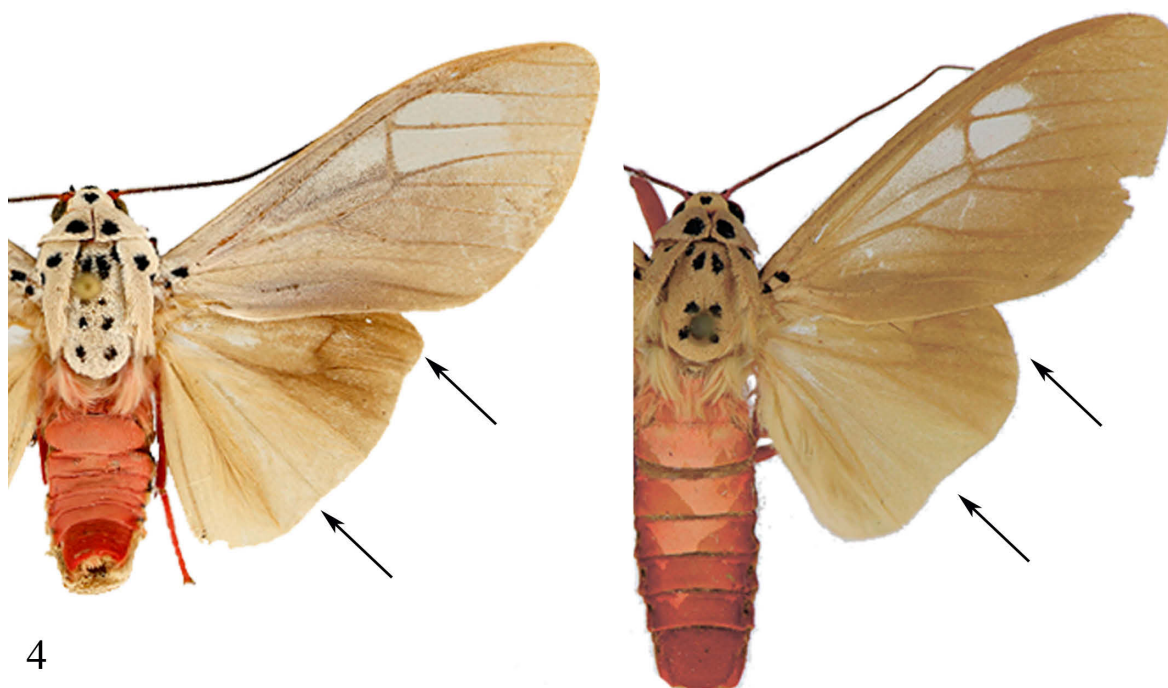


Fig. 4. Comparison of the hindwing shapes. Left – *A. smithi* sp. n.; right – *A. leucoptera*.

baso-medially; tarsus pale red. Mid- and hindleg similar in colouration to foreleg, middle tibia with two reddish spurs distally, outer of which half as long as inner one, tarsus uniformly reddish; hindleg coxa without dark distal scales, tibia armed with two pairs of reddish spurs situated postmedially and apically, where outer spur ca. half as long as inner one. Forewing triangular, apically rounded, costal margin straight in its proximal two-thirds, then slightly curved; ventral margin almost straight; termen is broad. Ground colour brown, with three black basal dots; cell gradually semitransparent distad, areas between veins R5–M1 and M1–M2 semitransparent until middle of veins. Ventral side colour similar to dorsal side, but basal area with a short, narrow reddish subcostal stripe. Hindwing triangular, sub-equilateral; apex rounded; outer margin shallow convex medially, and shallow convex anteriorly towards apex; ventral margin gently arcuate. Ground colour brown, discal zone pale brown. Ventral side as dorsal side, but dorsum lighter. **Abdomen.** Segments 1 to 7 covered in short reddish scales dorsally, creamy white ventrally; each segment with a pair of black ovoid dots laterally, where dorsal dot larger than ventral one. **Male genitalia** (Fig. 111). Uncus short, triangular, apically pointed. Tegumen of average size of the genus, arms narrow; vinculum very short, broadly rounded; saccus well developed, rounded. Valva broad, round, dorsal margin and apex evenly rounded, ventral margin almost straight, slightly convex subbasally and postmedially; valva surface with long, thin setae along margin. Harpe long, broad basally, curved ventrad subbasally, tapered distally into pointed apex, reaching outer margin of valva. Corema relatively short, base spherical, covered in fine, long setae. Juxta slightly sclerotized, rounded rectangular, unmodified. Aedeagus very short, dilated posteriorly, weakly sclerotized; vesica moderately

long, very thick, with a large, inflated basal diverticulum; cornutus situated distally, heavily sclerotized, long, thick, rod-like.

Female unknown.

Type material. Holotype ♂, “Indonesia / Bacan Island / 2–12. May 2008 / leg. St. Jakl” // “gen. slide / No. 36.308” (MWM/ZSM). Paratype ♂, with the same data as in the holotype.

Type locality. Indonesia, Bacan Isl.

Etymology. This new species is dedicated to Ms Florina Witt, daughter of Dr Verena Witt, one of the co-founders of the Witt Foundation.

Distribution. The species is known only from the Bacan Island of the Maluku archipelago, Indonesia.

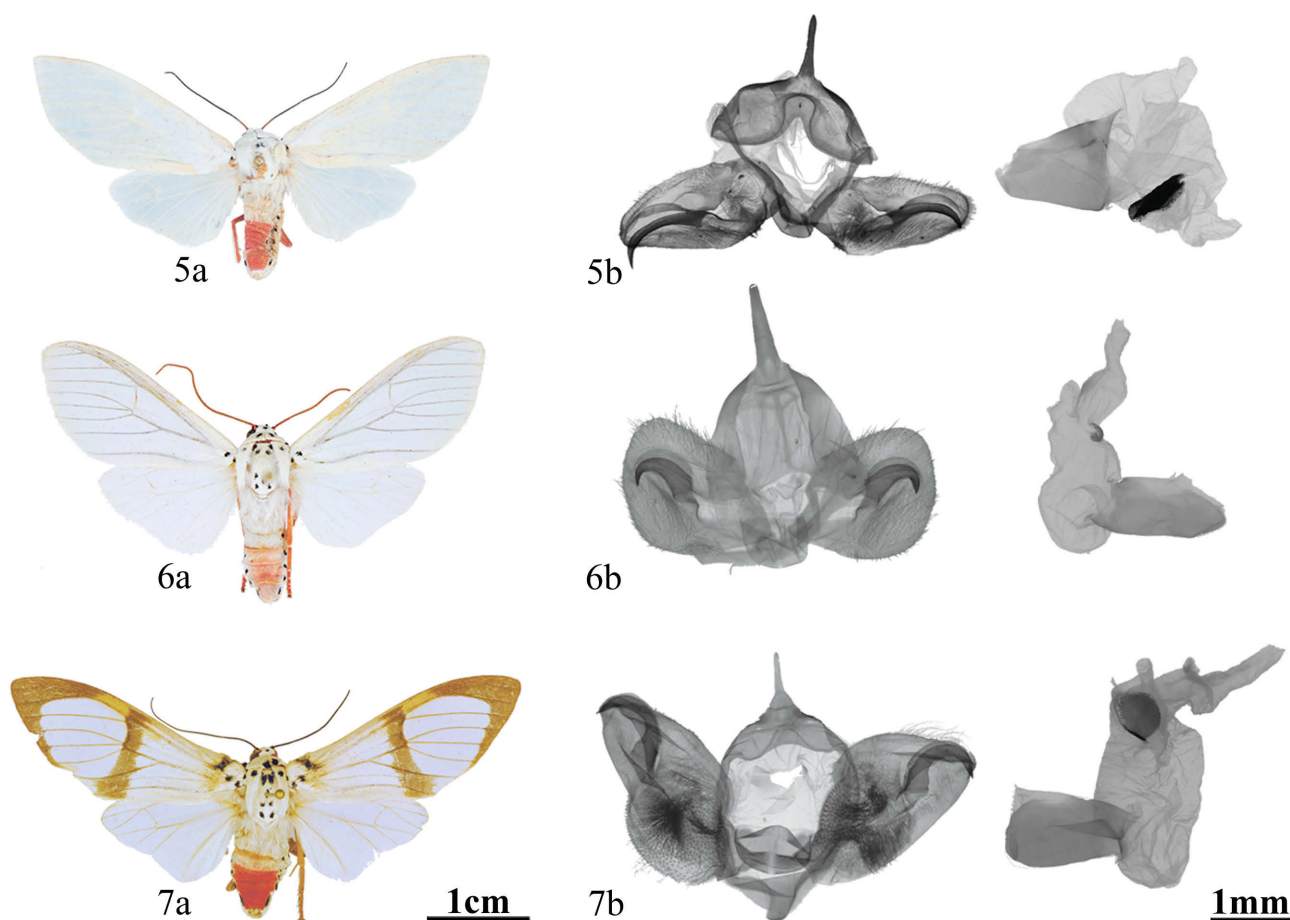
***Amerila smithi* László, sp. n.**

(Figs 4, 10a, 10b, 42, 83)

ZooBank taxon LSID:

C610CE89-196F-40D5-A2A4-5C037DEC1CAF

Diagnosis. The new species is reminiscent of its closely related sister taxon *A. leucoptera* (Fig. 11a), but in the male individuals it is easily distinguished by the greyish shade of the body and wings as opposed to the brownish ground colour of *A. leucoptera*, the more pointed forewing, the noticeably larger, more elongate semitransparent areas between veins R5–M1 and M1–M2 and the slightly produced apex of the hindwing which is evenly rounded in *A. leucoptera* (Fig. 4, 11a). It is important to note, that *A. pannosa* (Grünberg, 1908), a synonym of *A. leucoptera* was described from Uganda and the photograph of the holotype published in the original description was examined to exclude the possible conspecificity with the Zambian moth. The wing shape and the size and shape of the semitransparent forewing patches of *A. pannosa* are identical to those of *A. leucoptera*, in addition, a DNA barcoded specimen



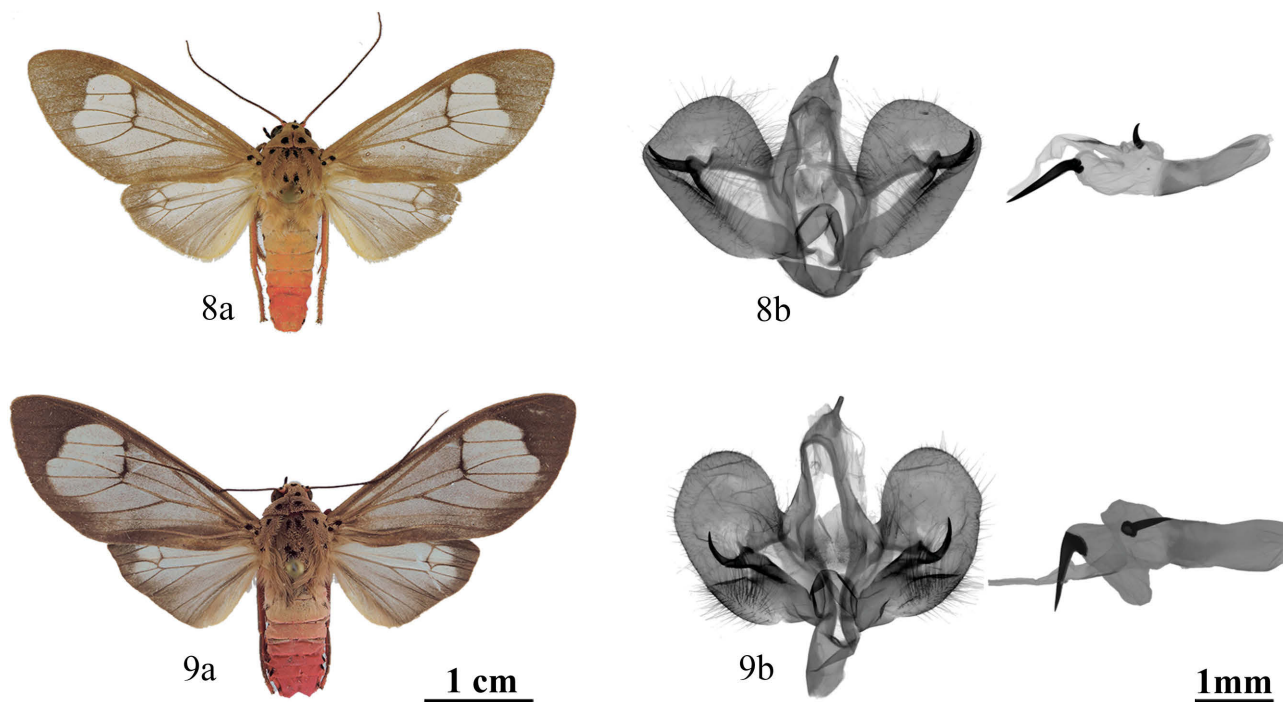
Figs 5–7. Male adults and genitalia of *A. magnifica* species complex. 5 – *A. francesae*, holotype (MWM/ZSM); 6 – *A. mulleri*, Tanzania (ANHRT). 7 – *A. magnifica*, Mozambique (ANHRT). a – adult; b – ventral view of genitalia (left), aedeagus (right).

from the North Kivu area being geographically very close to the type locality of *A. pannosa* has been recovered with *A. leucoptera*, thus the synonymy of the former name is retained here.

In the male genitalia, *A. smithi* has a considerably shorter, apically slightly bifurcate uncus (it is simply pointed in *A. leucoptera*), a distally more elongate and narrower valva, and a harpe with somewhat smaller lateral spines compared to those of *A. leucoptera*. The aedeagus and vesica configuration are nearly identical in the two species, however, *A. smithi* has somewhat shorter cornuti (Figs 10b, 11b).

In the females, *A. smithi* has a forewing venation highlighted in pale grey, whereas the venation of *A. leucoptera* is almost concolorous with the pure white forewing ground colour (Figs 41, 42). The female genitalia display the following differences between the two species: *A. smithi* has a considerably narrower, postero-medially less deeply incised postvaginal plate with more evenly arcuate posterior margin, a somewhat shorter posterior part of the signum bursae consisting of smaller spinulose signa, a markedly broader and somewhat longer longitudinal medial signum and a markedly larger rounded ventral plate of the corpus bursae compared to those characters of *A. leucoptera* (Figs 82, 83).

Description. Male (Fig. 10a). Forewing length: 21–24 mm. **Head.** Antenna filiform, brown; scapus and pedicellus barrel-shaped, red, scapus with black spot dorsally; flagellum has very thin and short ciliation, first 5–7 segments of flagellum covered in brownish-red scales dorsally. Frons slightly bulged, white or dirty white, with rounded black spot anteriorly; vertex whitish with large black rounded central spot and bordered by pink scales anteriorly. Compound eye large, globular; ocellus distinct; proboscis well developed. Labial palp upcurved, rounded apically, first segment approximately same in length as second one, pink baso-laterally, whitish ventrally, black distally, second segment pink in basal part with a few white scales ventrally, black distally, third segment ca. half as long as second, proximal half pink, apical half black. **Thorax.** Patagium, tegula, mesoscutum, mesoscutellum pale brown; patagium with large, round black postero-lateral, and antero-medial dot, tegula with postero-lateral postmedial dot. Mesoscutum with two black triangular spots posteriorly and two black dots anteriorly; mesoscutellum with two black dots medially. Metascutum covered in long pinkish hairs. Foreleg with inner side of coxa covered in pinkish, ventro-laterally in dirty white scales, with a small blackish dot sub-basally; femur bright pink dorsally, dirty white ventrally, distally with a belt of dark brown scales; tibia light brown dorsally, pinkish ventrally; tarsus pale brown ventrally.

