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Taxonomy and phylogeny of selected genera of Malagasy Syntomini (Lepidoptera: Erebidae: Arctiinae)

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Doctoral thesis

Supervisor

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Taksonomia i filogeneza wybranych rodzajów madagaskarskich Syntomini (Lepidoptera: Erebidae: Arctiinae)

Marcin Wiorek

Rozprawa doktorska

Promotor

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SUMMARY

The lineage of the tribe Syntomini that is endemic to Madagascar constitutes one of the largest known evolutionary radiation in Lepidoptera of the island, with around 100 species deriving from a single ancestor. However, their current systematics has been shown to comprise some polyphyletic genera, and thus demands a modern revision. This applies especially to the genera *Thyrosticta* Hampson, 1898 and *Melanonaclia* Griveaud, 1964, together constituting around 1/3 of the species diversity of Madagascan Syntomini.

The presented doctoral thesis consists of a series of three articles (**Wiorek et al. 2021**, PeerJ; **Przybyłowicz, Wiorek et al. 2021**, Zoologica Scripta; **Wiorek et al.**, **manuscript**), and is based on the verification of four research hypotheses, concerning the systematics, diversity and distribution of the genera *Thyrosticta* and *Melanonaclia*, using an integrative taxonomy approach.

The molecular part of the study is based on the sequences of up to eight markers: one mitochondrial – cytochrome c oxidase I (COI), and seven nuclear – elongation factor 1 alpha (EF1a), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), cytosolic malate dehydrogenase (MDH), isocitrate dehydrogenase (IDH), ribosomal protein S5 (RpS5), the wingless gene (Wgl400), and carbamoylphosphate synthase domain protein (CAD). In total, in the study were included 1016 sequences of a total length of 643 549 base pairs, which were obtained from 254 specimens (including outgroups).

The morphological and distributional analyses are based on 1402 specimens of both freshly collected and museum specimens, deposited in 12 collections. The morphological studies included genitalia dissections, wing venation preparations, and SEM visualisation of different phylogenetically informative structures, including scales and eggs – the latter described from the Madagascan Syntomini for the first time.

Obtained results confirmed that the reviewed genera are polyphyletic, and comprise nine distinct evolutionary lineages, of which seven are proposed to be described as new genera: *Skippernaclia* **gen. nov.**, *Kowalskinaclia* **gen. nov.**, *Privatenaclia* **gen. nov.**, *Julienaclia* **gen. nov.**, *Riconaclia* **gen. nov.**, *Mauricenaclia* **gen. nov.**, and *Mortinaclia* **gen. nov.**

The taxonomical status of all species was verified, including an elaboration of the intraspecific variation observed in some of them. As a result, three new species are proposed: *Skippernaclia leesi* Wiorek **sp. nov.**, *Mauricenaclia apatris* Wiorek **sp. nov.**, and *Melanonaclia ranomafana* Wiorek & Przybyłowicz **sp. nov.** Additionally, five species are considered as synonyms: *Thyrosticta incerta* **syn. nov.**, *Thyrosticta melanisa* **syn. nov.**, *Thyrosticta*

angustipennis **syn. nov.**, *Dysauxes subfenestrata* **syn. nov.**, and *Tritonaclia inauramacula* **syn. nov.** In total, 30 valid species are recognised in the study.

Although the reviewed taxa appeared to be highly diverse morphologically, it was possible to delineate clear apomorphies for each of the distinguished genera. Additionally, a set of characters with a presence/absence pattern that was stable within but varied among genera was found. Among these is the brush-like tuft of scales located at the base of the male foreleg. This structure, to our best knowledge, is reported in Syntomini for the first time, and potentially may have an androconial function.

The reviewed taxa occur broadly across in the entire span of Madagascar, but species ranges are usually restricted to different parts of the island. The highest species diversity is recorded from humid, evergreen forests of eastern Madagascar, while a few species are associated specifically with the dry to semi-arid biotopes of the southern and eastern parts of the island. The highest number of more or less sympatric species (eight) occurs in the Marojejy massif in northern Madagascar. Six species, including all three members of the genus *Privatenaclia* **gen. nov.**, are identified as local endemics, occurring only in relatively small areas in different parts of the island.

Except for general data on the preferred types of vegetation, the biology of the species covered in the thesis remains largely unknown. First records of nectaring are provided for five species, with indication of preference for Rubiaceae. The number of spermatophores or their remnants found in the dissected females indicates for the presence of polyandry in Madagascan Syntomini.

The Mauritian endemic "*Maculonaclia*" *florida* is proven to belong to the genus *Dysauxes* in which it was originally described, with the remaining species in the genus occurring only in the Palaearctic. Furthermore, the genus *Dysauxes*, the African species *Pseudonaclia puella*, and the genus *Mauricenaclia* gen. nov. are shown to constitute a monophyletic lineage named the "*Dysauxes* clade", which is inferred to have given rise to out-of-Madagascar dispersal to continental Africa and subsequently to Palaearctic.

The presented thesis constitutes a coherent revision of the diversity of a third of Madagascan Syntomini. It contributes to a better understanding of the islands' biodiversity, as well as a widening of the body of knowledge on the tribe Syntomini, arguably the least known group of tiger moths (Arctiinae).

STRESZCZENIE

Endemiczna dla Madagaskaru linia plemienia Syntomini stanowi jedną z największych znanych radiacji ewolucyjnych wśród Lepidoptera tej wyspy i liczy około 100 gatunków, wywodzących się od wspólnego przodka. Współczesna systematyka grupy okazała się zawierać polifiletyczne rodzaje, wymaga więc współczesnej rewizji. Dotyczy to szczególnie rodzajów *Thyrosticta* Hampson, 1898 i *Melanonaclia* Griveaud, 1964, łącznie stanowiących około 1/3 różnorodności gatunkowej madagaskarskich Syntomini.

Przedstawiona rozprawa doktorska składa się z serii trzech artykułów: (**Wiorek i in. 2021**, PeerJ; **Przybyłowicz, Wiorek i in. 2021**, Zoologica Scripta; **Wiorek et al.**, **manuskrypt**) i opiera się na weryfikacji czterech hipotez badawczych, dotyczących systematyki, różnorodności i rozmieszczenia rodzajów *Thyrosticta* i *Melanonaclia,* w ramach taksonomii integratywnej.

Molekularna część badań oparta jest o sekwencje ośmiu markerów: jednego mitochondrialnego – podjednostka pierwsza oksydazy cytochromowej, (COI), oraz siedmiu jądrowych – czynnik elongacyjny - 1 alfa (EF1a), dehydrogenaza aldehydu 3-fosfoglicerynowego (GAPDH), dehydrogenaza jabłczanowa (MDH), dehydrogenaza izocytrynianowa (IDH), białko rybosomalne S5 (RpS5), gen wingless (Wgl400), oraz syntetaza karbamoilofosforanowa (CAD). W sumie, w badaniach ujęto 1016 sekwencji, o całkowitej długości 643 549 par zasad, pochodzących ze 254 okazów (włączając grupy zewnętrzne).

Badania morfologiczne i nad rozmieszczeniem gatunków były oparte na 1402 okazach, zarówno świeżo zebranych, jak i muzealnych, zdeponowanych w 12 kolekcjach. Część morfologiczna obejmowała wykonanie preparatów z aparatów genitalnych oraz użyłkowania skrzydeł, a także wizualizację za pomocą SEM informatywnych filogenetycznie struktur, w tym łusek oraz jaj – tych ostatnich opisanych u madagaskarskich Syntomini po raz pierwszy.

Otrzymane wyniki potwierdziły polifiletyzm rewidowanych rodzajów, które okazały się zawierać dziewięć odrębnych linii ewolucyjnych, z których siedem zostało zaproponowane jako nowe rodzaje: *Skippernaclia* **gen. nov.**, *Kowalskinaclia* **gen. nov.**, *Privatenaclia* **gen. nov.**, *Julienaclia* **gen. nov.**, *Riconaclia* **gen. nov.**, *Mauricenaclia* **gen. nov.**, and *Mortinaclia* **gen. nov.**

Zweryfikowano status taksonomiczny wszystkich gatunków, włącznie z opracowaniem obserwowanych przypadków zmienności wewnątrzgatunkowej. Odkryte zostały trzy nowe gatunki: *Skippernaclia leesi* Wiorek **sp. nov.**, *Mauricenaclia apatris* Wiorek **sp. nov.**, oraz *Melanonaclia ranomafana* Wiorek & Przybyłowicz **sp. nov.** Dodatkowo, pięć gatunków

zostało uznane za synonimy: *Thyrosticta incerta* **syn. nov.**, *Thyrosticta melanisa* **syn. nov.**, *Thyrosticta angustipennis* **syn. nov.**, *Dysauxes subfenestrata* **syn. nov.** oraz *Tritonaclia inauramacula* **syn. nov.** W sumie, w rozprawie rozpoznano 30 ważnych gatunków.

Badane grupy okazały się bardzo zmienne morfologicznie, jednak możliwe było wskazanie jednoznacznych apomorfii dla wszystkich wyróżnionych rodzajów. Dodatkowo, znaleziono zestaw cech, których obecność lub brak są stałe w obrębie rodzajów, ale różnią się pomiędzy nimi. Spośród nich, pęczek wydłużonych łusek u nasady przedniego odnóża samców, według naszej wiedzy, jest stwierdzony u Syntomini po raz pierwszy i potencjalnie może pełnić funkcję feromonową (androkonium).

Rewidowane taksony są szeroko rozprzestrzenione na całym Madagaskarze, jednak zasięgi poszczególnych gatunków zwykle są ograniczone do określonych obszarów. Największa różnorodność gatunków występuje w wilgotnych, wiecznozielonych lasach wschodniego Madagaskaru, a kilka gatunków związane jest z suchymi biotopami południowej i wschodniej części wyspy. Największa liczba mniej lub bardziej sympatrycznych gatunków (osiem) występuje w masywie Marojejy w północnej części Madagaskaru. Sześć gatunków, w tym wszystkie trzy z rodzaju *Privatenaclia* **gen. nov.**, jest lokalnymi endemitami, występującymi jedynie na stosunkowo niewielkich obszarach w różnych częściach wyspy.

Poza ogólnymi informacjami o preferowanych typach roślinności, biologia gatunków ujętych w rozprawie pozostaje w większości nieznana. Podane są pierwsze dane o pobieraniu nektaru dla pięciu gatunków, z pewną preferencją marzanowatych (Rubiaceae). Liczba spermatoforów lub ich pozostałości stwierdzonych u spreparowanych samic wskazuje, że u madagaskarskich Syntomini występuje poliandria.

Potwierdzone została także przynależność maurytyjskiego endemitu "*Maculonaclia*" *florida* do rodzaju *Dysauxes,* w którym był oryginalnie opisany. Gatunki *Dysauxes* z Mauritiusu i Palearktyki, afrykański gatunek *Pseudonaclia puella*, oraz rodzaj *Mauricenaclia* **gen. nov.** należą do monofiletycznego "kladu *Dysauxes*", w którym najprawdopodobniej miała miejsce dyspersja z Madagaskaru do Afryki i Palearktyki.

Przedstawiona rozprawa stanowi spójną rewizję 1/3 różnorodności gatunkowej madagaskarskich Syntomini. Przyczynia się do lepszego zrozumienia bioróżnorodności Madagaskaru, a także do poszerzenia wiedzy o plemieniu Syntomini, będącym prawdopodobnie najsłabiej poznaną grupą niedźwiedziówek (Arctiinae).

PUBLICATIONS INCLUDED IN THE DOCTORAL DISSERTATION

ARTICLE 1

Wiorek M., Malik K., Lees D., Przybyłowicz Ł. 2021. Malagasy Polka Dot Moths (Noctuoidea: Erebidae: Arctiinae: Syntomini) of Ambohitantely—endemism in the most important relict of Central Plateau rainforest in Madagascar. PeerJ 9:e11688. doi:10.7717/peerj.11688.

PeerJ, IF (2.3), Ministry of Science and Higher Education score: 100

Contributions to the paper: paper concept, collecting Syntomini specimens in the field, conducting molecular and morphological analyses, interpreting the results, map preparation, and writing the manuscript. **I estimate my participation in the preparation of the publication as 60%.**

ARTICLE 2

Przybyłowicz Ł., **Wiorek M.**, Przystałkowska A., Wahlberg N. 2021. Alone on an island: The reassessment of an enigmatic species of Handmaiden Moth (Lepidoptera, Erebidae) endemic to Mauritius. Zoologica Scripta, 50, 752-768. doi:10.1111/zsc.12508.

Zoologica Scripta, IF (2.3), Ministry of Science and Higher Education score: 100

Contributions to the paper: conducting molecular and biogeographical analyses, interpreting the results, elaborating on the species' biology, map preparation, and writing the manuscript. **I estimate my participation in the preparation of the publication as 40%.**

ARTICLE 3

Wiorek M., Lees D.C., Wahlberg N., Przybyłowicz Ł. [2024]. Two becomes nine: integrative taxonomy revision of the genera *Thyrosticta* and *Melanonaclia* reveals even higher diversity of Madagascan endemic Polka Dot Moths (Noctuoidea: Erebidae: Arctiinae: Syntomini).

Manuscript prepared for submission to the Zoological Journal of the Linnean Society, IF (3.0), Ministry of Science and Higher Education score: 140

Contributions to the paper: paper concept, collecting Syntomini specimens in the field, analyses and data obtaining in museum collections, conducting molecular, morphological, and biogeographical analyses, interpreting the results, SEM photography, figure preparation, and writing the manuscript. **I estimate my participation in the preparation of the publication as 70%.**

INTRODUCTION

Madagascar is renowned for the high endemism of its flora and fauna, and is classified as a biodiversity hotspot (Fritz-Vietta et al. 2011). The levels of endemism in some groups reach up to around 90% of species, and the growth of knowledge about Madagascar's biodiversity has resulted in a general increase in these values over the last two decades (Goodman 2023).

In Lepidoptera, there are 1418 genera and 5016 species recorded from Madagascar (Lees and Minet 2022). The most species rich superfamily is the Noctuoidea, constituting around 40% of the island lepidopterofauna (Krüger 2007), whilst the general endemism of butterflies (Papilionoidea) can be estimated at 74% (Vences et al. 2009).

Madagascar broke away from Insular India around 88 mya (Yoder and Nowak 2006), and since then remained isolated from other landmasses. More or less at the same time, the large radiation of Lepidoptera began, especially in the Macroheterocera (Wahlberg et al. 2013). Thus, the majority of the Macroheterocera lineages present in Madagascar can be interpreted as deriving from subsequent colonisation events, rather than continental vicariance (Krüger 2007). Perhaps for the same reason, despite the high endemism of Madagascan Lepidoptera at a species level, substantial endemism of higher taxonomic units (subtribes to families) is rare, and there are only a few such examples, e.g. the family Whalleyanidae (summarised in **Wiorek et al. 2021**).

The largest known radiation of Madagascan Macroheterocera, although not classified as a separate taxonomic unit, is the lineage of the erebid tribe Syntomini, which evolved in the Malagasy region (Lees and Minet 2022, Przybyłowicz et al. 2019). There are around 100 endemic species of Syntomini in Madagascar (Viette 1990). All (but one) derive from a single ancestor and additionally gave rise to subsequent out-of-Madagascar re-colonisation events, since the Palaearctic genus *Dysauxes* Hübner, [1819] also belongs to that evolutionary lineage (Przybyłowicz et al. 2019). Additionally, there are two further syntomine species, *Pseudonaclia puella* Boisduval, 1847 and *Dysauxes florida* de Joannis, 1906 (“*Maculonaclia*” *florida* in Guillermet 2018), which are superficially similar to many of the Madagascan species, but their affinities with that lineage for a long time have remained unclear (see **Przybyłowicz, Wiorek et al. 2021**).

Numerous evolutionary radiations are another peculiarity of the Madagascan biota, with lemurs (Herrera and Dávalos 2016, Everson et al. 2023), and chameleons (Tolley et al. 2013, Giles and Arbuckle 2022) being perhaps the best studied. In general, evolutionary radiations are relatively well recognised in Madagascan vertebrates (Vences 2005), and many mechanisms have been proposed to interpret these patterns (e.g. Vences et al. 2009), whilst the knowledge of these phenomena among invertebrates is still scarce. Evolutionary radiations have been identified so far, for example, in Carabidae beetles (Moore and Robertson 2014), dung beetles (Miraldo et al. 2011), and – in non-insect arthropods – in millipedes (Wesener 2009). In this regard, Madagascan Syntomini remain largely neglected, even though they could be considered as a “charismatic” radiation in Madagascan insects, with their number of around 100 species being comparable to lemurs (Everson et al. 2023).

Another characteristic trait of the Madagascan biota is local endemism, i.e. occurrence of species restricted not only to the island of Madagascar but specifically to its certain regions. Such distributional patterns have been identified and relatively well explained – again – in vertebrates, like lemurs, chameleons, and geckos (Wilmé et al. 2006, Pearson and Raxworthy 2009). However, some contributions were made also to invertebrates, e.g. the already mentioned millipedes (Wesener et al. 2011). The distribution of Madagascan Syntomini also seems to have a specific pattern, with the majority of the species occurring in the eastern part of the island, which is covered with humid forests, distinctly different from e.g. dry forests of western Madagascar, or southern semi-arid, dry thickets (e.g. Vences et al. 2009). Some patterns of local endemism in Syntomini distribution were indicated already in Griveaud (1964), and further developed in **Wiorek et al. (2021), Wiorek et al. (manuscript)**.

Therefore, Madagascan Syntomini seem to be a suitable object for future evolutionary studies, allowing for elaboration of the mechanisms and phenomena well known from vertebrates, as an insect “model”, and thus for a better understanding of the biodiversity of Madagascar. But first, the group demands a modern systematic revision, to reveal the true relationships between species. The last elaboration of the group was done by Griveaud (1964), where their current systematics was established by him. However, initial molecular results (Przybyłowicz et al. 2019) questioned the monophyletic character of at least some of the 15 genera proposed by Griveaud (1964). This applies especially to the genus *Thyrosticta* Hampson, 1898, which comprises 23 superficially very variable species. The establishment of a stable, morphology-based systematics of Noctuoidea, to which Syntomini belong, has been challenging, and only very recently insights from molecular studies have allowed for some further progress (Zahiri et al. 2012). Thus, the tribe Syntomini itself, which has been a largely neglected group of Erebidae (Przybyłowicz et al. 2019), and especially its unique Madagascan lineage, demand a modern revision using an integrative taxonomy approach.

Remarkably, the immature stages and biology of Madagascan Syntomini have been completely unknown (Griveaud 1964), which thus constitutes a large gap in the knowledge of the diversity of tiger moths in general, and this has been addressed in **Wiorek et al. (manuscript)**. This is an important lacuna in the context of potential ecological traits, e.g. aposematism, undoubtedly exhibited by Madagascan Syntomini, with their vivid, usually black-white or black-yellow colouration. In tiger moths, aposematism is usually connected with pharmacophagy, as the advertisement of toxicity or unpalatability resulting from obtaining specific plant secondary compounds, which, however, has not been recorded in Syntomini so far (Zaspel et al. 2014).

In the thesis presented here, two genera of Madagascan Syntomini are reviewed: the genus *Thyrosticta*, and the genus *Melanonaclia* Griveaud, 1964 which in the course of the study appeared to be connected with *Thyrosticta* at the level of inter-specific relationships. In total, around 1/3 of the diversity of the Madagascan lineage of Syntomini is elaborated.

RESEARCH GOALS AND HYPOTHESES

The main research goal of the thesis was to reveal the true relationships among the reviewed taxa, in the context of their placement in the phylogeny of the Madagascan lineage of Syntomini, and their relationship to other, non-Madagascan Syntomini species from Africa and Mauritius.

The realisation of the thesis was based on the verification of four hypotheses, indicated in the Individual Research Plan:

H1. There are distinct, previously unrecognized morphological characters, which enable the unambiguous assignment of groups of reviewed taxa to actual evolutionary lines, and molecular studies confirm the apomorphic nature of these characters (**Wiorek et al. 2021, Wiorek et al. manuscript**).

H2. The reviewed genera comprise more species than are currently known due to: (a) the lack of α-taxonomic studies of museum materials, (b) the existence of cryptic species among the previously known taxa, (c) the existence of undescribed species resulting from the insufficient research of the Madagascar fauna (**Wiorek et al. 2021, Wiorek et al. manuscript**).

H3. The reviewed taxa are not widely distributed across Madagascar but they are characterized by selectivity concerning habitat conditions, such as humidity, elevation, and type of plant communities, among the diverse biotopes of Madagascar (**Wiorek et al. 2021, Wiorek et al. manuscript**).

H4. The reviewed Madagascan taxa are related to the East African representatives of the genus *Pseudonaclia*, the Palearctic genus *Dysauxes*, and the Mauritian endemic "*Maculonaclia*" *florida*, of undetermined generic affiliation. (**Przybyłowicz, Wiorek et al. 2021, Wiorek et al. manuscript**).

MATERIALS AND METHODS

MATERIALS

The study was based on specimens obtained during fieldwork trips, and visits to scientific museum collections of Lepidoptera, both conducted during realisation of the thesis.

Due to the specific behaviour of Madagascan Syntomini, with predominantly diurnal activity but limited flight, the main method of field collecting of the group is spotting the individuals sitting on vegetation, and catching them with an entomological net. The sampling can be supplemented by light-trapping at night but with limited results for most of the species (see **Przybyłowicz, Wiorek et al. 2021, Wiorek et al. manuscript** for further description of the methods).

The museum specimens included in the study are deposited in the collections of: Institute of Systematics and Evolution of Animals Polish Academy of Sciences, Kraków, Poland (ISEA PAS); African Natural History Research Trust, Leominster, UK; Zoological Museum of the Jagiellonian University, Kraków, Poland; Museum für Naturkunde, Berlin, Germany; Muséum national d'Histoire naturelle, Paris, France; Natural History Museum, London, UK; Národní Muzeum, Prague, Czech Republic; Naturhistoriska riksmuseet, Stockholm, Sweden; Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar; Senckenberg Naturmuseum, Frankfurt am Main, Germany; Staatliches Museum für Naturkunde, Stuttgart, Germany; private collection of Patrick Basquin, France.

The specimens were analysed during site visits, and borrowed specimens were further elaborated at ISEA PAS. In a few cases, the photographs of the specimens and labels, allowing for species identification, were provided by the courtesy of collection managers. The total number of Madagascan Syntomini specimens used for analyses is 1402 (**Wiorek et al. 2021**; Table S1 in **Wiorek et al. manuscript**). Additionally, the study included a number of specimens of *Dysauxes florida* from Mauritius and *Pseudonaclia puella* from East Africa (**Przybyłowicz, Wiorek et al. 2021, Wiorek et al. manuscript**; Table T1 in the supplementary information at the end of the text of thesis).

MORPHOLOGICAL ANALYSES

Morphological analyses were conducted predominantly at ISEA PAS, and also in Muséum national d'Histoire naturelle in Paris, and Natural History Museum in London.

The spreaded specimens from the ISEA PAS collection, and those borrowed from other collections for further elaboration, were photographed using a Canon EOS 70D camera provided with a macro lens EF 50 mm, before further procedures, especially destructive sampling (**Wiorek et al. 2021:** Fig. 3; **Wiorek et al. manuscript:** Figs 35, 48, 54-55, 64, 72, 75-76, 98-100, 119).

Details of body morphology were photographed using a stereoscope microscope Leica S9i system, with LasX software provided with stacking mode (**Wiorek et al. manuscript:** Figs 1, 7-9, 13, 18, 20, 28).

Genitalia slides were made with the standard method. Abdomens were macerated in a 10% solution of NaOH, rinsed in distilled water, and dissected in glycerine under a binocular microscope. Glycerine, due to its viscosity, allows for more precise manipulation of fragile structures, especially the eversion of the vesica in the male genitalia, than dissecting in water or ethanol. Prepared genitalia were stained in a water solution of chlorazol black (if necessary), mounted on microscope slide in glycerine, and photographed with the use of Leica S9i system stereoscope microscope (**Wiorek et al. 2021:** Figs 4-5; **Wiorek et al. manuscript:** Figs 36-37, 41-47, 49-53, 59-63, 67-69, 73-74, 77-82, 84-93, 97, 102-106, 108-114). For further details of capturing pictures see Materials and Methods in **Wiorek et al. (manuscript)**. Further, the genitalia were rinsed in ethanol, mounted in Euparal on labelled microscope slides, covered with coverslips and left for two weeks at 50°C for the medium to solidify.

Wing venation slides were made following the methodology by Banasiak (2015), with minor modifications. The wings were torn off, descaled under a binocular microscope with a fine brush in a Petri dish containing water with a droplet of detergent to remove surface tension, then rinsed in ethanol and left for at least 24h in a 10% eosin water solution. Stained wings were mounted on microscope slides, in a drop of water with detergent, covered with coverslips and photographed using the same binocular microscope and software, as mentioned above (**Przybyłowicz, Wiorek et al. 2021**: Fig. 5; **Wiorek et al. manuscript:** Figs 14-17)

Preparations for SEM visualisation were made from dry specimens, by removing the relevant body parts, or loose wing scales under a binocular microscope, and placing them on carbon disc. Only eggs required rehydration to remove dust, then dehydration with ethanol as described in **Wiorek et al. (manuscript)**, and placed on carbon disc. The preparations were further coated with gold and photographed using a HITACHI SU8600 Ultrahigh-Resolution Scanning Electron Microscope, in the Laboratory of Scanning Electron Microscopy and Microanalysis of the Institute of Geological Sciences, Jagiellonian University in Kraków.

MOLECULAR ANALYSES

Laboratory methods

The laboratory part of the molecular research was done in the laboratories at Lund University, Sweden, and at ISEA PAS, following the same methods and procedures in all three articles included in the thesis (**Wiorek et al. 2021, Przybyłowicz, Wiorek et al. 2021, Wiorek et al. manuscript**).

The molecular study was based on Sanger sequencing, thus only fresh specimens, i.e. collected not earlier than in the 1990s. were used, to provide appropriate DNA quality. Two legs of each specimen were used for DNA extraction. Preferably midleg and hindleg from one body side were sampled, to retain at least one leg from a pair for morphological analyses. The legs were further crushed with the microhomogenisator in an Eppendorf tube. Genomic DNA extraction was conducted with the NucleoSpin Tissue kit (Macherey-Nagel, Germany), according to the manufacturer's protocol. DNA extracts were stored in a fridge, at 4°C. These conditions do not affect the quality of extracts, whilst storage at -20°C causes multiple freeze-thaw cycles during using samples for analyses, and the formation of ice crystals during freezing induces DNA fragmentation.

In total, during realisation of the thesis, 1016 sequences of the total length of 643 549 base pairs, obtained from 254 specimens were used (including outgroups, see Table T1).

Sequences of up to eight molecular markers, one mitochondrial and seven nuclear (Tab. T2) were amplified, using the primers designated by Wahlberg and Wheat (2008); some of them are amplified in two or three fragments (Tab. T2). These markers have been widely used in molecular research on Noctuoidea (e.g. Przybyłowicz et al. 2019, Zahiri et al. 2012, Zenker et al. 2017). Additionally, in the case of samples with DNA too degraded to obtain the barcode region sequence with the standard primers, amplification with special primers was conducted, amplifying the barcode region in two pieces (Tab. T2). All primers are hybridized with an universal sequences T7Promoter(F) 5' TAA TAC GAC TCA CTA TAG GG 3' (forward), and T3(R) 5' ATT AAC CCT CAC TAA AGG G 3' (reverse) facilitating sequencing by use of these universal primers for all gene regions.

PCR reactions were conducted with the use of Bioline 2x MyTaq HS Red Mix (Meridian Bioscience, USA), in a total volume of 12.5 µl. The composition of the reagent mix was as follows: ddH_2O – 4 µl, forward primer – 0.625 µl, reverse primer – 0.625 µl, Bioline 2x MyTaq HS Red Mix – 6.25 µl, DNA extract – 1.0 µl.

Successful PCR products were either sequenced using BrilliantDye Terminator v.3.1 kit (NimagGen, the Netherlands) following the manufacturers protocol, and read with an ABI Prism 3130xl sequencing machine at ISEA PAS, or sent for sequencing to Macrogen Europe (Amsterdam, the Netherlands). Sequences obtained were curated manually in BioEdit (Hall 1999), i.e. compared with the relevant chromatograms and reference sequences, and ambiguous sites were coded according to IUPAC nucleotide code. Such prepared sequences were uploaded to VoSeq database (Peña and Malm 2012), and further usage of the data was managed in that platform.

Phylogenetic analyses

The phylogenetic analyses included in the thesis were conducted within the Maximum Likelihood framework (ML) (**Wiorek et al. 2021, Przybyłowicz, Wiorek et al. 2021, Wiorek et al. manuscript**), and the Bayesian Inference (BI) framework (**Wiorek et al. manuscript**).