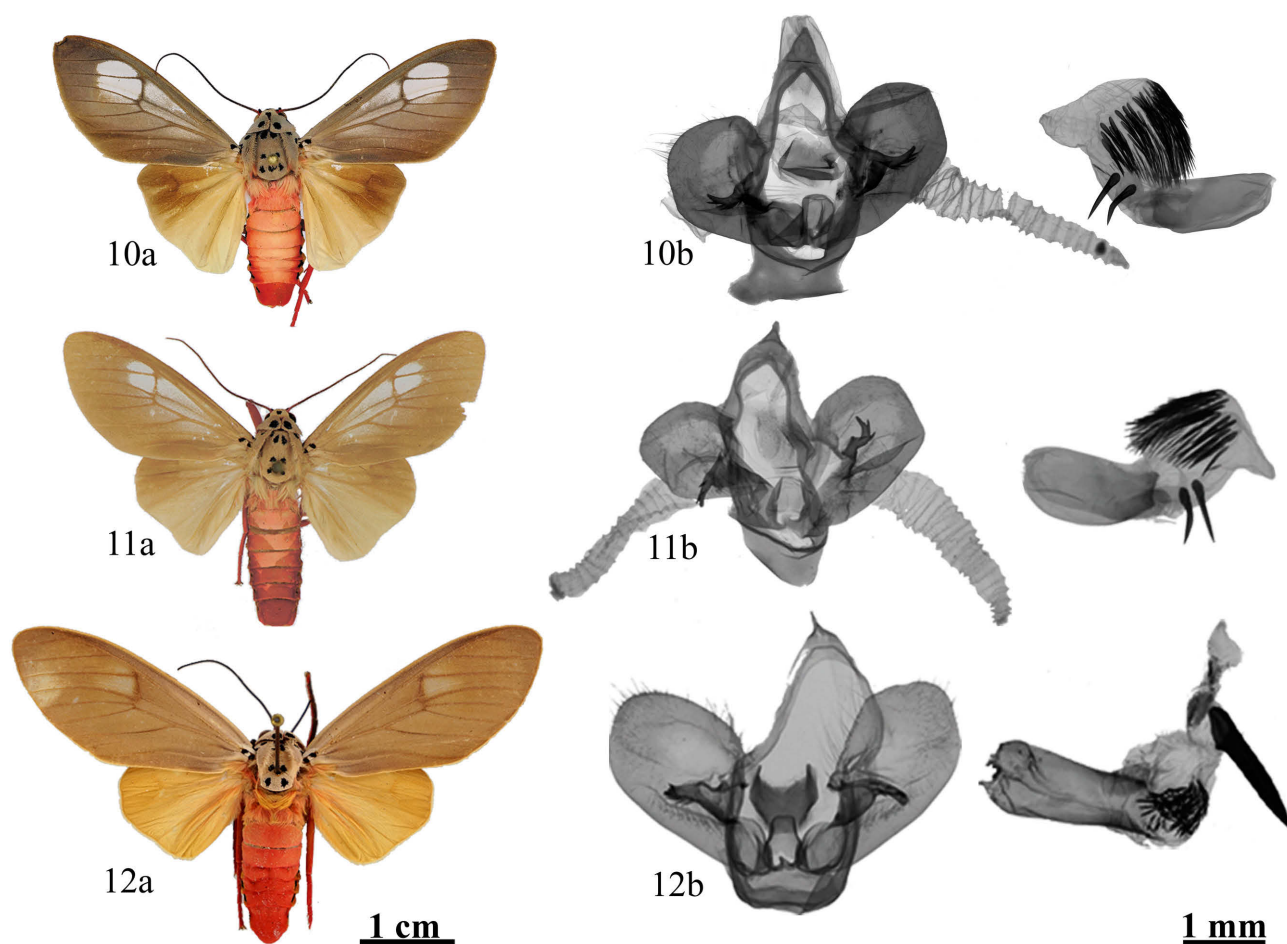


Figs 8–9. Male adults and genitalia of *A. luteibarba* species complex. 8 – *A. affinis*, Ivory Coast (ANHRT); 9 – *A. luteibarba*, Uganda (CHS). a – adult; b – ventral view of genitalia (left), aedeagus (right).

pinkish dorso-laterally with groups of brown scales dorsally. Mid- and hindleg similar in colouration to foreleg, midleg tibia with two pinkish spurs distally, outer one half as long as inner one, tarsus uniformly pinkish. Hind coxa without dark distal scales, tibia armed with two pairs of pinkish spurs situated postmedially and apically, where outer spur ca. half as long as inner one. Forewing relatively narrow, elongate triangular, apically rounded, costal margin straight in its proximal two-thirds, then slightly curved; ventral margin almost straight; termen is obtuse angled. Ground colour pale greyish brown with three black basal dots; cell gradually semitransparent distad, areas between veins R5–M1 and M1–M2 semitransparent until middle of veins. Ventral side colour similar to dorsal side but dorso-medial area covered in darker brown scales, and basal area with a short, narrow pinkish subcostal stripe. Hindwing almost equilateral; apex produced into a short, rounded lobe; outer margin convex medially; ventral margin gently arcuate. Ground colour light brown, costal third gradually darkened towards termen with a dark brown streak along M3. Ventral side as dorsal side, but somewhat darker. **Abdomen.** Segments 1–6 covered in short pale pink scales dorsally, creamy white ventrally; 7th segment salmon dorsally, bright white ventrally; each segment with a pair of black ovoid dots laterally where dorsal dots larger than ventral one. **Male genitalia** (Fig. 10b). Uncus short, triangular, apex bifid with two very short processes. Tegumen of average size for the genus, arms rather narrow; vinculum short, broadly rounded; saccus well developed, rounded. Valva short broad, round, dorsal margin gently arched, apex broadly rounded, ventral margin rounded subbasally and postmedially; valva surface with long, thin setae along distal part of ventral margin and apex. Harpe

moderately long, very broad basally, abruptly tapered medially, curved dorsad, apex pointed, ventral margin with 4–5 acute spikes. Corema long and relatively narrow, base spherical, apex covered in middle-sized setae. Juxta weakly sclerotized, rounded rectangular, unmodified. Aedeagus very short moderately thick, tubular, slightly curved posteriorly; vesica short, proximal section dilated, tapered distally, subbasally armed with 2 robust, rather long dorso-lateral cornuti, ventro-medially with a field of numerous long, thin, acute spines.

Female (Fig. 42). Forewing length 23–27 mm. Head and thorax pattern, colouration of legs as in male, ground colour bright white throughout, forewing venation highlighted in pale grey, area between veins semitransparent. First abdominal segment dirty white, segments 2–7 salmon, 8th segment bright red dorsally, all segments bright white ventrally, lateral surface of each segment with a pair of black round blotch where dorsal blotch larger than ventral one. Female genitalia (Fig. 83) with ovipositor very broad and short, papilla analis rounded quadrangular, apophysis posterioris relatively long, thin, apically pointed. Eight tergite short, distal margin almost straight, proximal margin evenly convex, laterally tapered into narrow marginal sclerotization connected with short and pointed apophysis anterioris. Lamella postvaginalis well-developed, relatively long and broad, distal margin gently arched with short and narrow medial notch, proximal margin gently concave. Ostium bursae rather broad, membranous, ductus bursae very short; corpus bursae amorphous with a short, dome-shaped proximal projection; cervix bursae fused with bursa copulatrix, situated anterolaterally. Signum bursae complex consisting of a row of small, scobinate-spinulose rounded plates along the distal and right lateral margin decreasing in



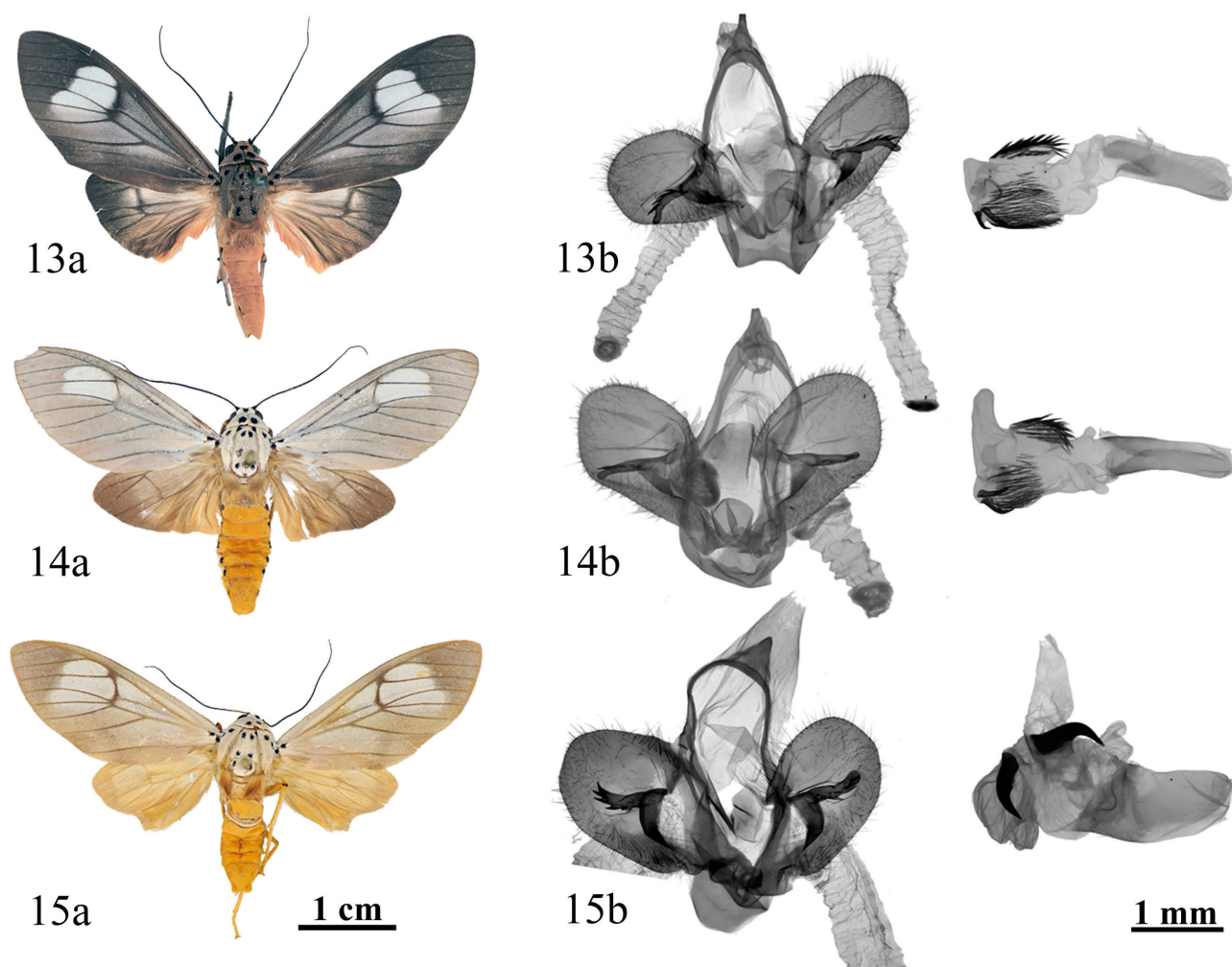
Figs 10–12. Male adults and genitalia of *A. phaedra* species complex. 10 – *A. smithi* sp. n., holotype, Zambia (ANHRT); 11. *A. leucoptera*, Ivory Coast (ANHRT); 12 – *A. phaedra*, Kenya (ZSM). a – adult; b – ventral view of genitalia (left), aedeagus (right).

size proximally, an elongate, densely scobinate-spinulose, invaginated, longitudinal mediodorsal, and a less heavily sclerotized, large, rounded rectangular ventral plate of smooth surface.

Genetic information. *Amerila smithi* sp. n. has been assigned the BIN URI: BOLD:AEJ3161. The intraspecific divergence ranges between 0.15–0.31%. The nearest neighbour of the species is *A. phaedra* Weymer, 1892 (Figs 12, 39, 81) with pairwise distances in the range of 2.82–3.30%. The pairwise distance between *A. leucoptera* (Hampson, 1901), the morphologically closest sister of *A. smithi*, and the new species is 2.98–3.63%.

Type material. Holotype ♂, “ZAMBIA 1400 m / Hillwood, Ikelenge / S11°16'02", E24°18'59" / 17–24.iii.13 Light Trap / leg. Smith, R. & Takano, H.” // “ANHRTUK / 00194259”, Gen. slide No. LG 6015, DNA barcode/BOLD process id.: ANHRTUK00194259/ANLMN3407-21 (ANHRT). Paratypes: Zambia. 4♂, with the same data as in the holotype; 4♂, 2♀, same locality and collectors, 25.–27.xi.2014, gen. slide No.: LG 4524 (♂); 1♀, same locality, 30.iv.–11.v.2014, leg. Smith R., Takano H., Chmurova L. & Smith L.; 1♀, same locality and collectors, 21.–28.x.2013; 2♂, 4♀, same locality, 23.–30.i.2019, leg. Bashford M., Miles W., Mulvaney L., Smith R.; 9♂, 5♀, Chitunta Plain (Miombo/Dambo mosaic), 1396 m, 11°29'12"S, 24°24'18"E, 29.xi.–4.xii.2019, MV, LepiLED and actinic light trap, leg. Bashford M., Miles W., Mulvaney L., DNA barcode/BOLD pro-

cess id.: ANHRTUK00125267/ANLMN3408-21 (♂); 1♂, 3♀, Nyangombe Falls, (Miombo/Riverine forest mosaic), 1300 m, 11°48'25"S, 24°32'12"E, 17.–23.xi.2019, MV and actinic light trap, leg. Bashford M., Miles W., Mulvaney R., Smith R., gen. slide No.: LG 6016 (♂); 7♀, Zambezi Rapids (Miombo/Riverine forest mosaic), 1205 m, 11°7'30"S, 24°11'6"E, 4.–9.i.2018, MV and actinic light trap, leg. Aristophanous M., Dérozier V., László G., Oram D., gen. slide No.: LG 5642, DNA barcode/BOLD process id.: ANHRTUK00054876/ANLMN3409-21 (♂); 1♀, Nkwaji, Mwinilunga, 1316 m, S11°36'22", E24°33'17", 5.–8.v.2014, Light Trap, leg. Smith R., Takano H., Chmurova L., Smith L.; 1♂, 1♀, Camp near Kanyama, (Miombo/Riverine/Dambo mosaic), 1375 m, 11°25'36"S, 24°40'00"E, 4.–7.xii.2019, MV and actinic light trap, leg. Bashford M., Miles W., Mulvaney L.; 1♀, Jiwundu Swamp, (Miombo/Riverine forest mosaic), 1340 m, 11°51'54"S, 25°33'20"E, 29.x.–4.xi.2018, actinic Light Trap, leg. Aristophanous M., Dérozier V., László G., Oram D.; 1♂, same locality, 23.–30.x.2017, leg. Carter M., Lloyd A., Miles W., Oram D., Smith R.; 1♀, same locality, 21.–24.xi.2014, leg. Smith R. & Takano H.; 2♂, Lukwakwa, West Lunga NP, 1147 m, S12°39'40", E24°26'13", 28.–29.iv.2014, Light Trap, leg. Smith R., Takano H., Chmurova L. & Smith L.; 1♂, same site, 4.–8.xi.2013, leg. Smith, Takano & Oram; 1♀, Greystone, Kitwe, Copperbelt Province, 1179 m, S12°55'50", E28°14'29", 17.–21.v.2013, Light Trap, leg. Smith R., Takano H. & Oram D.; 1♂, Jan Fisher's Farm, Chingola (Miombo/Riverine forest mosaic), 1365 m, 12°36'10"S, 27°55'48"E, 14.–17.xi.2019, MV Light Trap, leg. Bashford M., Miles W., Mulvaney L. leg.; 1♂, Ntumbachushi Falls, Ngona River, Lua-



Figs 13–15. Male adults and genitalia of *A. bipartita* species complex. 13 – *A. brunnea*, Uganda (CHS); 14 – *A. bipartitoides* stat. rev., Tanzania (ANHRT); 15 – *A. bipartita* Tanzania (ANHRT). a – adult; b – ventral view of genitalia (left), aedeagus (right).

pula Prov., 1166 m, S09°51'12", E28°56'40", 1.–3.ii.2019, MV light trap, leg. Dérozier V., Mulvaney L., Takano H.; 1♂, Luman-gwe Falls, Kalungwishi River, 1187 m, S09°32'33", E29°23'17", 20.–22.xi.2012, Light Trap, leg. Smith R., Takano H. & Oram D.; 1♂, Lake Kashiba, Mpongwe, 1160 m, 13°26'55"S, 27°56'40"E, 4.–5.v.2015, Light Trap, leg. Smith R., Takano H., Aristophanous M.; 1♂, Chisimbe Falls, Kasama, 1320 m, S10°06'31", E30°55'02", 27.–29.iv.2013, Light Trap, leg. Smith R., Takano H. & Oram D.; 1♂, Kapishya Hot Springs, Shiwa N'gandu Estate, 1437 m, S11°10'13", E31°36'00", i.2015, M.T. Harvey coll., leg. Smith R. & Takano H.; 1♂, same locality and collectors, i.–iii.2016; 1♀, same locality and collectors, iii.2015, DNA barcode/BOLD process id.: ANHRTUK00194261/ANLMN3415-21; 1♀, same locality, 24.–27.iv.2013, leg. Smith R., Takano H., Oram D.; 1♀, same locality and collectors, v.2015; 2♀, same locality, 16.–17.v.2019, Dérozier V., László G., Miles W. (ANHRT). Tanzania. 1♂, Kagera District, Near Kasato, 25.x.2012, leg. Elk Ott & H. Sulak (CHS); 1♂, same locality, gen. slide No. 34.700 (CHS).