In **Przybyłowicz, Wiorek et al. (2021)**, and **Wiorek et al. (manuscript)**, the ML analyses were conducted in both IQ-TREE and RAxML software. Different programs using the ML approach, although based on the same principles, differ in the implementation of computational methods, thus in some cases can give non-identical results (Zhou et al. 2018). Thus, the usage of different programs allows for a more accurate elaboration of the phylogenetic relationships.

Phylogenetic analyses conducted in IQ-TREE (Nguyen et al. 2015) were done on the web server (Trifinopoulos et al. 2016). The dataset was partitioned by gene region (i.e. 11 partitions, see Table T2), as such approach has been proven for the data based on the eight markers used in the study (Przybyłowicz et al. 2019). The best substitution model for each partition was found using the model-finding tool implemented in IQ-TREE (Kalyaanamoorthy et al. 2017). Node support values were provided with Ultrafast Bootstrap (Hoang et al. 2017) and SH-like approximate likelihood test (Guindon et al. 2010), both with 1000 replicates.

The RAxML (Stamatakis 2014) analyses were conducted with the same data partitioning, and input parameters as implemented on the CIPRES platform (Miller et al. 2010).

The BI analyses were done in MrBayes (Ronquist et al. 2012) on CIPRES (Miller et al. 2010). Two independent runs of 10 million generations were conducted, each consisting of four chains, which were sampled every 1000 generations. The convergence was verified visually, with a 25% burn-in applied.

The obtained trees were visualised with FigTree v.1.4.4 software.

Species delimitation analyses

In **Wiorek et al. (2021)**, the verification of the taxonomic status of the two morphotypes of *Thyrosticta dilata* Griveaud, 1964 (i.e. *Kowalskinaclia dilata* **comb. nov.** in **Wiorek et al. manuscript**) was done solely based on the p-distance between the DNA barcode regions of COI gene (Tab. T2) (Kekkonen and Hebert 2014).

In **Wiorek et al. (2024)**, more species delimitation analyses were implemented to explore the patterns observed in the obtained phylogenetic trees (**Wiorek et al. manuscript**: Fig. 5A-B, Figs S1-S2), suggesting the existence of cryptic species complexes. One cluster-based method, Automatic Barcode Gap Discovery (ABGD) (Puillandre et al. 2012), and one tree-based method, the ML implementation of Poisson Tree Processes (PTP) (Zhang et al. 2013) were used, separately for COI-begin, EF1a-begin and GAPDH regions (Tabs T1, T2), to provide evidence in both mitochondrial and nuclear genes.

In both methods, single-locus data are used as the input. In ABGD, it was aligned FASTA files with the sequences of relevant regions. The samples with more than around 50-70 ambiguous base pairs (“Ns”) at either end were removed from the dataset, except for the species represented only by a single sample. The input parameters were set as indicated in **Wiorek et al. (manuscript:** File S1). For PTP analyses, as the input were used ML trees in Newick format, constructed in IQ-TREE (Nguyen et al. 2015) based on the same alignments that were used in ABGD.

The results of the Bayesian implementation of PTP (bPTP), i.e. the arrangement of partitions found by simple heuristic search were not included in the results (**Wiorek et al. manuscript**), as they comprised partitioning into a high number of single-sample “species” with very poor support. Thus, only the partitioning based on Maximum Likelihood support is shown.

Additionally, another commonly used tree-based method of species delimitation is Generalized Mixed Yule Coalescent (GMYC) (Fujisawa et al. 2013, Kekkonen and Hebert 2014), but it requires a strictly ultrametric, i.e. time-calibrated tree. Obtaining such a tree, thus involving inference of divergence times, was beyond the scope of the thesis. Although there are tools allowing for a transformation of an un-calibrated tree into an ultrametric-like one, e.g. the R “ape” package (Paradis and Schliep 2019), the tree obtained with this method failed to provide a reliable GMYC output (not shown).

DISTRIBUTIONAL ANALYSES

Patterns of local endemism in Madagascan Syntomini were initially elaborated in **Wiorek et al. (2021)**, for the Reserve SpéAmbohitantely.

For a complex elaboration of the distribution of the taxa covered in the thesis, label data from all specimens included in the study were gathered (**Wiorek et al. manuscript:** Table S1). Based on that, 191 collecting localities were identified (**Wiorek et al. manuscript:** Table S3) and geolocalised referring to Dorr (1997), Viette (1991), and Moat and Smith (2007), if coordinates were not indicated in the labels. The distributional maps were prepared in the QGIS program. Data on primary vegetation were taken from Du Puy and Moat (1996) and Moat and Smith (2007), and the dataset on 2000-2020 deforestation – from LOFM (2022).

We were unable to provide the coordinates only for a few localities. This usually results from a very general mention of the collecting area in the label, or the existence of a few places with the same name in Madagascar and lack of additional clues in the data, or the misspelling of the actual name in the label (for further details of methodology and remarks see Materials and Methods, and Results, respectively, in **Wiorek et al. manuscript**).

Elevational data were collected predominantly from the labels, if available. Since many of the localities were secondarily geolocalised, thus with a possible error, inferring elevation based on these coordinates would bring additional errors to the data. Nevertheless, we used Google Earth Pro to obtain elevational data for a few species, which missed this information in the specimens from the lower elevations, especially in coastal regions. In these parts of Madagascar, the elevation is relatively equal even within larger areas, contrary to e.g. the eastern slope of Madagascar, where the elevation ascends steeply to over 1600 m a.s.l. in the Central Plateau **(Wiorek et al. 2021)**.

ETYMOLOGY OF THE NEW GENERIC NAMES

The new genera described in **Wiorek et al. (manuscript)** are named after the characters from "The Penguins of Madagascar" television series (see the manuscript for the details), with a traditional ending 'naclia' (as precented for *Toulgoetinaclia*, *Soganaclia*, although these were named after real persons)**.**

RESULTS

The results obtained during realisation of the thesis allowed for comprehensive verification of the four research hypotheses.

H1. (Wiorek et al. 2021, Wiorek et al. manuscript)

The reviewed genera *Thyrosticta* and *Melanonaclia* are confirmed to be polyphyletic, with nine distinct evolutionary lineages recognised within them (**Wiorek et al. manuscript:** Fig. 5A-B, Figs S1-S2). Additionally, some species belonging to these two genera turn out to be closely related to each other and should be treated as congeneric.

In the genus *Thyrosticta*, the majority of the seven morphological "groups" *sensu* Griveaud (1964) appear to be monophyletic and constitute separate evolutionary lineages, established here as new genera. The genus *Thyrosticta* becomes monotypic, with its only species *Thyrosticta sylvicolens* (Butler, 1878). The "group of *Thyrosticta lacrimata*" is therein described as *Skippernaclia* **gen. nov.**, "group of *Thyrosticta vieui*" as *Kowalskinaclia* **gen. nov.**, "group of *Thyrosticta triangulifera*" as *Privatenaclia* **gen. nov.**, "group of *Thyrosticta pauliani*" as *Julienaclia* **gen. nov.**, and "group of *Thyrosticta minuta*" as *Mauricenaclia* **gen. nov.** The "group of *Thyrosticta trimacula*" comprises closely unrelated species, from which *Thyrosticta trimacula* (Mabille, [1879]) and *T. dujardini* Griveaud, 1969 are moved to the genus *Melanonaclia*, and *Thyrosticta bimacula* Griveaud, 1964 constitutes a distinct lineage, moved to its own, monotypic genus *Riconaclia* **gen. nov.**

In the genus *Melanonaclia*, the majority of the species appeared to belong to a monotypic lineage. Only *Melanonaclia moerens* (Oberthür, [1911]) is revealed to be sister to *Thyrosticta pauliani* Griveaud, 1964, and moved to the genus *Julienaclia* **gen. nov.**, and *Melanonaclia perplexa* Griveaud, 1964 to its own, monotypic genus (but see below).

Therefore, the species previously belonging to *Thyrosticta* and *Melanonaclia* (*sensu* Griveaud 1964) are arranged in nine genera. For each of them, we were able to recognize "distinct, previously unrecognized morphological characters" (**H1**), designated as apomorphies of the new genera. These characters are located mostly in the genitalia, but also other body parts, e.g. in the 8th sternite of the male abdomen in *Julienaclia* **gen. nov.** (**Wiorek et al. manuscript:** Fig. 66). Additionally, we identified a number of further morphological characters, described and illustrated in detail, whose presence and structure make an almost uniform pattern within genera but vary among them. These are: the shape of antennae, presence/absence of male foreleg scale tuft, presence/absence and number of additional hindleg tibial spurs, number of forewing radial veins, and presence/absence of female ventral pheromone glands (**Wiorek et al. manuscript:** Tab. 3, Figs 6-17, 29).

Identification of these characters was possible also thanks to first descriptions, including the genitalia, of previously unknown males or females of certain species, and redescription of the genitalia of the remaining species. In the thesis, for the first time are described: the females of: *Skippernaclia vestigii* (Griveaud, 1964) **comb. nov.** (**Wiorek et al. 2021:** Figs 3D, 4C), *Skippernaclia ankaratra* (Griveaud, 1964) **comb. nov.**, *Kowalskinaclia vieui* (Griveaud, 1964) **comb. nov.**, *Privatenaclia ratovosoni* (Griveaud, 1964) **comb. nov.**, *P. seguyi* (Griveaud, 1964) **comb. nov.**, *Julienaclia pauliani* **comb. nov.**, *Riconaclia bimacula* **comb. nov.**, and the male of *Melanonaclia dujardini* **comb. nov.** (**Wiorek et al. manuscript:** Figs 45, 48G-I, 52, 54E, 62, 63, 64C, E, 69, 72C, 74, 100E 114). Additionally, the first correct description of the male genitalia of *Thyrosticta sylvicolens,* and the female of *Skippernaclia lacrimata* (Griveaud, 1964) **comb. nov.**, misidentified in Griveaud (1964), are provided (**Wiorek et al. manuscript:** Figs. 36, 48B, 44).

Also, the eggs of four species: *Kowalskinaclia vieui* **comb. nov.**, *Privatenaclia seguyi* **comb. nov.**, *Mauricenaclia minuta* (Boisduval, 1833) **comb. nov.**, and *M. octopunctata* (Rothschild, 1924) **comb. nov.** are described and illustrated for the first time, providing the first insight into the immature stages of Madagascan Syntomini (**Wiorek et al. manuscript:** Figs 30-33).

H2. (Wiorek et al. 2021, Wiorek et al. manuscript)

During realisation of the thesis, three new species were discovered and described: *Skippernaclia leesi* Wiorek **sp. nov.**, *Mauricenaclia apatris* Wiorek **sp. nov.**, and *Melanonaclia ranomafana* Wiorek & Przybyłowicz **sp. nov.** (**Wiorek et al. manuscript**: Figs 47 48K-L, 76I-J, 85, 100H-J, 108).

The description of these species results mostly from the reason "(a) the lack of α-taxonomic studies of museum materials", but also "(c) [...] the insufficient research of the Madagascar fauna" indicated in hypothesis **H2**. The specimens of *S. leesi* **sp. nov.** and *M. ranomafana* were collected relatively recently (considering that the studies of Madagascan Syntomini reach back to the 1830s – see Boisduval 1833): in 1993 in the case of the former, and 2004 and 2018 in the case of the latter species. The materials have been deposited in NHMUK and ISEA PAS, and examined during the realisation of the thesis. Because *S. leesi* is superficially almost identical to *S. ankaratra* and *S. lacrimata*, and *M. ranomafana* resembles *Melanonaclia trimacula*, identifying them as new species demanded molecular and morphological research (genitalia dissection) to indicate their apomorphies (**Wiorek et al. manuscript**).

The description of *M. apatris* **sp. nov.** results directly from "(a) the lack of α-taxonomic studies of museum materials" (hypothesis **H2**). The three known specimens of the species were found among mixed, unidentified materials from Madagascar during a research visit of Marcin Wiorek and Łukasz Przybyłowicz to the Muséum national d'Histoire naturelle in Paris. The superficial distinctiveness of the specimens suggested them directly to represent a new species, but the similarity of genitalia to those of *Mauricenaclia rothschildi* **comb. nov.** required detailed morphological analyses to reveal the diagnostic characters (**Wiorek et al. manuscript**).

Additionally, the potential "existence of cryptic species among the previously known taxa", indicated in hypothesis H2 was examined with the use of species delimitation analyses. In **Wiorek et al. (2021)** the two discrete morphotypes of *Kowalskinaclia dilata* **comb. nov.**, "yellow" one and "black" were confirmed to be conspecific based on both molecular (no difference in the DNA barcoding region of COI gene, with p-distance equal to 0.0), and morphological evidence (lack of differences in the male genitalia) (**Wiorek et al. 2021**: Figs 3E-F, 5D-E, 6, Tab. S2). Further, six potential cryptic species complexes were found, within: *Kowalskinaclia cowani* **comb. nov.**, *K. vieui* **comb. nov.**, *Melanonaclia luctuosa* (Oberthür, 1911), *M. trimacula* **comb. nov.**, *Mortinaclia perplexa* **comb. nov.**, and *Mauricenaclia minuta* **comb. nov.** (**Wiorek et al. manuscript**: Figs 5A-B, S1-S7, File S1). However, in the case of *Melanonaclia luctuosa*, *M. trimacula* **comb. nov.**, the results of ABGD and PTP analyses were not congruent with each other. Additionally, except in the case of *M. perplexa* **comb. nov.**, we were unable to identify any morphological characters diagnostic to the potential species. Despite that, the "western" population of *M. minuta* **comb. nov.** (specimen DL_02-325) seems to be a true species, as it appears as clearly distinct in all analyses, based on both mitochondrial and nuclear markers (**Wiorek et al. manuscript**: Figs S3-S7). In the case of *M. perplexa* **comb. nov.**, numerous differences in both male and female genitalia were found, suggesting the existence of two or three species (not shown). However, further molecular research is needed to assign males and females to the proper species.

Finally, in **Wiorek et al. (manuscript)**, five new synonyms are established: *Thyrosticta incerta* Griveaud, 1964 syn. nov. of *Kowalskinaclia cowani* **comb. nov.**, *Thyrosticta melanisa* Griveaud, 1969 syn. nov. of *Julienaclia moerens* **comb. nov.**, *Thyrosticta angustipennis* Le Cerf, 1921 syn. nov. and *Dysauxes subfenestrata* Aurivillius, [1900] syn. nov. of *Mauricenaclia* *minuta* **comb. nov.**, and *Tritonaclia inauramacula* Griveaud, 1964 syn. nov. of *Melanonaclia luctuosa*. In total, 30 valid species are recognised in this paper.

H3. (Wiorek et al. 2021, Wiorek et al. manuscript)

The reviewed species were recorded in 191 localities across the entire area of Madagascar (Wiorek et al. manuscript: Figs 34, 39, 56, 58, 65, 71, 94-96, 115-117). Most of them occur in the eastern and central parts of the island, and their ranges often are narrow latitudinally but extended longitudinally, corresponding with the area of humid, evergreen "eastern" forests.

There are only a few taxa restricted to other parts of Madagascar, including one genus – *Julienaclia* **gen. nov.**, from which *J. moerens* **comb. nov.** is associated with northern Madagascar, and mainly its western coast, and *J. pauliani* **comb. nov.**, occurs along the western and southern coast of the island (**Wiorek et al. manuscript**: Fig. 71A-B). Additionally, in the genus *Mauricenaclia* **gen. nov.**, three species: *M. raharizonina* Griveaud, 1964 **comb. nov.**, *M. rothschildi* Griveaud, 1964 **comb. nov.**, and *M. octopunctata* **comb. nov.** occur also mostly along the southern and western coast of Madagascar, in the areas covered with deciduous, seasonally dry forests, but also semi-arid, thorny bushes and thickets.

In **Wiorek et al. (2021)**, the Reserve Spéciale d'Ambohitantely was recognised as a centre of local endemism of Syntomini in the Central Highlands. Of the eight species recorded in the paper, five occurred only there, including *Skippernaclia vestigii* **comb. nov.** and *Kowalskinaclia cowani* **comb. nov.** However, **Wiorek et al. (manuscript)** the latter species is reported also from Parc National d'Andasibe.

In **Wiorek et al. (manuscript)**, six species in total are found to be local endemics of certain areas: *Privatenaclia seguyi* **comb. nov.** and *P. triangulifera* **comb. nov.** are endemic to Marojejy, and *P. ratovosoni* **comb. nov.** to the Moramanga region, *Skippernaclia vestigii* **comb. nov.** to Ambohitantely, *S. leesi* **sp. nov.** to Masoala, and *Melanonaclia ranomafana* **sp. nov.** to PN Ranomafana. Thus, in the genus *Privatenaclia* **gen. nov.** all species are local endemics, and *P. ratovosoni* appears also to be the most endangered species, because of the intensive deforestation of the area of its occurrence (**Wiorek et al. manuscript**: Fig. 65).

In total, Marojejy is a centre of diversity of Syntomini, with eight out of 30 species covered in the thesis being recorded from that massif.

H4. (Przybyłowicz, Wiorek et al. 2021, Wiorek et al. manuscript)

The Mauritian endemic "*Maculonaclia*" *florida,* originally described as *Dysauxes florida* de Joannis 1906 is proved indeed to be closely related to the other species of the genus *Dysauxes,* and sister to its Palaearctic clade, based on both molecular and morphological research (**Przybyłowicz, Wiorek et al. 2021**: Figs 3, 5, 9, S1).

Both *D. florida* and *Pseudonaclia puella* belong to a monophyletic clade, called by us "*Dusauxes* clade", together with the genus *Mauricenaclia* **gen. nov.**, comprising species from the "group of *T. minuta*" of the reviewed genus *Thyrosticta* (**Przybyłowicz, Wiorek et al. 2021**: Figs 3 S1; **Wiorek et al. manuscript:** Fig. 5B, S1-S2). Additionally, the male and female genitalia of *P. puella* were described for the first time in Wiorek et al. (manuscript: Figs 86, 97), allowing for a proper identification of the apomorphies of *Mauricenaclia* **gen. nov.**

Additionally, all available data on the biology of *D. florida*, including observation of nectaring on *Ixora parviflora* (Rubiaceae) were gathered together (**Przybyłowicz, Wiorek et al. 2021**: Fig. 4).

Therefore, all four hypotheses have been addressed in the thesis, and verified positively, i.e. the statements made therein have been confirmed.

Additionally, in **Wiorek et al. (manuscript:** Fig. 118) the first observations of nectaring in Madagascan Syntomini are included, as well as the information on the number of spermatophores or their remnants found in the dissected females, allowing for the inference, that polyandry is present in Madagascan Syntomini.

DISCUSSION

The results obtained in the thesis confirm the monophyletic character of the Madagascan lineage of Syntomini, inferred by Przybyłowicz et al. (2019). However, the exact relationship between the nine genera introduced here and the other taxa of Madagascan Syntomini still require further research, as well as the relationship with the "basal", African clades of Syntomini (the former Thyretini *sensu* Przybyłowicz 2009).

The results of the thorough morphological analysis of the reviewed taxa revealed the group to be highly diverse, with a pattern of presence/absence and variation in many characters. Thus, the proper arrangement of the species into higher taxa reflecting their true evolutionary relationships would be much more difficult, if not impossible, without molecular phylogenetic inferences. Additionally, the general morphology of Madagascan Syntomini requires further study in the other lineages, as these insights can provide important information about the overall diversity of the tribe - especially since some morphological characters used to be indicated as the apomorphies of Syntomini, in this study (**Wiorek et al. manuscript**) appeared to be still ambiguous (e.g. the fusion of the hindwing veins along the costal margin) or even erroneous (the loss of the male frenulum) (Jacobson and Weller 2002, Kitching and Rawlins [1999]).

Additionally, some of the structures can have an important function in the biology of the species, like e.g. the male foreleg tuft, composed of potential scent scale, which to our best knowledge is reported in Syntomini for the first time in **Wiorek et al. (manuscript)**.

The first descriptions of the eggs of four species of Madagascan Syntomini provided in **Wiorek et al. (manuscript)**, together with the description of the egg of the closely related *Dysauxes florida* from Mauritius that was done in **Przybyłowicz, Wiorek et al. (2021)** constitute the first insights into the diversity of immature stages of this lineage of Syntomini. Elsewhere in Lepidoptera, morphological analyses of immature stages have allowed e.g. for the discovery of apomorphic characters of Mycalesina (Nymphalidae: Satyrinae), based on the larvae of species of also large Madagascan radiation (Roos 2003).

The morphological and molecular analyses, including the evaluation of intraspecific variation, allowed for the verification of taxonomic status and recognition of 30 valid species within the reviewed genera *Thyrosticta* and *Melanonaclia* (**Wiorek et al. 2021, Wiorek et al. manuscript**). The two new species, *Skippernaclia leesi* **sp. nov.** and *Melanonaclia ranomafana* **sp. nov.** described in **Wiorek et al. (manuscript)** were collected in the last 30 years, and the second of them additionally was found in one of the best-studied national parks of Madagascar (Goodman et al. 2018). This indicates, that despite the quite intensive research in Madagascan

Lepidoptera in the previous decades, there can still be more unknown species to discover, especially considering that even a short survey can yield new records to the studied area (**Wiorek et al. 2021**).

The presumed cryptic species complexes, as well as the potential factors maintaining intraspecific variation within certain species, require further examination. The observed incongruency between the molecular results obtained with mitochondrial and nuclear genes, and from morphological analyses can result from multiple factors, e.g. incomplete lineage sorting (Steenwyk et al. 2023) or early stages of speciation (de Queiroz 2007). This variation is especially interesting in the context of interactions between the aposematic coloration, potential mimicry rings within Madagascan Syntomini and sexual selection. The observed variation within some species can be the result of various factors, as differently coloured individuals of tiger moths can be differently recognised by conspecifics, but also by predators (Henze et al. 2018).

In the light of rather poor overall distributional data available for Madagascan Lepidoptera (Iannella et al. 2019), the state of knowledge on Madagascan Syntomini can now be considered as respectable. The associations of Madagascan Syntomini mostly with centre of species richness in eastern, evergreen, humid forests inferred in Lees et al. (1999) are confirmed in this study. Additionally, a few taxa are identified to be associated mostly with drier habitats of western and southern Madagascar. Their distribution and relationships to other species, as well as the mechanism which have led to the observed patterns, can be an interesting study bearing potentially of more general mechanisms shaping the biodiversity of Madagascar (Vences et al. 2009). Also, the patterns of microendemism (see Introduction) in Madagascan Syntomini require further study, especially since some of the least known species are not necessarily true local endemics, as indeed turned out to be the case for *Kowalskinaclia dilata* **comb. nov.** (**Wiorek et al. 2021, Wiorek et al. manuscript**).

Except for the general information on the vegetation types preferred by the reviewed taxa, the knowledge of their biology and ecology remains rudimentary. For *Kowalskinaclia dilata* **comb. nov.** that we observed in Ambohitantely, this the species generally does not fly out of wooded areas (**Wiorek et al. 2021**). Typically, the active flight in syntomine species that belong to the Madagascan radiation is reduced to short distances, usually only to escape in the surrounding vegetation, as was also observed in *Dysauxes florida* (**Przybyłowicz, Wiorek et al. 2021**), and *D. ancilla* (Linnaeus, 1767) (Betzholtz 2002). Additionally, although Madagascan Syntomini are considered generally diurnal lepidopterans (**Wiorek et al. 2021, Przybyłowicz, Wiorek et al. 2021**), some species, especially from the genera *Kowalskinaclia* and *Melanonaclia*, are attracted to light seemingly more often than others. This possibly can be associated with different vision adaptations in certain lineages of Syntomini, since moths are known to be attracted preferentially to the UV and blue parts of the light spectrum (Brehm et al. 2021). In this context also, compound eye morphology should be analysed, especially in view that e.g. males of *Kowalskinaclia dilata* **comb. nov.** have eyes significantly larger than females (**Wiorek et al. 2021**), which indicates a potentially important role of visual signals in the behaviour of this species, while such strong dimorphism in the eye size – and generally, such eye enlargement – have not been observed in other species covered in this study (not shown).

The foodplants of the larvae of Madagascan Syntomini, as well as the larvae themselves, remain frustratingly unknown. However, based on information on the biology of *D. ancilla* (Betzholtz 2002, 2003a, b) and *P. puella* (Staude et al. 2023: 382), we can hypothesize that Madagascan Syntomini, and especially members of the genus *Mauricenaclia* belonging to the "*Dysauxes* clade" can also develop in the litter (see **Wiorek et al. manuscript**). Regards the adults, **Wiorek et al. (manuscript)** provide the first records of nectaring on certain plant species. The fact that *Melanonaclia trimacula* **comb. nov.** was observed nectaring on *Psychotria* (*Mapourea*) sp., and *Mauricenaclia minuta* was apparently reported from *Cinchona succirubra* (however with significant doubts considering the plant identity, since this is an Andean taxon) (**Wiorek et al. manuscript**), together with *D. florida* being observed nectaring on *Ixora parviflora* in Mauritius (**Przybyłowicz, Wiorek et al. 2021**) all indicate a prevalence of Rubiaceae among this so far scarce dataset. This plant family is known to contain different alkaloids and other potentially toxic compounds (Gutiérrez-Grijalva et al. 2020). The phenomenon of pharmacophagy i.e. obtaining such secondary compounds – especially pyrrolizidine alkaloids – although widespread in tiger moths and connected with aposematism, as mentioned in the introduction, is completely unknown in Syntomini, and demands examination, not least in the Madagascan lineage of the tribe.

CONCLUSIONS

Results obtained during realisation of the thesis allowed for a complex elaboration of the systematics and diversity of the genera *Thyrosticta* and *Melanonaclia*. The following conclusions can be formulated:

1. The genera *Thyrosticta* and *Melanonaclia* in the arrangement by Griveaud (1964) are proven to be polyphyletic, and comprise nine distinct evolutionary lineages, of which seven are described as new genera. For each of them clear morphological characters – apomorphies – are indicated, and morphological and molecular results are congruent. These results contribute to a better understanding of the diversity of Madagascan Syntomini.

2. Verification of the taxonomic status of analysed specimens allowed for the description of three new species, and the establishment of five new synonyms. In total, 30 valid species are recognised in the thesis. The taxonomic status of the potential cryptic species found in the study requires further verification.

3. The reviewed taxa occur across the entire island Madagascar, but the ranges of occurrences of individual species are usually restricted to specific areas. The majority of the species occur in the humid, evergreen forest of the east of Madagascar, and a few species are associated with dry habitats in the southern and western parts of the island. Apart from information about preferred habitats and single observations of nectaring, the biology of the reviewed taxa remains unknown and demands further research, including the ecological aspects.

4. Among the reviewed taxa, the former “group of *Thyrosticta minuta*”, described in this study as *Mauricenaclia* **gen. nov.**, is closely related to Mauritian endemic *Dysauxes florida*, the Palaearctic *Dysauxes* species, and African species *Pseudonaclia puella*. These taxa constitute a monophyletic lineage referred to as the “*Dysauxes* clade”. These results indicate the extraordinary inference that this lineage gave rise to out-of-Madagascar dispersal, but the exact relationships with the non-Madagascan species, and especially the route of *Dysauxes* dispersal to Palaearctic, require further studies.

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TABLES T1 & T2

Table T1. All samples used in molecular studies in the three arctiles included in the thesis.