Type locality. Zambia, Hillwood, Ikelenge, 1400 m 11°16'02"S, 24°18'59"E.

Etymology. The new species is dedicated to Mr Richard Smith, Chairman of the Board of Trustees, African Natural History Research Trust, founder of the entomological research museum of the Trust. Mr Smith is a committed promoter of entomological research in Africa and he is one of the collectors of this new species.

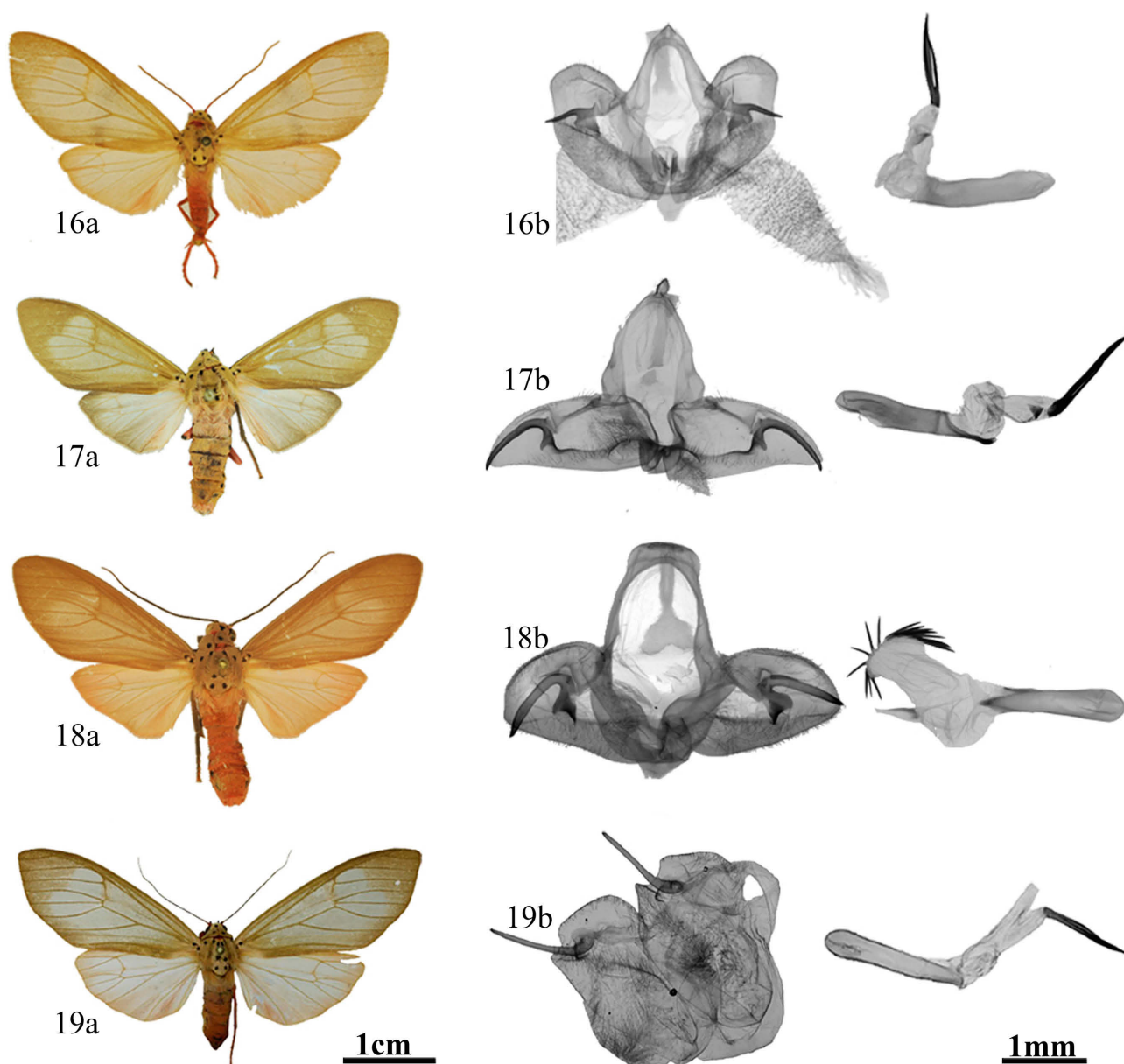
Distribution. *Amerila smithi* is widely distributed in the Zambian plateau, inhabiting miombo woodlands. The species has also been collected in northwestern Tanzania (Kagera district) and most probably occurs in Katanga (DRC) as well.

Comparative material of *Amerila leucoptera* (Hampson, 1901) examined

Type material. Holotype of *Rhodogastria leucoptera* Hampson, 1901. ♀, red ring label "Type" // "S. Leone. / 94-214." // [with handwritten] "Rhodogastria / leucoptera. / type ♀. Hmpsn." // "ARCTIIDAE ♀ / Genitalia Slide / VU no. 831" // "Arctiidae / genitalia slide / No. 3048" // QR code label with unique id.: NHMUK 010915779 (NHMUK).

Holotype of *Rhodogastria sarconota* Hampson, 1911. ♀, red ring label "Type" // [partly handwritten] "S. Nigeria. / Aro / 1.iii.1910. / C.M. Gray / 1910-257" // [with handwritten] "Rhodogastria / sarconota. / type ♀. Hmpsn." // "Arctiidae genitalia slide No. 4393" // QR code label with unique id.: NHMUK 010915780 (NHMUK).

Additional material. Cameroon. 1♂, Adamawa Region, Adamawa Plateau, 7.3 km West of Bazanga, Chute De Tello, 1246 m, 07°13'50.6"N, 13°56'29.2"E, 24.–30.ix.2018, MV Light Trap, Sáfian, Sz., Simonics, G. leg., ANHRT:2018.36, DNA barcode/BOLD process id.: ANHRTUK00070065/ANLMN3403-21;



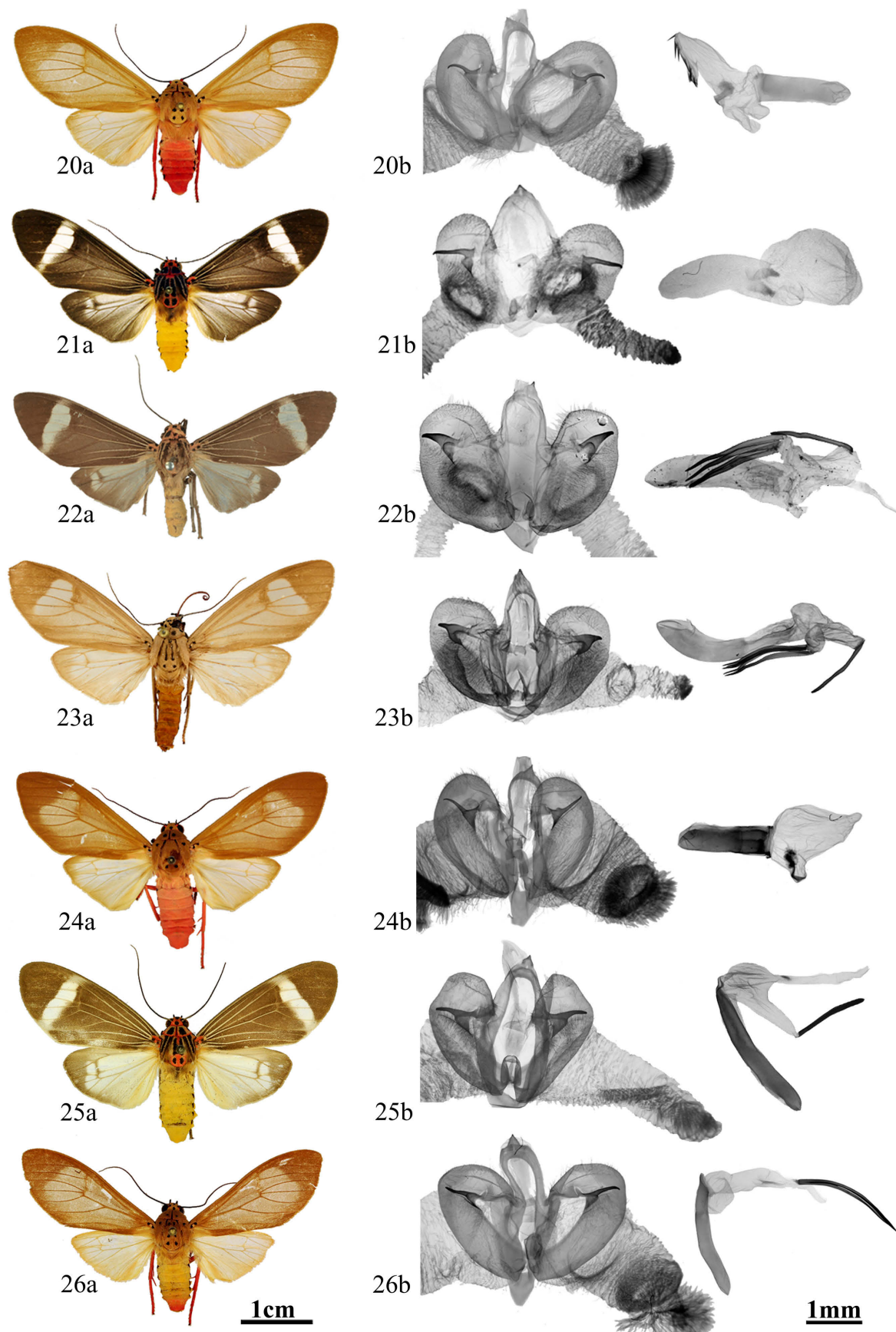
Figs 16–19. Male adults and genitalia of *A. carneola* species complex. 16 – *A. carneola* stat. rev., DRC (ANHRT); 17 – *A. castanea*, Congo (MWM/ZSM); 18 – *A. accra*, Liberia (ANHRT); 19 – *A. femina*, Cameroon (NEJCU). a – adult; b – ventral view of genitalia (left), aedeagus (right).

1♀, North Region, Wack (La Falaise), 900 m, 07°40'16.5"N, 13°33'18.4"E, 2.–21.x.2018, LepiLED Light Trap, Sáfián, Sz., Simonics, G. leg. ANHRT:2018.36, DNA barcode/BOLD process id.: ANHRTUK00077379/ANLMN3405-21 (ANHRT). DRC. 1♀, Kanyatsi, Nord-Kivu, 1700 m, 1°22'S, 28°59'E, vi.2017 ex coll. A. Colley, ANHRT:2018.22, gen. slide No.: LG 6017, DNA barcode/BOLD process id.: ANHRTUK00190105/ANLMN7899-21 (ANHRT). Guinea. 1♂, Ditinn, Chute de Ditinn, 771 m, 10°49'08"N, 12°11'30"W, 18.–25.ix.2019, MV Light Trap, Geiser M., Koivagui S., Leno M., Miles W., Mulvaney L., Sáfián Sz. Leg., ANHRT: 2019.19, gen. slide No.: LG 6014, DNA barcode/BOLD process id.: ANHRTUK00140257/ANLMN3404-21 (ANHRT). Ivory Coast. 1♂, Kakpin Village, Comoe 0, Open forest, 259 m, 08°39'07"N, 03°46'58.8"W, 27.vi.–02.vii.2015, Light Trap, Aristophanous M., Moretto P., Ruzzier E. leg., ANHRT:2017.14, gen. slide No.: LG 4525; 2♀, Gbando Village, (Sudanese forest with Gallery forest), 417 m, 9°34'17.1"N, 6°41'1.1"W, 15.–22.vi.2018, MV Light Trap, Aristophanous M.,

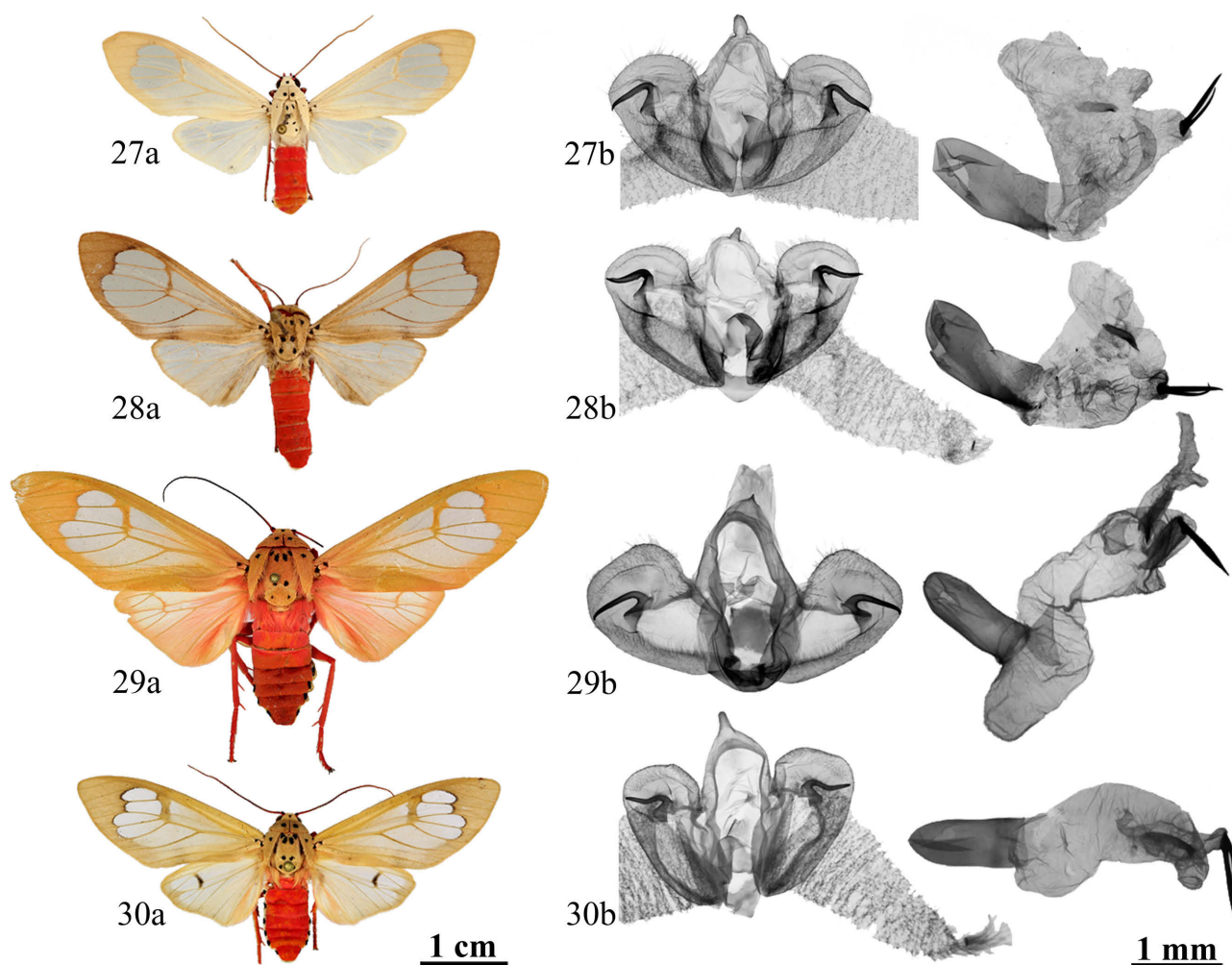
Miles W., Moretto P., Outtara Y. leg., ANHRT:2018.28, gen. slide Nos: LG 5641, LG 5615, DNA barcode/BOLD process ids: ANHRTUK00103782/ANLMN3406-21, ANHRTUK00103781/ANLMN3418-21 (ANHRT).