Code	Genus	Species	CAD	COI-begin	COI-end	EF1a-begin	EF1a-center	EF1a-end	GAPDH	IDH	MDH	RpS5	Wgl400	N of bases
LN018	*Alytarchia*	*leonina*		KX360797		KX360855							KX361075	2417
LN035	*Amata*	*atricornis*		MK158506		MK158599							MK158857	2417
LN038	*Amata*	*aurantiaca*		MK158507		MK158600							MK158860	2417
AYK-04-5607	*Amata*	*fortunei*		KF491527									JQ786661	1070
LN061	*Amata*	*ganssuensis*		MK158508										670
LN017	*Amata*	*leucerythra*	MK158596	MK158509	MK158509	MK158601						MK158779	MK158847	3882
RZ8	*Amata*	*phegea*	X	HQ006238	HQ006941		HQ006425	HQ006425	HQ006492	X	HQ006656	HQ006749	HQ006846	5860
LN024	*Amata*	sp.		MK158510									MK158851	1876
LN026	*Amata*	sp.		MK158511		MK158602							MK158852	2417
LN027	*Amata*	sp.		MK158512		MK158603							MK158853	2417
LN031	*Amata*	sp.		MK158513		MK158604							MK158855	2382
LN032	*Amata*	sp.		MK158514		MK158605							MK158856	2417
LN034	*Amata*	sp.		MK158515										1476
LN039	*Amata*	sp.		MK158516		MK158606							MK158861	2417
AMSP13GE1	*Amata*	sp.		KX050203									KX050614	1876
LN037	*Amatula*	*kikiae*		MK158517									MK158859	1876
RZ404	*Amerila*	*astreus*	X	JN401288	JN401170	JN401403	JN401514	JN401514	JN401612	JN401715		JN401910		5594
LN015	*Amerila*	*brunnea*		KX300223	KX300223	KX300346	KX300346	KX300346	KX300609	KX300688	KX300779	KX300895	KX301005	5416
LN014	*Amerila*	*vitrea*		KX300224		KX300347							KX301006	2417
LN005	*Anapisa*	*holobrunnea*		MK158518		MK158607							MK158837	1611
LN011	*Anapisa*	*monotica*		MK158519	MK158519	MK158608	MK158608	MK158608	MK158683	MK158717		MK158775	MK158843	5009
MM05380	*Antichloris*	*viridis*		HQ006151		HQ006249							HQ006760	2417
MM05843	*Apisa*	*canescens*		HQ006146									HQ006765	1876
LN030	*Apisa*	*cinereocostata*		MK158520									MK158854	1876
MM03713	*Arctia*	*caja*		GU828693									GU829573	1876
LN003	*Automolis*	*crassa*		MK158521									MK158836	1070
LN060	*Automolis*	*meteus*		MK158522									MK158879	1876
LN043	*Balacra*	*affinis*		MK158523									MK158865	1876
LN041	*Balacra*	*compsa*		MK158524		MK158612							MK158863	2417
LN042	*Balacra*	*flavimacula*		MK158525		MK158613							MK158864	2417

Code	Genus	Species	CAD	COI-begin	COI-end	EF1a-begin	EF1a-center	EF1a-end	GAPDH	IDH	MDH	RpS5	Wgl400	N of bases
LN010	*Balacra*	*furva*		MK158526		MK158614							MK158842	2417
LN045	*Balacra*	*herona*		MK158527		MK158615							MK158867	2417
LN046	*Balacra*	*preussi*		MK158528										1476
LN040	*Balacra*	*pulchra*		MK158529									MK158862	1876
LN044	*Balacra*	*rattrayi*		MK158530									MK158866	1674
LN006	*Balacra*	*rubricincta*		MK158531		MK158618							MK158838	1611
LN008	*Balacra*	*rubrostriata*	MK158593	MK158532	MK158532		MK158619	MK158619	MK158680	MK158715		MK158772	MK158840	5453
RZ397	*Barsine*	sp.		JN401286		JN401401							JN400968	2417
RZ28	*Brunia*	*antica*		HQ006193		HQ006289							HQ006801	2417
LN063	*Caeneressa*	*fouqueti*		MK158533									MK158880	1876
RZ136	*Callimorpha*	*dominula*		HQ006169		HQ006266							HQ006778	2417
MZ038	*Calonotos*	*acutipennis*		KX360805		KX360863							KX361082	2417
LN058	*Ceryx*	sp.		MK158536		MK158621							MK158877	2417
AM-94-0396	*Cisseps*	*fulvicollis*		GU828535		GU828881							GU829442	2417
MM05671	*Coscinia*	*cribraria*		HQ006149		HQ006247							HQ006758	2417
LN001	*Creatonotos*	*omanirana*		KX360812		KX360871							KX361074	1611
RZ30	*Creatonotos*	*transiens*	HQ006991	HQ006198	HQ006902	HQ006294	HQ006387	HQ006387	X	HQ006537	HQ006619	HQ006711	HQ006806	6401
RZ398	*Cyana*	sp.	JN401073	JN401285	JN401167	JN401400	JN401511	JN401511	JN401610	JN401712	JN401816	JN401876	JN400967	6401
LN028	*Dubatolovia*	sp.		MK158537										1476
DL1799	*Dubianaclia*	*amplificata*		MK158539	MK158539	MK158624	MK158624	MK158624	MK158669			MK158755	MK158820	4287
DL1810	*Dubianaclia*	*amplificata*		MK158590	MK158590	MK158664	MK158664	MK158664	MK158674			MK158761	MK158826	4410
DL1862	*Dubianaclia*	cf. *eleonora*		MK158538	MK158538	MK158623	MK158623	MK158623				MK158766	MK158833	3719
LN067	*Dysauxes*	*famula*				MK158626							MK158884	1747
LN068	*Dysauxes*	*famula*		MK158542	MK158542				MK158708				MK158885	2295
MM00154	*Dysauxes*	*famula*	GU828120	GU828619	GU828417	GU828954		GU829244		GU830008	GU830328		GU829514	4914
MAD_180	*Dysauxes*	*florida*		MZ255000	X	X	X	X	X			X	MZ270506	4410
MAD_182	*Dysauxes*	*florida*		MZ255001	X	X	X	X	X			X	MZ270507	4410
MAD_186	*Dysauxes*	*florida*		MZ255002	X	X	X	X	X		X	X	MZ270508	4817
ISEZ-DNA_574	*Dysauxes*	*parvigutta*		MZ254999	X	MZ270189			X	X	X	X	MZ270505	4840
RZ88	*Dysschema*	*leucophaea*		HQ006240		HQ006334							HQ006848	1611
RZ695	*Elysius*	*rabusculum*		KJ723705		KJ723691								2017

Code	Genus	Species	CAD	COI-begin	COI-end	EF1a-begin	EF1a-center	EF1a-end	GAPDH	IDH	MDH	RpS5	Wgl400	N of bases
MZ018	*Epidesma*	*ursula*	KX360779	KX360818	KX360818	KX360876	KX360876	KX360876	KX360917	KX360944	KX360986	KX361025	KX361077	6401
LN023	*Epitoxis*	*myopsychoides*		MK158543		MK158627							MK158850	2417
LN066	*Epitoxis*	*namaqua*											MK158883	1206
LN036	*Eressa*	sp.		MK158545		MK158628							MK158858	2417
T1	*Estigmene*	*tenuistrigata*		KP081793		KP082336							KP082726	1611
LN020	*Euchromia*	*guineensis*		KX300260		KX300380							KX300906	2417
LN004	*Euchromia*	*lethe*		KX300259		KX300379							KX300905	1611
RZ400	*Eugoa*	*bipunctata*		JN401284		JN401399							JN400966	2417
DL1790	*Fletcherinia*	*decaryi*		MK158546	MK158546	MK158629	MK158629	MK158629	MK158668		MK158726	MK158751	MK158817	4817
RZ399	*Garudinia*	*simulana*	JN401071	JN401283	JN401165	JN401398	JN401509	JN401509	JN401609	JN401710	JN401814	JN401905	JN400965	6401
LN049	*Hippurarctia*	*ferrigera*		MK158549									MK158869	1876
NSGJZ020	*Hippurarctia*	*ferrigera*		KF533447									KF533575	1059
GBA010	*Homoeocera*	*staminea*		KX300272		KX300389							KX300904	2417
LN064	*Lempkeella*	cf. *vanoyei*		MK158550									MK158881	1876
RZ694	*Leucanopsis*	*setosa*		KJ723706									KJ723684	1876
RZ692	*Lophocampa*	*propinqua*		KJ723707										1476
DL1800	*Maculonaclia*	*leopardina*		MK158552	MK158552	MK158633	MK158633	MK158633	MK158670			MK158756	MK158821	4287
DL1804	*Maculonaclia*	*leopardina*		MK158551	MK158551	MK158632	MK158632	MK158632	MK158673			MK158759	MK158824	4410
MAD_143	*Maculonaclia*	*tampoketsya*		MW817638										670
MAD_149	*Maculonaclia*	*tampoketsya*		MW817643										670
LN051	*Mecistorhabdia*	*haematoessa*		MK158553									MK158871	1876
LN012	*Meganaclia*	*sippia*	MK158594	MK158554		MK158635	MK158635	MK158635	MK158684	MK158718		MK158776	MK158844	5188
DL_2980	*Melanonaclia*	*luctuosa*		X										670
DL_SC3	*Melanonaclia*	*luctuosa*		X	X								X	1876
DL_SF11	*Melanonaclia*	*luctuosa*		X	X	X	X	X	X	X	X		X	4936
DL_SG29	*Melanonaclia*	*nigra*		X										670
DL_SG30	*Melanonaclia*	*nigra*		X	X	X	X	X	X			X	X	4410
DL_2985	*Mortinaclia*	*perplexa*		X	X			X				X	X	2985
DL1770	*Mortinaclia*	*perplexa*		MK158576	MK158576	MK158652	MK158652	MK158652	MK158666			MK158749	MK158815	4410
MAD_286	*Mortinaclia*	*perplexa*	X	X	X	X						X	X	3882
DL1801	*Melanonaclia*	*toulgoeti*		MK158584	MK158584	MK158657	MK158657	MK158657	MK158671			MK158757	MK158822	4287

Code	Genus	Species	CAD	COI-begin	COI-end	EF1a-begin	EF1a-center	EF1a-end	GAPDH	IDH	MDH	RpS5	Wgl400	N of bases
ISEZ-DNA_519	*Melanonaclia*	*toulgoeti*		X	X	X								2017
ISEZ-DNA_538	*Melanonaclia*	*toulgoeti*		X	X									1476
MAD_009	*Melanonaclia*	*toulgoeti*		X	X									1476
MAD_074	*Melanonaclia*	*toulgoeti*		X										670
MAD_082	*Melanonaclia*	*toulgoeti*		X										670
MAD_084	*Melanonaclia*	*toulgoeti*		X	X	X	X	X	X	X		X	X	5132
MAD_085	*Melanonaclia*	*toulgoeti*		X										670
MAD_127	*Melanonaclia*	*toulgoeti*		X										670
MAD_128	*Melanonaclia*	*toulgoeti*		X										670
MAD_129	*Melanonaclia*	*toulgoeti*		X	X								X	1876
MAD_133	*Melanonaclia*	*toulgoeti*		X										670
MAD_134	*Melanonaclia*	*toulgoeti*		X										670
LN007	*Melisa*	*diptera*		MK158556									MK158839	1070
MZ062	*Metaloba*	*argante*		KX360835		KX360892							KX361083	1611
LN074	*Metarctia*	*cinnamomea*		MK158557		MK158638							MK158889	2417
LN070	*Metarctia*	*nigricornis*		MK158558									MK158886	1876
LN053	*Metarctia*	*sarcosoma*												806
LN072	*Metarctia*	sg. *Thyretarctia*		MK158560									MK158888	1876
LN054	*Metarctia*	sp.		MK158561									MK158873	1876
DL1852	*Micronaclia*	sp1_cf_*imaitsa*		MK158562	MK158562	MK158640							MK158831	2417
LN016	*Nacliodes*	*microsippia*	MK158595	MK158563	MK158563	MK158641	MK158641	MK158641	MK158686		MK158732	MK158778	MK158846	5679
LN029	*Nanna*	sp.		KX300292		KX300409							KX300926	2417
LN009	*Neophemula*	*vitrina*		MK158564		MK158642							MK158841	2417
RZ387	*Nyctemera*	*baulus*		JN401287		JN401402							JN400969	2417
MZ168	*Ochrodota*	*pronapides*		KX300298		KX300415							KX300998	2417
RZ689	*Opharus*	*consimilis*		KJ723708		KJ723694							KJ723685	1572
MZ032	*Paraethria*	*mapiria*		KX360842		KX360900							KX361079	2417
LN013	*Paramelisa*	*dollmani*		MK158565									MK158845	1876
RZ691	*Phaegoptera*	*decrepidoides*		KJ723709									KJ723686	1876
MZ066	*Poliopastea*	*anthracina*		KX300310		KX300427							KX300899	2417
LN071	*Pseudmelisa*	sp.		MK158566		MK158644							MK158887	2210

Code	Genus	Species	CAD	COI-begin	COI-end	EF1a-begin	EF1a-center	EF1a-end	GAPDH	IDH	MDH	RpS5	Wgl400	N of bases
BCRSA2471	*Pseudonaclia*	*puella*											MZ270504	400
MAD_241	*Pseudonaclia*	*puella*	X	MZ255003	X	MZ270190			X			X	MZ270509	3765
MAD_245	*Pseudonaclia*	*puella*		MZ255004									MZ270510	1070
MAD_246	*Pseudonaclia*	*puella*		MZ255005										670
LAA05	*Pseudonaclia*	sp.		MK158567		MK158645							MK158835	2417
LN021	*Pseudonaclia*	sp.		MK158568									MK158849	1876
06-srnp-35191	*Pseudophaloe*	*troetschi*		GU828534		GU828880							GU829441	2417
LN055	*Pseudothyretes*	*carnea*		MK158569		MK158647							MK158874	2417
LN056	*Pseudothyretes*	*obscurus*		MK158570	MK158570	MK158648	MK158648	MK158648	MK158701		MK158741	MK158802	MK158875	4694
LN057	*Pseudothyretes*	*obscurus*		MK158571		MK158649							MK158876	2417
LN048	*Rhabdomarctia*	*rubrilineata*		MK158572									MK158868	1876
LN047	*Rhipidarctia*	*forsteri*		MK158573										1476
LN052	*Rhipidarctia*	sp.		MK158574		MK158651							MK158872	2417
MZ194	*Romualdia*	*elongata*		KX300325		KX300441							KX300992	2417
M5	*Spilosomina*	sp.		KP081794		KX050360							KP082727	1611
DL1834	*Stictonaclia*	sp11_cf_*subflava*		MK158575										670
DL1805	*Tenuinaclia*	sp2_cf_*andapa*		MK158577		MK158653							MK158825	2417
MO76629	*Tervurenia*	*eloumdeni*		MK158578									MK158892	1876
LN065	*Thyretes*	*caffra*		MK158579									MK158882	1876
LN050	*Thyretes*	*negus*		MK158580	MK158580	MK158654	MK158654	MK158654	MK158698		MK158739	MK158798	MK158870	4817
LN080	*Thyrogonia*	*efulensis*		MK158581	MK158581							MK158812	MK158891	2479
MAD_260	*Mauricenaclia*	*angustipennis*		X										670
MAD_287	*Mauricenaclia*	*angustipennis*		X	X	X						X	X	3020
MAD_288	*Mauricenaclia*	*angustipennis*		X	X	X						X	X	3020
MAD_108	*Skippernaclia*	*ankaratra*		X	X	X							X	2417
MAD_110	*Skippernaclia*	*ankaratra*		X	X	X	X	X	X				X	3807
MAD_111	*Skippernaclia*	*ankaratra*		X										670
DL_06-040	*Riconaclia*	*bimacula*		X		X			X	X		X	X	3627
DL_06-291	*Riconaclia*	*bimacula*		X	X	X	X	X	X	X		X	X	5132
ISEZ-DNA_518	*Riconaclia*	*bimacula*		X	X	X			X				X	3108
MAD_073	*Riconaclia*	*bimacula*		X	X	X	X	X	X			X	X	4410

Code	Genus	Species	CAD	COI-begin	COI-end	EF1a-begin	EF1a-center	EF1a-end	GAPDH	IDH	MDH	RpS5	Wgl400	N of bases
MAD_218	*Riconaclia*	*bimacula*		X	X	X	X	X	X	X		X	X	5132
DL1811	*Mauricenaclia*	*bruneata*		MK158555	MK158555	MK158636						MK158762	MK158827	3020
ISEZ-DNA_521	*Kowalskinaclia*	*cowani*		X	X	X						X	X	3020
ISEZ-DNA_522	*Kowalskinaclia*	*cowani*	X	X	X	X	X	X	X	X		X	X	5994
ISEZ-DNA_558	*Kowalskinaclia*	*cowani*		X	X	X	X	X	X			X	X	4410
MAD_025	*Kowalskinaclia*	*cowani*		X	X							X	X	2479
MAD_029	*Kowalskinaclia*	*cowani*		X	X								X	1876
MAD_075	*Kowalskinaclia*	*cowani*		X	X	X							X	2417
MAD_100	*Kowalskinaclia*	*cowani*		X										670
MAD_137	*Kowalskinaclia*	*dilata*		MW817635										670
MAD_141	*Kowalskinaclia*	*dilata*		MW817636										670
MAD_142	*Kowalskinaclia*	*dilata*		MW817637		X						X		1814
MAD_144	*Kowalskinaclia*	*dilata*		MW817639	X	X	X	X	X	X			X	4529
MAD_145	*Kowalskinaclia*	*dilata*		MW817640										670
MAD_146	*Kowalskinaclia*	*dilata*		MW817641										670
MAD_147	*Kowalskinaclia*	*dilata*		MW817642										670
MAD_151	*Kowalskinaclia*	*dilata*		MW817644										670
MAD_152	*Kowalskinaclia*	*dilata*		MW817645										670
MAD_153	*Kowalskinaclia*	*dilata*		MW817646	X		X	X				X	X	3178
MAD_154	*Kowalskinaclia*	*dilata*		MW817647										670
MAD_155	*Kowalskinaclia*	*dilata*		MW817648										670
MAD_156	*Kowalskinaclia*	*dilata*		MW817649										670
MAD_157	*Kowalskinaclia*	*dilata*		MW817650	X									1476
MAD_158	*Kowalskinaclia*	*dilata*		MW817651										670
MAD_159	*Kowalskinaclia*	*dilata*		MW817652										670
MAD_160	*Kowalskinaclia*	*dilata*		MW817653										670
MAD_162	*Kowalskinaclia*	*dilata*		MW817654										670
MAD_164	*Kowalskinaclia*	*dilata*		MW817655										670
MAD_165	*Kowalskinaclia*	*dilata*		MW817656										670
MAD_171	*Kowalskinaclia*	*dilata*		MW817657										670
MAD_191	*Kowalskinaclia*	*dilata*		MW817658										670

Code	Genus	Species	CAD	COI-begin	COI-end	EF1a-begin	EF1a-center	EF1a-end	GAPDH	IDH	MDH	RpS5	Wgl400	N of bases
MAD_193	*Kowalskinaclia*	*dilata*		MW817659										670
MAD_194	*Kowalskinaclia*	*dilata*		MW817660										670
MAD_195	*Kowalskinaclia*	*dilata*		MW817661										670
MAD_198	*Kowalskinaclia*	*dilata*		MW817662										670
MAD_199	*Kowalskinaclia*	*dilata*		MW817663										670
MAD_200	*Kowalskinaclia*	*dilata*		MW817664										670
MAD_202	*Kowalskinaclia*	*dilata*		MW817665										670
ISEZ-DNA_556	*Kowalskinaclia*	*incerta*		X	X	X	X	X	X	X		X	X	5132
MAD_273	*Kowalskinaclia*	*incerta*		X									X	1070
CLV_3	*Skippernaclia*	*lacrimata*	X	X	X							X	X	3341
CLV_7	*Skippernaclia*	*lacrimata*	X	X	X	X						X	X	3882
DL_02-325	*Mauricenaclia*	*minuta*		X	X	X	X	X	X			X		4010
DL1802	*Mauricenaclia*	*minuta*		MK158582	MK158582	MK158655	MK158655	MK158655	MK158672		MK158727	MK158758	MK158823	4817
MAD_020	*Mauricenaclia*	*minuta*		X	X	X	X	X	X			X	X	4410
MAD_282	*Mauricenaclia*	*minuta*		X	X		X	X				X	X	3178
DL_02-26	*Mauricenaclia*	*octopunctata*		X	X							X	X	2479
DL_2966	*Mauricenaclia*	*octopunctata*		X	X	X	X	X	X	X		X	X	5132
MA_16-9	*Mauricenaclia*	*octopunctata*		X	X	X						X	X	3020
MAD_263	*Mauricenaclia*	*octopunctata*		X	X	X	X	X	X	X	X	X	X	5539
MAD_272	*Mauricenaclia*	*octopunctata*		X										670
DL_02-109	*Julienaclia*	*pauliani*	X	X	X	X	X	X	X			X	X	5272
DL_02-92	*Julienaclia*	*pauliani*		X	X				X			X	X	3170
DL1788	*Julienaclia*	*pauliani*		MK158583	MK158583	MK158656	MK158656	MK158656	MK158667			MK158750	MK158816	4287
MA_16-6	*Julienaclia*	*pauliani*	X	X	X	X						X	X	3882
DL1792	*Mauricenaclia*	*peyrierasi*		MK158547	MK158547	MK158630						MK158752	MK158818	3020
MAD_008	*Privatenaclia*	*ratovosoni*		X										670
DL_05-857	*Mauricenaclia*	*rothschildi*		X	X	X	X	X	X		X	X	X	4817
MAD_212	*Mauricenaclia*	*rothschildi*		X	X	X			X	X	X		X	4237
DL_06-320	*Privatenaclia*	*seguyi*		X										670
DL_06-321	*Privatenaclia*	*seguyi*		X										670
DL_06-324	*Privatenaclia*	*seguyi*		X										670

Code	**Genus**	**Species**	**CAD**	**COI-begin**	**COI-end**	**EF1a-begin**	**EF1a-center**	**EF1a-end**	**GAPDH**	**IDH**	**MDH**	**RpS5**	**Wgl400**	**N of bases**
DL_06-327	*Privatenaclia*	*seguyi*		X										670
DL_06-347	*Privatenaclia*	*seguyi*		X										670
DL_06-406	*Privatenaclia*	*seguyi*		X	X	X		X	X	X			X	4336
DL_2968	*Privatenaclia*	*seguyi*		X	X	X	X	X	X			X	X	4410
DL_2973	*Privatenaclia*	*seguyi*		X	X	X	X	X	X	X		X	X	5132
DL_2974	*Privatenaclia*	*seguyi*		X	X	X	X	X	X			X	X	4410
DL1769	*Melanonaclia*	*ranomafana* sp. n.		MK158585	MK158585	MK158658	MK158658	MK158658	MK158665		MK158725	MK158748	MK158814	4694
MAD_018	*Melanonaclia*	*ranomafana* sp. n.		X	X	X	X	X	X	X	X	X	X	5539
MAD_019	*Melanonaclia*	*ranomafana* sp. n.		X	X	X			X			X	X	3711
DL1795	*Thyrosticta*	*sylvicolens*		MK158540		MK158625						MK158754	MK158819	2214
MAD_274	*Privatenaclia*	*triangulifera*		X										670
DL_05-424	*Melanonaclia*	*trimacula*		X	X	X			X			X	X	3711
DL_06-975	*Melanonaclia*	*trimacula*		X	X	X	X	X				X	X	3719
DL_14Z-002	*Melanonaclia*	*trimacula*		X	X	X			X			X	X	3711
DL1794	*Melanonaclia*	*trimacula*				MK158659								541
ISEZ-DNA_539	*Melanonaclia*	*trimacula*		X		X	X	X	X			X		3204
ISEZ-DNA_540	*Melanonaclia*	*trimacula*		X	X	X	X	X	X			X	X	4410
ISEZ-DNA_541	*Melanonaclia*	*trimacula*		X	X	X			X			X	X	3711
ISEZ-DNA_542	*Melanonaclia*	*trimacula*		X	X	X			X				X	3108
ISEZ-DNA_543	*Melanonaclia*	*trimacula*		X	X	X	X	X	X			X	X	4410
ISEZ-DNA_544	*Melanonaclia*	*trimacula*		X	X	X			X			X	X	3711
ISEZ-DNA_545	*Melanonaclia*	*trimacula*		X	X	X			X			X	X	3711
ISEZ-DNA_546	*Melanonaclia*	*trimacula*		X	X	X	X	X	X			X	X	4410
MAD_081	*Melanonaclia*	*trimacula*		X	X	X	X	X				X	X	3719
MAD_126	*Melanonaclia*	*trimacula*		X	X									1476
MAD_130	*Melanonaclia*	*trimacula*		X										670
MAD_211	*Melanonaclia*	*trimacula*		X	X									1476
MAD_169	*Skippernaclia*	*vestigii*		X										670
DL_14R-218	*Kowalskinaclia*	*vieui*		X	X	X						X	X	3020
MAD_005	*Kowalskinaclia*	*vieui*		X	X									1476
MAD_131	*Kowalskinaclia*	*vieui*		X	X	X						X	X	3020

Code	**Genus**	**Species**	**CAD**	**COI-begin**	**COI-end**	**EF1a-begin**	**EF1a-center**	**EF1a-end**	**GAPDH**	**IDH**	**MDH**	**RpS5**	**Wgl400**	**N of bases**
DL1860	*Toulgoetinaclia*	*obliquipuncta*		MK158548	MK158548				MK158676			MK158765	MK158832	3047
LN059	*Trichaeta*	sp.		MK158586		MK158660							MK158878	2417
DL1816	*Tritonaclia*	*melania*		MK158587	MK158587	MK158661	MK158661	MK158661				MK158763	MK158828	3719
DL1863	*Tritonaclia*	*melania*		MK158588	MK158588	MK158662			MK158677		MK158729	MK158767	MK158834	4118
DL1817	*Tritonaclia*	sp13		MK158589	MK158589		MK158663	MK158663	MK158675		MK158728	MK158764	MK158829	4276
NW17810	*Utetheisa*	*lotrix*		KX360851		KX360907							KX361117	2417
DL1833	*Vitrionaclia*	sp1_cf_*veronica*		MK158591									MK158830	1876

Table T2. Molecular markers and the relevant primers used in the three articles included in the thesis.

Molecular marker	Gene region	Primers
Cytochrome c oxidase I (COI)	COI-begin, 670 bp	**HybLCO** 5' TAA TAC GAC TCA CTA TAG GGG GTC AAC AAA TCA TAA AGA TAT TGG 3' **HybHCO** 5' ATT AAC CCT CAC TAA AGG GT AAA CTT CAG GGT GAC CAA AAA ATC A 3'
Cytochrome c oxidase I (COI)	COI-end, 806 bp	**HybJerry** 5' TAA TAC GAC TCA CTA TAG GGC AAC AYT TAT TTT GAT TTT TTG G 3' **HybPat** 5' ATT AAC CCT CAC TAA AGG GA TCC ATT ACA TAT AAT CTG CCA TA 3'
Elongation factor 1 alpha (EF1a)	EF1a-begin, 541 bp	**HybStarsky** 5' TAA TAC GAC TCA CTA TAG GGC ACA TYA ACA TTG TCG TSA TYG G 3' **HybMonicaR** 5' ATT AAC CCT CAC TAA AGG GC ATR TTG TCK CCG TGC CAR CC 3'
Elongation factor 1 alpha (EF1a)	EF1a-center, 193 bp + EF1a-end, 506 bp	**HybAlF** 5' TAA TAC GAC TCA CTA TAG GGG AGG AAA TYA ARA ARG AAG 3' **HybEFrcM4** 5' ATT AAC CCT CAC TAA AGG GA CAG CVA CKG TYT GYC TCA TRT C 3'
Glyceraldehyde-3-phosphate dehydrogenase (GAPDH)	GAPDH, 691 bp	**HybFrigga** 5' TAA TAC GAC TCA CTA TAG GGA ARG CTG GRG CTG AAT ATG t 3' **HybBurre** 5' ATT AAC CCT CAC TAA AGG GG WTT GAA TGT ACT TGA TRA GRT C 3'
Cytosolic malate dehydrogenase (MDH)	MDH, 407 bp	**HybMDHF** 5' TAA TAC GAC TCA CTA TAG GGG AYA TNG CNC CNA TGA TGG GNG T 3' **HybMDHR** 5' ATT AAC CCT CAC TAA AGG GA GNC CYT CNA CDA TYT TCC AYT T 3'
Isocitrate dehydrogenase (IDH)	IDH, 722 bp	**IDHdeg27F** 5' TAA TAC GAC TCA CTA TAG GGG GWG AYG ARA TGA CNA GRA THA THT GG 3' **IDHdegR** 5' ATT AAC CCT CAC TAA AGG GT TYT TRC AIG CCC ANA CRA ANC CNC C 3'
Ribosomal protein S5 (RpS5)	RpS5, 603 bp	**HybrpS5degF** 5' TAA TAC GAC TCA CTA TAG GGA TGG CNG ARG ARA AYT GGA AYG A 3' **HybrpS5degR** 5' ATT AAC CCT CAC TAA AGG GC GGT TRG AYT TRG CAA CAC G 3'
Wingless (Wgl400, without gaps)	Wgl400, 400 bp	**HybLepWG1** 5' TAA TAC GAC TCA CTA TAG GGG ART GYA ART GYC AYG GYA TGT CTG G 3' **HybLepWG2** 5' ATT AAC CCT CAC TAA AGG GA CTI CGC ARC ACC ART GGA ATG TRC A 3'
Carbamoylphosphate synthase domain protein (CAD, first part)	CAD, 862 bp	**CAD743nF** 5' TAA TAC GAC TCA CTA TAG GGG GNG TNA CNA CNG CNT GYT TYG ARC C 3' **CADmidR** 5' ATT AAC CCT CAC TAA AGG GC ATT CWG CKG CWA CTG TAT C 3'
Cytochrome c oxidase I (COI), degraded material, HybLCO/K699 + Ron/Nancy	COI-begin, 670 bp	**HybLCO** 5' TAA TAC GAC TCA CTA TAG GGG GTC AAC AAA TCA TAA AGA TAT TGG 3' **K699** 5' ATT AAC CCT CAC TAA AGG GWG GGG GGT AAA CTG TTC ATC C 3' **Ron** 5' TAA TAC GAC TCA CTA TAG GGG GAG CYC CWG ATA TAG CTT TCC C 3' **Nancy** 5' ATT AAC CCT CAC TAA AGG GCC TGG TAA AAT TAA AAT ATA AAC TTC 3'

ARTICLES

ARTICLE 1

Malagasy Polka Dot Moths (Noctuoidea: Erebidae: Arctiinae: Syntomini) of Ambohitantely—endemism in the most important relict of Central Plateau rainforest in Madagascar

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ABSTRACT

Malagasy Syntomini (Polka Dot Moths) are one of the largest endemic lineages of Lepidoptera on the island, belonging to the Tiger Moth subfamily (Arctiinae). This diverse radiation comprises nearly 100 valid described species that share a single ancestor. Despite a monograph in 1964 by Paul Griveaud, systematics of the group greatly needs modern revision, and their distribution on the island is still poorly known. This contribution concerns the diversity of Syntomini of the Réserve Spéciale d'Ambohitantely, which protects the largest remaining, but already highly fragmented, vestige of Central Plateau rainforest in Madagascar. Here we provide an annotated checklist of the eight species occurring in the Reserve. Two species are recorded from the forest for the first time, while five endemics are until now known only from Ambohitantely. We also describe for the first time the female of *Thyrosticta vestigii* Griveaud, 1964 and of *Maculonaclia tampoketsya* Griveaud, 1969, as well as a yellow morphotype of *Thyrosticta dilata* Griveaud, 1964, and we redescribe and illustrate the genitalia of the remaining species. The significance of such colour pattern variation in aposematic moths and the role of this Reserve as a local centre of diversity of Malagasy Syntomini together with its importance in the protection of the biodiversity of Madagascar are discussed.

Subjects Biodiversity, Entomology, Molecular Biology, Taxonomy, Zoology
Keywords Madagascar, Central Plateau, Syntomini, Endemism, Evolutionary radiation, Intraspecific variation, Taxonomy

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Additional Information and Declarations can be found on page 28

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INTRODUCTION

The biodiversity of Madagascar is characterised by high overall endemism rates of flora and fauna. Despite the fact that an estimated 74% of Malagasy butterfly species live solely there (*Vences et al., 2009*), endemism of higher taxonomic units within the Lepidoptera fauna is very rare (species- and generic-level endemism predominates), and the few higher-rank exceptions encompass small number of species (Whalleyanidae—2 spp.,

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Callidulidae: Griveaudiinae—3 spp., Hesperiidae: Malazinae—3 spp.; Drepanidae: Nidarini—5 spp., Erebidae: Phryganopterygina—20 spp.) (*Lees & Minet, 2003*; *Zhang et al., 2020*; see also *Twort et al., 2020*). However, the most outstanding example of Lepidoptera endemism on the island are members of the tribe Syntomini. Presently they comprise 99 valid described species in 15 genera, entirely endemic to Madagascar (*Viette, 1990*; with exclusion of *Euchromia* spp. in Arctiini, *Zenker et al., 2017*). Fourteen of these genera (98 spp.) belong to a single evolutionary lineage deriving from a megadiverse radiation, which also gave raise to what have been interpreted as out-of-Madagascar dispersal events, reaching Africa (*Pseudonaclia puella* (Boisduval, 1847)), Mauritius and even the Palaearctic (genus *Dysauxes*) (*Przybyłowicz et al., 2019*; Przybyłowicz et al., 2021, unpublished data). However, since the "Amatidae" monograph of *Griveaud (1964)*, little attention has been paid to the systematics and biogeography of the group, with only a few additional species described by P. Griveaud and P. Viette that were listed in *Viette (1990)*, until the phylogenetic paper of *Przybyłowicz et al. (2019)*. The latter paper and our further examinations show that the present systematic arrangement comprises several genera which are artificial assemblages of not closely related species rather than evolutionary monophyletic units. Thus, the diversity of Malagasy Syntomini demands wider investigation and revision to reveal real relations within the clade, and this we are undertaking.

Here we focus on the Syntomini of the Réserve Spéciale d'Ambohitantely, showing that it appears to be a centre of local richness and endemism for this group, despite its small size (currently around 1,300 hectares, in one large and many small fragments). The Reserve is located in the Central Highlands (usually known as the Central Plateau) of Madagascar. This Plateau covers about 40% of the area of the island, but at the same time is one of the most neglected regions in terms of conservation (*Goodman & Raherilalao, 2003*; *Kull, 2012*).

A checklist of Syntomini species of the Reserve is provided for the first time, with the further remarks on each of them. Females of *Thyrosticta vestigii* Griveaud, 1964 and *Maculonaclia tampoketsya* Griveaud, 1969 are described, as well as a yellow morphotype of *Thyrosticta dilata* Griveaud, 1964 which was omitted in its original description. We also redescribe the genitalia of collected species and illustrate them with photographs. These species have already been described and illustrated by *Griveaud (1964*, *1969)*, but in a very general and schematic way. This paper is the first of a series planned to adequately describe the syntomine fauna of the island. In terms of diversity, endemism and importance for biodiversity conservation and evaluation this rich radiation may be of similar importance to the lemurs (*Mittermeier et al., 2010*) but has been neglected in recent surveys.

MATERIALS & METHODS

Study area

Research was conducted in the Réserve Spéciale d'Ambohitantely, 80 km north-northwest as measured linearly (though about 130 km by the road) from the capital city Antananarivo (Fig. 1A). The Reserve, situated mostly between 1,250–1,500 m elevation,

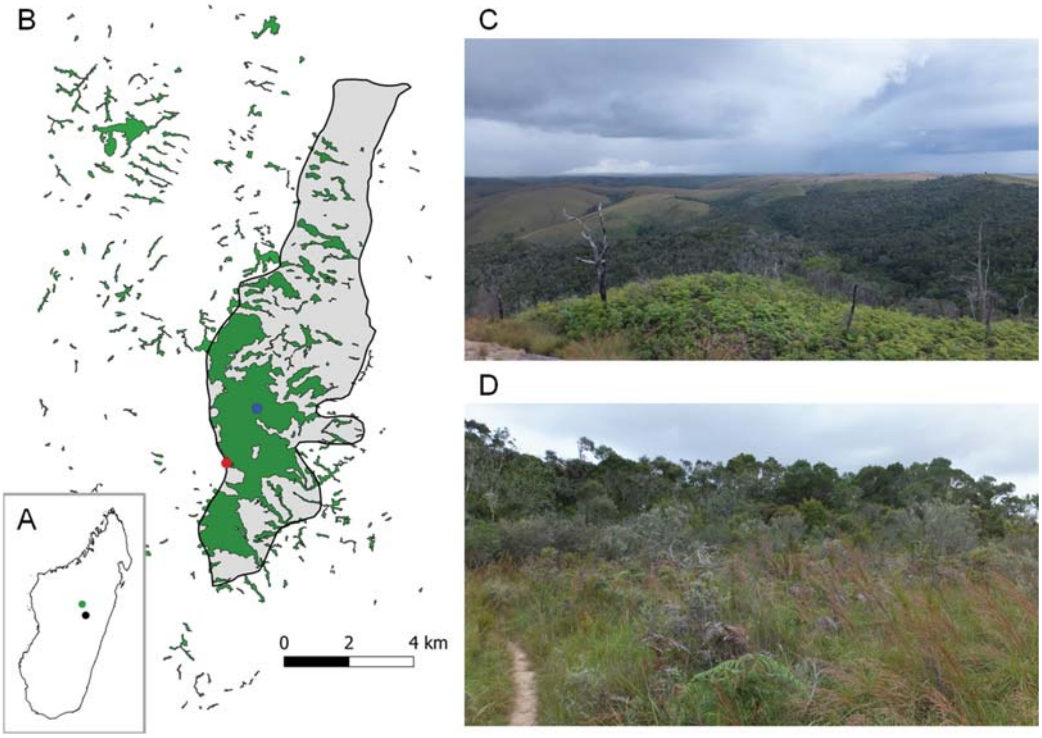

Figure 1 **Réserve Spéciale d'Ambohitantely.** (A) General localisation on Madagascar, black dot indicates the capital city Antananarivo, green dot—Ambohitantely Reserve. (B) Detailed map of the Reserve, remnant patches of forest marked in green, area of the Reserve hatched, red dot—the light trap setup point ca. 100 m from the forest edge, blue dot—the furthest point on the daytime transect, near the waterfall. (C) General view of the southern part of the Reserve, with the forest covering hilltops (in the middle and on the right side), while in surrounding areas it is constrained to valley bottoms (background), foreground covered with ferns being an important element of herbaceous vegetation in the area. (D) Intermediate zone of shrubby vegetation between grassland (foreground) and forest (background) occurring in some fragments of the Reserve. Map Data: © 2021 Maxar Technologies, © 2021 CNES/Airbus. Photo credit: Marcin Wiorek. Full-size DOI: 10.7717/peerj.11688/fig-1

with the highest point at about 1,670 m, is located in the Central Highlands of Madagascar, in the eastern part of the geological/vegetational formation referred as Tampoketsa (high plateau) d'Ankazobe (*Abraham et al., 1996*; *Goodman, Raherilalao & Wohlhauser, 2018*). Its total surface equals to 4,950 ha (5,600 ha in the original creation decree) (*Goodman, Raherilalao & Wohlhauser, 2018*), and comprises the only significant area of forest in the Ankazobe region (*Klein, 2004*) and actually one of the last remnants in the Central Highlands at all (*Ratsirarson et al., 2003*), along with Ankazomivady (*Goodman et al., 1998*), today very degraded.

The most up-to-date map of vegetation of the area, including different types of land coverage, based on the analysis of satellite images from 2017 will be published soon by S.M. Goodman (2021, unpublished data). The map prepared by us (Fig. 1B), based on aerial photographs from Google Earth Pro taken in 2016, shows fragmentation of woody vegetation into numerous patches, including areas covered with dense forest, as well as small groups of trees growing in ravines, which are not necessarily comparable in quality and composition to closed-canopy forest. It corresponds with the commonly cited (e.g., *Langrand & Wilmé, 1997*; *Vallan, 2000*, *2003*) map of *Langrand (1995)* based on the aerial photographs from 1991. Fragments of forest in the Reserve and in the 10 km wide peripheral zone cover together a calculated 1,302.4 ha and are separated by grasslands and marshy patches (*Goodman, Raherilalao & Wohlhauser, 2018*; S.M. Goodman, 2021, unpublished data).

Forest in the Reserve is not constrained to valley bottoms as in surrounding areas but covers also hilltops (Fig. 1C). It can be generally classified as medium elevation moist evergreen forest, a formation characteristic of the floristic Central Domain of Madagascar (*Gautier et al., 2018*), with few variants of vegetation composition identified there, depending on topography and probably corresponding with different stages of its restoration (*Goodman, Raherilalao & Wohlhauser, 2018*). This type of forest is subject in Ambohitantely to a cool, humid tropical climate, with a high rainfall (around 1,460 mm per year), falling mostly in the warm rainy period lasting for about half a year from October–November to March–April, and high air humidity causing frequent morning mists (*Langrand, 2003*; *Goodman, Raherilalao & Wohlhauser, 2018*). High Plateau forests are considered relict, nonetheless grassland is also a naturally occurring vegetation type of the Central Plateau of Madagascar (*Solofondranohatra et al., 2020*), but nowadays is highly degraded. In Ambohitantely secondary grasslands cover 40% of the protected area (*Ratsirarson et al., 2003*; *Goodman, Raherilalao & Wohlhauser, 2018*). The ecotone between forest and grassland is most often sharp (*Vallan, 2000*), but relatively narrow intermediate zones of secondary shrubby vegetation are also present in some parts of the Reserve (Fig. 1D). Human impact on the environment of the Central Plateau is undeniable (*Langrand, 2003*; *Goodman, Raherilalao & Wohlhauser, 2018*), however its extent has been a subject of a great debate, reaching back to the 19th century (*Klein, 2004*; see also discussion).

Sampling methods and morphological studies

Field collecting was undertaken under the permits Nos. 251/06/MINENV.EF/SG/DGEF/DPB/SCBLF/RECH and 292/19/MEDD/SG/DGEF/DGRNE from Direction Generale de l'Environment et des Forets and Direction de la Gestion des Ressources Naturelles Renouvelables et des Ecosystemes. Material was collected during three visits: 6–7 December 2006, 11–12 December 2019 and 13–16 March 2020, in the southern part of the Reserve (S 18.1969°, E 47.2847°), close to the camp located near the largest patch of forest (S 18.1981°, E 47.2816°). Moths were sampled at night with the use of automatic light traps with UV-A (blacklight) or a 6 W white fluorescent light source, or at a three spectral peak LEPI-LED (*Brehm, 2017*) inside a reflective screen column, and during the day, between 10 am and 5 pm, by walking slowly through the forest paths and looking for individuals sitting on the upper side of leaves and catching them with a standard entomological net, which is the most efficient method of collecting Malagasy Syntomini (Ł. Przybyłowicz et al., 2021, unpublished data). Day collecting was conducted within a distance of few hours of slow walk from the camp, the final point marked at a cascade near the centre of the largest patch of the forest (Fig. 1B). The light traps were set at dusk (about 6 pm) and left overnight in proximity of the camp site in different habitats: inside the dense forest, as well as among shrubby vegetation on its edges and on sparse trees in grassland surrounding the forest, ca. 100 m from the forest edge (Fig. 1B). In the latter case the light trap was clearly visible to moths flying out from the forest. Collected moths were killed with ethyl acetate and pinned on standard entomological pins. Individuals were spread after legs were sampled for molecular studies and photographed with a Canon 70D camera before the further examination. The images were adjusted with Adobe Photoshop. Specimens are deposited in the collection of ISEA PAS, Kraków, Poland, accession numbers of the specimens are provided in Table S1.

Genitalia were dissected from one specimen of each sex of collected species, except for males of *Tsarafidynia perpusilla*, where two slides of the same sex were prepared. Abdomens were macerated in 10% KOH in a water bath, then the genitalia were stained with chlorazol black, embedded in Euparal (Agar Scientific, Essex, UK) and mounted on slides. Photographs of the genitalia were taken with the use of a stereoscope microscope Leica S9i system. Images were adjusted with the Adobe Photoshop programme.

The general morphological terminology follows *Miller (1991)*, and for genitalia we refer to *Koda (1987)*. Measurement of forewing length (in mm) was taken with the use of a digital caliper from base to apex of the wing.

We summarise our results with updated data published on distribution and ecology of Syntomini species occurring in the Réserve Spéciale d'Ambohitantely. Official names of protected areas mentioned in the text follow *Goodman, Raherilalao & Wohlhauser (2018)*. The most important collections of Malagasy Syntomini, including type specimens of majority of the species, are deposited in three institutions: MNHN in Paris, NHMUK in London and PBZT in Antananarivo. However, we may have missed some information, as in the latter collection, red paratype labels are pinned under the main labels, thus in available photographs were visible partially, if at all. Moreover, some species have more specimens labelled as paratype than designated in *Griveaud (1964)*, even taking into consideration only London and Paris collections, where the photographed labels are clearly visible. These last collections were inaccessible for examination at the time of writing (due to COVID-19). Thus, to make some morphological and taxonomical remarks and to confirm localisation of type specimens of species that are dealt with in the paper, we relied on photographs of specimens and genital slides taken by ŁP in MNHN in 2015 and in PBZT in 2019. Detailed photographs of type specimens and their labels from NHMUK are available on AfroMoths (*De Prins & De Prins, 2011*) and from MNHN are available in the Museum online database of the Lepidoptera collection (https://science.mnhn.fr/institution/mnhn/collection/el/item/search).

Molecular studies

For molecular investigation, two legs from each specimen were sampled. Isolation of genomic DNA was done with the NucleoSpin Tissue kit (Machery-Nagel, Germany), following the manufacturer's protocol. Sequences of the first part of the mitochondrial gene cytochrome c oxidase subunit I (COI) were obtained with the use of HCO/LCO primers pair hybridised with the universal primer pair T7/T3, described by *Wahlberg & Wheat (2008)*. PCR was done with the use of hot-start ready PCR mix (StartWarm

HS-PCR Mix; A&A Biotechnology, Poland), protocol followed manufacturer's instructions. Obtained sequences were compared with chromatograms, aligned manually with a template sequence in BioEdit software (*Hall, 1999*). Ambiguous sites were coded in accordance to the IUPAC nucleotide code.

Prepared sequence files were managed with VoSeq database (*Peña & Malm, 2012*). Sequences were analysed in a Maximum Likelihood framework in IQ-TREE (*Nguyen et al., 2015*) on the web server (*Trifinopoulos et al., 2016*) with 1,000 replications of Ultrafast Bootstrap (*Minh, Nguyen & von Haeseler, 2013*). The p-distance between barcode sequences was calculated in MEGA X (*Kumar et al., 2018*). The outgroup sequence of *Fletcherinia decaryi* Griveaud, 1964 (GenBank accession code MK158546) was obtained from the study of *Przybyłowicz et al. (2019)*. DNA sequences are deposited in GenBank (MW817635–MW817665) and accession codes are provided in Table S2.

RESULTS

Checklist of Syntomini of Réserve Spéciale d'Ambohitantely and general remarks

During three expeditions to Ambohitantely 58 specimens of Syntomini belonging to seven species in four genera were collected. In total, the fauna of Syntomini of the Reserve comprises eight species, of which two are recorded for the first time (marked with '!'). At the current stage of knowledge on distribution of Malagasy Syntomini, five species appear to occur only in this area (marked with '*'):

**Maculonaclia altitudina* Griveaud, 1964
!*Maculonaclia ankasoka* Griveaud, 1964
**Maculonaclia brevipenis* Griveaud, 1964
**Maculonaclia tampoketsya* Griveaud, 1969
**Thyrosticta dilata* Griveaud, 1964
**Thyrosticta vestigii* Griveaud, 1964
Tritonaclia stephania (Oberthür, 1923)
!*Tsarafidynia perpusilla* (Mabille, 1880)

Three species: *Maculonaclia ankasoka*, *Tritonaclia stephania* and *Tsarafidynia perpusilla* are known from several localities in central, eastern and southern parts of Madagascar (Fig. 2). Most of them are located near or within protected areas, as indicated in the text. In all these areas, as well as in Ambohitantely, the dominant type of vegetation is medium elevation moist evergreen forest (sensu *Gautier et al., 2018*). The above three more widely distributed species occur between 800 and 1,600 m elevation, with Ambohitantely being the highest observed locality in all the cases.

Type specimens of the most of Malagasy Syntomini species, including all described by P. Griveaud, are deposited in three collections, but in *Griveaud (1964)* only details concerning holotypes and allotypes were given. Generally, holotypes as well as part of paratypes are housed in MNHN Paris, remaining paratypes are in NHMUK London and in PBZT Antananarivo.

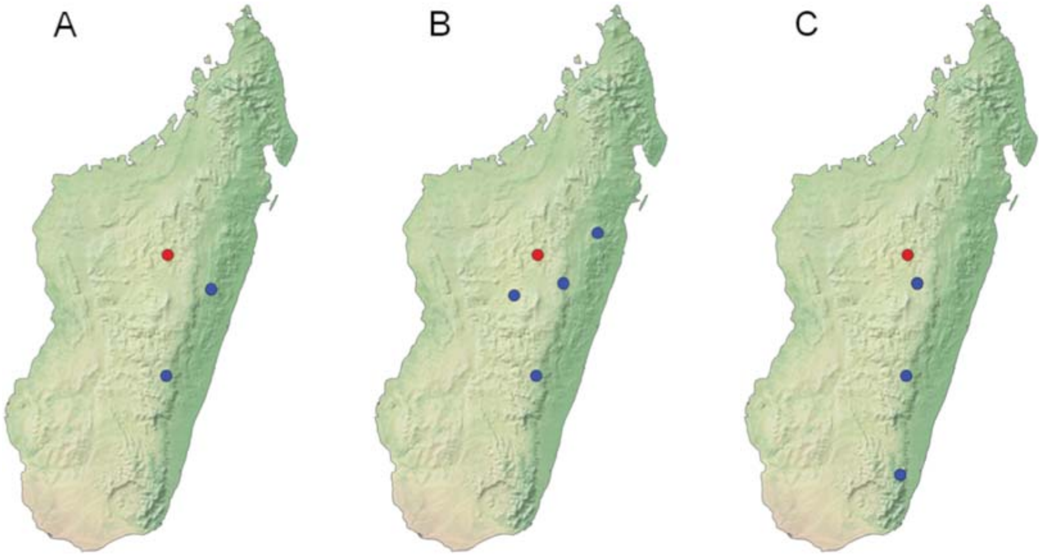

Figure 2 **Records of widely distributed species occurring in the Réserve Spéciale d'Ambohitantely.** (A) *Maculonaclia ankasoka*. (B) *Tritonaclia stephania*. (C) *Tsarafidynia perpusilla*, red dot indicates Ambohitantely, blue dots—remaining localities listed in the text.

Full-size DOI: 10.7717/peerj.11688/fig-2

Specimen data, descriptions and remarks on the species

Maculonaclia altitudina Griveaud, 1964

Distribution

Until now recorded only in the Réserve Spéciale d'Ambohitantely.

Remarks

Maculonaclia altitudina is the only Syntomini species occurring in the Reserve, which was not collected during our study. This species is known only from type series, consisting of the male holotype and seven paratypes, all collected in the Reserve by A. Robinson in May 1961 at an elevation of 1,550 m. The female remains unknown (Griveaud, 1964). The holotype and three paratypes are deposited in MNHN, and one paratype is in NHMUK. A further three specimens are in PBZT, and their collecting data labels are identical to those of specimens in Paris and London, thus they probably are the remaining paratypes. Among specimens labelled as paratype of *Maculonaclia altitudina* in Paris there is one additional specimen, undoubtedly belonging to the species *Maculonaclia brevipenis*, which is similar in general appearance, but distinctly differs in details of forewing pattern. As discussed below, the type series of *Maculonaclia brevipenis* in Paris contains many more specimens labelled as paratypes than stated by Griveaud (1964), and all the specimens of both species were collected in the same place, at the same time and by the same collector.

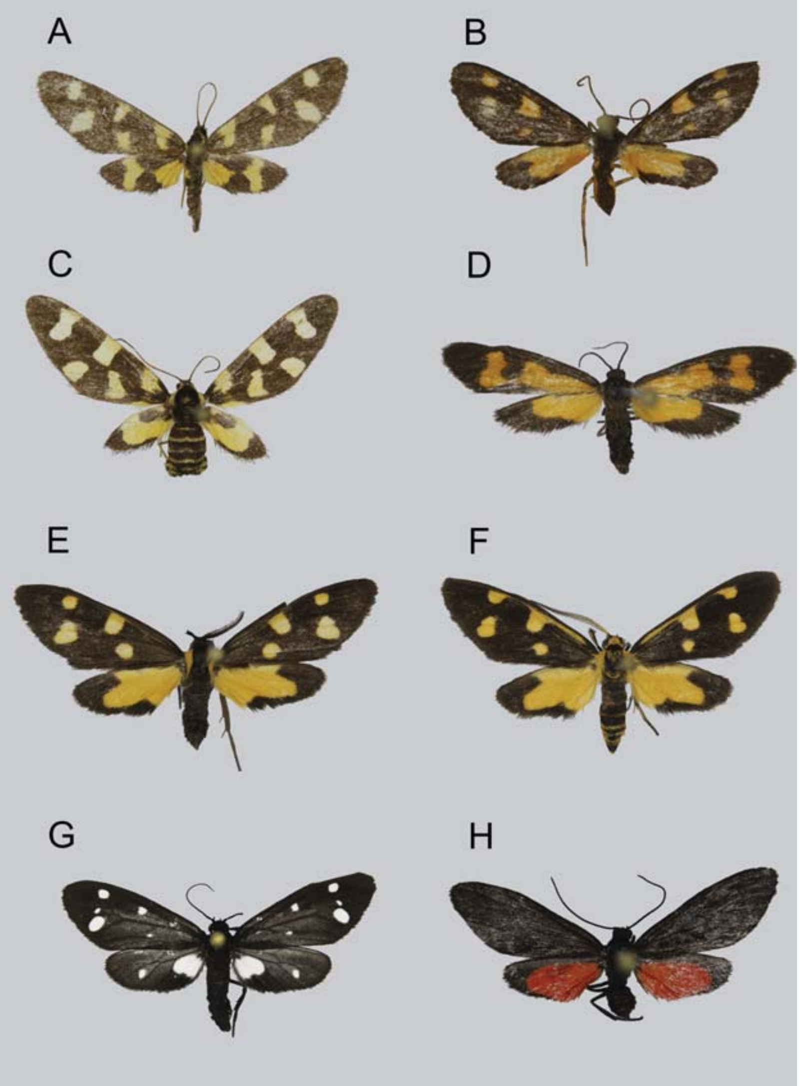

Figure 3 Syntomini of Ambohitantely, resting posture. (A) *Maculonaclia ankasoka*, female. (B) *Maculonaclia brevipenis*, male. (C) *Maculonaclia tampoketsya*, female. (D) *Thyrosticta vestigii*, female. (E) *Thyrosticta dilata*, black morphotype, male. (F) *Thyrosticta dilata*, yellow morphotype, male. (G) *Tritonaclia stephania*, male. (H) *Tsarafidynia perpusilla*, male.
Full-size DOI: 10.7717/peerj.11688/fig-3

All the known specimens of *Maculonaclia altitudina* were collected in May, in the cool dry period.

***Maculonaclia ankasoka* Griveaud, 1964** (Figs. 2A, 3A, 4A)

Material (1 specimen). 1♀, 8.xii.2006, Ankazobe District, Ambohitantely Reserve (1,600 m), lgt. Ravo Ranaivosolo.

Distribution (Fig. 2A)
The species is recorded for the first time from the Ambohitantely Reserve. Until now it has been known from four localities given by *Griveaud (1964)* (from north to south): Périnet

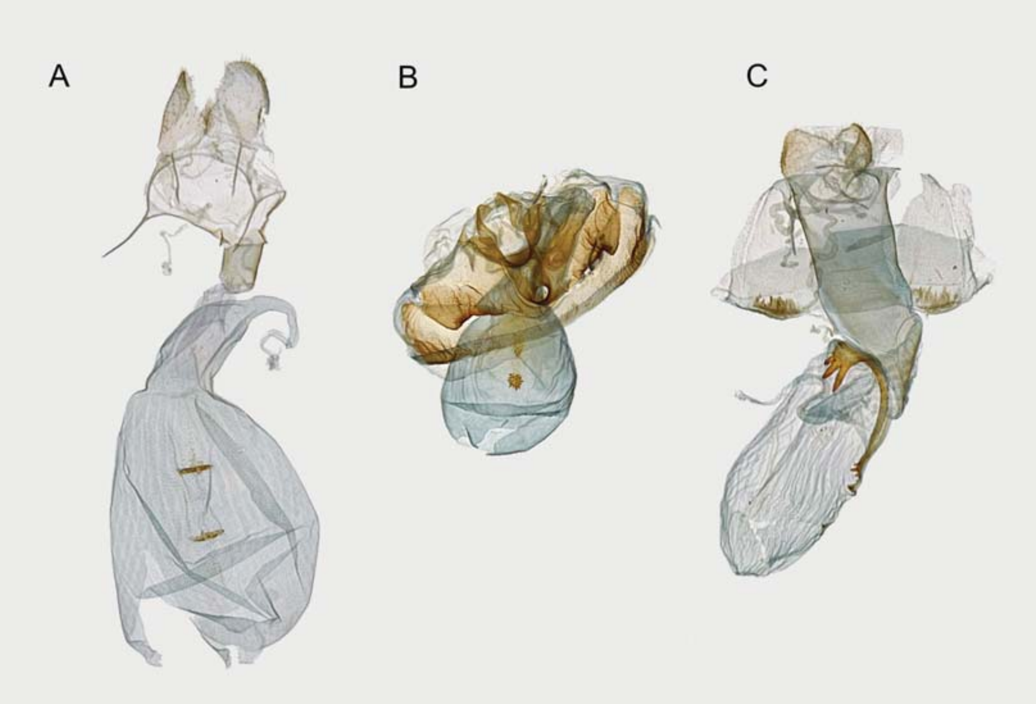

Figure 4 **Female genitalia of syntomini of Ambohitantely.** (A) *Maculonaclia ankasoka*. (B) *Maculonaclia tampoketsya*. (C) *Thyrosticta vestigii*. Full-size DOI: 10.7717/peerj.11688/fig-4

[=Andasibe], Ankasoka and Sandrangato—all three located close to each other in the area of the southern parts of the Réserve de Ressources Naturelles du Corridor Ankeniheny-Zahamena and Parc National d'Analamazoatra (on the map all three marked as one point); Tsarafidy—a few kilometres W from Parc National de Ranomafana and about 32 km NNE of Fianarantsoa. It occurs between 900 and 1,600 m elevation. Ambohitantely is so far the northernmost locality.