DISCUSSION

The phylogenetic analyses (ML, BI) resulted in topologies that divide the genus into two main clades with *A. magnifica*, *A. mulleri* and *A. francesae* (Figs 5–7, 31, 32, 75, 76) forming a well-supported cluster (ML 85.5/98, BI 0.98) that is sister to all other *Amerila* lineages. This latter clade is subdivided into 13 (BI) or 14 (ML) lineages recognised here as species groups. The most derived lineage is the Indomalayan-Australasian clade that is the sister group to the predominantly Afrotropical *A. vitrea* species complex that includes an unidentified Indomalayan species (*A. cf. vitrea* 1, BOLD sample id.: NIGBE MOT-01523).



Figs 20–26. Male adults and genitalia of *A. syntomina* species complex. 20 – *A. cf. vidua*, Mozambique (ANHRT); 21 – *A. alexandrae* Tarcz & László, 2019; 22 – *A. syntomina* (Butler, 1878), lectotype (BMNH); 23 – *A. thermochroa* (Hampson, 1916) Ethiopia (MWM/ZSM); 24 – *A. invidua* (Bethune-Baker, 1925), Liberia (ANHRT); 25 – *A. rubondoi* Häuser & Boppré, 1997, Guinea (ANHRT); 26 – *A. puella* (Fabricius, 1794), Guinea (ANHRT). a – adult; b – ventral view of genitalia (left), aedeagus (right).



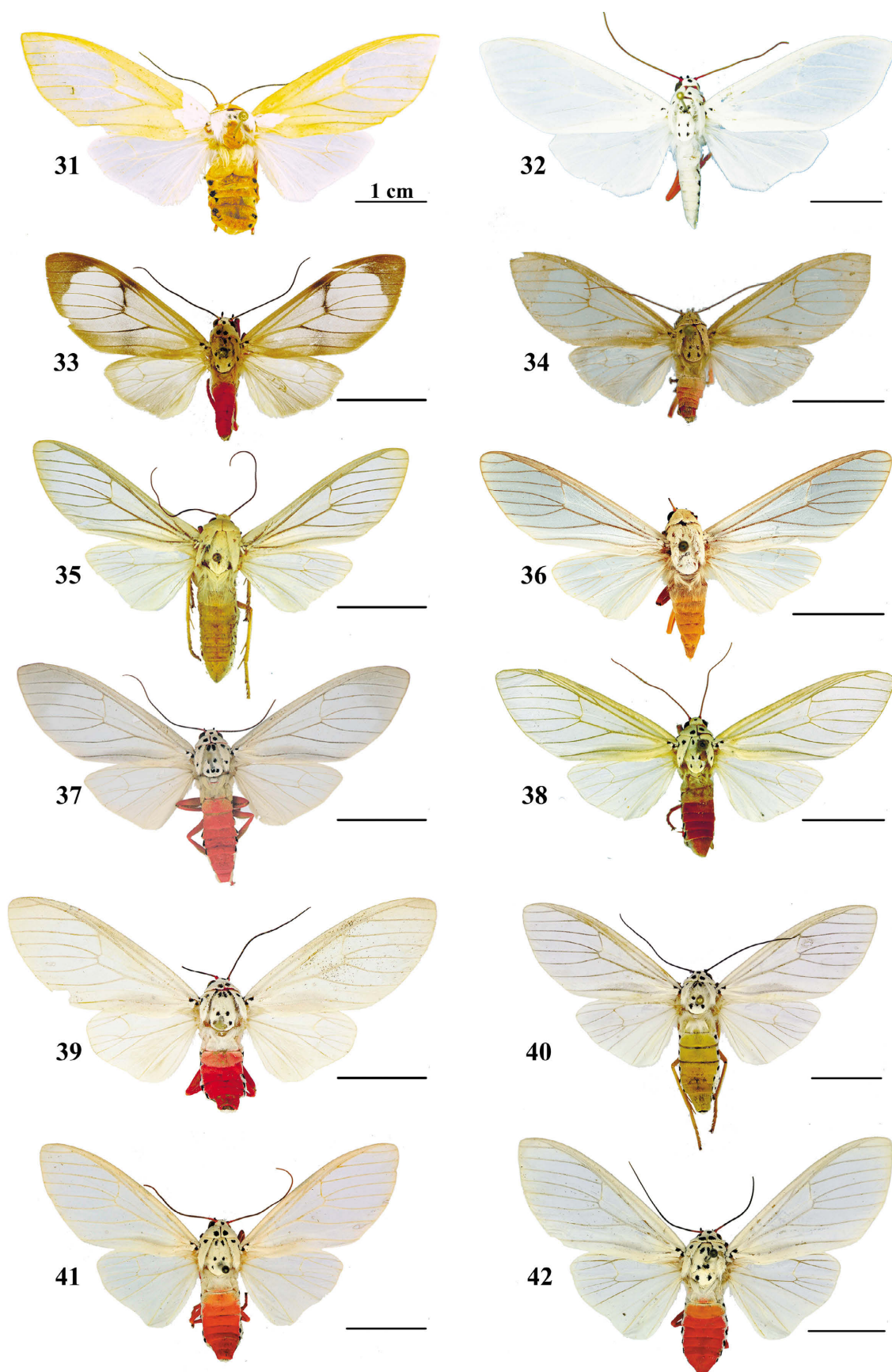
Figs 27–30. Male adults and genitalia of *A. vitrea* species complex. 27 – *A. cf. vitrea*, Yemen (CGM); 28 – *A. vitrea*, Tanzania (MWM/ZSM); 29 – *A. madagascariensis*, Madagascar (ANHRT); 30 – *A. saalmuelleri* stat. rev., Madagascar (ANHRT). a – adult; b – ventral view of genitalia (left), aedeagus (right).

The basal *A. magnifica* clade (Figs 5–7, 31, 32, 75, 76) was analysed in detail by Ignatev et al. (2022) who recognised several shared traits such as adult colour (Figs 5a, 6a, 7a, 31, 32) where all three species have a white wing ground colour, and the males display diagnostic semi-red/semi-white dorsal colouration of the abdomen. Further shared characters in the male genitalia (Figs 5b, 6b, 7b) include a conspicuously short aedeagus, vesica with plate-like sclerotization, instead bearing a true cornutus, and a simple, elongate uncus that is ca. five times longer than that of other *Amerila* species. These shared morphological characters are fully congruent with the distinct genetic position of the *A. magnifica* complex within the genus.

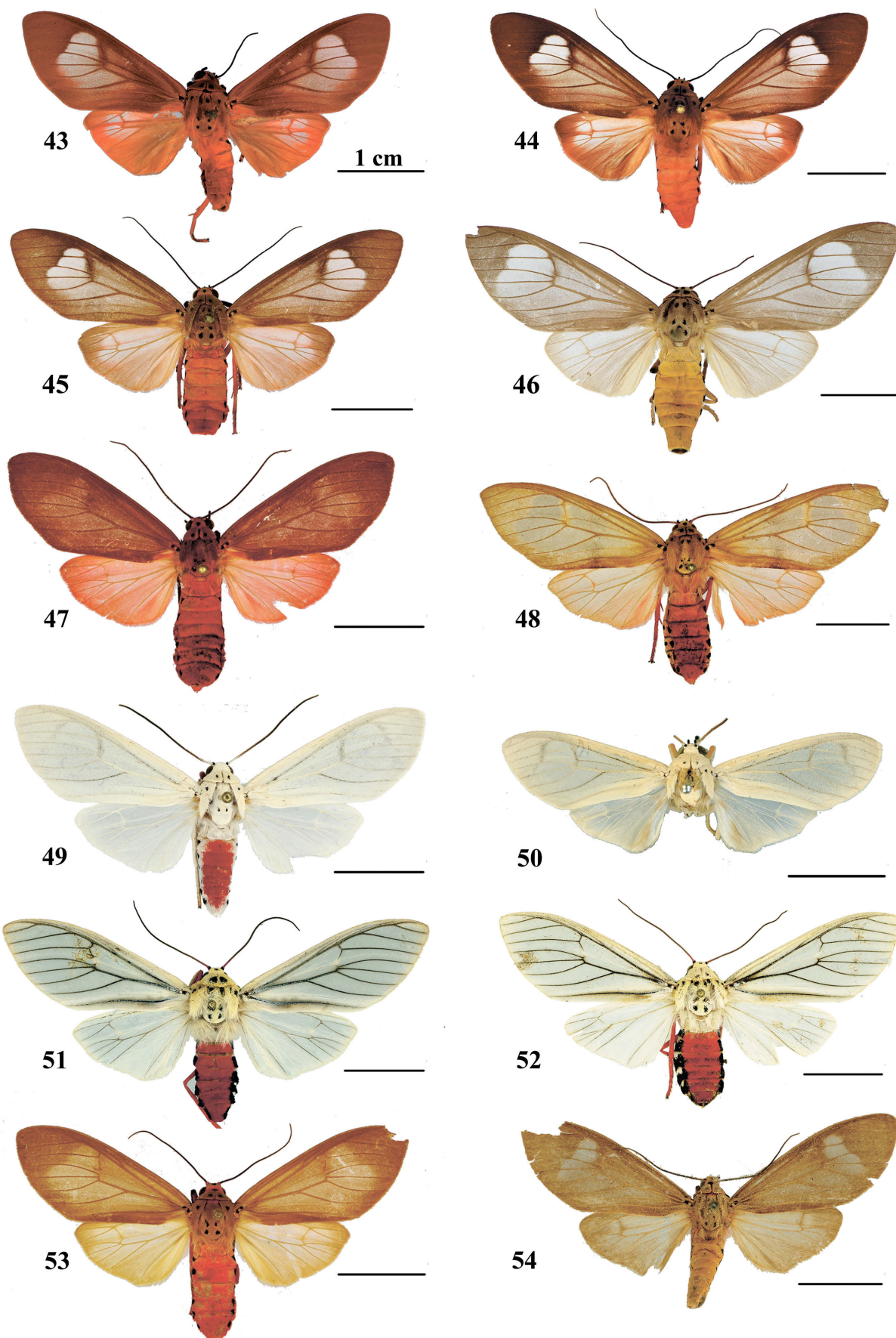
While the second main clade of *Amerila* has good support (ML 92.3/83), it includes a basal polytomy between the *A. nigroapicalis* – *A. bubo* group (white ground colour species), the *A. luteibarba* species group (semitransparent window surrounded by a dark brown marginal colour), and the clade comprising all other species. The *A. luteibarba* species group comprises *A. affinis* and *A. luteibarba*, as well as an unidentified taxon from Gabon (*A. cf. luteibarba*) (Figs 1, S1) that has robust support in both genetic analyses (ML 94.2/99, BI 1). Adults of these taxa share a

brown ground wing and an extensive semitransparent inner area (Figs 8a, 9a, 33, 34). Males of both species share autapomorphies of the male genitalia (Figs 8b, 9b), where the uncus is short and slightly tapered distally, the vesica bears two distinct, well-developed cornuti and the harpe of the valva is directed distally.

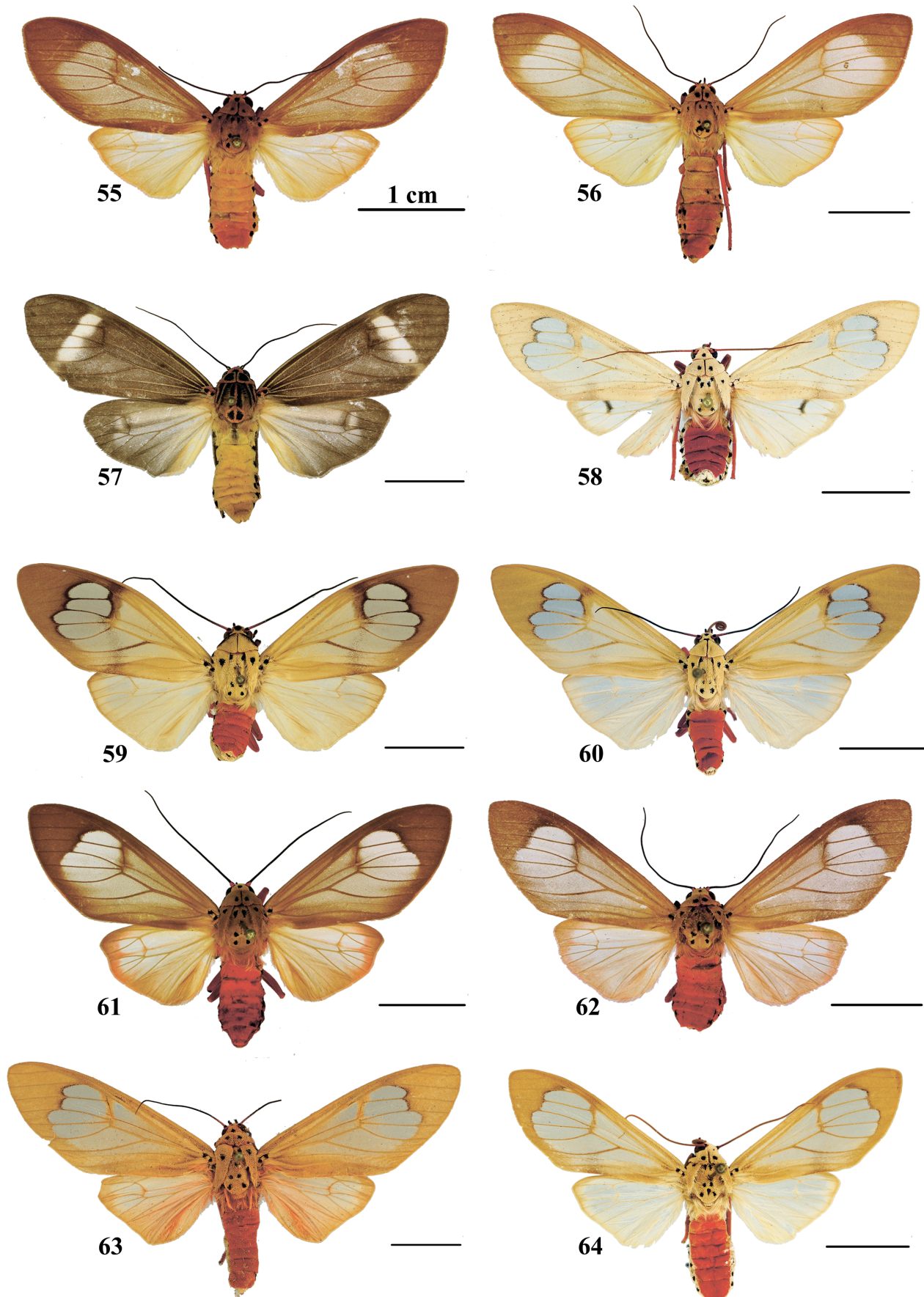
The phylogenetic position of and the relationship between *A. nigroapicalis* and *A. bubo* is uncertain due to the inconsistent results of the ML and BI analyses (Figs 1, S1). In the ML analysis, these two species are recovered as sister taxa, but with relatively low branch support (ML 34.1/55), whereas the BI tree results in a polytomy for both *A. bubo* and *A. nigroapicalis* (Fig. S1). Adult morphology of the two species includes both shared and unique characters. They share a whitish ground colour (Figs 35–38) and a comparably elongate tegumen in the male genitalia (Figs 105, 106). The uncus is apically bifurcate in *A. bubo*, whereas it is pointed triangular in *A. nigroapicalis*. Additional molecular studies involving further gene regions may clarify the phylogenetic position of these species, but based on our results we consider these two taxa as representatives of two separate monotypic species complexes.



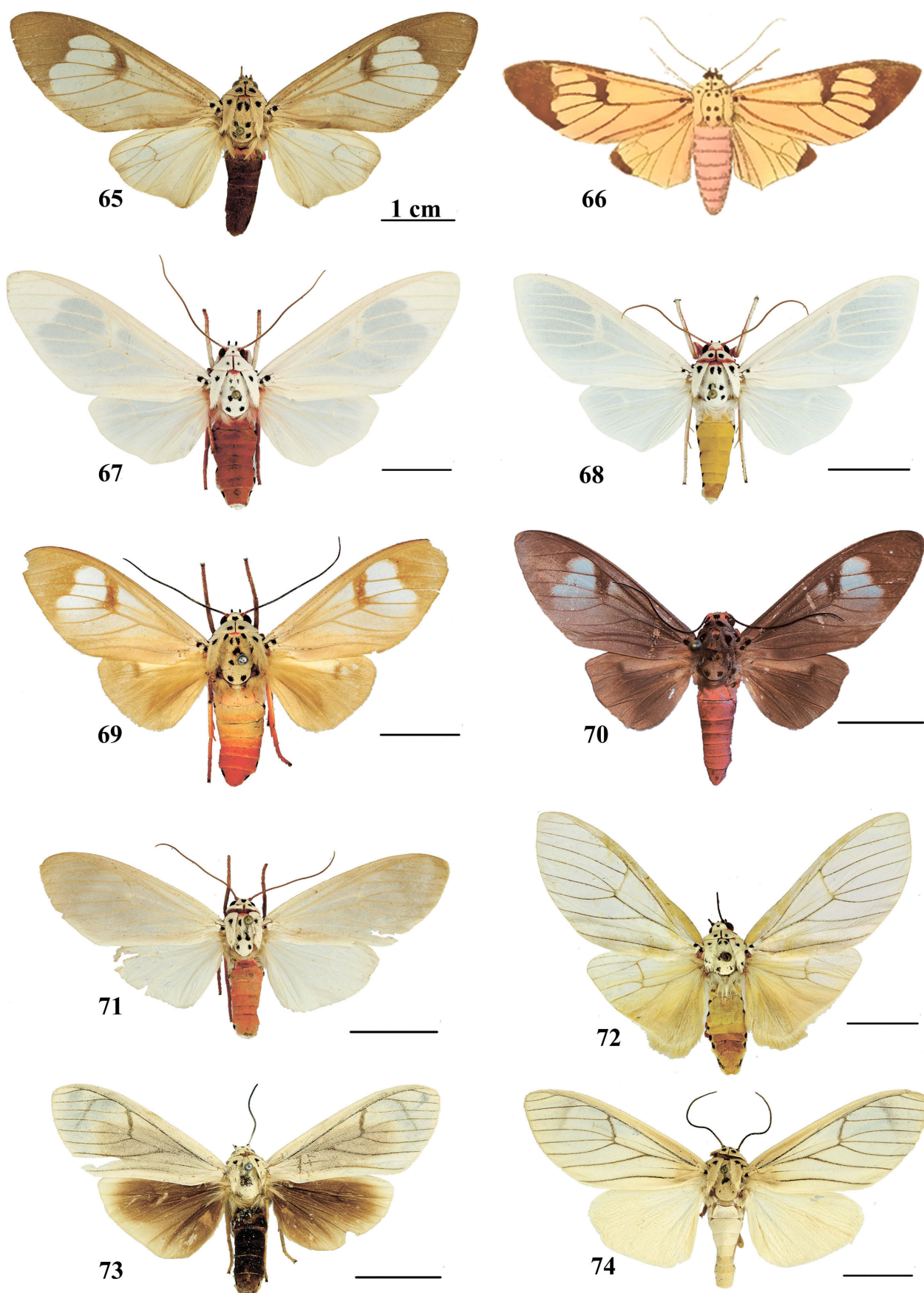
Figs 31–42. Adults of *Amerila* species. 31 – *A. francesae* paratype ♀, Tanzania (MWM/ZSM); 32 – *A. mulleri*, ♀, Cameroon (NECJU); 33 – *A. affinis*, ♀, DRC (ANHRT); 34 – *A. luteibarba*, ♀, Uganda (MWM/ZSM); 35 – *A. bubo*, ♂, Rwanda (ANHRT); 36 – *A. bubo*, ♀, Uganda (CHS); 37 – *A. nigroapicalis*, ♂, Zambia (ANHRT); 38 – *A. nigroapicalis*, ♀, Rwanda (ANHRT); 39 – *A. phaedra*, ♀, Mozambique (ANHRT); 40 – *A. bipartita*, ♀, Mozambique (ANHRT). 41 – *A. leucoptera*, ♀, Ivory Coast (ANHRT); 42 – *A. smithi* sp. n., paratype ♀, Zambia (ANHRT).



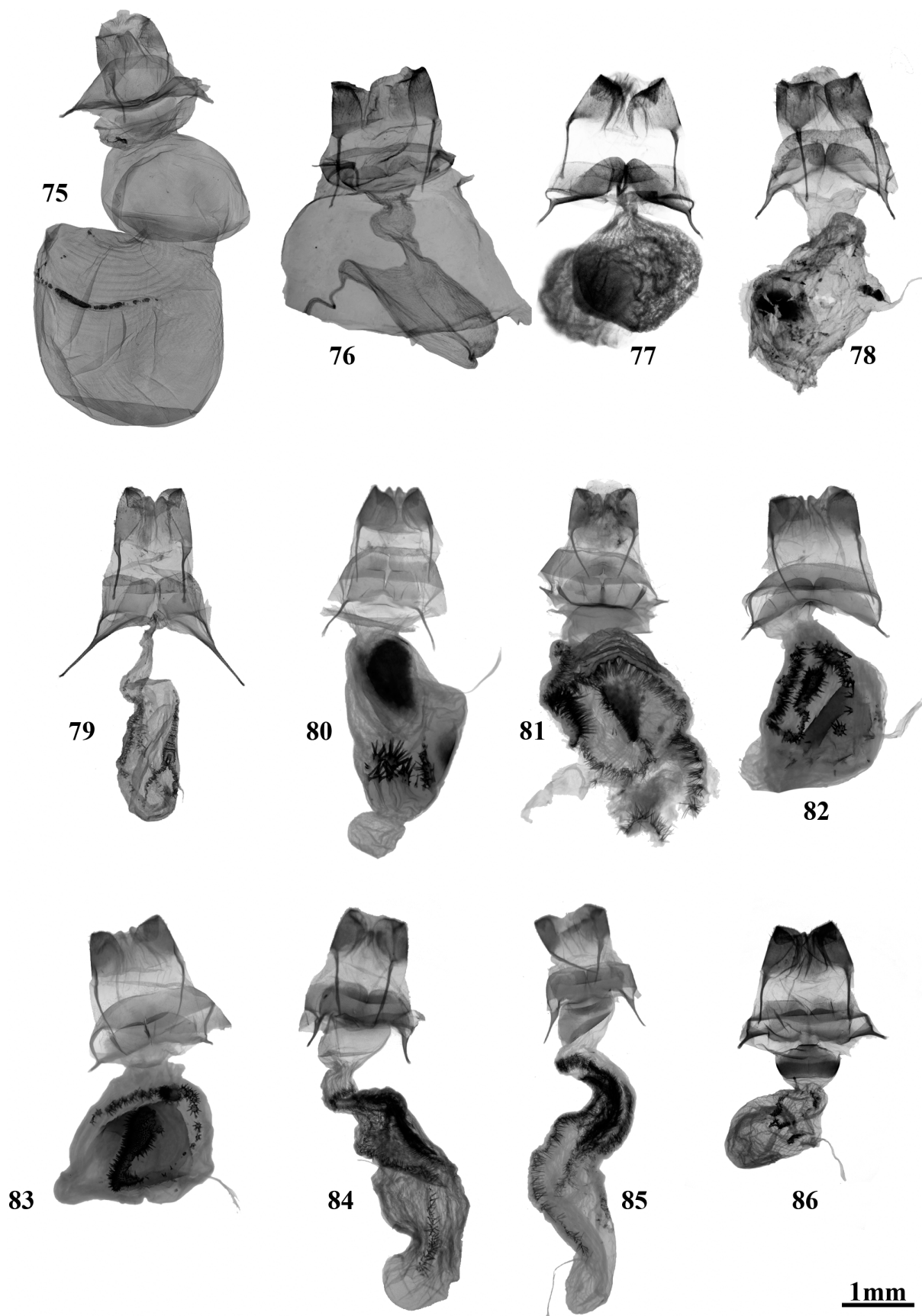
Figs 43–54. Adults of *Amerila* species. 43 – *A. fennia*, ♂, DRC (ANHRT); 44 – *A. fennia*, ♂, Liberia (ANHRT). 45 – *A. fennia*, ♀, Guinea (ANHRT); 46 – *A. brunnea*, ♀, Ivory Coast (ANHRT); 47 – *A. accra*, ♀, Sierra Leone (ANHRT); 48 – *A. carneola* stat. rev., ♀, Tanzania (ANHRT); 49 – *A. lupia*, ♀, South Africa (SMNS); 50 – *A. lupia*, ♂, holotype, Mozambique (NHMUK); 51 – *A. nigrivenosa*, ♂, Uganda (CHS); 52 – *A. nigrivenosa*, ♀, Uganda (CHS); 53 – *A. invidua*, ♀, Guinea (ANHRT); 54 – *A. thermochroa*, ♀, Uganda (CHS).



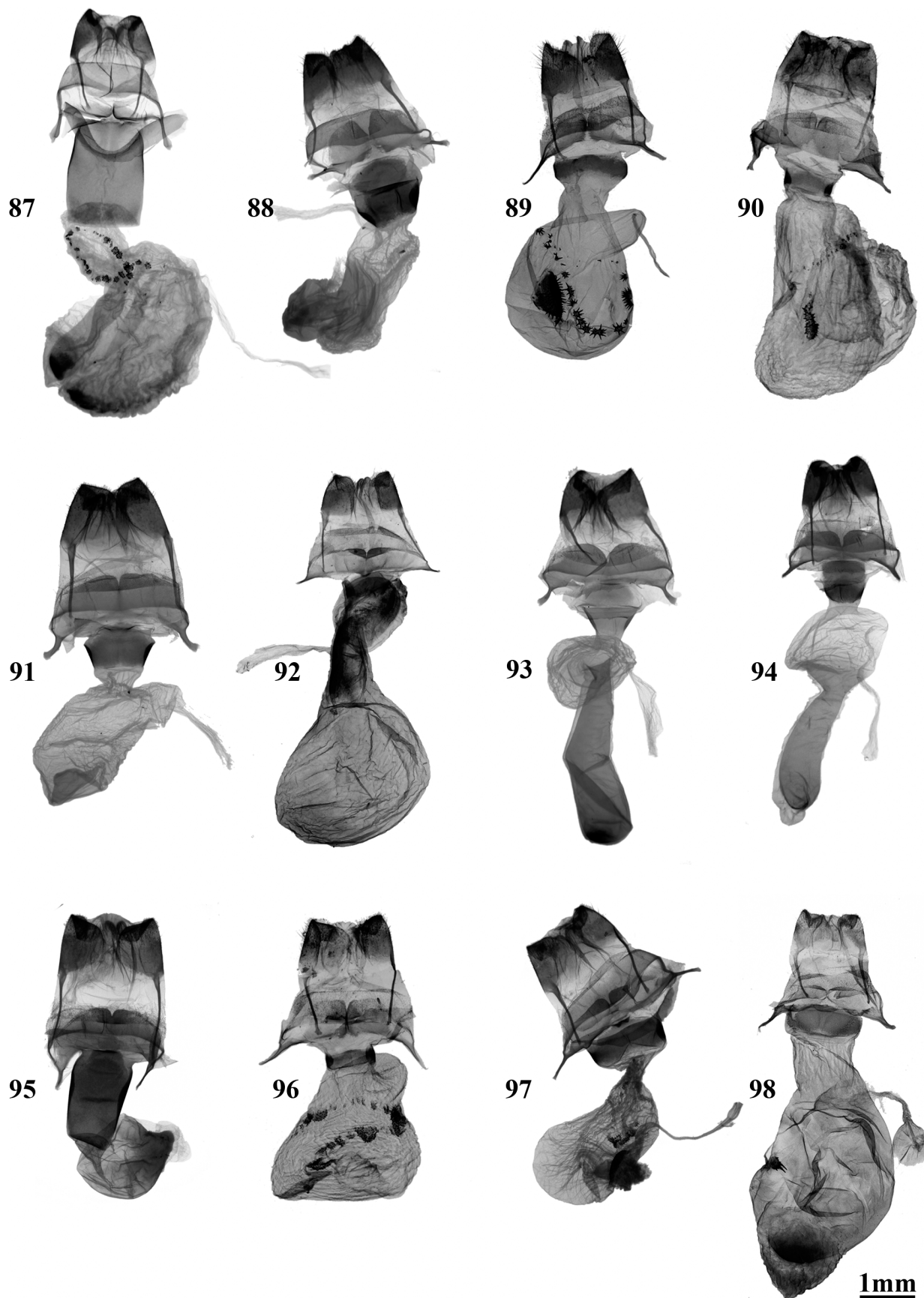
Figs 55–64. Adults of *Amerila* species. 55 – *A. puella*, ♀, Guinea (ANHRT); 56 – *A. puella*, ♀, São Tomé and Príncipe (ANHRT); 57 – *A. rubondoii*, ♀, Guinea (ANHRT); 58 – *A. saalmuelleri* stat. rev., ♀, Madagascar (CHS); 59 – *A. bauri*, ♂, South Africa (MWM/ZSM); 60 – *A. bauri*, ♀, South Africa (MWM/ZSM); 61 – *A. roseomarginata*, ♂, Gabon (ANHRT); 62 – *A. roseomarginata*, ♀, Ivory Coast (ANHRT); 63 – *A. madagascariensis*, ♀, Madagascar (ZSM); 64 – *A. vitrea*, ♀, Kenya (MWM/ZSM).