Redescription of female genitalia (Fig. 4A)
Papillae anales subtriangular with rounded protrusion at base of dorsal margin, covered with short erect setae, much denser on the protrusion; dorsal and ventral pheromone glands present in form of very narrow, elongate, not anastomosing membranous tubes; apophyses posteriores almost as long as papillae anales, straight and narrow, needle-like; apophyses anteriores of similar shape and size as apophyses posteriores; ostium bursae rounded; antrum well developed, sclerotised, cylindrical, slightly longer than wide; ductus bursae membranous, slightly widening towards corpus bursae, terminal portion with sublateral diverticulum directed distally, from which narrow, membranous ductus seminalis originates; corpus bursae forming a membranous, oval pouch bearing indistinct, irregular zones of minute, diffuse scrobinations; central portion with a pair of signa in form of short, parallel ridges consisted of tiny subtriangular sclerotised plates, leaning on each other; along a longitudinal axis designated by the signa, scrobinations are slightly strongly articulated.

Remarks

Male and female genitalia were described and illustrated by Griveaud (1964: *Figs. 87–90)*. Corpus bursae is depicted to possess scrobinations only in the rhomboidal areas surrounding each of two signa. In the genital slide of the allotype (MNHN) these areas are indeed more prominent than in the slide prepared from our specimen (Fig. 4A), where minute scrobinations are diffuse over whole corpus bursae, and only slightly larger around signa. It could be a matter of intraspecific variation, but also an effect of different staining technique, as slides of Griveaud are prepared with eosin, whereas our ones with chlorazol black. This issue needs further examination in the future on larger series of specimens.

Type series of *Maculonaclia ankasoka* designated by *Griveaud (1964)* is given to comprise 10 specimens: male holotype, and nine paratypes (one male and eight females of which one labelled as allotype). The holotype and the male paratype were collected by P. Griveaud in November 1956 in Ankasoka at an elevation of 1,000 m (however original label of the holotype says "1,130 m"), the allotype and the remaining female paratypes in February 1961 at Périnet, elevation 900 m (*Griveaud, 1964*). The holotype, allotype and three other paratypes are deposited in MNHN. In Paris are also other seven specimens: four collected by P. Griveaud and R. Vieu in 1956 and three collected in 1959, 1963 and 1964 by P. Viette (detailed collecting data illegible in the photographs). A further about 30 specimens determined as *Maculonaclia ankasoka* are in the PBZT collection, collected mostly by P. Griveaud. Three of them are most probably remaining paratypes, as their labels agree with data given by *Griveaud (1964)*.

Maculonaclia brevipenis **Griveaud, 1964** (Figs. 3B, 5A)

Material (7 specimens). 2♂♂, 12.xii.2019, Ankazobe District, Ambohitantely Reserve (1,600 m), S 18.1969°, E 47.2847°, lgt. ŁP; 5♂♂ as above but 14–15.iii.2020 (all collected by netting at day).

Distribution

Until now recorded only in the Réserve Spéciale d'Ambohitantely.

Redescription of male genitalia (Fig. 5A)

Tegumen narrow, moderately sclerotised, almost completely fused with vinculum; uncus elongate, dorso-ventrally flattened, slightly concaved in ventral surface; of the same width up to sharply narrowed, ventrally incurved hook-like tip; dorsally covered with erect setae, longer in basal portion; vinculum narrow, produced with a prominent saccus of triangular shape; juxta well developed, divided into transverse ventral plate and a pair of lateral, rectangular plates; valva approximately the length of uncus with terminal half of triangular shape; costa evenly convex, widely folded towards inner zone; tiny, tooth-like protrusion in the 1/3 of folded costal margin; saccular margin shallowly sinusoidal; margins and some regions of internal and external surface with short erect setae; aedeagus weakly sclerotised, short, tubular, slightly narrowing towards apex; vesica

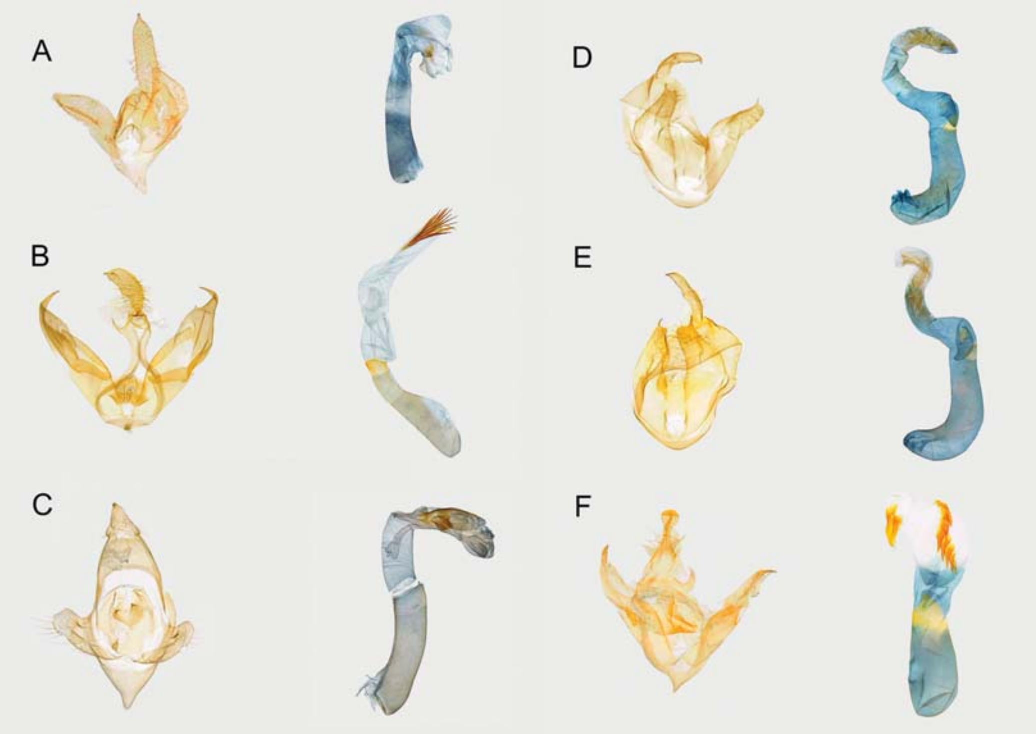

Figure 5 **Male genitalia of Syntomini of Ambohitantely.** (A) *Maculonaclia brevipenis*. (B) *Maculonaclia tampoketsya*. (C) *Tsarafidynia perpusilla*. (D) *Thyrosticta dilata*, yellow morphotype. (E) *Thyrosticta dilata*, black morphotype. (F) *Tritonaclia stephania*. Full-size DOI: 10.7717/peerj.11688/fig-5

membranous, bag-like, with four small sclerotised plates of irregular shape in latero-distal portion.

Remarks

Male genitalia were described and illustrated by Griveaud (1964: *Figs. 95–97)*. Figures show valva with sharply terminated apex, narrow elongate saccus, and vesica was uneverted. In fact the valva is dully terminated and saccus is triangular, but not elongate, vesica as described above.

Until now the species has been known from the type series, according to *Griveaud (1964)* consisting of the male holotype and two paratypes, collected by A. Robinson in May 1961 at an elevation of 1,550 m. The female remains unknown. However, in MNHN, except the holotype, are deposited 10 specimens marked as paratypes, labelled with identical collecting data as given above. Further two paratypes are deposited in NHMUK. Another 13 specimens with identical labels are in PBZT collection, at least one of which is also labelled as a paratype, because a fragment of a red label is visible from under the collecting data label.

All the known specimens were collected in December, March and May, during the warm rainy period and at the beginning of the cool dry period.

Maculonaclia tampoketsya **Griveaud, 1969** (Figs. 3C, 4B, 5B, 6)

Material (2 specimens). 1♂, 11–12.xii.2019, Ankazobe District, Ambohitantely Reserve (1,600 m), S 18.1969°, E 47.2847°, lgt. ŁP; 1♀ as above (all attracted by light).

Distribution

Until now recorded only in the Réserve Spéciale d'Ambohitantely.

Redescription of male genitalia (Fig. 5B)

Tegumen completely fused with vinculum, very narrow, moderately sclerotised, with a pair of prominent, sharp, claw-like protrusions directed ventrally, close to the uncus base; uncus large, elongated, bent ventrally, laterally flattened, with tiny spike-like protrusion at the tip; basal half with numerous long setae; saccus short, terminated with tiny, narrow protrusion; valva elongate, reaching almost to uncus tip, narrowed terminally into sclerotised, hook-like process slightly curved ventrally; costal margin widely sclerotised, concaved submedially, with some undulation in its basal portion; concavity marked with a narrow, membranous, joint-like articulation; sacculus sclerotised, reaching till 2/3 of valva length, with short erect setae, extending beyond; a short spike-like protrusion at dorsoterminal margin beyond sacculus; central inner portion of valva membranous; aedeagus tubular, widened subbasally, slightly bent dorsally in distal portion; vesica in form of membranous tube evenly widened in proximal 2/3 of its length, bearing a dense bunch of elongate, needle-like cornuti in terminal portion.

Remark: The short spike-like protrusion at dorsoterminal margin beyond sacculus visible only on right valva. Left valva with indistinct convexity.

Description of female (Fig. 3C)

Head. Proboscis well developed, brown, apex and base pale brown; frons pale yellow, with longitudinal ochraceous stripe from clypeal portion towards second third; vertex ochraceous with admixture of pale yellow scales, lateral margins yellow, ochraceous stripe between scapi; palpi three-segmented, porrect, yellow, ventrally with elongate scales, dorsally with admixture of ochraceous scales, terminal palpomere dorsally entirely ochraceous; antennae filiform, ochraceous with admixture of creamy scales, except terminal, dark ochraceous quarter.

Thorax. Patagia of piliform scales, submedially ochraceous with tiny yellow spot in central portion, laterally pale yellow; tegulae pale yellow with elongate scales almost piliform in distal portion, terminally with admixture of ochraceous; subventral zone ochraceous; mesothorax ochraceous, medially with longitudinal narrow yellow stripe and yellow spot in disto-median portion; metathorax ochraceous; ventral portion of pleurites ochraceous, with yellow blotches at base of coxa; foreleg: pale yellow, epiphysis absent; midleg: pale yellow, tibia with one pair of terminal spurs of similar length; hindleg: coxa and femur pale yellow; remaining parts of the hindleg unavailable.

Abdomen. Ochraceous, distal margin of each segment with yellow stripe.

Forewing. Length of costa 11 mm ($n = 1$); upperside background ochraceous, with short, yellow, narrow streak along proximal portion of dorsum and additional 5 pale yellow to creamy blotches of subrectangular shape and similar size: 1 at basal 2 at medial and 2 at distal portion of wing; basal one elongate, from costal margin to the half of the wing width, with a prominent narrow projection towards wing base on R vein; first medial one of rectangular shape, form costal margin to hind margin of DC; second medial one of irregular shape, from cubital vein, widening towards termination before inner margin; first distal one elongate, from costal margin to M3, constricted in medial portion along M1; second distal one below CuA1, of irregular shape, separated from outer margin by narrow ochraceous stripe; underside with the same pattern, with addition of zone of scattered pale yellow scales between the basal blotch and 1A + 2A; cilia ochraceous.

Hindwing. Elongate, reaching about half of forewing; basal portion yellow, reaching to the baso-distal angle and to 3/4 of the length of costal margin, with large, 8-shaped elongate ochraceous blotch, originating from the wing base and including most of DC, but not reaching to its outer margin nor the costal margin of the wing; outer area ochraceous; underside pattern the same but lateral portion of brown blotch reaches the costal margin; piliform scales along wing margins, longer on baso-distal margin; frenulum present.

Female genitalia (Fig. 4B)

Papillae anales semicircular, covered with short, dense, erect setae; dorsal pheromone glands present in form of narrow, rather stright, not anastomosing tubes, of about three lengths of apophyses posteriores; apophyses posteriores strongly sclerotised, straight and narrow, needle-like; apophyses anteriores in form of subtriangular, short lobes, half of the length of apophyses posteriores; 7th and 8th segments heavily sclerotised; 7th sternite wide and narrow with shallowly concave distalomedian margin and a pair of shallow depressions at anterolateral corners; 8th sternite with distinct, expanded, subtriangular wrinkled cavities at anterolateral margin; posterior margin in form of prominent, sclerotised ridge provided medially with deep, U-shaped slit connected with ostium bursae by well-defined concavity of parallel margins; ostium bursae rounded, strongly sclerotised; antrum well developed, strongly sclerotised, distinctly bent distally to the left (according to body axis); ductus bursae strongly bent to the right towards the medial axis, membranous, of length of antrum, slightly widened terminally, with plicae in form of longitudinal parallel ridges; ductus seminalis from anterior portion of antrum just below the ostium; corpus bursae membranous, pear-shaped, bearing extensive, irregular zone of minute, diffuse scrobinations; central portion of which with a pair of spiny signa, proximal one elongate, terminal one rounded with longer spines than in proximal one.

Remarks

We collected one specimen of each sex, thus in this case we could confirm that they are conspecific not only by morphological, but also molecular examination (Fig. 6). The genetic distance between barcode sequences (p-distance) is 0% (Table S2).

The male was illustrated as a line drawing by Griveaud (1969: *pl. I, Fig. B*), but in the figure caption was referred as "*Melanonaclia tampoketsya*", which is certainly an unintended error, as in the description this species is explicitly attributed to the genus *Maculonaclia* and to the section of *Maculonaclia ankasoka* established within the genus by *Griveaud (1964)*. The male genitalia were described and illustrated in the same paper (Griveaud, 1969: *Figs. 9–12*), but with an uneverted vesica of the aedeagus, which is described above.

Until now the species has been known only from male holotype collected by P. Griveaud in April 1967, deposited in MNHN (*Griveaud, 1969*). In the male the general body colouration and pattern are similar to the female, with differences listed below: eyes much larger, with tuft of yellow scales at the eye margin, below scapus; frons narrower; vertex uniformly ochraceous, with yellow lateral margins and small yellow spot in central part, over axis between scapi; antennae serrate, shaft dorsally golden-yellowish, each pectine with golden-yellowish lobe directed downwards, cowered with short, dense, erect setae; hindleg tibia possess one pair of spurs of slightly uneven length; all legs have well-developed arolium; retinaculum is present. Male palpi are similar to female, i.e., yellow, dorsally with admixture of ochraceous scales, terminal palpomere dorsally entirely ochraceous, but in original description (*Griveaud, 1969*) are referred as entirely ochraceous, which can be intraspecific variation and needs to be revised in MNHN collection.

All the known specimens were collected in April and December, thus both in cool dry and warm rainy period.

Thyrosticta dilata **Griveaud, 1964** (Figs. 3E, 3F, 5D, 5E and 6)

Black morphotype

Material (23 specimens). 12♂♂, 11–12.xii.2019, Ankazobe District, Ambohitantely Reserve (1,600 m), S 18.1969°, E 47.2847°, lgt. ŁP; 2♂♂ as above but 11.xii.2019; 6♂♂ as above but 13–15.iii.2020 (all above attracted at light); 2♂♂ as above but 14–15.iii.2020; 1♂ as above but 12.xii.2019 (latter 3 collected by netting at day).

Yellow morphotype

Material (22 specimens). 15♂♂, 11–12.xii.2019, Ankazobe District, Ambohitantely Reserve (1,600 m), S 18.1969°, E 47.2847°, lgt. ŁP; 5♂♂ as above but 13–15.iii.2020 (all above attracted at light); 1♂ as above but 12.xii.2019; 1♂ as above but 14–15.iii.2020 (latter 2 collected by netting at day).

Distribution

Until now recorded only in the Réserve Spéciale d'Ambohitantely.

Taxonomic status

This species is represented by two morphotypes, described in detail below. Despite variation within and clear differences between them, our morphological and molecular results confirm that they belong to the same species. There is no difference in male genitalia (Figs. 5D and 5E), also p-distance between barcode sequences of specimens varies from 0–0.2% with no regard to morphotypes (Table S2), and all the specimens represent a single clade on the tree (Fig. 6).

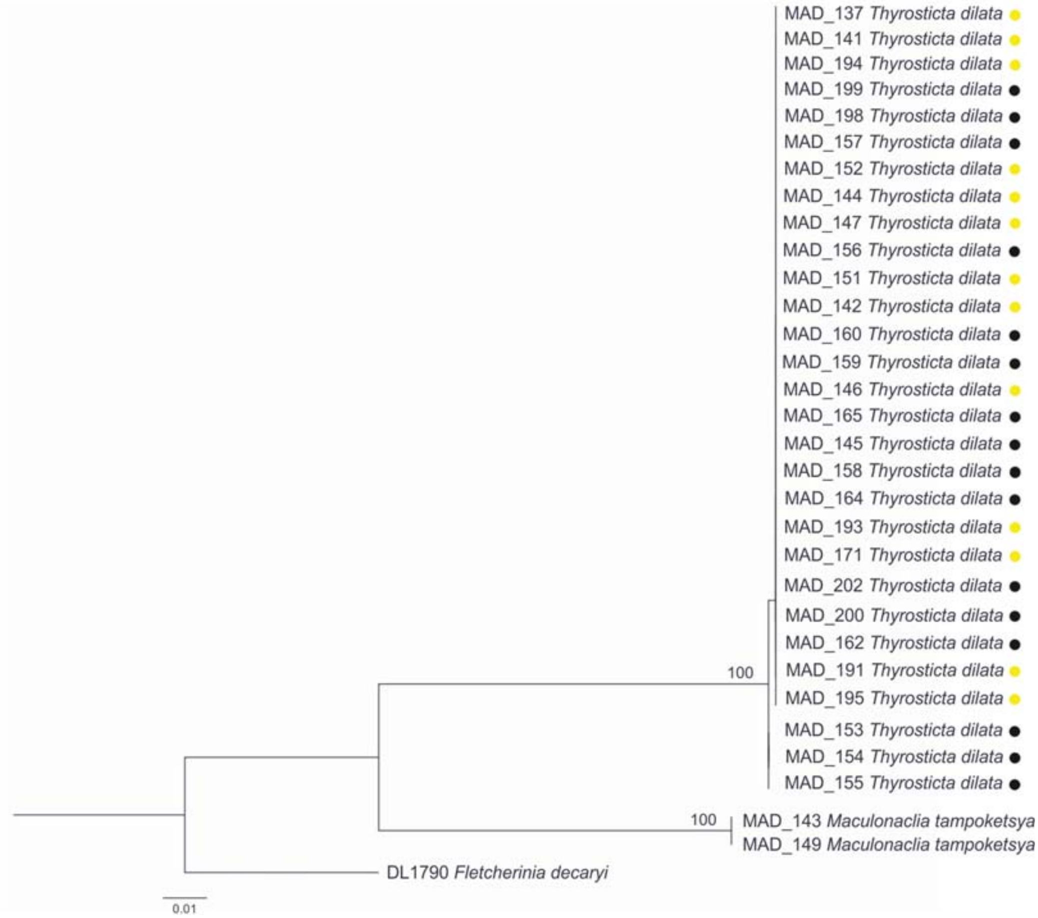

Figure 6 **Phylogenetic tree based on a Maximum Likelihood analysis of the barcode region.** Yellow dots indicate the yellow morphotype of *T. dilata*, black dots—black morphotype. Node labels—ultrafast bootstrap values (see Materials & Methods), scale bar—number of substitutions per site.

Full-size DOI: 10.7717/peerj.11688/fig-6

Description of the yellow form (Fig. 3F)

Head. Proboscis well developed, black, with ochraceous-yellowish apex; frons yellow, few pale ochraceous scales close to eye margin; vertex yellow, with black stripe between scapi and ochraceous longitudinal spot in median part; palpi porrect, terminally curved downward; palpomeres of comparable length, elongated, at least three times longer than wider; first two palpomeres yellow, with ochraceous scales on dorsal part; first with piliform scales on ventral part; third palpomere ochraceous, with admixture of yellow scales; antennae bipectinate; Scapus yellow ventrally, ochraceous dorsally; shaft black ventrally, dorsally yellow at base, distally from base with admixture of ochraceous scales, increasing towards entirely ochraceous apex; pectines black with numerous dense, short, erect setae; on each pecten 3 yellowish-ochraceous setae of uneven length, apical one the longest and most visible.

Thorax. Patagia black with admixture of ochraceous and yellow scales in lateral parts; tegulae yellow, black basally; mesothorax yellow with dark ochraceous central portion;

metathorax with elongated scales, medially yellow, laterally ochraceous; ventral pleurites yellowish-ochraceous with yellow spots at base of mid and hind coxa; foreleg: coxa ochraceous with pale yellow stripe on lateral and distal margins; femur and tibia ochraceous medially, yellow laterally; epiphysis ochraceous, reaching 3/4 the length of tibia; tarsus ochraceous, segments 1–3 partially pale yellow; midleg: coxa pale ochraceous; femur yellow, ochraceous terminally; tibia pale ochraceous medially, pale yellow laterally, one pair of pale yellow terminal spurs of uneven length; tarsus pale yellow with pale ochraceous admixture; hindleg: coxa pale ochraceous; femur pale yellow with pale ochraceous terminal portion; tibia pale yellow with pale ochraceous admixture, two pairs of pale yellow spurs; tarsus pale ochraceous with pale yellow admixture.

Abdomen. Ochraceous, each segment with yellow, differently expressed distal margin, gradually broadened towards the abdomen termination, hardly visible on the first tergite.

Forewing. Upperside background ochraceous, with narrow, yellow streak from wing base to its half between costal margin and Sc, and additional four yellow blotches of different shape: two at medial and two at distal portion of wing; the largest first medial blotch in DC, U-shaped, fusing with the yellow streak; second rounded, between CuA2 and 1A + 2A; third one in apical region, round, with comma-shape projection towards first medial one; fourth one 8-shape, between M2 and CuA1; underside with the same pattern; inner margin with piliform scales; cilia ochraceous; retinaculum present.

Hindwing. Elongate, reaching beyond half of forewing; basal portion including DC, half of the costal margin and basal portion of hind margin-yellow, and in central part forming a round projection into outer ochraceous zone; underside pattern the same, with ochraceous costal margin, broadened at wing base, and tiny protrusion from the margin towards central part of yellow zone; hind and outer margins with elongated scales, piliform at the wing base; frenulum present.

Redescription of male genitalia (Figs. 5D and 5E)
Tegumen moderately sclerotised, widened in dorsal portion, laterally narrowed, almost completely fused with vinculum; uncus narrow, elongate, dorsally with long, erect setae; slightly constricted in distal third, terminated in form of a sclerotised, sharp, dorso-ventrally flattened tip; vinculum very narrow, U-shaped, without produced sacculus; valva moderately elongated, subtriangular, narrowed till dull apex; terminal half including margins with short, erect setae, inner portion with shallow, longitudinal convexity; costal margin of sinusoidal shape, terminally with spike-like inwards curved protrusion, outer margin shallowly concave in distal portion; saccus not developed; aedeagus moderately elongate, of approximately equal width, L-shaped; vesica membranous, elongate, tubular; short subbasal portion distinctly bent parallel to aedeagus base; its left lateral zone with pocket-like diverticulum provided with a indistinct field of minute scrobinations, opposite membranous wall without diverticulum but with more extensive field of distinctly thicker scrobinations; remaining portion of vesica delicately spiral, provided with a belt-like

longitudinal zone of granular sclerotisations covering less than a half of the vesical membrane circumference.

Remarks

The specimens representing the yellow morphotype strongly resemble *Thyrosticta vieui* Griveaud, 1964, especially in the black-yellow striped abdomen and the general pattern of the forewing. The main differences are: (i) shape of the basal blotch of the forewing, in *Thyrosticta dilata* forming a narrow, yellow streak between costal margin and Sc, while in *Thyrosticta vieui* present as a wider, irregular, suboval blotch with fuzzy margins, close to the costal margin; (ii) shape of the projection of yellow blotch of the hindwing, distinctly narrower in *Thyrosticta vieui* than in *Thyrosticta dilata*.

The black morphotype distinctly differs from the yellow one in the characters listed below (Figs. 3E and 3F): head (including palpi and antennae) and thorax (including patagia) are entirely black, tegulae yellow with piliform scales. Legs are fully dark ochraceous, including spurs. Forewing has the same shape and pattern as in yellow form, but elongate streak along costal margin is always absent. Abdomen is entirely black dorsally and ventrally, first tergite possesses elongated black scales.

As already mentioned, no intermediate form of *Thyrosticta dilata* has been detected, however both morphotypes exhibit internal variation in the colouration described below.

In the yellow morphotype ($n = 22$) ochraceous scales on frons, close to eyes margin, are absent in some specimens. The ochraceous stripe on vertex varies from a very narrow band to a globular blotch, reaching or not to the black stripe between antennae. The elongate streak on costal margin of forewing reaches half of the wing and fuses with the second U-shaped blotch or terminates before. In some specimens also a comma-shape projection of apical blotch reaches close to or fuses with the DC blotch, up to the fusion of these three blotches, creating a yellow stripe along costal margin fused with them. When the wing pattern is strongly developed, the U-shaped (the largest) and round (the second) blotches nearly touch each other, but never fuse.

In the black morphotype ($n = 23$) some specimens have a general body colouration of dark ochraceous rather than blackish. In some specimens with strongly developed wing pattern the U-shaped (the largest) and round (second) blotches nearly touch each other, up to their fusion.

The species has until now been known only from the type series designated by *Griveaud (1964)*, stated to consist of the male holotype and four paratypes. The female remains unknown. The holotype was collected by P. Griveaud on 27.xii.1956 at an elevation of 1,600 m. Paratypes are said to have been collected in May 1961 and to have the same provenance and collector as the holotype (*Griveaud, 1964*), but according to their labels, all the five specimens from May 1961 were collected by A. Robinson at an elevation of 1,550 m, not by P. Griveaud at 1,600 m.

The holotype and one paratype are deposited in MNHN, another paratype is in NHMUK. A further three specimens with labels identical as those of the paratypes in Paris and London are in PBZT, thus most probably among them are the remaining two paratypes. In PBZT there are also an additional four specimens, collected in April 1967 by

P. Griveaud (two specimens), in October 1974 by A. Peyrieras (one specimen) and in the 1970s (one specimen, exact year and name of collector illegible in the photograph). All of them were collected in the area of Tampoketsa d'Ankazobe as well, however the specimen from 1974 remains uncertain because of an illegible locality on the label, except "central Madagascar".

For the reason given below, we assume that Griveaud was aware of the intraspecific variation when describing the species, but for some reason omitted it. The original description and colour illustration (Griveaud, 1964: *pl. I, Fig. 60*) refer to the black morphotype. However, the holotype deposited in MNHN represents the yellow morphotype, while the paratype in the same collection belongs to the black one. The genitalia were described and illustrated in Griveaud (1964: *Figs. 224–226)*, but with an uneverted vesica on the aedeagus, which is described above.

As indicated in the Materials section, almost all of the fresh specimens of *Thyrosticta dilata* were collected at light traps with both UV or non-UV white light sources, which allowed us to obtain a series of well-preserved specimens. According to our observations, this is rather exceptional among Malagasy Syntomini, although DCL has observed it for some members of genera *Thyrosticta* and *Tritonaclia* at other sites. As a general rule, syntomines are attracted to light rather rarely and usually just in small numbers, which makes day netting the most efficient collecting method for the vast majority of taxa.

***Thyrosticta vestigii* Griveaud, 1964** (Figs. 3D and 4C)

Material (1 specimen). 1♀, 12.xii.2019, Ankazobe District, Ambohitantely Reserve (1,600 m a.s.l.), S 18.1969°, E 47.2847°, lgt. ŁP (collected by netting at day).

Distribution

Until now recorded only in the Réserve Spéciale d'Ambohitantely.

Description of female (Fig. 3D)

Head. Entirely blackish ochraceous, including palpi and antennae; palpi projected downward; proboscis well developed; antennae filiform, flagellum with numerous short, erect setae.

Thorax. Concolorous with head both dorsally and ventrally, including patagia and filiform tegulae; metascutellum with partially filiform scales; legs entirely blackish ochraceous, with exception of paler epiphysis on foreleg; mid and foreleg tibia with one pair of terminal spurs.