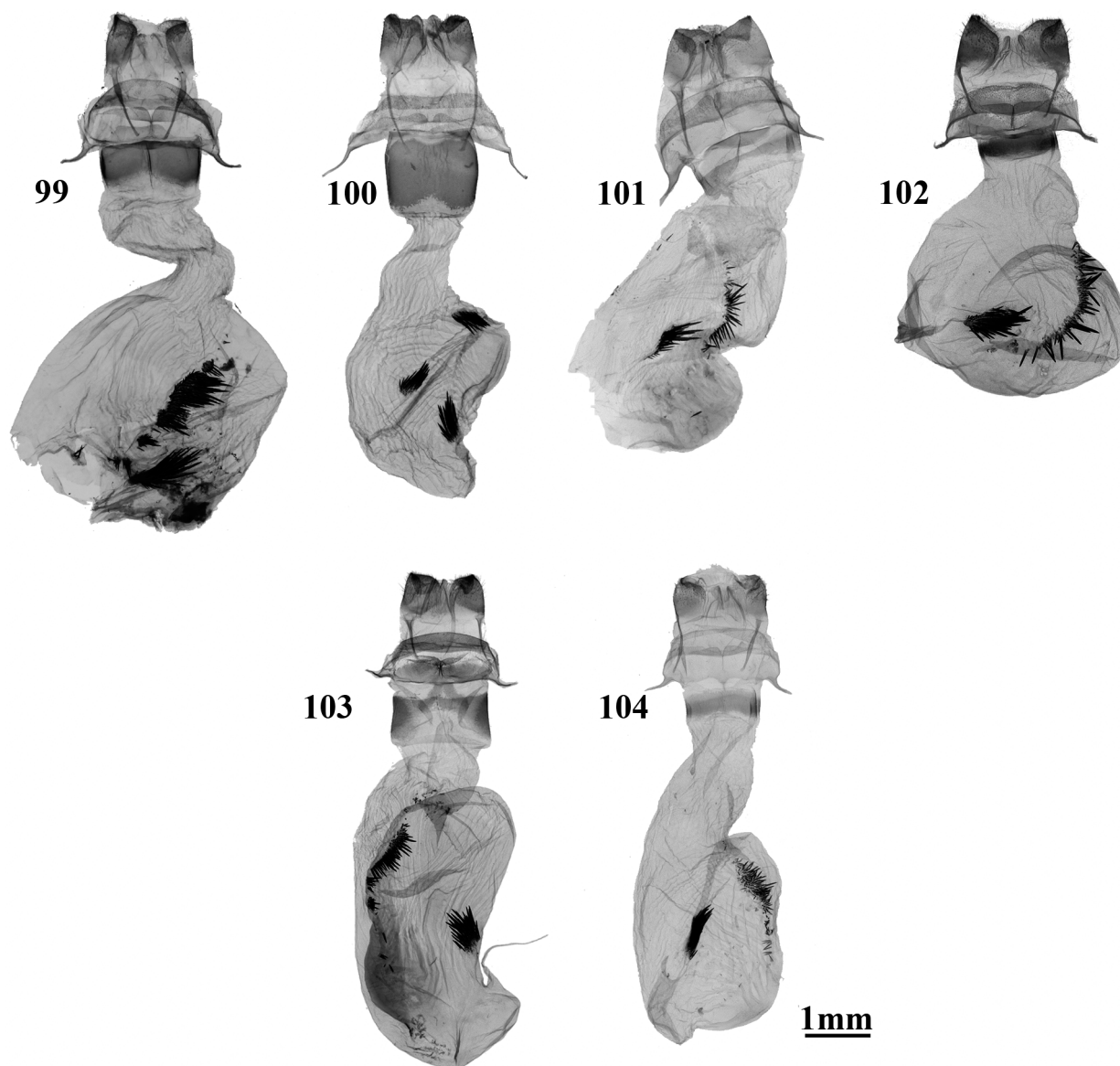
Figs 65–74. Adults of *Amerila* species. 65 – *A. cf. astreus*, ♀, India (MWM/ZSM); 66 – *A. astreus*, picture from the original description; 67 – *A. alberti*, ♀, Australia (SMNS); 68 – *A. rubripes*, ♀, Australia (SMNS); 69 – *A. timolis*, ♂, Australia (NHMUK); 70 – *A. florinae* sp. n., ♂, Indonesia (MWM/ZSM); 71 – *A. serica*, ♀, Australia (SMNS); 72 – *A. howardi*, ♂, Tanzania (ANHRT); 73 – *A. androfusca*, ♂, Kenya (ZSM); 74 – *A. shimbaensis*, ♂, Tanzania (ZSM).



Figs 75–86. Female genitalia of *Amerila* species. 75 – *A. francesae*, Tanzania (MWM/ZSM); 76 – *A. mulleri*, Cameroun (NECJU); 77 – *A. affinis*, DRC (ANHRT); 78 – *A. luteibarba*, Uganda (CHS); 79 – *A. bubo*, Uganda (CHS); 80 – *A. nigroapicalis*, Rwanda (ANHRT); 81 – *A. phaedra*, Mozambique (ANHRT); 82 – *A. leucoptera*, Ivory Coast (ANHRT); 83 – *A. smithi* sp. n., Zambia (ANHRT); 84 – *A. bipartita*, Mozambique (ANHRT); 85 – *A. brunnea*, Ivory Coast (ANHRT); 86 – *A. fennia*, Guinea (ANHRT).



Figs 87–98. Female genitalia of *Amerila* species. 87 – *A. accra*, Sierra Leone (ANHRT); 88 – *A. carneola* stat. rev., Tanzania (ANHRT); 89 – *A. lupia*, South Africa (SMNS); 90 – *A. nigrivenosa*, Uganda (CHS); 91 – *A. invidua*, Guinea (ANHRT); 92 – *A. thermochroa*, Uganda (CHS); 93 – *A. puella*, Guinea (ANHRT); 94 – *A. puella*, São Tomé and Príncipe (ANHRT); 95 – *A. rubondoii*, Guinea (ANHRT); 96 – *A. bauri*, South Africa (MWM/ZSM); 97 – *A. roseomarginata*, Ivory Coast (ANHRT); 98 – *A. saalmuelleri* stat. rev., Madagascar (CHS).



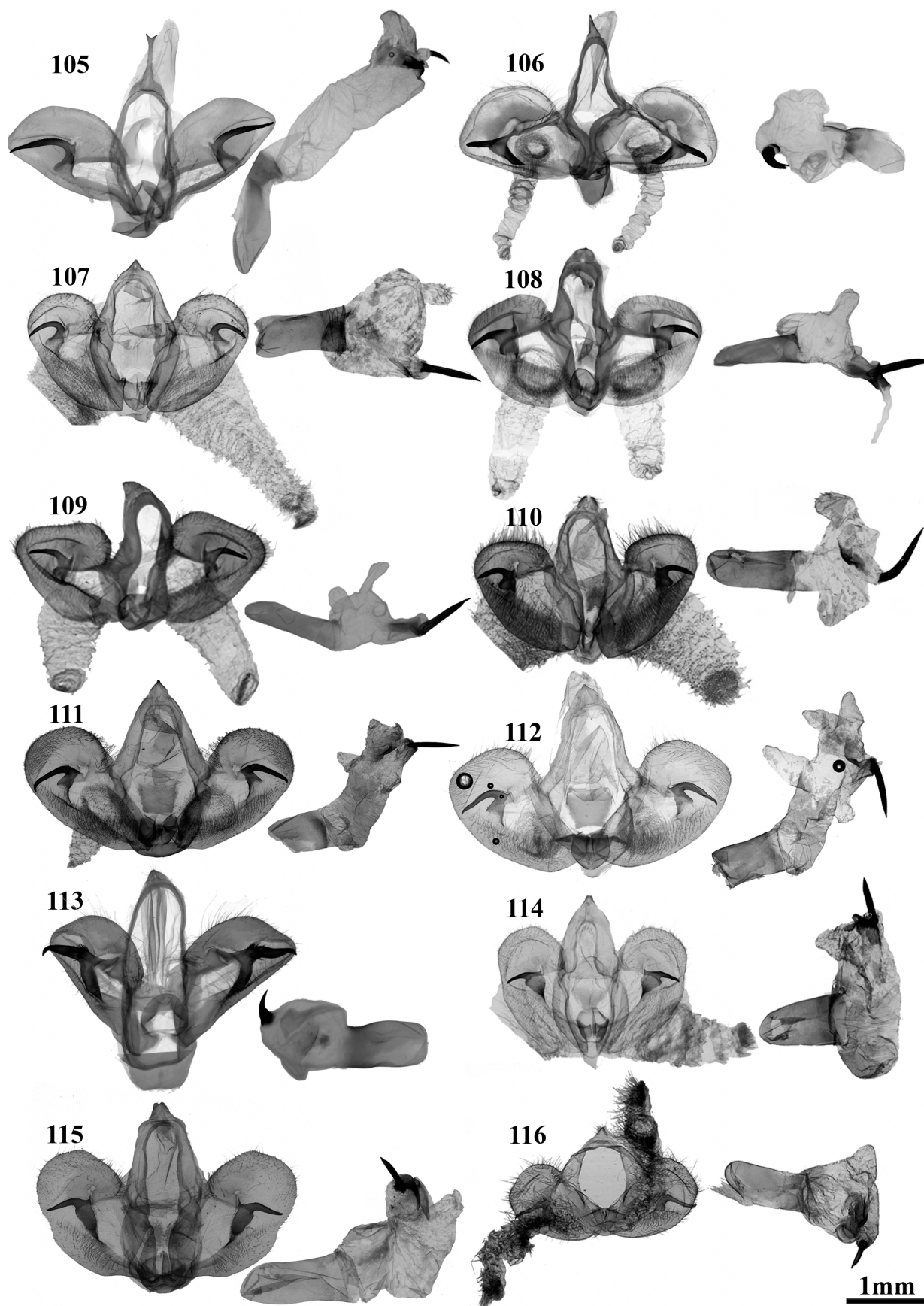
Figs 99–104. Female genitalia of *Amerila* species. 99 – *A. madagascariensis*, Madagascar (ZSM); 100 – *A. vitrea*, Kenya (MWM/ZSM); 101 – *A. cf. astreus*, India (MWM/ZSM); 102 – *A. serica*, Australia (SMNS); 103 – *A. alberti*, Australia (SMNS); 104 – *A. rubripes*, Australia (SMNS).

The next species group is recovered with strong support (ML 92.7/98, BI 1) and comprises three sister taxa: *A. leucoptera*, *A. smithi* sp. n. and *A. phaedra*. All three taxa share a colour pattern where the abdomen is reddish, and the wing ground colour is brownish in males and white in females (Figs 10–12, 39, 41, 42) – a remarkable display of sexual dimorphism. In the male genitalia of this complex, the vesica has a distinct field of numerous and small acute cornuti (Figs 10b–12b). The sister group to the *A. phaedra* species complex is the *A. bipartita* species group, also recovered with good support (ML 74.6/94, BI 0.76) (Figs 1, S1). Shared traits in the male habitus include dorsally yellow colour of the abdomen and the presence of a narrow yellow stripe in the ventral margin of the hindwing (Figs 13a, 14a, 15a). Several features, such as the presence of an extensive field of small, but acute, cornuti in the vesica, and the unique configuration of the harpe with serrate lateral margin (Figs 13b, 14b, 15b) support a close relation-

ship with the *A. phaedra* species group. Adults of the *A. bipartita* species complex also exhibit sexual dimorphism, where the female of *A. bipartita* has white ground colour on the wings, similar to *A. phaedra*, but the abdomen of the *A. bipartita* female is yellow dorsally rather than red (Figs 39, 40). The female of *A. brunnea* differs from the male in having a much paler colouration overall (Figs 13a, 46).

Amerila fennia is recovered as a monotypic lineage in both ML, and BI analyses (Figs 1, S1). The isolated phylogenetic position of the species is corroborated by several unique morphological characters, such as the semitransparent area of the forewing suffused with brown scales within the cell (Figs 43, 44, 45). In the male genitalia, the triangular valva of *A. fennia* is conspicuously rounded unlike in other taxa of the genus (Fig. 109).

The *A. carneola* species complex is recovered with a support of 90.6/85, however with only PP 0.5 in BI. This group comprises five species – *A. accra*, *A. femina*, *A.*



Figs 105–116. Male genitalia of *Amerila* species. 105 – *A. bubo*, Rwanda (ANHRT); 106 – *A. nigroapicalis*, Zambia (ANHRT); 107 – *A. bauri*, South Africa (MWM/ZSM); 108 – *A. roseomarginata*, Gabon (ANHRT); 109 – *A. fennia*, Liberia (ANHRT); 110 – *A. nigrivenosa*, Uganda (CHS); 111 – *A. florinae* sp. n., Indonesia (MWM/ZSM); 112 – *A. timolis*, Australia (NHMUK); 113 – *A. howardi*, Tanzania (ANHRT); 114 – *A. androfusca*, Kenya (ZSM); 115 – *A. shimbaensis*, Tanzania (ZSM); 116 – *A. lupia*, holotype, Mozambique (NHMUK).

castanea, *A. carneola* stat. rev., and an undescribed sister taxon of the latter (Figs 1, S1). All taxa of the *A. carneola* lineage display similar external habitus characterised by brown ground colour of variable shading and the presence of an extensive semitransparent field in the central area of the forewing where the cell is just slightly darker than the remaining area of the field (Figs 16a–19a). In the male reproductive organs, species of this complex possess a pair of long cornuti of the vesica (Figs 16b, 17b, 19b), with the exception of *A. accra* (Fig. 18b) where a cluster of medium-sized cornuti is present. While *A. accra* shares the same main external features with other members of the species group, it displays certain unique features in the male genitalia, such as the largely dilated, quadrangular uncus, and the numerous medium-sized acute cornuti of the vesica (Fig. 18b).

In ML and BI analyses, *A. nigrivenosa* and *A. lupia* form an unresolved polytomy with monotypic branches, but their positions relative to other species groups differ between the ML, and BI trees (Figs 1, S1), most likely because of insufficient taxon sampling with only a single specimen of *A. nigrivenosa* from Uganda (Table S3). Both species share a similar colour with the abdomen dorsally bright red, and ventrally pure white. Another distinctive feature expressed by the black-highlighted veins of the forewing in both species may suggest a close relationship (Figs 49–52). However, according to the results of molecular analyses, we consider *A. lupia* and *A. nigrivenosa* to represent two distinct monotypic species groups.

A morphologically diverse, but highly supported (ML 98/99, BI 1) monophyletic lineage is the *A. syntomina* species group, comprising *A. invidua*, *A. cf. vidua*, *A. thermochroa*, *A. alexandrae*, *A. puella*, *A. rubondoi*, and *A. syntomina* (Figs 20–26). In addition to the molecular support, the male genitalia include corroborating features such as a very broad and short valva with evenly rounded margin, and ventrodistally oriented harpe (except for *A. alexandrae* where the harpe is projected ventrad) (Figs 20b–26b). *Amerila puella uniformis* (Berio, 1935), described from Saõ Tomé island, was previously synonymised with *A. puella* (Fabricius, 1794) by Häuser & Boppré (1997), and that synonymy is confirmed by our results (Figs 55, 56, 93, 94).

The *A. syntomina* species complex analysed by Przybyłowicz et al. (2019b) comprised four species: *A. thermochroa*, *A. alexandrae*, *A. syntomina* and *A. rubondoi*. The latter three have confusingly similar facies characterised by a blackish forewing ground colour with a conspicuous whitish, oblique postmedial fascia, while *A. thermochroa* has male genitalia with a configuration almost identical to the externally dissimilar *A. syntomina*. Przybyłowicz et al. (2019b) provided evidence of monophyly for the complex through molecular analysis supported by shared morphological features across the taxa which can easily be recognised in both wing pattern and the structures of male copulatory organ. However, the extended taxon sampling in the present study revealed that *A. invidua*, *A. cf. vidua* and *A. puella* (Figs 20a, 24a, 26a), despite their largely different habitus being reminiscent

only of *A. thermochroa*, clearly belong to the *A. syntomina* lineage (Figs 1, S1).

The lack of sufficiently high-resolution sequencing data may be a contributing factor to the contradictory placements of *A. bauri* and *A. roseomarginata* (Figs 1, S1). The results presented in ML and BI analyses suggest different monotypic species groups. The adult morphology confirms the monotypic phylogenetic position of the two taxa expressed by the unique forewing shape of *A. bauri* where the costal margin is characteristically arched medially (Figs 59, 60). Moreover, the forewing of *A. bauri* is covered by pale ochreous scales from the base to the medial area, and by pale brown scales from the medial area to the termen, displaying a unique feature in the entire *Amerila* genus. *Amerila roseomarginata* (Figs 61, 62) is similar to *A. castanea*, *A. invidua*, *A. puella*, *A. carneola* (Figs 17a, 24a, 26a, 48, 53, 55, 56), but a distinctive and unique diagnostic character is found in the hindwing colouration, where the transparent area is well defined by a narrow but conspicuous pinkish margin.

The most derived monophyletic *Amerila* clade is subdivided into two sister sub-clades with robust support in both analyses (ML 97/99, BI 1): the *A. vitrea* species-group comprising mostly Afrotropical species and the Indomalayan-Australasian subclade of exclusively Asian and Australian taxa.

The *A. vitrea* species complex (Figs 27–30) includes, besides the eponymous species, *A. saalmuelleri* stat. rev., *A. madagascariensis*, a taxon from Somalia (*A. cf. vitrea* 2), and an undescribed Indomalayan species from the Sindh province of Pakistan (*A. cf. vitrea* 1) with strong support (ML 98.6/100, BI 1) in analyses (Figs 1, S1). The results of this study suggest the species-level status of the Madagascan taxon *A. saalmuelleri* (Rothschild, 1911) stat. rev., which was doubtfully treated by Häuser & Boppré (1997) as a subspecies of *A. vitrea* Plötz, 1880.

The sister clade of the *A. vitrea* complex comprising Indomalayan-Australasian taxa (Figs 1, S1), also received strong support (ML 80.8/99, BI 0.92) with the following species: *A. astreus*, *A. cf. astreus* 1, 2 (unconfirmed identification), *A. rubripes*, *A. crokeri*, *A. timolis*, *A. serica*, *A. alberti*, *A. cf. alberti* (unconfirmed identification), and *A. nigropunctata*. *Amerila astreus* and *A. alberti* appear repeatedly in the analyses, which can be attributed to inaccurate taxonomic interpretations in GenBank and BOLD databases, as well as the existence of several cryptic, undescribed species. Ancient DNA sequencing of the holotype specimens of *A. astreus* and *A. rubripes* could shed light on the real status of the mis- or unidentified taxa and their attributions to species groups.

In agreement with Przybyłowicz et al. (2019b), our study confirms that the Indomalayan-Australasian species of the *Amerila* genus form a subclade with a sister group connection to an African-Pakistan clade. In both analyses, the Indomalayan-Australasian subclade was recovered as the sister group of the *A. vitrea* species group, which is widely distributed in Africa reaching Yemen in the north along with two Madagascan taxa, *A. saalmuelleri* and *A. mada-*

gascariensis. The morphology of the male reproductive organs demonstrates prominent resemblances between *A. vitrea* and some of the Asian taxa, where the males have a single, medium-sized bifurcate cornutus of the vesica (Figs 27b, 28b, 111, 112). The resolution of the ML and BI trees was not impacted by the lack of adequate sampling for Indomalayan-Australasian taxa. However, we suggest that extended taxon sampling from the Indomalayan and Australasian regions, together with DNA sequencing and morphological examination of primary type specimens could further clarify the relationship of taxa within this clade.

The phylogenetic hypotheses presented in this study will help elucidate the potential reasons of *Amerila*'s evolutionary success in Indomalayan-Australasian region and allow evaluation of how the evolution of host plant use has affected speciation. Further detailed studies are required to clarify the relationships of the taxa within the Indomalayan-Australasian subclade.

It is well known that numerous other insect groups are known to have a similar Palaeotropical distribution pattern to that of *Amerila*. For example, several butterfly lineages have disjunct distributions across Asia and Africa (Aduse-Poku et al., 2009; Kaliszewska et al., 2015; Toussaint & Balke, 2016). Long-distance migration between continents is often cited as one of the primary mechanisms shaping the distribution pattern of butterflies (Condamine et al., 2013; Chazot et al., 2021). For instance, the genus *Charaxes* Ochsenheimer, 1816 (Lepidoptera: Nymphalidae: Charaxinae), includes approximately 250 species, with the majority occurring on the African continent. The remaining ca. 30 species are distributed in the tropical Indomalayan-Australasian realm.

According to Aduse-Poku et al. (2009), the common ancestor of *Charaxes* split off from the common ancestor of *Palla* in the mid-Eocene (45 million years ago) in (Central) Africa and started an intensive radiation resulting in a highly diverse genus as it is known today. Aduse-Poku et al. (2009) believe the Indo-Australian *Charaxes* are most likely the descendants of three separate Miocene colonisations of Asia by African *Charaxes* (Aduse-Poku et al., 2009). The subfamily Limenitidinae (Nymphalidae) shows a similar biogeographic pattern. (Tseng et al., 2022) proposed a centre of origin in eastern Asia in the early Eocene (ca. 52 Ma) followed by dispersal to Africa before the end of the Eocene. Then in the Miocene, the genus *Junonia* is believed to have dispersed from Africa to Asia and then to the New World (Kodandaramaiah & Wahlberg, 2007).

CONCLUSIONS

- The ML and BI trees display similar topologies. These trees, along with a detailed morphological analysis of male reproductive organs and habitus of adults, support the division of the genus into the species groups recognised here.
- Integrative analysis of adults allowed us to support 14 species groups. Due to insufficient data, the Indomalayan-Australasian taxa could not be fully resolved.

- Multiple analyses allowed the recognition of 2 new species, *A. florinae* sp. n. (Indonesia) and *A. smithi* sp. n. (Zambia and reaching Tanzania).
- Taxonomic status was revised for the following taxa: *A. bipartitoides* stat. rev., *A. saalmuelleri* stat. rev., and *A. carneola* stat. rev.
- The species *A. invidua*, *A. cf. vidua*, and *A. puella*, were added to the previously circumscribed *A. syntomina* species group (Przybyłowicz et al., 2019b).

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DATA AVAILABILITY STATEMENT. The COI-5P sequences and metadata of ANHRT samples are accessible in the BOLD public dataset DS-AMERILA (<https://dx.doi.org/10.5883/DS-AMERILA>). Accession numbers are also provided in Table S3.

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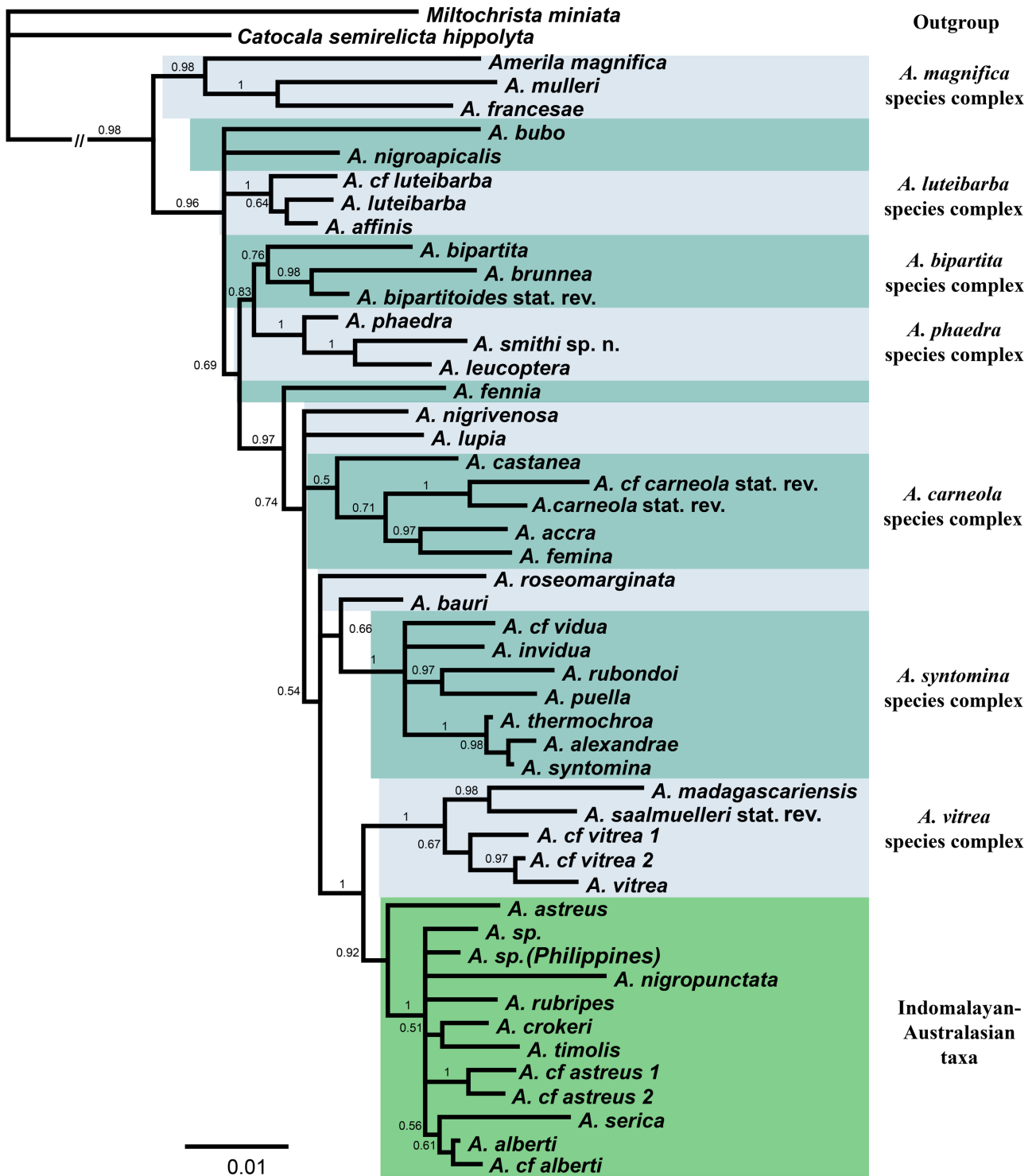


Fig. S1. Phylogenetic tree of the genus *Amerila* Walker, 1855 inferred by Bayesian Inference. Branch labels display the posterior probability values.

Table S1. Partitioning scheme with substitution models selected by PartitionFinder based on BIC statistics.

Subset	Substitution model	# sites	Partition names
1	F81	219	COIa
2	TRN+G	218	COIb
3	TRNEF+I+G	352	wingless1, COIc,
4	JC	1831	rps1, atp1, argkin1, rps2, ef2, ef1, atp3, wingless2
5	K80	738	argkin3, argkin2, atp2, rps3
6	K80+G	536	ef3, wingless3

Table S2. Summary of the distinctive characters of the *Amerila* species groups.

Species group	Habitus of adults	Male genitalia structures
<i>Amerila magnifica</i>	semi-white, semi-red dorsal colouration of abdomen (Figs 5a–7a)	plate-like sclerotization on vesica, simple, elongated uncus which is ca. 5 times longer than at other <i>Amerila</i> species (Figs 5b–7b)
<i>A. luteibarba</i>	semi-light brown/semi-red dorsal colouration of abdomen (Figs 8a, 9a)	distally directed harpe of valva; vesica bear two distinct different size, well-developed cornuti (Figs 8b, 9b)
<i>A. phaedra</i>	ground colour is brown in males, and white in females. Abdomen is dorsally red in both sexes (Figs 10a–12a, 39, 41, 42)	vesica bears a distinct field of numerous acute cornuti of small size (Fig. 10b–12b)
<i>A. bipartita</i>	hind wing with narrow yellow stripe near ventral margin, abdomen is yellow or pale orange in both sexes (Figs 13a–15a, 40, 46)	vesica has two large equal size cornuti (<i>A. bipartita</i>), or two extensive fields of small, acute cornuti, along with two middle sized cornuti (Figs 13b–15b)
<i>A. carneola</i>	forewing with slight, not clear-cut semitransparent field in the medial area (Figs 16a–19a, 47, 48)	aedeagus almost straight, relatively narrow, elongated; vesica bear a pair of long fused basally cornuti, (Figs 16b, 17b, 19b) or numerous medium-sized acute cornuti (<i>A. accra</i>) (Fig. 18b)
<i>A. syntomina</i>	forewing with the oblique white band, or with semitransparent area in it's central part (Figs 20a–26a, 53–57)	broad and evenly rounded valva (Figs 20b–26b); harpe of valva towards ventro-distally (Figs 20b, 22b–26b)
<i>A. vitrea</i>	uniformly bright red dorsal colouration of abdomen along with clear-cut semitransparent areas on fore- and hindwing (Figs 27a–30a, 58, 63, 64)	vesica distally with two medium sized, slightly curved, fused basally cornuti, and with a narrow plate-like sclerotization (Figs 27b–30b)
<i>A. fennia</i>	forewing dark-ochre, its discal semitransparent area suffused with brown scales (Figs 43–45)	valva somewhat triangular shaped; vesica with two distinct elongated papillae (Fig. 109)
<i>A. bubo</i>	uniformly white colouration of fore- and hindwing along with dorsally yellow colored abdomen (Figs 35, 36)	long bifurcated apically uncus; vesica bears distally small slightly curved cornutus and narrow plate-like sclerotization (Fig. 105)
<i>A. nigroapicalis</i>	apex, costal, and ventral margin of forewing covered with light gray scales (Figs 37, 38)	triangular uncus slightly elongated apically; vesica distally with strong, short, hook-like cornutus (Fig. 106)
<i>A. nigrivenosa</i>	weakly scaled whitish forewing with remarkably dark veins (Figs 51, 52)	small blunt uncus slightly bifurcated apically; vesica bears two fused basally, large cornuti, and distinct field of numerous tiny cornuti (Fig. 110)
<i>A. lupia</i>	relatively small-sized (forewing 18–21mm) whitish coloured adults; discal vein finely covered with light-gray scales; postdiscally with a gray line (Figs 49, 50)	vesica distally with two small basally fused, pointed apically cornuti, and with narrow plate-like sclerotization (Fig. 116)
<i>A. roseomarginata</i>	transparent area of forewing is well defined by pinkish scales (Figs 61, 62)	almost identical with <i>A. fennia</i> (Fig. 108)
<i>A. bauri</i>	forewing covered with pale ochre scales from the basal part to discal area, and by pale brown scales from discal area to outer margin; costal margin of forewing evenly arched (Figs 59–60)	vesica is dome-shaped (Fig. 107)

Table S3. Accession numbers.