Abdomen. Entirely blackish ochraceous dorsally and ventrally, with admixture of piliform scales.

Forewing. Length of costa 7 mm ($n = 1$); upperside blackish ochraceous, with two partially fused yellow blotches; first one prominent, reaching from the wing base up to half of the wing length terminating at DC outer margin; costal portion along R stem with indistinct, shallow, concavity in its half-length; opposite margin in proximal part along narrow ochraceous streak of inner margin of wing, in distal part directed to a right-angle-shaped terminating blotch; second blotch in postdiscal zone, of dumbbell-shape, fusing narrowly in inner posterior angle with the tip of first blotch; cilia and scales along inner margin elongate concolorous with background; underside pattern the same.

Hindwing. Oval, elongated, reaching beyond the half of forewing; basal part including DC with yellow oval zone, reaching to the baso-distal angle and beyond the half of the costal margin; outer zone brown, with narrow brown margin along costa; underside pattern the same, with addition of short brown protrusion from brown costal margin towards central part of yellow zone; elongated scales on outer and hind margins, with dominance of piliform scales close to wing base; frenulum present.

Female genitalia (Fig. 4C)

Papillae anales subtriangular, covered with erect setae, much denser and longer in ventral portion; dorsal pheromone glands well developed, in form of four very narrow, elongate, twisted, rarely anastomosing membranous tubes; two sublateral, much longer than two submedial; apophyses straight and narrow, needle-like; posteriores as long as papillae anales, anteriores slightly shorter; ostium bursae membranous, with lateral projections of subtriangular shape, covered with minute scrobinations; antrum well developed, wide and at least two times longer than wide, plain, weakly sclerotised; proximal margin of 7th segment laterally with symmetrical pocket-like cavities covered with scales; ductus bursae membranous, constricted in middle portion, inner wall in form of sclerotised plate, outer one membranous with well defined, longitudinal, parallel plicae; corpus bursae in form of membranous, elongate pouch, entirely covered with conspicuous plicae in form of longitudinal, parallel ridges; signum singular, prominent, forming a strongly sclerotised, narrow, elongate longitudinal buckle, located at laterobasal portion of corpus bursae; initial portion of signum widened and folded inwards, palm-shaped, formed of four subtriangular plates of different size; terminal portion straight, reaching half of corpus bursae, with longitudinal row of spine-like protrusions of different length directed inwards corpus bursae, and row of few scrobinations on outer surface; below the signum, in terminal third of corpus bursae three tiny spine-like scrobinations directed inwards; ductus seminalis narrow, from membranous diverticulum in basal portion of corpus bursae.

Remarks

Body colouration and wing pattern of female is generally the same as in male. All the blackish-ochraceous body parts have golden-yellowish reflections.

The male and its genitalia were described and illustrated in Griveaud (1964*: Pl. I, Fig. 56; Figs. 208–210).*

Until now the species has been known only from male holotype and two paratypes collected by A. Robinson in May 1961 at an elevation of 1,550 m (*Griveaud, 1964*). The holotype and one paratype are deposited in MNHN. One specimen has an identical label, thus being most probably the second paratype is in PBZT. In the latter collection there is also one additional worn specimen, labelled as collected in "Tampoketsa d'Ankazobe" in October 1974 by A. Peyrieras. Thus, this specimen was collected somewhere around the Ambohitantely Reserve, and the species remains endemic to the area.

All the specimens known to us were collected in October, December and May, so both during the warm rainy period and at the beginning of the cool dry period.

***Tritonaclia stephania* (Oberthür, 1923)** (Figs. 2B, 3G, 5F)

Material (1 specimen). 1♂, 11–12.xii.2019, Ankazobe District, Ambohitantely Reserve (1,600 m a.s.l.), S 18.1969°, E 47.2847°, lgt. ŁP (attracted by light).

Distribution (Fig. 2B)

This species is known from the few localities given by *Griveaud (1964)* (from north to south): "Réserve Naturelle III"—present Parc National de Zahamena; Réserve Spéciale d'Ambohitantely; La Mandraka—ca. 10 km S of Paysages Harmonieux Protégé du Complexe Anjozorobe-Angavo; "Ampolomita"—east of Belanitra (for details see *Griveaud, 1957*); Tsarafidy/Ankafina—about 32 km NNE of Fianarantsoa; "préfecture de Fianarantsoa" (not shown on the map, see remarks). Occurs between 800 and 1,600 m elevation, Ambohitantely being the highest recorded locality.

Redescription of male genitalia (Fig. 5F)

Tegumen narrow, moderately sclerotised, not fused with vinculum, with a pair of lateral, flattened protrusions, slightly curved dorso-distally and densely covered with short setae; uncus base trapezoidal, recessed into disto-dorsal wall of tegumen, surrounded laterally by short tegumen arms; uncus prominent, bent ventrally, of arrowhead shape; narrowed in medial portion, with dorsal, longitudinal rib in distal portion; subdorsally covered with long, erect setae directed laterally; apex bulbous with round, concave tip; vinculum narrow, tendril-like laterally, produced medially into short, triangular, sharply terminated saccus; valva elongate, of claw-like shape, narrowed in terminal half with sharp tip slightly curved inward, terminally with few erect setae; costa at 1/3 of its length with nodular protrusion, folded towards central, membranous part of valva; sacculus sclerotised, reaching to the half of valvae length, with erect setae on margin then in form of membranous, sclerotised, textured lobe, reaching nearly till the end of valva, on outer margin with thin, erect setae; aedeagus massive, tubular, widened basally, gradually narrowing towards termination; vesica membranous, tubular, widened in basal portion, with longitudinal row of eight sharp, thick, spike-like cornuti bent towards the base of vesica; terminal portion with a pair of adhered to each other, sclerotised plates of subtriangular shape of which the outer one much larger than the inner one.

Remarks

Tritonaclia stephania was originally described and illustrated by Oberthür (1923*: 135, pl. 566, Fig. 4882)* from southern Madagascar (*Sud de Madagascar Reçu de M. Lamberton en Avril 1922*), but he did not mention number nor sex of specimens. Generally, Charles Lamberton block locality labels, and especially this one, are unreliable, even as to the part of the island (Viette, 1962*: 15*) as also seen for some butterflies so labelled which are expected only to occur in the North (D.C. Lees, 2020, personal observations). However, the male specimen deposited now in NHMUK has a label indicating a collecting locality agreeing with that given in the original description and another label with information that the specimen was a model for the illustration in the original description. Griveaud (1964: *80, Figs. 184–187)* described the male and female genitalia and designated the aforementioned male specimen (NHMUK010620988) from London as lectotype, and another specimen (female) from MNHN, which he apparently recognized as a part of the type series, as "neallotype". According to the labels both specimens were obtained from Ch. Lamberton in 1922, but collecting dates are unknown. However, *Griveaud (1964)* probably recognized the locality "Fianarantsoa" where the "neallotype" was collected as a very general area and gave "préfecture de Fianarantsoa", which was a larger unit of the former administrative division of Madagascar. For this reason, the locality is not shown on the map (Fig. 2B), but the southernmost locality Tsarafidy is ca. 30 km NE of the city of Fianarantsoa, thus this exclusion does not change the general range of the species significantly.

There are further 21 specimens deposited in MNHN, collected by P. Griveaud, P. Soga and R. Vieu, and 20 specimens in PBZT, collected mostly by P. Griveaud.

***Tsarafidynia perpusilla* (Mabille, 1880)** (Figs. 2C, 3H, 5C)

Material (1 specimen). 1♂, 14-15.iii.2020, Ankazobe District, Ambohitantely Reserve (1,600 m a.s.l.), S 18.1969°, E 47.2847°, lgt. ŁP (collected by netting at day).

Distribution (Fig. 2C)

The species is recorded for the first time from the Ambohitantely Reserve; it has so far been recorded from three localities (*Griveaud, 1964*) (from north to south): Antananarivo; Tsarafidy forest (erroneously written as "Tsarafify")—a few kilometres W from Parc National de Ranomafana; "sous-préfecture de Midongy du Sud"—currently district Midongy du Sud, in large part overlapping with the Parc National de Befotaka-Midongy du Sud, which is marked on the map. Occurs at an elevation between 950 and 1,600 m.

Redescription of male genitalia (Fig. 5C)

Uncus short, subtriangular, at base with lateral indistinct protrusions dorsally covered with short erect setae directed outwards; apex ventrally provided with bulbous protrusion, terminating with claw-like hook incurved ventrally; valva short, suboval, dully terminated, without extended costal portion; costa and sacculus convex, in terminal portion costa with tiny shallow concavity; outer margin covered with several prominent, erect setae, distinctly longer than those on uncus; vesica membranous with numerous diverticuli and elongate, narrow, tubular ductus ejaculatorius; cornuti in form of multidimensional sclerotised block-like structure in median portion and single elongate sublateral sclerotisation originating close to vesica base and terminating in its distal third.

Contrary to the original description (Griveaud, 1964: *56, Figs. 124–126*) the major differences observed in two examined specimens can be summarized as follows (Fig. 5C): uncus not laterally flattened (*uncus aplati latéralement*), but rather three-dimensional due to ventral bulbous protrusion; valva without elongate costal portion as can be seen in Griveaud's Figs. 124–125, but rather subquadrate; sclerotised cornuti much more complicated and of different shape compared to Fig. 126 where only single cornutus is visible.

Remarks

Tsarafidynia perpusilla with its red and black colouration is one of the most distinctive Malagasy Syntomini, hard to confuse with any other species. However, the original description of genitalia (Griveaud, 1964*: 56, Figs 124–126*) is schematic and these illustrations do little justice to their real appearance. Thus, here we redescribe the male genitalia basing on two specimens to make sure that observed differences are not a result of intraspecific variation.

The species has been described by *Mabille (1880)* as "*Aglaope* ? *perpusilla*", doubtfully placed in the Zygaenidae genus *Aglaope* Latreille, 1809. In the original description given in Latin the hindwing is divided into two colour zones, but both of them are described as "black" with the use of the same word, what does not tell them apart and is most probably a typo (*Alae posticae margine antico usque ad medium alae nigro*; *caetera pars nigra est, fimbriaque nigra. Alae subtus similes. Corpus nigrum; antennae simplices, nigrae*). Currently on the pin of the presumed holotype in NHMUK (NHMUK010354697), of about the right dimensions (about 15.5 mm apex–apex, 16 mm maximum), there is a French-language handwritten label in the writing style of Ch. Oberthür notifying this fact: "Not in accordance with the description. Hindwings are indicated black in the description." (*Pas conforme á la description. Les ailes inférieures sont indiquées noires dans la description*). The labels "Madag" and "Aglaope perpusilla Mab." also attached to this specimen are in a script consistent for P. Mabille. There is no part of the description in French, except that Mabille writes: "♂, 17 mill…Un mâle (coll. H.-G. Smith). Concinna species, sedis incertae". *Jordan (1928)* was the first who mentioned this issue in a publication and proposed that the outer hindwing zone should had been referred as "vitreous" (*pars vitrea*), but he did not see the holotype and guessed that it had gone missing. This may rise from the fact that the type specimens of many species described by P. Mabille have been unrecognized for a long time, as only rarely being directly labelled by him. *Viette & Fletcher (1968)* finally localised what they considered to be the holotype of *A. perpusilla* in NHMUK. *Rothschild (1911)* independently described the species as *Micronaclia bicolor* based on one female (holotype) and two males collected in Antananarivo by Chulliat. This locality, long devoid of native forest, apparently was not confirmed by *Griveaud (1964)*, and is mentioned separately and in quotation mark. Conspecifity of *Aglaope perpusilla* and *Micronaclia bicolor* was, according to *Viette (1965)*, established first in the collection of MNHN by H. de Toulgoët, and then published by *Griveaud (1964)*, who created a separate genus *Tsarafidynia* for it. Therein, the outer zone of the hindwing should have been referred as red or carmine (certainly not black nor vitreous!) in the original description. The type species of *Aglaope*, *Sphinx infausta* Linnaeus, 1767 (Zygaenidae—see also *Viette, 1965*) which has pectinate antennae and is patterned just like the presumed type of *Aglaope perpusilla*, black with the basal part of hindwing red. It is likely for this reason alone that Mabille's description was simply inaccurate, while he wrote the identity label correctly; more likely he meant to write *caetera pars rubra est*, and the second use of black in the same sentence in any case makes no logical sense.

Holotypes of *Tsarafidynia perpusilla* and *Micronaclia bicolor* are deposited in NHMUK London. There are further 15 specimens in MNHN and 35 in PBZT. In these collections are also specimens collected in 1970s, so a few years after the monograph of *Griveaud (1964)* and range of the species needs to be reassessed including all the specimens.

DISCUSSION

Significance of Réserve Spéciale d'Ambohitantely as a local centre of diversity of Malagasy Syntomini and in protection of the biodiversity of Madagascar

Madagascar is one of the world's richest biodiversity hotspots (*Ganzhorn et al., 2001*) with very high levels of endemism (*Goodman & Benstead, 2005*), attributed to long lasting isolation from other continents and "explosive" evolutionary radiations (*Dewar & Richard, 2007*; *Yoder & Nowak, 2006*). An illuminating example of such a radiation within Lepidoptera is the endemic Malagasy lineage of the tribe Syntomini (*Przybyłowicz et al., 2019*). In the Réserve Spéciale d'Ambohitantely eight species in four genera have been recorded, and five of them are known so far only from this place. This means that 5% of total species-level diversity (*Viette, 1990*) of the group is currently recorded just from less than two thousand hectares of forest, making the Reserve a centre of the local diversity of Syntomini.

Our results provide further evidence for importance of this Reserve, comprising one of the last considerable fragments of forest in the entire Central Plateau of Madagascar (*Ratsirarson et al., 2003*), as an important complement for preservation of the remaining biodiversity of Madagascar. The uniqueness of the area is so far underscored by three endemic plants and three endemic frog species (*Goodman, Raherilalao & Wohlhauser, 2018*). Also, in terms of phylogeography the reserve conserves unique genetic diversity in otherwise widespread species of butterflies (*Linares et al., 2009*). At the same time, the biodiversity of this place is still not fully documented, especially regarding arthropods. Here we recorded two Syntomini species new for Ambohitantely. In the last few years, several taxa new to science have been described from the Reserve: four species of subsocial *Anelosimus* spiders (*Agnarsson et al., 2015*), the mite *Atropacarus distinctus* Niedbała & Starý, 2014, and two rove beetles: *Squamiger elegans* Hlaváč & Baňař, 2016 and *Ambohitantella banari* Hlaváč & Nakládal, 2016, with a new genus created for the latter species.

The montane moist evergreen forest present in Ambohitantely, as well as its floristic and faunistic species composition indicate close affinities with the region of eastern Madagascar (*Langrand, 2003*; *Gautier et al., 2018*). Syntomini of the Reserve also match this pattern, as the three more widely distributed species, *Maculonaclia ankasoka*, *Tritonaclia stephania* and *Tsarafidynia perpusilla*, are known from several localities in the eastern and central Madagascar (*Griveaud, 1964*), and Ambohitantely is one of their northern- and westernmost sites (Fig. 2); moreover, all these localities share the same general type of forest (*Gautier et al., 2018*). This is also the case in another arctiine genus, *Cyana* in the Lithosiini (*Karisch, 2013*; *Volynkin, 2020*). As the highest diversity of Syntomini species occurs in the longitudinal zone of tropical forests extending throughout the eastern part of the island (*Lees, Kremen & Andriamampianina, 1999*), it is possible that the entire Syntomini fauna present in the area of Ambohitantely derives from the so called "eastern" forests.

Knowledge on the distribution of Malagasy insects, including Lepidoptera, is still far incomplete, selective and biased towards protected and easily accessible areas (*Iannella, D'Alessandro & Biondi, 2019*). Malaise trap studies have started to show a remarkable level of previously unknown diversity, even in one of the best studied reserves, Parc National d'Analamazoatra [= "Andasibe"], notably among the micromoths (*Lopez-Vaamonde et al., 2019*). However, considering all published records (*Griveaud, 1964*, *1966*, *1969*, *1970*, *1972*, *1974*; *Viette, 1987*), we can infer that that the distribution of Syntomini in the area east from Ambohitantely has been studied far more intensively than other regions of the island. An exception for areas readily accessible from the capital is Paysages Harmonieux Protégé du Complexe Anjozorobe-Angavo ("Anjozorobe"), where the fauna of syntomines is still poorly studied (D.C. Lees, 2004–2018, personal observations). This still forested part of the Angavo Massif is the first major patch of forest encountered eastwards of Ambohitantely (ca. 90 km E as the crow flies). Therefore, in terms of understanding the past forest connectedness of Ambohitantely, more intense efforts should be made to examine this area. For example, *Tritonaclia stephania* was already recorded at a similar elevation along the once unfragmented Angavo Massif, at La Mandraka (*Griveaud, 1964*). It may turn out that ranges of at least part of the Syntomini species known only from Ambohitantely are wider than currently known, and they are not actually endemic to the area. Moreover, it is supposed that forests of Ambohitantely and Anjozorobe-Angavo were connected to each other only a few hundred years ago (*Rakotondravony & Goodman, 1998* in *Goodman & Raherilalao, 2003*), but there is no direct evidence when the separation occurred, and it was most probably before 1900 (see *Linares et al., 2009*), if not long before. Rather surprisingly in this context, results of *Linares et al. (2009)* suggest that Ambohitantely has remained as an isolated patch of forest long enough for genetic drift to fix a unique COI haplotype in three species of *Heteropsis* butterflies occurring in the Reserve. However, the also dense forest restricted riodinid *Saribia tepahi* (Boisduval, 1833) exhibited a similar haplotype to the population in Tsaratanana (*Linares et al., 2009*), 450 km to the north, perhaps suggesting that a forest connection northwards may have existed within the time of human colonisation.

The current landscape of the Central Plateau and its most recent historical forest cover, has been widely debated since the 19th century. Ambohitantely, as one of the last remnants of forest in the Central Plateau, is of particular interest for such speculations. Three main approaches to the vegetational history of the Central Highlands can be distinguished, as summarized in *Yoder et al. (2016)*: the "forest", "grassland" and "mosaic" hypotheses. Recent studies, not only botanical, but also those on distribution of mouse lemur species, support the latter one. This assumes that landscape composed of patches of forest and grassland had existed in the High Plateau long before human arrival, in cycles of isolation and reconnection of forest fragments driven by climate, and with a rapid fragmentation and separation from the eastern rainforests near the last glacial maximum (*Yoder et al., 2016* and papers cited therein; *Joseph & Seymour, 2020*; *Tiley et al., 2020*). In that light, referring to the forest fragments of Ambohitantely as "relict" is not quite correct if it presumes Ambohitantely was part of an extensive and continuous former dense tropical forest (*Klein, 2004*). Despite this, the "lost paradise" line of thinking, connected with the "forest" hypothesis promoted by the French colonizers at the end of 19th century (but see *Grandidier, 1898*) is still present, influencing discussions on the environmental policy on Madagascar (*Pollini, 2010*; *Amelot, 2017*).

However, it is undeniable that current deforestation and fragmentation of the forest is primarily anthropogenic (S.M. Goodman, 2021, unpublished data). The danger to Ambohitantely's main forest block of fires started in the adjacent grasslands has been at least partly mitigated by installed firebreaks (*Goodman, Raherilalao & Wohlhauser, 2018*). However, direct deforestation, the second main threat for Ambohitantely, is still increasing at alarming rates, and concerns also forest within the borders of the Reserve. Between 2010 and 2017 alone, over 400 ha of forest disappeared in the Reserve and adjacent areas, whilst the rate of natural forest regeneration since 1949 up to 2017 was virtually negligible. This has caused not only decrease of forest coverage, but also its further fragmentation (S.M. Goodman, 2021, unpublished data).

Effects of this fragmentation in Ambohitantely have already been studied on herpetofauna (*Vallan, 2000*), birds (*Langrand & Wilmé, 1997*) and insectivorous mammals (*Goodman & Rakotondravony, 2000*), but to our knowledge it has never been assessed in regard to invertebrates (except in the context of phylogeography of butterflies: *Linares et al., 2009*). According to our observations, Malagasy syntomines are rather sedentary species, and do not fly between forest fragments, and thus their relatively abundant fauna can make Ambohitantely an excellent site for the future studies on the mobility of species belonging to this group, as well as potential impact of forest fragmentation on their populations. An especially suitable model could be *Thyrosticta dilata* with its behaviour, rather unusual among Malagasy Syntomini, of being lured to light in large number of individuals. During our study, 40 of total 45 specimens were attracted in this way. Moreover, all of them were trapped within the forest, and no individual was recorded in the shrubby vegetation of the ecotone (Fig. 1D) nor collected by a light trap set in the grassland, ca. 100 m from the forest's edge (Fig. 1B).

As already mentioned, further investigation of the distribution of Syntomini in remnant patches of forest in the area of Central Plateau is crucial to understanding their overall patterns of distribution. Also research on biology of Madagascan Syntomini and their potential food resources may shed some light on their ecological connections with certain types of vegetation. At the same time, with five Syntomini species known so far only from Ambohitantely, it cannot be excluded that some of them will turn out indeed to be endemic for the area, as local endemism is characteristic for many evolutionary lineages within the fauna of Madagascar (*Wilmé, Goodman & Ganzhorn, 2006*), also within arthropods, spectacularly so for examples among the giant pill millipedes (*Wesener, 2009*), dung beetles (*Knopp et al., 2011*) or mayflies (*Benstead et al., 2003*). Up until now several hypotheses have been proposed to explain these unique patterns of distribution, but they were addressed mostly to vertebrates and results show that in many cases a pluralistic approach is required rather than emphasis on a single environmental factor (*Wilmé, Goodman & Ganzhorn, 2006*; *Pearson & Raxworthy, 2009*; *Vences et al., 2009*).

Polymorphism of males of *Thyrosticta dilata*

We described here a yellow morphotype of *Thyrosticta dilata*, omitted by Griveaud (1964) in the original description. This species possesses two discrete forms with continuous variation between individuals within each of them. A similar example from the tribe Arctiini is recently described in the Amazonian species *Watsonidia fulgida* Grados, 2019, where both males and females represent two separate morphotypes within one species, but with continuous variation in male genitalia among specimens of both morphotypes. As for *W. fulgida* (*Grados, 2019*), the intraspecific variation in *Thyrosticta dilata* is not related to any sexual dimorphism (indeed the female remains unknown), nor to geographic, environmental or seasonal dimorphism, because specimens of both types were collected simultaneously in the same place, and moreover the species is known only from the Ambohitantely Reserve. Other, but more phylogenetically distant examples in Lepidoptera are: the Asian clearwing moth *Bembecia rushana* Gorbunov, 1992 with two differently coloured morphotypes and the African nymphalid *Euphaedra eberti* Aurivillius, 1896, with two significantly different wing patterns. In both cases, genetic and morphological analyses confirmed conspecifity of the forms (*Zúbrik et al., 2019*; *Garrevoet, Bartsch & Lingenhöle, 2013*). However, causes of variation in all three abovementioned species remain unknown (*Grados, 2019*; *Zúbrik et al., 2019*; *Garrevoet, Bartsch & Lingenhöle, 2013*).

As common in Arctiinae moths (*Simmons, 2009*), nearly all members of Malagasy Syntomini, including *Thyrosticta dilata*, are aposematically coloured. They usually have black, brown or ochraceous wings as background with white, yellow, orangish-ochraceous and hyaline spots, up to nearly transparent wings, a few species loosely resembling wasps, and often possess black-yellow abdomens (*Griveaud, 1964*). However, it is not clear that the majority are close wasp mimics, and some species exhibit a possibly Müllerian resemblance with procridine zygaenids that fly in the vicinity (D.C. Lees, Masoala 1993, Ranomafana 1995, Ankazomivady 2003, personal observations). According to the theory of aposematism, each individual should strictly replicate a single pattern that predators learn to avoid. However, numerous examples of variation within species or even single populations are observed across virtually all groups of warning coloured animals (see review by *Briolat et al., 2019*). Such variation is not uncommon also in tiger moths, and in some cases having an extreme form causes taxonomic complications due to assignation of conspecific males and females to different species (*Moraes et al., 2016*). This even occurs for Syntomini, e.g., in the genus *Pseudothyretes* (*Przybyłowicz & Tarcz, 2015*). According to our observations, other examples of the intraspecific variability among

Malagasy Syntomini are shown by some members of genera *Stictonaclia* and *Dubianaclia*, and by *Thyrosticta cowani* Griveaud, 1964, but the taxonomic status of these forms still demands revision. Recently, we described continuous variability in the wing pattern in the Mauritian endemic *Dysauxes florida* de Joannis, 1906, a species which is shown to derive from the Malagasy radiation (Ł. Przybyłowicz et al., 2021, unpublished data). Numerous and elaborate explanations of the variation within aposematic species have been proposed, but theoretical models often do not meet with observations (*Briolat et al., 2019*). Variability of colouration in tiger moths can be determined genetically, as for the three major phenotypes of *Euplagia quadripunctaria* (Poda, 1761) (*Liebert & Brakefield, 1990*), but causes of this phenomenon in *Thyrosticta dilata* remain unknown and need further research, especially in the context of similarity of the yellow morphotype to *Thyrosticta vieui Griveaud, 1964*, which may prove illuminating.

CONCLUSIONS

Our results contribute towards an adequate description of diversity of Malagasy Syntomini, indicating that the Réserve Spéciale d'Ambohitantely is a centre of local richness of the group, about 63% of which appear also to be endemic there. It provides further evidence for the importance of the area in protection of the remaining biodiversity of Madagascar. It also highlights the Malagasy Syntomini, whose early stage biology is as yet completely unknown, as an important new study system for the study of adaptive radiation in relation to the diversification of colour pattern.

ABBREVIATIONS

ISEA PAS	Institute of Systematics and Evolution of Animals Polish Academy of Sciences, Kraków, Poland
MNHN	Muséum national d'Histoire naturelle, Paris, France
NHMUK	Natural History Museum, London, United Kingdom
PBZT	Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar
DCL	David C. Lees
ŁP	Łukasz Przybyłowicz

WING VENATION

1A + 2A	anal vein
CuA1–CuA2	cubital veins
DC	discal cell
M1–M3	medial veins
R1–R5	radial veins

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The authors declare that they have no competing interests.

Author Contributions

- Marcin Wiorek conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Kamila Malik analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- David Lees conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Łukasz Przybyłowicz conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

Field collecting was approved by Direction Generale de l'Environment et des Forets and Direction de la Gestion des Ressources Naturelles Renouvelables et des Ecosystemes of the Republic of Madagascar. Field collection was undertaken under permit Nos. 251/06/MINENV.EF/SG/DGEF/DPB/SCBLF/RECH and 292/19/MEDD/SG/DGEF/DGRNE.

DNA Deposition

The following information was supplied regarding the deposition of DNA sequences:

The cytochrome c oxidase subunit I sequences are available at GenBank: MK158546 and MW817635 to MW817665.

Data Availability

The following information was supplied regarding data availability:

The ISEA PAS collection accession numbers of the specimens are available in the Supplemental Table.

Supplemental Information

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ARTICLE 2

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ORIGINAL ARTICLE

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Alone on an island: The reassessment of an enigmatic species of Handmaiden Moth (Lepidoptera, Erebidae) endemic to Mauritius

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Abstract

Maculonaclia florida (de Joannis, 1906) has been one of the most mysterious moths of Mauritius, a small volcanic island located some 900 km east from Madagascar. Here, we reviewed its generic placement, phylogenetic relationships and the potential evolutionary scenarios leading to the current distribution of this unique Mauritian member of Syntomini. The species, known previously only from a few old museum specimens, is redescribed based on newly collected material including both sexes and eggs. The generic affiliation to the Palaearctic *Dysauxes* is confirmed based on morphological and molecular data. A hypothesis is presented on the colonization of Mauritius by the ancestor of *D. florida* from Madagascar through the now submerged stepping stone islands of the Mascarene ridge. Behavioural data and environment preferences of *D. florida* are assessed for the first time. The species prefers shrubby vegetation with a humid understory, and presence of endemic shrub *Ixora parviflora* seems to play a role in selecting the suitable microhabitat. Additionally, based on IUCN criteria, a CR threat category is proposed, highlighting the major risk factors affecting the species. The significant variation in wing venation of *D. florida* is noted and provisionally correlated with environmental stress, which is the consequence of human-caused habitat degradation. Finally, the study provides further evidence for the significant role of Madagascar in the diversification of continental biota, indicating a Malagasy origin of the African syntomine *Pseudonaclia puella*.