DNA sample ID	Collection	Taxon	Gene region	Sequence accession No.	Publication
ABCNA001-06	RCRB	<i>Catocala semirelictica</i>	COI-5P	MF126536	Zahiri et al., 2017
ABOLA123-14	LMK	<i>Mitochondria miniata</i>	COI-5P	MG522231	Huemer et al., 2018
NI202	ZFF	<i>Amerila cf. vitrea</i> 2	COI-5P	PP275850	this study
NI204	ZFF	<i>A. sp.</i>	COI-5P	PP275853	this study
CAM159	NECJU	<i>A. mulleri</i>	COI-5P	MG596295	Przybyłowicz et al., 2019
CAM102	NECJU	<i>A. mulleri</i>	COI-5P	MG596293	Przybyłowicz et al., 2019
CAM158	NECJU	<i>A. mulleri</i>	COI-5P	MG596294	Przybyłowicz et al., 2019
CAM101	NECJU	<i>A. mulleri</i>	COI-5P	MG596292	Przybyłowicz et al., 2019
ANLMN3427-21	ANHRT	<i>A. francesae</i>	COI-5P	OM158447	Ignatev et al., 2022
NI141	MWM/ZSM	<i>A. francesae</i>	COI-5P	OM169367	Ignatev et al., 2022
ANLMN3308-21	ANHRT	<i>A. magnifica</i>	COI-5P	OM158448	Ignatev et al., 2022
ANLMN3309-21	ANHRT	<i>A. magnifica</i>	COI-5P	OM158446	Ignatev et al., 2022
AYK-03-0912	UM	<i>A. bauri (saalmuelleri)</i>	COI-5P	GU696215	unpublished
AYK-03-0911	UM	<i>A. bauri</i>	COI-5P	GU696163	unpublished
AYK-03-0910	UM	<i>A. bauri</i>	COI-5P	GU696162	unpublished
MAMOT-01523	NIBGE	<i>A. cf. vitrea</i> 1	COI-5P	KX860667	Ashfaq et al., 2017
MAMOT-00356	NIBGE	<i>A. cf. vitrea</i> 1	COI-5P	HQ991050	Ashfaq et al., 2017
MAMOT-00355	NIBGE	<i>A. cf. vitrea</i> 1	COI-5P	HQ991049	Ashfaq et al., 2017
NI129	MWM/ZSM	<i>A. vitrea</i>	COI-5P	PP275854	this study
NI166	MWM/ZSM	<i>A. vitrea</i>	COI-5P	PP275852	this study
NI088	MWM/ZSM	<i>A. vitrea</i>	COI-5P	PP275855	this study
LN014	ISEA	<i>A. vitrea</i>	COI-5P	KX300224	Zenker et al., 2017
LN014	ISEA	<i>A. vitrea</i>	EF-1a:	KX300347	Zenker et al., 2017
MGABB741-10	MNHN	<i>A. sp.</i>	COI-5P	HM893333	Unpublished
ISEZ381	ISEA	<i>A. rubondoi</i>	COI-5P	MG596297	Przybyłowicz et al., 2019
ISEZ374	ISEA	<i>A. rubondoi</i>	COI-5P	MG596296	Przybyłowicz et al., 2019
NI159	ZSM	<i>A. sp.</i>	COI-5P	PP275856	this study
RZ404	nd	<i>A. astreus</i>	COI-5P	JN401170	Zahiri et al., 2012
RZ405	nd	<i>A. astreus</i>	GADPH	JN401612	Zahiri et al., 2012
RZ406	nd	<i>A. astreus</i>	RpS5	JN401910	Zahiri et al., 2012
GBGL14121-14	nd	<i>A. sp.</i>	COI-5P	KF533441	Zaspel et al., 2014
10ANIC-01120	ANIC	<i>A. nigropunctata</i>	COI-5P	HQ921253	Hebert et al., 2013 (UNP)
10ANIC-01119	ANIC	<i>A. nigropunctata</i>	COI-5P	HQ921252	Hebert et al., 2013 (UNP)
NI169	ZSM	<i>A. sp.</i>	COI-5P	PP275857	this study
10ANIC-01129	ANIC	<i>A. serica</i>	COI-5P	HQ921261	Hebert et al., 2013 (UNP)
10ANIC-01128	ANIC	<i>A. serica</i>	COI-5P	HQ921260	Hebert et al., 2013 (UNP)
10ANIC-01127	ANIC	<i>A. timolis</i>	COI-5P	HQ921259	Hebert et al., 2013 (UNP)
AYK-04-0590-08	UM	<i>A. astreus</i>	COI-5P	GU696216	unpublished
AYK-04-1280-03	UM	<i>A. astreus</i>	COI-5P	KF491530	unpublished
10ANIC-01134	ANIC	<i>A. rubripes</i>	COI-5P	HQ921266	Hebert et al., 2013 (UNP)
10ANIC-01137	ANIC	<i>A. rubripes</i>	COI-5P	HQ921269	Hebert et al., 2013 (UNP)
10ANIC-01136	ANIC	<i>A. rubripes</i>	COI-5P	HQ921268	Hebert et al., 2013 (UNP)
10ANIC-01135	ANIC	<i>A. rubripes</i>	COI-5P	HQ921267	Hebert et al., 2013 (UNP)
LTOLB249-09	UM	<i>A. sp.</i>	COI-5P	HM377804	this study
NI139	MWM/ZSM	<i>A. castanea</i>	COI-5P	PP275858	this study
NI086	MWM/ZSM	<i>A. brunnea</i>	COI-5P	PP275860	this study
I_H3	ISEA	<i>A. bubo</i>	COI-5P	MG596289	Przybyłowicz et al., 2019
I_B9	ISEA	<i>A. bubo</i>	COI-5P	MG596288	Przybyłowicz et al., 2019
TDGAB-2029	MNHN	<i>A. cf. luteibarba</i>	COI-5P	HM892650	unpublished
TDGAB-0046	MNHN	<i>A. cf. luteibarba</i>	COI-5P	HM390275	unpublished
TDGAB-0629	MNHN	<i>A. cf. luteibarba</i>	COI-5P	HM390275	unpublished
CAM105_I	NECJU	<i>A. luteibarba</i>	COI-5P	MG596279	Przybyłowicz et al., 2019
TDGAB-1249	MNHN	<i>A. luteibarba</i>	COI-5P	HM892856	Unpublished
Lope11-0342	MNHN	<i>A. luteibarba</i>	COI-5P	MK187680	Delabye et al., 2018
TDGAB-0907	MNHN	<i>A. luteibarba</i>	COI-5P	HM892432	Delabye et al., 2018
TDGAB-0409	MNHN	<i>A. luteibarba</i>	COI-5P	HM891955	Delabye et al., 2018
TDGAB-0197	MNHN	<i>A. luteibarba</i>	COI-5P	HM390415	Delabye et al., 2018
TDGAB-0168	MNHN	<i>A. luteibarba</i>	COI-5P	HM390386	Delabye et al., 2018
CAM106_I	NECJU	<i>A. luteibarba</i>	COI-5P	MG596280	Przybyłowicz et al., 2019
Lope11-0292	MNHN	<i>A. luteibarba</i>	COI-5P	MK187571	Delabye et al., 2018
TDGAB-0174	MNHN	<i>A. luteibarba</i>	COI-5P	HM390392	Delabye et al., 2018
TDGAB-0637	MNHN	<i>A. luteibarba</i>	COI-5P	HM892176	Delabye et al., 2018
TDGAB-0407	MNHN	<i>A. luteibarba</i>	COI-5P	HM891953	Delabye et al., 2018
TDGAB-0486	MNHN	<i>A. luteibarba</i>	COI-5P	HM892028	Delabye et al., 2018
TDGAB-0047	MNHN	<i>A. luteibarba</i>	COI-5P	HM390276	Delabye et al., 2018
Lope11-0524	MNHN	<i>A. luteibarba</i>	COI-5P	MK187509	Delabye et al., 2018
TDGAB-1228	MNHN	<i>A. luteibarba</i>	COI-5P	HM892835	Delabye et al., 2018
TDGAB-0464	MNHN	<i>A. luteibarba</i>	COI-5P	HM892007	Delabye et al., 2018
II_B10	ISEA	<i>A. brunnea</i>	COI-5P	MG596287	Przybyłowicz et al., 2019

Table S3 continued. Accession numbers.

DNA sample ID	Collection	Taxon	Gene region	Sequence accession No.	Publication
LN015	ISEA	<i>A. brunnea</i>	COI-5P	KX300223	Zenker et al., 2017
LN015	ISEA	<i>A. brunnea</i>	EF-1a:	KX300346	Zenker et al., 2017
LN015	ISEA	<i>A. brunnea</i>	GADPH	KX300609	Zenker et al., 2017
TDGAB-1223	MNHN	<i>A. brunnea</i>	COI-5P	HM892830	Delabye et al., 2018
TDGAB-0717	MNHN	<i>A. brunnea</i>	COI-5P	HM892249	Delabye et al., 2018
TDGAB-1240	MNHN	<i>A. brunnea</i>	COI-5P	HM892847	Delabye et al., 2018
ISEZ384	ISEA	<i>A. nigroapicalis</i>	COI-5P	MG596281	Przybyłowicz et al., 2019
TDGAB-1715	MNHN	<i>A. nigroapicalis</i>	COI-5P	HM893310	Delabye et al., 2018
TDGAB-0793	MNHN	<i>A. nigroapicalis</i>	COI-5P	HM892323	Delabye et al., 2018
TDGAB-0020	MNHN	<i>A. nigroapicalis</i>	COI-5P	HM390253	Delabye et al., 2018
NI134	ZSM	<i>A. bipartitoides</i>	COI-5P	PP275862	this study
ISEZ302	ISEA	<i>A. phaedra</i>	COI-5P	MG596283	Przybyłowicz et al., 2019
NI118	MWM/ZSM	<i>A. phaedra</i>	COI-5P	PP275863	this study
NI051	MWM/ZSM	<i>A. leucoptera</i>	COI-5P	PP275864	this study
NI128	MWM/ZSM	<i>A. leucoptera</i>	COI-5P	PP275865	this study
10ANIC-01121	ANIC	<i>A. nigropunctata</i>	COI-5P	HQ921254	Hebert et al., 2013
Sph694	nd	<i>A. cf. astreus</i> 2	COI-5P	MG735264	Bolotov et al., 2018
Sph693	nd	<i>A. cf. astreus</i> 2	COI-5P	MG735263	Bolotov et al., 2018
10ANIC-01126	ANIC	<i>A. timolis</i>	COI-5P	KF389092	Hebert et al., 2013
LTOLB246-09	UM	<i>A. sp.</i>	COI-5P	GU696214	unpublished
10ANIC-01132	ANIC	<i>A. cf. alberti</i>	COI-5P	HQ921264	Hebert et al., 2013
10ANIC-01133	ANIC	<i>A. alberti</i>	COI-5P	HQ921265	Hebert et al., 2013
10ANIC-01131	ANIC	<i>A. alberti</i>	COI-5P	HQ921263	Hebert et al., 2013
10ANIC-01124	ANIC	<i>A. crokeri</i>	COI-5P	HQ921257	Hebert et al., 2013
10ANIC-01123	ANIC	<i>A. crokeri</i>	COI-5P	HQ921256	Hebert et al., 2013
10ANIC-01122	ANIC	<i>A. crokeri</i>	COI-5P	HQ921255	Hebert et al., 2013
SCDNA240	nd	<i>A. crokeri</i>	COI-5P	KF533440	Zaspel et al., 2014
NI175	ZSM	<i>A. sp.</i>	COI-5P	PP275866	this study
CAM156	NECJU	<i>A. femina</i>	COI-5P	MG596278	Przybyłowicz et al., 2019
CAM155	NECJU	<i>A. femina</i>	COI-5P	MG596277	Przybyłowicz et al., 2019
CAM154	NECJU	<i>A. femina</i>	COI-5P	MG596276	Przybyłowicz et al., 2019
CAM153	NECJU	<i>A. femina</i>	COI-5P	MG596275	Przybyłowicz et al., 2019
CAM109	NECJU	<i>A. femina</i>	COI-5P	MG596274	Przybyłowicz et al., 2019
CAM108	NECJU	<i>A. femina</i>	COI-5P	MG596273	Przybyłowicz et al., 2019
CAM103	NECJU	<i>A. femina</i>	COI-5P	MG596272	Przybyłowicz et al., 2019
IL_C1	ISEA	<i>A. fennia</i>	COI-5P	MG596290	Przybyłowicz et al., 2019
TDGAB-0730	MNHN	<i>A. roseomarginata</i>	COI-5P	HM892261	Delabye et al., 2018
TDGAB-0137	MNHN	<i>A. roseomarginata</i>	COI-5P	HM390357	Delabye et al., 2018
TDGAB-0006	MNHN	<i>A. roseomarginata</i>	COI-5P	HM390239	Delabye et al., 2018
I_B3	ISEA	<i>A. fennia</i>	COI-5P	MG596291	Przybyłowicz et al., 2019
Lope11-0677	MNHN	<i>A. roseomarginata</i>	COI-5P	MK187538	Delabye et al., 2018
Lope11-0526	MNHN	<i>A. roseomarginata</i>	COI-5P	MK187480	Delabye et al., 2018
CAM157	nd	<i>A. roseomarginata</i>	COI-5P	MG596284	unpublished
Lope11-0658	MNHN	<i>A. fennia</i>	COI-5P	MK188052	Delabye et al., 2018
NI135	SMNS	<i>A. lupia</i>	COI-5P	PP275868	this study
NI137	MWM/ZSM	<i>A. nigroapicalis</i>	COI-5P	PP275861	this study
25919	ANHRT	<i>A. alexandrae</i>	COI-5P	MN258513	Przybyłowicz et al., 2019
25923	ANHRT	<i>A. alexandrae</i>	COI-5P	MN258516	Przybyłowicz et al., 2019
25920	ANHRT	<i>A. alexandrae</i>	COI-5P	MN258514	Przybyłowicz et al., 2019
25918	ANHRT	<i>A. alexandrae</i>	COI-5P	MN258513	Przybyłowicz et al., 2019
25921	ANHRT	<i>A. alexandrae</i>	COI-5P	MN258515	Przybyłowicz et al., 2019
ISEZ403	ISEA	<i>A. thermochroa</i>	COI-5P	MG596285	Przybyłowicz et al., 2019
ISEZ379	ISEA	<i>A. syntomina</i>	COI-5P	MG596271	Przybyłowicz et al., 2019
CAM100	NECJU	<i>A. syntomina</i>	COI-5P	MG596270	Przybyłowicz et al., 2019
NI 114	MWM/ZSM	<i>A. roseomarginata</i>	COI-5P	PP275866	this study
25922	ANHRT	<i>A. rubondoi</i>	COI-5P	MN258517	Przybyłowicz et al., 2019
25924	ANHRT	<i>A. rubondoi</i>	COI-5P	MN258518	Przybyłowicz et al., 2019
NI158	ZSM	<i>A. sp.</i>	COI-5P	PP275851	this study
NI203	MWM/ZSM	<i>A. nigrivenosa</i>	COI-5P	PP275859	this study
SCDNA239	ANIC	<i>A. alberti</i>	EF-1a	KF533512	Zaspel et al., 2014
SCDNA240	ANIC	<i>A. alberti</i>	RpS5	KF533634	Zaspel et al., 2014
RZ436	nd	<i>A. sp.</i>	EF-1a	KF533513	Zaspel et al., 2014
RZ437	nd	<i>A. sp.</i>	RpS5	KF533635	Zaspel et al., 2014
nd	nd	<i>A. brunnea</i>	RpS5	KX300895	Zenker et al., 2017
SCDNA240	nd	<i>A. crokeri</i>	RpS5	KF734451	Zaspel et al., 2014
nd	nd	<i>A. alberti</i>	Wgl	KF533568	Zaspel et al., 2014
nd	nd	<i>A. brunnea</i>	Wgl	KX301005	Zenker et al., 2017
nd	nd	<i>A. crokeri</i>	Wgl	KF533569	Zaspel et al., 2014
nd	nd	<i>A. sp.</i>	Wgl	KF533570	Zaspel et al., 2014
nd	nd	<i>A. vitrea</i>	Wgl	KX301006	Zenker et al., 2017