KEYWORDS

Arctiinae, *Dysauxes florida*, endemics, *Maculonaclia*, Mascarene Islands, Mauritius, phylogeny, redescription, Syntomini

1 | INTRODUCTION

Mauritius, located about 900 km east from Madagascar, is renowned for its high level of endemicity among the major groups of terrestrial organisms inhabiting the island (see Florens, 2013; Motala et al., 2007), contributing to its extraordinary value as a biodiversity hot spot (Myers et al., 2000). However, as with most island biotopes, it is well documented that almost all groups of organisms have tremendously suffered from human settlement and industry. Human impacts affect many endemic insular species and, in extreme cases, cause their extinction (Leclerc et al., 2020). Unfortunately, Mauritius is far from an exception. It is an illuminating example of one of the most 'ecologically devastated' islands of the world. Characterized by a long list of unique but extinct species, beginning with the iconic dodo and its dramatic loss of over 98% of natural habitats (Florens, 2013; Hammond et al., 2015), the remaining endemic diversity on Mauritius is under extreme threat. Therefore, to save what is left, it is crucial to document the endemic species and to characterize the evolutionary pathways and processes that have led to their present distribution and their current conservation status. Despite a growing interest in Mauritian biodiversity, relatively little attention has been paid to the insects (but see Bradler et al., 2015). Among them, Lepidoptera are characterized by one of the highest numbers of endemic species (99 of 317 recorded Lepidoptera species, including 94 of 280 Heterocera species), preceded only by Coleoptera and Hemiptera (Motala et al., 2007).

Dysauxes florida de Joannis, 1906 (Lepidoptera: Erebidae: Arctiinae: Syntomini) has been one of the most mysterious moths known from Mauritius. This results from the taxonomic negligence of the species and the overall superficial similarity in external morphology, that is size, proportions of body parts, pattern and colouration, to some members of the same tribe belonging to the lineage endemic to Madagascar (Griveaud, 1964; Przybyłowicz et al., 2019). It was described by Joseph de Joannis in 1906, based on two female syntypes, preserved at the Natural History Museum in Paris (de Joannis, 1906). However, for more than a century thereafter, neither morphological nor genetic studies have been undertaken on it. Published information has been restricted almost solely to mentions of the taxon in general catalogues (Hampson, 1914; Seitz, 1930; Zerny, 1912) and checklists of Lepidoptera of the Mascarene Islands (Guillermet, 2018; Vinson, 1938). The only exception is an ecological study of the pollination networks in Mauritian heathland habitats that included data on *D. florida* (Kaiser-Bunbury et al., 2009). Interestingly, the taxon was originally described as a member of the Palaearctic genus *Dysauxes* Hübner, [1819], but later transferred by Guillermet (2018) to the Malagasy endemic genus *Maculonaclia* Griveaud, 1964 with no justification provided. Furthermore, this species is the only representative of the tribe Syntomini known so far from any of the Western Indian Ocean Islands (with the exception of Madagascar).

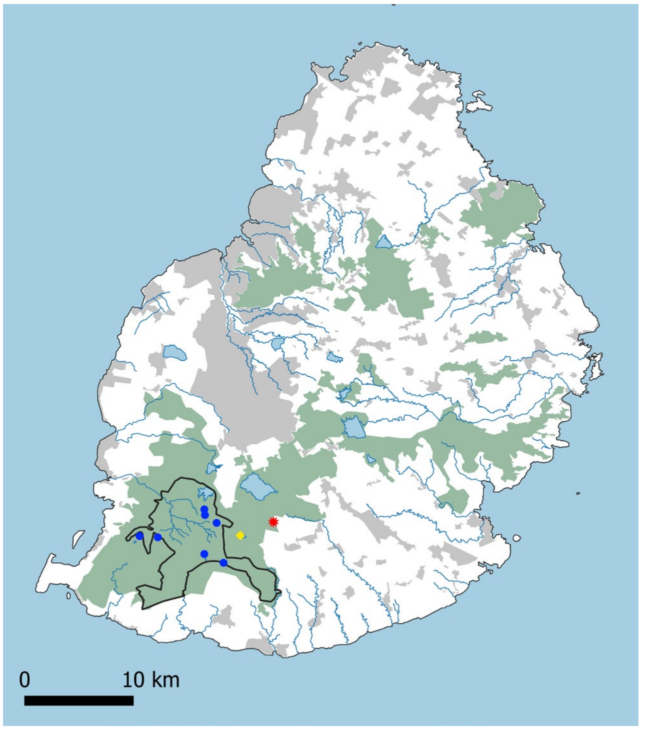


FIGURE 1 Known localities of *Dysauxes florida* on Mauritius. Black line—border of the Black River Gorges National Park; blue dots—modern (21st century) localities extracted from Kaiser-Bunbury et al. (2009), provided by P. Libourel, as well as those discovered in 2019; yellow diamond—Grand Bassin locality; red asterisk—type locality Kanaka Crater

The aim of this study was to sum up all available data on *Dysauxes florida*. It includes fresh material from a recent field expedition to Mauritius, allowing for a re-examination of the species both morphologically and genetically. We provide a detailed morphological redescription based on both sexes, including the first description of the male. We also clarify the phylogenetic position of the taxon within Syntomini and propose a revised generic affiliation, focusing on its relations with the Malagasy clade. Finally, we gather all available details concerning the behaviour, biology, life history, distribution and possible threats of this unique endemic species. We also discuss the possible origin and dispersal routes leading to the presence of *D. florida* on Mauritius in the context of the biogeography of the entire *Dysauxes* genus.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling method

The sampling was undertaken in the Black River Gorges National Park (Figure 1), located in south-west part of

Mauritius, during December 2019. The region of the island, as well as the period of the year, was selected based on data extracted from the original description of the species and labels attached to the type specimens. The potential habitats were identified through consultation with Vincent Florens, an ecologist with experience of Mauritian biota.

Specimens were collected during the day, using a standard entomological net. The collecting was conducted during sunny days, between 10:00 and 17:00, using methodology focused on collecting Syntomini, developed by the first author during his several fieldwork trips to Madagascar. It is described in detail below. The methodology is very simple, albeit provides significantly better results than two typical and most widely implemented techniques used by Lepidoptera collectors, that is (a) butterfly day collecting in usually sunny places, at open meadows or along the forest edges and (b) collecting with lights at night. Malagasy Syntomini, as well as the Mauritian species, are inconspicuous moths, as a rule attracted in very low numbers by lights. They inhabit damp, shady places inside the forests or forest edges with high herbaceous vegetation or shrubby areas.

Thus, the best method to collect specimens of Malagasy (and Mauritian) Syntomini is to undertake long, at least 2–3 hr, walks during the day across relatively humid parts of the forest. One should go slowly, looking for small, inconspicuous specimens sitting on the upper surface of broad leaves, from the ground level up to heights that are accessible. The best option is to choose narrow paths leading through the forest, designed either for tourists or by local villagers. The alternative exploration of patches of forest away from paths results in shaking the surrounding vegetation hence missing the inconspicuous specimens. The specimens sitting on leaves may resemble small holes, droppings of birds, moss or lichen particles or pieces of decaying matter fallen from above. Sometimes, especially around midday, syntomines can be spotted when flying actively. A very important factor is the number of collectors—the higher it is, the better is the success of a single walk. In this respect, help from the local guides or hired villagers equipped with the entomological nets can significantly increase the collecting success. Local people are very skilled at noticing different forms of wildlife in the forest, and thus, a short training session based on showing 2–3 specimens sitting nearby and how to collect them leads to raising overall collecting results markedly. A collecting walk gives the best results if undertaken between 10:00 and 18:00, when the specimens are the most active or exposed sitting on leaves. The collector should be aware of the evasive habits of resting specimens. They stay motionless until the very last moment before catching, showing no indication that collector was perceived. Then, they escape in a straight, fast flight, usually towards the nearest vegetation.

Collected specimens were killed with ethyl acetate, pinned and stored in dry conditions and kept safe from destruction by insects. Beside adults, eggs were obtained from a single female placed within a vial and conserved in 99% alcohol immediately after laying.

2.2 | Morphology

The studied material consists of 21 specimens. They come essentially from the recent expedition to Mauritius (19 specimens – 7♂♂, 10♀♀, 1 sex unknown through a destroyed abdomen, 1 in alcohol) and the type series consisting of two females. However, due to the poor condition of these specimens (descaled fragments of body, broken legs and antennae), the redescription is based on the freshly collected material. In this particular case, there is no doubt that the types and collected specimens represent the same species due to the overall similarity in all morphological characters (size, pattern, colouration) as well as the morphology of female genitalia. Redescription of both sexes is done by examination of specimens collected on December 15, 2019 by a path on Mt Cocotte. To complete the list of all known museum specimens, label information from three additional specimens housed in Muséum national d'Histoire naturelle (Paris, France) is included. Biological and distributional data are also extracted from observations of additional specimens which have not been collected. A list of such records is provided after the list of all examined specimens. Illustrated specimens were photographed using a Canon EOS 70D camera with macro lens EF 50 mm.

To make the veins more visible, preparations from the fore and hindwings were made based on Banasiak (2015) with a few modifications. The wings from a selected specimen were gently torn off with tweezers, then placed individually in Petri dishes with water and a small drop of detergent to reduce surface tension hence to prevent a wing from floating on the water surface. The scales were gently pulled off with a paintbrush. After thorough cleaning and rinsing, the wings were placed in a small container with 1% eosin for 20 hr. On the following day, the wings were rinsed in water and placed on a basic slide in a drop of glycerine and the preparation was closed with a cover slide. The preparations were photographed using a stereoscopic microscope Leica S9i. The images were edited in Adobe Photoshop. Additionally, the variation in the locations of the forewing R veins was examined and illustrated. However, in order to not damage the limited material further, the relevant area of the wing was photographed without descaling and the position and diverging points of veins were marked by the colour lines during postprocessing in Adobe Photoshop.

Dissection and preparation of genitalia slides were performed using standard protocols described in detail by Lafontaine (2004) with chlorazol black as a stain. The genitalia were embedded in Euparal (Essex, UK) and mounted on slides. Each genital slide was labelled. Genitalia photographs were taken with a stereoscope microscope Leica S9i system. The images of genital slides were edited in Adobe Photoshop.

SEM photographs were taken to illustrate eggs of *D. florida* and, for comparison, of the Malagasy syntomine *Maculonaclia tenera* (Mabille, 1878), as well as the retinaculum region of the *D. florida* male forewing. The wing was torn off, descaled with a paintbrush and along with the eggs, coated with a layer of gold. The photographs were taken using the scanning microscope JEOL JSM5410 at the Institute of Zoology and Biomedical Research of Jagiellonian University (retinaculum region) and HITACHI S-4700 at the Institute of Geological Sciences of Jagiellonian University (eggs). The images were edited in Adobe Photoshop.

The terminology used for the general morphology follows Miller (1991). The terminology for the genitalia was taken from Koda (1987) and for eggs from Salkeld (1984).

2.3 | Molecular methods

One or two legs were sampled from specimens of *D. florida* collected in 2019, as well as *Pseudonaclia puella* (Boisduval, 1847) collected in 2013 (Ethiopia, Arba Minch) and 2014 (RSA, Mashovhela Lodge) and *Dysauxes parvigutta* (Christoph, 1889) collected in 2018 (Iran, Golestan National Park). Genomic DNA was extracted using NucleoSpin Tissue kit (Macherey-Nagel), according to the manufacturer's protocol. We amplified three markers using PCR protocols and primers described in Wahlberg and Wheat (2008) and Zenker et al. (2017). The three markers were 657 bp of cytochrome c oxidase subunit I (COI), 400 bp of wingless and 540 bp of elongation factor 1-alpha (EF1α). Successful PCR products were Sanger sequenced either by Macrogen Europe (Amsterdam), or at the Institute of Systematics and Evolution of Animals Polish Academy of Sciences with an ABI Prism 3130xl sequencing machine. Chromatograms of the obtained sequences were checked manually and aligned with a reference sequence using the BioEdit software (Hall, 1999), ambiguous sites were coded according to IUPAC nucleotide code. Sequence files were managed with the VoSeq database (Peña & Malm, 2012). Remaining molecular data included in the study were obtained from Przybyłowicz et al. (2019). All taxa are listed in Table S1, together with collection localities, voucher codes and GenBank accession numbers.

2.4 | Phylogenetic analysis

The new sequences were combined with the COI, EF1-α and wingless sequences from the study by Przybyłowicz et al. (2019) and analysed partitioned by gene in a maximum-likelihood framework. We used the program IQ-TREE (Nguyen et al., 2015) to infer the most likely topology, based on the best fitting model for each partition selected by the model finding feature in IQ-TREE (Kalyaanamoorthy et al., 2017). Robustness of the tree was estimated using 1,000 replicates of Ultrafast Bootstrap (Hoang et al., 2017) and 1,000 replicates of the SH-like approximate likelihood test (Guindon et al., 2010). We also analysed the data using RAxML (Stamatakis, 2014). The data were partitioned by gene, and the GTR+G model was assigned to each gene. Robustness of the tree was estimated using 1,000 replicates of bootstrap.

2.5 | Abbreviations

CuA1-CuA2, cubital veins: 1A+2A, anal vein; DC, discal cell; M1-M3, medial veins; R1-R5, radial veins; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMUK, Natural History Museum, London, United Kingdom.

3 | RESULTS

Redescription of *Dysauxes florida* de Joannis, 1906

A detailed redescription of *Dysauxes florida* with remarks on intraspecific variation is provided in Appendix S1.

3.1 | Immature stages

Immature stages remain unknown, except the egg. The morphology of the egg is based on the examination of eggs obtained from a single female.

Egg (Figure 2b-f): Subspherical, diameter 0.72–0.84 mm; (n = 12). Cellular-type exochorion sculpture covers entire egg surface. Micropylar area rosette-like, composed of 9–10 petaloid cells of different lengths (Figure 2f). Clear transition between cells of micropylar area and remaining egg surface absent, although an indistinct band of similar shape and size cells can be noticed. Central portion of rosette with five micropylar openings. Remaining polygonal cells arranged irregularly on chorion with 4 to 7 thin walls, although single cells with up to 8 or 9 walls are also present in the photograph (Figure 2d). Aeropyles small, slightly expressed at walls junctions, not protruding above the wall edge (Figure 2e).

A detailed description of the putative species-specific characters of the egg chorion, as well as any differential diagnosis regarding members of the Madagascar clade or even any Syntomini in general, is impossible, due to the lack of comparative morphological data. To show the overall similarity of the egg of *D. florida* to those of other members of Syntomini, especially the Madagascar lineage, an SEM

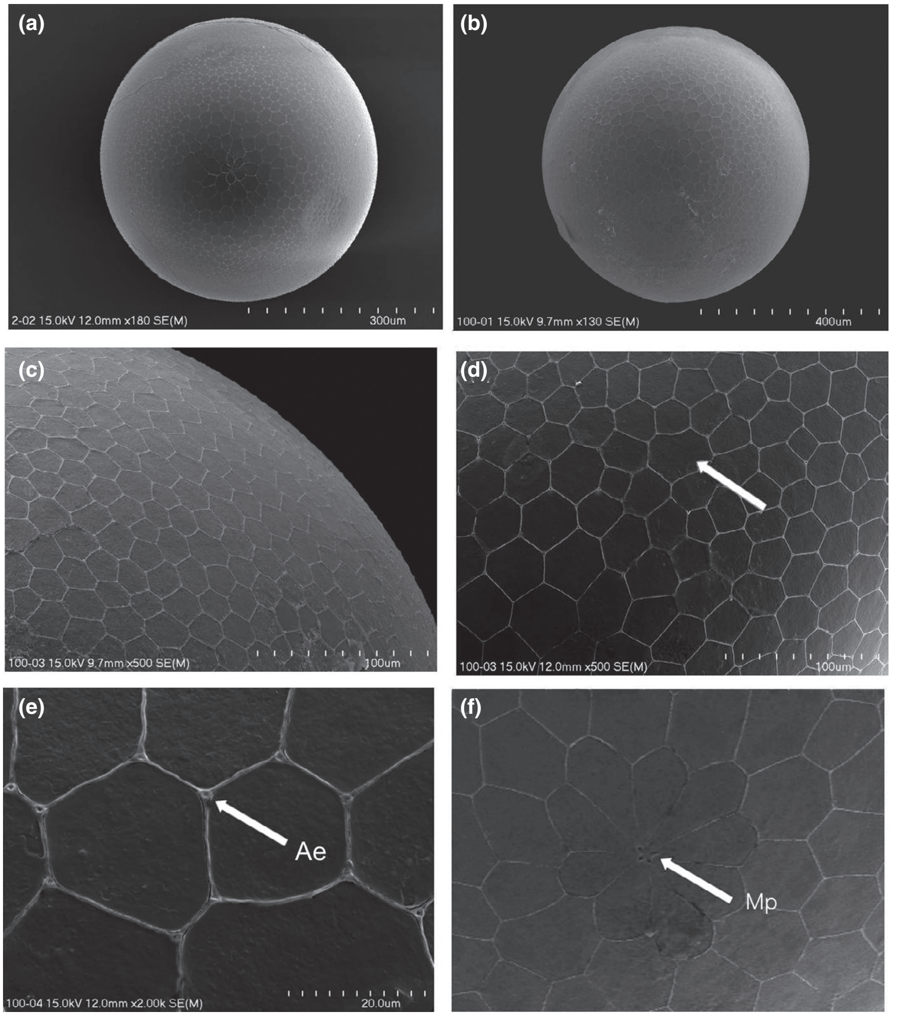


FIGURE 2 Egg morphology visualized by SEM, (a) *Maculonaclia tenera* dorsal view, (b) *Dysauxes florida* dorsal view, (c) lateral view, (d) details of chorion with exceptional, octagonal, unsymmetrical cell (white arrow), (e) details of polygonal cells and aeropyles (Ae) and (f) micropylar area (Mp)

photograph of the egg of *Maculonaclia tenera* (Mabille, 1878) is presented (Figure 2a).

3.2 | Remarks on generic characters

Generic characters and detailed morphological characterization of the genus *Dysauxes* are given by Ignatyev and Zolotuhin (2006). The placement of the Mauritian taxon in the purely Palaearctic genus does not affect its diagnostic coherence. This applies particularly to external characters such as the body colouration and pattern, which in the case of *D. florida* falls exactly within diagnosis of the genus. Male and female reproductive organs show some peculiarities not observed in remaining members of the genus, for example the upward curved uncus, massive cornutus or lack of the deep depression of the ostium, combined with a sclerotized proximal portion of the ductus bursae. However, these morphological structures are highly variable among Lepidoptera, even in closely related species. Therefore, we interpret them as species-specific characters and the detected differences as interspecific variability typical for every non-monotypic genus. Also, molecular results (see below) support placement of *D. florida* back in the genus *Dysauxes*, where it had originally been described.

3.3 | Phylogenetic relationships

Our analyses show strong affinities between Palaearctic *Dysauxes* species and *D. florida*, both in the IQ-TREE analysis (Figure 3) and in the RAxML analysis (Figure S2). With the inclusion of one more *Dysauxes* taxon (*D. parvigutta*), *D. florida* and *P. puella* specimens, the topology of the '*Dysauxes* clade' containing *Dysauxes* and *Dubianaclia* Griveaud, 1964 did not change in comparison with the results published in Przybyłowicz et al. (2019). The taxon *florida* appeared to be the sister species to the two other studied species of the genus *Dysauxes* with high (93.5/91) SH-Like support (Figure 3). The genus *Dysauxes* forms a group sister to some members of the larger genus *Thyrosticta* Hampson, 1898. Such an arrangement strongly suggests that the latter genus is in fact an artificial, polyphyletic assemblage of unrelated taxa (see also Przybyłowicz et al., 2019). Further down the tree, we find *Pseudonaclia puella* + Genus indet spS1 (albeit this node has

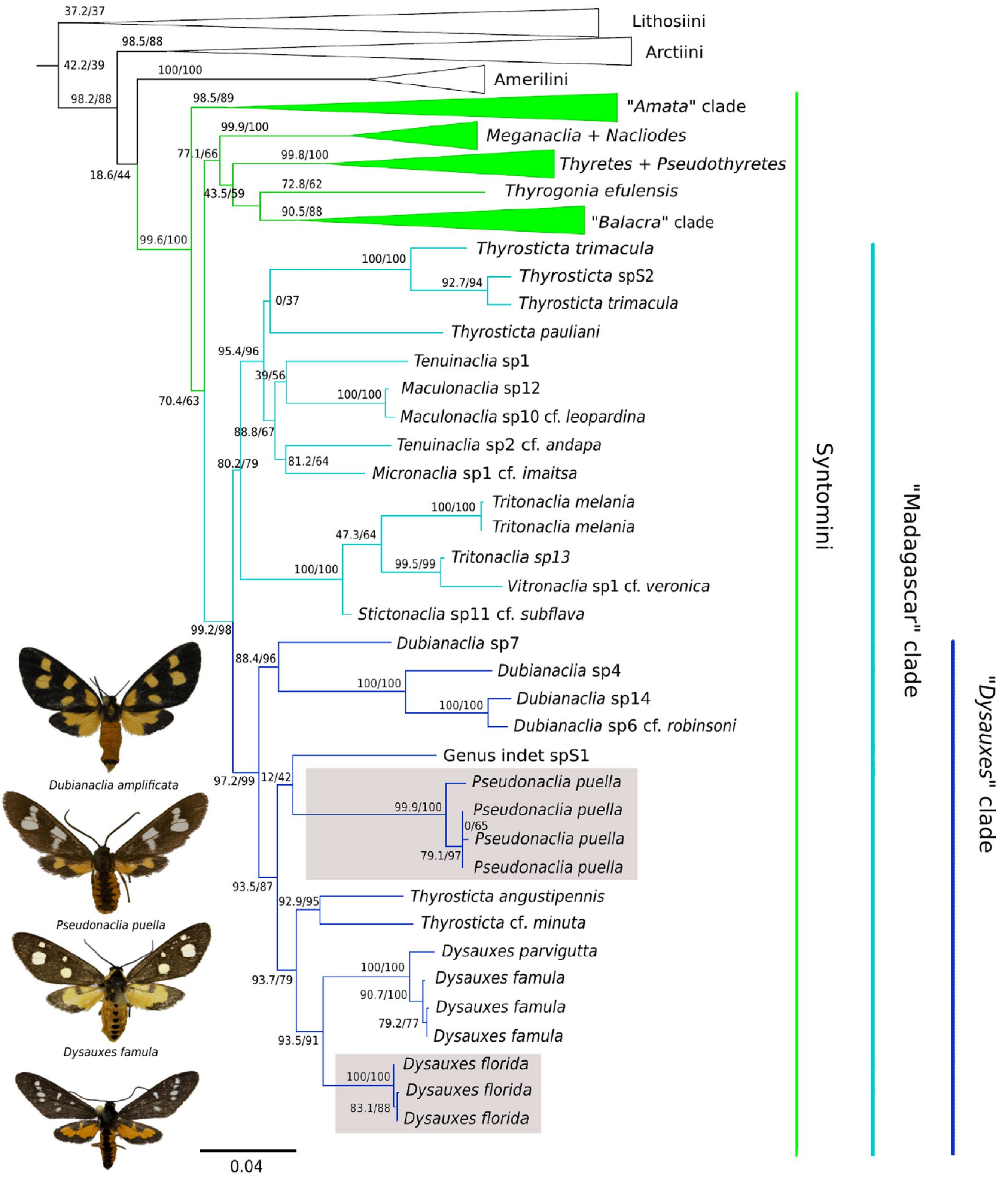


FIGURE 3 Phylogenetic relationships of *Dysauxes florida* and *Pseudonaclia puella* based on a maximum-likelihood analysis of three gene regions. Clades that are not relevant to this study are shown as collapsed (see Figure S1 for full tree). Support values at nodes are SH-like/Ultrafast Bootstrap (see text for details)

the weakest (12/42) support within the whole clade) as the sister group to the (*Dysauxes* + *Thyrosticta*) lineage. We were unable to identify specimen Genus indet spS1 properly to the genus or species level due to the lack of material. The specimen is stored at NHMUK and currently inaccessible for study. However, the image of the unspread specimen made available to us by David Lees provides some information on the general appearance and forewing pattern, matching the general pattern typical for all the taxa within the *Dysauxes* clade. Moreover, the previous molecular study also placed this specimen within that clade (Przybyłowicz et al., 2019). Finally, the sister genus to all the above-mentioned taxa is *Dubianaclia* represented here by four specimens from four different species.

3.4 | Habitat, environmental requirements, behaviour, biology and life history

As already mentioned, published information on *D. florida* is limited only to general morphological description of the female (Hampson, 1914; de Joannis, 1906), and thus, the biology and ecology of this species, as for many other afrotropical Syntomini (Przybyłowicz & Ochse, 2017; Przybyłowicz & Tarcz, 2015), remain unknown. Also, the short period and the methodological design of the fieldwork conducted in this study do not allow for a full description of the annual cycle of development and the detailed habitat requirements of the species. However, some facts can be provided based on the new observations and the data extracted from published sources.

Copulating pairs (Figure 4f-h; four observations on the 15th and 18th of December, at 15:00 and 16:00, on the path towards Mt Cocotte) were noticed among the shrubs and the surrounding thick herbaceous vegetation, close to the ground surface and up to 2 m. According to these observations, mating certainly takes place in the early afternoon hours. However, these are extemporaneous observations, and the extent of the period remains unknown. In the most cases, pairs were sitting motionless and well exposed on the upper surface of leaves of the alien, invasive Cattley guava (*Psidium cattleyanum*). Also, single individuals were often observed sitting motionless on a flat, undamaged surface of a leaf, thus contrasting with the background and being easily recognizable from a distance. They remained in this position until approached to within a metre, after which they escaped rapidly with a fast and jerky flight into nearby vegetation. They almost never flew towards open space.

FIGURE 4 Habitat of *Dysauxes florida* on Mauritius, (a) Black River Gorges National Park, S20°23′58″ E57°27′28″, 655 m, trail crossing, (b) Black River Gorges NP, S20°23′40″ E57°27′26″, 635 m, near trail, (c-d) microhabitat at path on Mt Cocotte, S 20°26′30″ E57°28′27″, 705–720 m, yellow arrow indicates resting moth, (e) specimen feeding on the nectar of *Ixora parviflora*, with extended proboscis penetrating deep into a tubular corolla of a flower, (f-h) a couple in typical position (the male and the female oriented in opposite directions with unevenly overlapping wings) among flowers of *I. parviflora*, on the upper surface of a guava leaf and among low grass

Some data regarding relations of this moth with certain plant species can be extracted from the research on pollination webs in Black River Gorges National Park on Mauritius done by Kaiser-Bunbury et al. (2009 and pers. comm.). *Dysauxes florida* was recorded at two sites located about 0.5 km from each other around Pétrin, where some of the last remnants of *Erica*/*Phylica*-heath plant community are found on the island. Flowers of 18 species belonging to 10 families were recorded to be visited by *D. florida*. All of them were native, and 12 were endemic to Mauritius. These species are (scientific names cited from the paper except *Myonima violacea* which is a younger synonym of *Ixora parviflora*): *Faujasiopsis flexuosa* ssp. *erecta*, *Helichrysum proteoides*, *Psiadia terebinthina* (Asteraceae), *Grangeria borbonica* (Chrysobalanaceae), *Dracaena reflexa* var. *angustifolia* (Dracaenaceae), *Erythroxylum macrocarpum* (Erythroxylaceae), *Antidesma madagascariense*, *Phyllanthus phillyreifolius* var. *telfairianus*, *Croton fothergillifolius*, *C. grangerioides* (Euphorbiaceae), *Aphloia theiformis* (Flacourtiaceae), *Bertiera zaluzania*, *Ixora parviflora*, *Psathura terniflora* (Rubiaceae), *Toddalia asiatica* (Rutaceae), *Molinaea alternifolia* (Sapindaceae), *Sideroxylon cinereum* and *S. puberulum* (Sapotaceae). *Dysauxes florida* was much more common in the control, unrestored site, than in the restored one (163 vs. 5 observed flower visits), where all non-native plant species had been removed. This can be attributed mainly to the presence of *I. parviflora*, and to a lesser extent *P. terebinthina*, and *F. flexuosa* in the unrestored site, as their flowers were the most visited. Especially, *I. parviflora* seems to be important, as no visits to the flowers of *P. terebinthina* and *F. flexuosa* were recorded in the restored area (C. Kaiser-Bunbury, pers. comm.). Moreover, further evidence for the importance of *I. parviflora* is that a single individual was observed by the first author nectaring on flowers of this plant during the day (Figure 4e). However, it must be emphasized that the observations of Kaiser-Bunbury et al. (2009) do not give definite evidence for *D. florida* feeding on the nectar of certain flower species, as the study was focused on pollinators and included all visitors touching the sexual parts of flowers, not necessarily drinking nectar. On the other hand, particularly the frequency of visits in the restored versus unrestored site strongly imply some ecological connection between this moth and the three plant species mentioned, as the small distance between study areas most likely excludes the possible impact of other factors.

4 | DISCUSSION

4.1 | Taxonomic comments

The originally proposed generic combination *Dysauxes florida* was changed for the first time by Guillermet (2018), but without formal explanation and certainly without objective reasons for the choice of *Maculonaclia* as the best generic placement for the species. Most likely it resulted from the overall similarity of *D. florida* with some members of *Maculonaclia* in wing pattern and colouration of forewing, especially *M. delicata* Griveaud, 1964 and *M. truncata* Griveaud, 1964. The same combination is used on the AfroMoths website (De Prins & De Prins, 2011-2019).

The condition of R veins of forewing with the absence of R4 (Figure 5) encountered in *D. florida* is typical for the genus *Dysauxes* and all Malagasy Syntomini, except for the genera *Vitronaclia* Griveaud, 1964 (two species) and *Fletcherinia* Griveaud, 1964 (monotypic), in which all five veins are present (Griveaud, 1964). The same condition (five veins) is characteristic for the syntomine genus *Amata* Fabricius, 1808 (Holloway, 1988).

4.2 | Generic affiliation

To assess the correct generic placement for *D. florida,* we compared it morphologically and molecularly with three different genera, which superficially, based on the external morphology, appeared to be the most closely related lineages: Palaearctic *Dysauxes*, Malagasy *Maculonaclia* and Ethiopian *Pseudonaclia puella* (Figure 6). As our previous molecular results suggested that the genus *Pseudonaclia* is not monophyletic and needs revision (Przybyłowicz et al., 2019), we base our morphological comparison on *P. puella*, the type species of its genus. Detailed comparison of these taxa led to the conclusion that *florida* is most similar morphologically to *Dysauxes*, which is corroborated by our phylogenetic hypothesis, where they form a monophyletic lineage (Figure 3). We did notice a single, albeit very significant morphological character, differentiating *florida* from all potentially related taxa, namely the lack of the male retinaculum (Figure 7). This character is present in *Pseudonaclia puella*, *Dysauxes* and all known Malagasy Syntomini (except *F. decaryi*, see below). It is a well sclerotized, involuted structure of the forewing underside, originating close to the wing base near the subcostal vein, interlocking with the frenulum of hindwing. The reason why *D. florida* lacks this character remains unknown, although it is certainly a result of secondary loss rather than a plesiomorphic condition. The evolution of wing-coupling mechanisms in certain groups of insects is thought to have improved their flight abilities (Wootton, 2002), and the retinaculum/frenulum coupling mechanism is one of the apomorphies of Heteroneura, comprising 99% of all Lepidoptera (Nielsen, 1982). Thus, this mechanism seems to be an important component of the evolutionary history of Lepidoptera.

In the case of *D. florida*, the loss of the retinaculum may be related to reduced flight capabilities, which is characteristic for some insular insect species. One of the most commonly

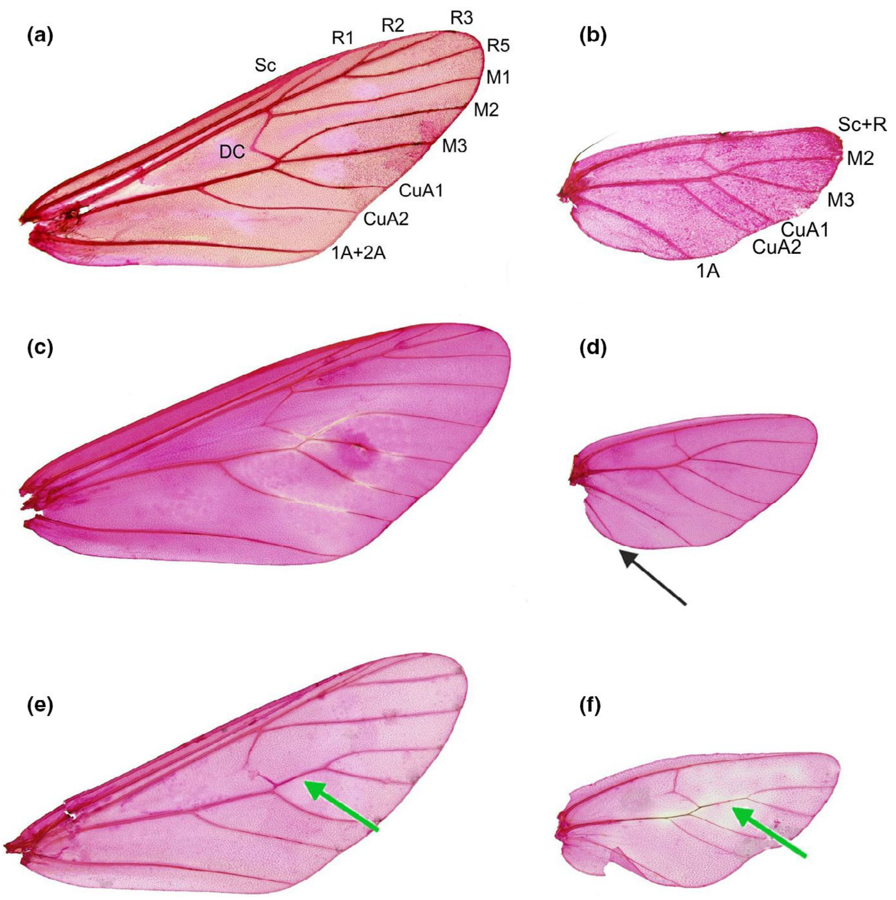


FIGURE 5 Wing venation (a-b) *Dysauxes florida*, (c-d) *D. famula*, (e-f) *Pseudonaclia puella*. Black arrow indicates rudimentary vein 2A in *D. famula*. Green arrows indicate fused basal portion of median veins in *P. puella*

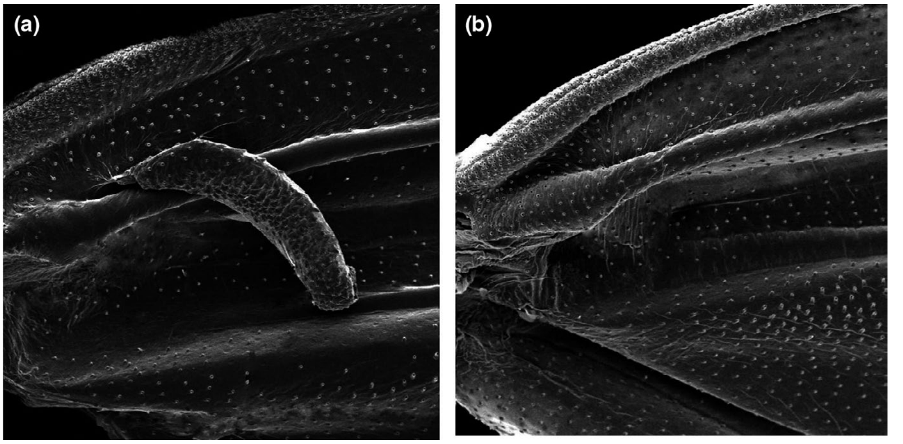
provided explanations of the phenomenon is selection against active flight in the face of strong oceanic winds, potentially blowing insects away (Gillespie & Roderick, 2002; Medeiros & Gillespie, 2011, but see Leihy & Chown, 2020). Almost all Malagasy syntomines possess the retinaculum, but based on our observations, they are not long-distance fliers; rather, they use short, fast flight for escape and fly actively only for about one hour around midday. Similar observations have been made on individuals of the closely related *Dysauxes ancilla* from an isolated population on the island of Öland, Sweden (Betzholtz, 2002), with the longest recorded flight distance being 144 m. Reduction in the retinaculum is rather unusual in Lepidoptera, more often it is the frenulum that is lost (Sattler, 1991). However, our observations suggest that the retinaculum is commonly lost in Syntomini, especially in the '*Amata* clade' (Przybyłowicz et al. in prep.), suggesting that these moths may be more prone to the loss of the character than other Lepidoptera.

As described above, *D. florida* shows some differences from the Palaearctic *Dysauxes* species, and its range is limited to a small oceanic island, located about 1,700 km south from the Equator and over 5,000 km from the closest populations of Palaearctic *Dysauxes* (Figure 8a). Considering this, an issue arises whether this species should be included in the genus *Dysauxes*, or rather placed in its own genus. Since genera should reflect the evolutionary history of taxa by consolidating monophyletic lineages, considering the Malagasy origin of *Dysauxes* and finally evaluating the morphological relations of *florida* and *Dysauxes*, we feel that including the Mauritian species in *Dysauxes* is preferable to creating a new, monotypic genus for it.

The position of *D. florida* within the genus requires some additional comments. *Dysauxes* has been divided by Ignatyev and Zolotuhin (2006) into two subgenera: *Dysauxes* s.s. and *Adauxes*. The subgenus *Adauxes* contains only two West-Palaearctic species *D. punctata* and *D. servula*. The latter had been for a long time regarded as a colour form of the former, and its taxonomic distinctiveness still remains unclear. Both taxa differ from the remaining ca. six species of *Dysauxes* by a very short and terminally rounded valva. However, members of *Dysauxes* s.s. are not uniform with respect to the morphology of the male genitalia, with *D. ancilla* being the most distant from congeners. This unclear pattern becomes even more complicated after examination of female reproductive organs. Here, the general morphotype has a large, concave ostium bursae, which, however, is missing in *D. fraterna*, *D. kaschmiriensis* and *D. punctata*. All of these suggest that the division of *Dysauxes* into two subgenera may not reflect phylogenetic relations within the group. Therefore, we decided not to place *D. florida* (Figure 9) in any of the subgenera

FIGURE 6 *Dysauxes florida* (a-g) and phenotypically similar taxa (h-j); (a) lectotype upper side. (b) lectotype underside, (c) lectotype labels, (d) male reduced pattern, (e) male extended pattern, (f) female reduced pattern, (g) female extended pattern, (h) *Dysauxes punctata,* (i) *Pseudonaclia puella*, (j) *Thyrosticta peyrierasi*

FIGURE 7 Male forewing underside retinaculum region under SEM microscope, (a) *Dysauxes ancilla* with well-developed retinaculum, (b) *D. florida* with retinaculum entirely atrophied



(however, it automatically goes to the nominal one) until a robust phylogenetic study of the entire genus using molecular data is undertaken.

4.3 | Variation in wing venation

In addition to *D. florida* (Figure 10), intraspecific variation or even individual asymmetry in wing venation is already known in Malagasy Syntomini species, for example *Toulgoetinaclia obliquipuncta* (Rothschild, 1921) and members of genus *Dubianaclia* (Griveaud, 1964). Moreover, this kind of variability seems not to be unusual for tiger moths (Lafontaine et al., 1982; Sotavalta, 1964). However, causes behind this phenomenon are unknown, and the number of examples among Lepidoptera has been growing. So far it has been studied or at least noticed in individual populations of *Agathiphaga vitiensis* Dumbleton, 1952 (Agathiphagidae)

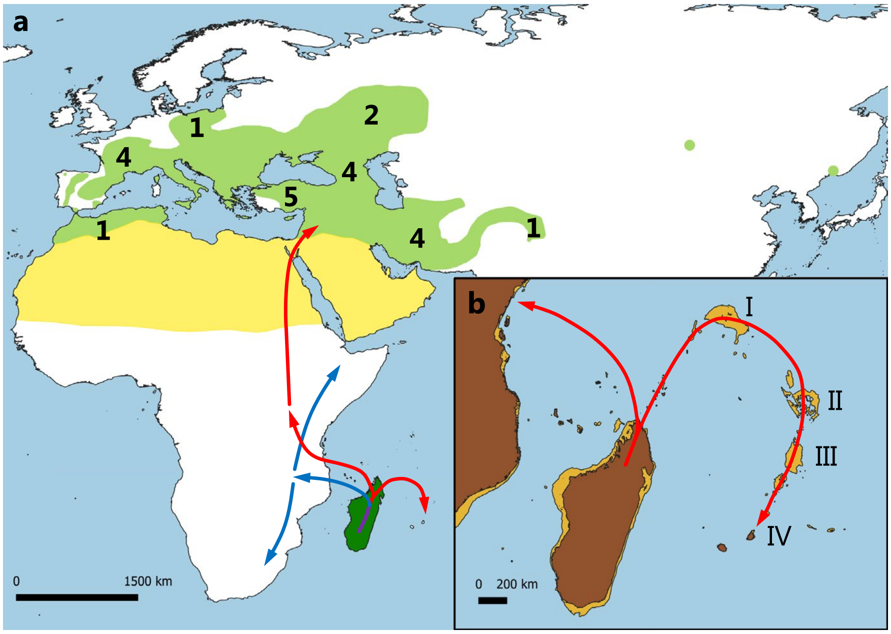


FIGURE 8 Hypothesis of dispersal in ancestral *Dysauxes*: (a) red arrows indicate possible dispersal routes by *Dysauxes*; blue arrows indicate *Pseudonaclia* recolonization event and its present distribution in continental Africa; light green area shows the present range of *Dysauxes* with numbers giving an overview of the species richness in different parts of the range (based mainly on Ignatyev & Zolotuhin, 2006, note that four species in SW Europe comes from treating the controversial *D. servula* as a separate species); yellow area shows the desert belt of N Africa and Arabian Peninsula acting as a barrier currently separating Ethiopian and Palaearctic fauna; (b) Malagasy Region illustrating the *stepping stones* hypothesis to explain the present distribution of *D. florida*; roman capitals illustrate major islands of the Mascarene Plateau. The putative ages of their origin are as follows: I—Saya De Malha, 41.5 mya, II—Nazareth Bank, 33–35 mya, III—St. Brandon, 31–35 mya, Mauritius—8–10 mya (from Bradler et al., 2015). Dark brown areas represent current land surfaces, and light brown is hypothetical land areas, if the sea level were 120 m below present, assuming constant topology of the ocean bottom

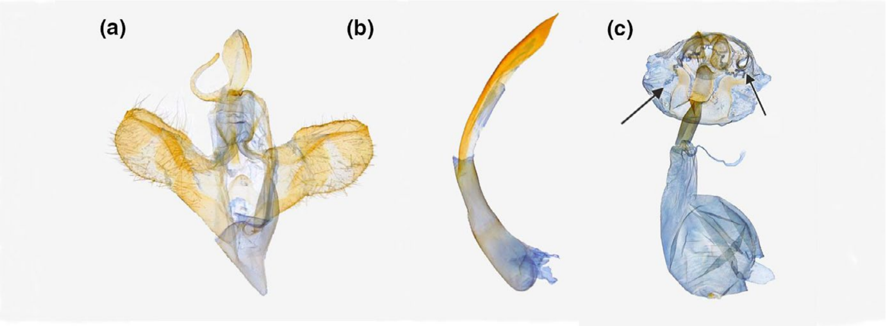


FIGURE 9 Variants of the forewing radial veins pattern in *Dysauxes florida,* (a) R2 proximally from R5, (b) R2 distally from R5. Both specimens represent the same sex (female)

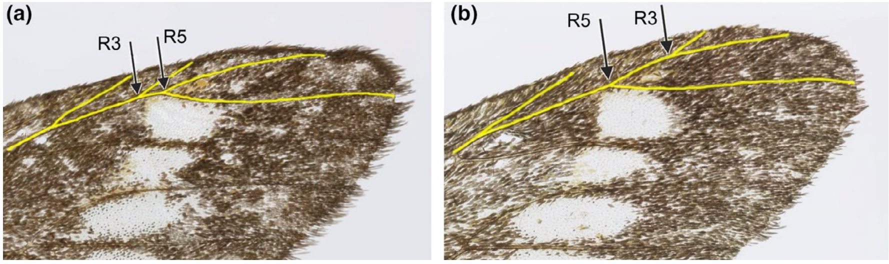


FIGURE 10 Reproductive organs of *D. florida*, (a) male genitalia, (b) aedeagus and (c) female genitalia. Black arrows indicate the presence of elongate, narrow, tubular, paired dorsal pheromone glands

(Schachat & Gibbs, 2016), in a few *Lichaneaula* Meyrick, 1890 species (Xyloryctidae) (Schachat, 2017) and in *Hydriomena costipunctata* Barnes & McDunnough, 1912 (Geometridae) (Schachat, 2019). In Elachistidae, intraspecific variation turned out to be even greater than interspecific differences, which had been used to distinguish taxa within the family (Albrecht & Kaila, 1997).

Fluctuating asymmetry in wing venation detected in an isolated population of the congeneric *Dysauxes ancilla* living on the island of Öland (Sweden) has been attributed to the environmental stress factor of dwelling in a constrained area of an ecologically marginal habitat (Betzholtz, 2000). Environmental stress has also been shown to cause variation in the location of vein junctions in *Helicoverpa punctigera* (Noctuidae) and *Epiphyas postvittana* (Tortricidae), but not in other traits such as wing size (Hoffmann et al., 2002, 2005). Thus, variation in wing venation in *D. florida* may also be an effect of environmental stress, due to the possible reduction in its range through habitat destruction. However, data are far too limited at the moment to make any definitive statements and interpretations.

4.4 | Biogeographic Inferences and colonization of Mauritius

The origin of the *D. florida* population on Mauritius and the dispersal routes leading to its current distribution remain unknown. Due to the uncertainty regarding the few known fossils of Arctiinae (Sohn et al., 2012), we are unable to calibrate the timescale of evolution for Syntomini confidently and thus to estimate time of colonization of Madagascar and Mauritius. However, indirect molecular datation already existing suggests that the whole tribe evolved not earlier than about 36 million years ago (Kawahara et al., 2019; Wahlberg et al., 2013), that is in the Late Eocene, and probably much later.

Przybyłowicz et al. (2019) hypothesized that the common ancestor of *Dysauxes* dispersed from Madagascar to the Palaearctic through Africa. However, the presence of *D. florida* on Mauritius raises the question whether the dispersal event towards the continent by the ancestors of *Dysauxes* might have been so simple and direct. Two possible scenarios can be proposed. Scenario S1, following the hypothesis of Przybyłowicz et al. (2019), must imply two, subsequent dispersal events, with one westwards from Madagascar to Africa and another eastwards from Africa to Mauritius. In the alternative scenario S2, the ancestor of *Dysauxes* would have dispersed simultaneously in two opposite directions: westward to Africa (and further north to Palaearctic, where speciation into the extant ca. 8 species occurred) and eastward, as a lineage represented now by *D. florida*, to Mauritius. Scenario S2 is suggested by our phylogenetic hypothesis, as the first divergence within *Dysauxes* is between *D. florida* and the Palaearctic members of the genus (based on our limited taxon sampling). This means that the common ancestor would have been widely distributed before diverging into the Mauritius and the Palaearctic lineages.

To understand how Mauritius may have been colonized from Madagascar, we need to consider the geology of the Western Indian Ocean and the hypothetical role of now submerged islands of the Mascarene Ridge as stepping stones (Figure 8b). These volcanic islands developed gradually over the past 40 million years (Myr) (see Figure 8 caption) (Bradler et al., 2015). Even after becoming inactive and being eroded to shallow banks, they were appearing and submerging periodically with the changes in the sea level. Figure 8b, based on the Global Relief Model (Amante & Eakins, 2009; NOAA, 2009), illustrates a situation when the sea would be 120 m below current level, assuming a constant topography of the ocean bottom. A map for an 80 m decrease would be nearly identical due to ocean's shallowness in the region. Based on the data summarized by Warren et al. (2010), such a decrease occurred ca. 46 times within the last 1.3 Myr, including nine times in the last 100,000 years. Although we still do not know the timeline for the colonization of Mauritius, it does appear that the geological dynamics of the Mascarene Ridge may have been involved in the dispersal of the common ancestor of *Dysauxes* towards Mauritius.

Our results indicate additionally that *P. puella* colonized Africa independently, and can be seen as another case of out-of-Madagascar dispersal in the 'clade *Dysauxes*'.

4.5 | Behaviour and ecology

The *D. florida* habit of sitting motionless on exposed surfaces of leaves and escaping at the last moment by fast flight into surrounding dense vegetation is shared with members of the Malagasy lineage of the tribe Syntomini.

Individuals of *D. florida* have been observed to visit flowers of 18 plant species; however, nectaring is confirmed only for *Ixora parviflora* (Figure 4e). Larval host plants are unknown, as with all Malagasy syntomines. It is hard to assume that *I. parviflora* is one of them based solely on adult feeding observations, as only about 54% of adult lepidopterans feed on nectar of their larval host plants (Altermatt & Pearse, 2011), and this relationship seems too weak to make general conclusions.

All observations of *D. florida* were made in places with secondary shrubby vegetation (Figure 4a,b), where the invasive guava *Psidium cattleyanum* was a dominant plant. This may suggest that the species is not strictly dependent on natural, undisturbed habitats. It can be therefore speculated that the food source for the caterpillar may be not necessarily vascular plants, but also, for example mosses, lichens or decaying matter covering the soil surface, like in larvae of many Syntomini, including the closely related *Dysauxes ancilla* (Betzholtz, 2003a, 2003b; Kitching & Rawlins, 1998).

Lastly, it has been shown that alien plant species can constitute an ecological trap for Lepidoptera. Females may choose to oviposit on invasive plant species that appear to be suitable but in reality are unfavourable for larval development (Yoon & Read, 2016). In the case of *D. florida,* further research on its biology is crucial to investigate the reasons behind its observed high attraction to unrestored habitat with alien plant species.

4.6 | Range and threats

Dysauxes florida is not widespread on Mauritius, and all known localities are concentrated in the SW part of the island (Figure 1). Its range extends for ca. 13 km west to east and ca. 5 km north to south. The type locality Kanaka Crater, which is also the easternmost known locality, was strongly deforested in 1975–1989 (de Boer et al., 2013), and the occurrence of the species there, as well as in the nearby Grand Bassin, has not been confirmed during our recent expedition. All the individuals were observed over an altitudinal range of 390–720 m a.s.l. Areas at this elevation were originally covered by moist and wet montane forests (Vaughan & Wiehe, 1937) and also by the upper parts of lower montane forest and azonal *Erica*-heaths (de Boer et al., 2013). The highest species diversity of Malagasy Syntomini is observed in tropical rainforests (Lees et al., 1999). Therefore, it can be hypothesized that the present range of *D. florida* at the higher elevations, with a mean annual precipitation of 2,000–4,000 mm (de Boer et al., 2013), arises from the species preferences for more humid forest biomes. Still, neither the larval host plant nor the specific microhabitat requirements of *D. florida* are known, so we are not able to predict its original range reliably. The environment of Mauritius is highly degraded, and only about 2% of primary vegetation remains (Florens, 2013). Thus, we may speculate that the present-day range of *D. florida* is only a restricted fragment of the previous distribution, especially taking into consideration that around 50% of the island was covered with wet forest before human colonization (de Boer et al., 2013). Moreover, the species is rarely collected by lepidopterists and found among the secondary vegetation, and thus, further localities are likely to be discovered in unexplored areas of the island with suitable environmental conditions. Potentially promising locations could be especially the forests surrounding Mare aux Vacoas, north-east from the known localities and at a similar altitude, or even the relatively less devastated area between Curepipe in the west, almost to the coast in the east. This elongated belt of better preserved seminatural habitats and protected areas (Domaine De L'Etoile or Kestrel Valley) may be considered as potentially favourable habitats for *D. florida*. Another target area, although fragmented by small villages and fields, could be the belt of wooden and shrubby vegetation extending along the north part of the island from Port Louis up to the Bras d'Eau National Park on the east coast.

Applying the IUCN Red List criteria (IUCN 2019) to our current knowledge, *D. florida* can be categorized as Critically Endangered (CR), based on criterion B1a, b(iii). The extent of occurrence (EOO) has surface of about 18 km^2, taking into consideration only locations documented in 21st century (Figure 1). Even including the type locality, the range covers ca. 28 km^2, which is much smaller than the <100 km^2 threshold for CR category. In practice, the EOO covers only a single location, comprising part of the Black River Gorges National Park and its closest surroundings. This is, however, positive for the survival of the species, since this area protects the largest comparatively undisturbed patch of the forest on the island. But even there, the species is found in fragments of partially disturbed habitats, with considerable presence and gradual encroachment of alien, invasive plant species (Florens et al., 2016). Moreover, areas outside the national park are under especially high risk of loss of even those secondary habitats, due to agricultural pressures and urbanization (Hammond et al., 2015; Figure 1). An illuminating example of such a scenario can be inferred from the specimen collected in Grand Bassin in 1945 and now housed in MNHN. The location is not far from other places where specimens were recently collected. However, in 1945 the Grand Bassin area had much better quality patches of native vegetation and far fewer buildings and parking areas. At that time, the site was frequently visited by biologists collecting samples of plants and animals, including insects (V. Florens, pers. comm.).

Vinson (1938) notes that "This moth is only found in certain forests of the upper regions of Mauritius (Les Mares, etc.) where it is not very rare". Thus, we can imagine that even 100 years ago the species was more abundant than now and that this situation can soon deteriorate. Decreasing population sizes and ranges can lead to other possible threats, such as bottleneck effects, leading to the loss of genetic variation and inbreeding (Remón et al., 2012). We have no knowledge of genetic variation in *D. florida* and thus cannot evaluate potential effects of loss of such variation. In general, it is known that island endemic insects do not tend to have lower genetic variation compared with mainland populations, in contrast to other groups of organisms (Frankham, 1997). Indeed, it has been observed that genetic diversity within small isolated marginal populations can be even higher than in the centre of the range, for instance in a comparison of a small, isolated population of *Dysauxes ancilla* living on the island of Öland (Sweden) and a continental German one (Betzholtz, 2000). It is clear that further efforts are needed to investigate the distribution, life history and population genetics of *D. florida* in order to protect this unique element of the Mauritian fauna.

4.7 | Remarks on the collector of two specimens from Paris museum

The identity of the collector of the two specimens housed in MNHN Paris is somewhat doubtful. The name printed on the label is “J. M. Vinson”. The Vinson family is clearly connected to studies on the Mauritian biota through Joseph Lucien Jean Vinson (1906–1966) [commonly used given names are underlined]. He had two sons, Marie Jean Michel Vinson and Marie Jean Michel Joseph Vinson, who were born in 1937 and 1939, respectively (V. Florens, pers. comm.). Considering the older son as a putative collector of the specimens, he would have been only 8 years old when collecting them. Most likely he had helped his father with collecting and then was honoured by him by being listed as the collector.

5 | CONCLUSIONS

We find that the single species of the tribe Syntomini endemic to Mauritius belongs to the Palaearctic genus *Dysauxes*, based on both morphological and molecular data. Thus, the original name combination *Dysauxes florida* de Joannis, 1906 should be applied to this species. The position of *D. florida* as sister to the two sampled Palaearctic *Dysauxes* species, which is a clade found deep within a clade of Malagasy endemics, suggests that the common ancestor of *Dysauxes* was a widespread species that colonized Mauritius and the Palaearctic through Africa before diversifying into the current ca. 8 species. It is likely that the currently submerged islands of Mascarene Plateau were used as stepping stones to reach Mauritius. A similar scenario has been proposed for Mascarene stick insects (Bradler et al., 2015) and extinct giant tortoises (Kehlmaier et al., 2019).

Dysauxes florida can, without exaggeration, be considered to be critically endangered, taking into account its very narrow range, anthropogenic pressure on the natural habitats of Mauritius and virtually unknown life cycle and habitat requirements. The observed phenotypical variation may be a reaction to the environmental stress factors affecting the population.

Therefore, we recommend that in-depth studies on the life-history requirements of the species, and appropriate assessment of all threats for the population, should be done as soon as possible. In addition, a detailed phylogeographic study on the genus *Dysauxes*, including examination of all species and subspecies from the whole range, is needed to elucidate the evolutionary history of the genus *Dysauxes*.

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SUPPORTING INFORMATION

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ARTICLE 3

Two becomes nine: integrative taxonomic revision of the genera *Thyrosticta* and *Melanonaclia* reveals even higher diversity of Madagascan endemic Polka Dot Moths (Noctuoidea: Erebidae: Arctiinae: Syntomini)

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Any taxonomic acts in this manuscript have no official status for the purposes of the Zoological Code.

ABSTRACT

The endemic lineage of Syntomini from Madagascar represents a large evolutionary radiation and constitutes a potentially suitable model system for further evolutionary studies. However, their systematics demands a modern re-elaboration. Here we present a systematic revision of the genera *Thyrosticta* and *Melanonaclia*. Both genera turn out to be polyphyletic and comprise nine distinct evolutionary lineages, well supported in molecular and morphological results. Seven new genera are described: *Skippernaclia* **gen. nov.**, *Kowalskinaclia* **gen. nov.**, *Privatenaclia* **gen. nov.**, *Julienaclia* **gen. nov.**, *Riconaclia* **gen. nov.**, *Mauricenaclia* **gen. nov.** and *Mortinaclia* **gen. nov.** We also describe three new species: *Skippernaclia leesi* **sp. nov.**, *Mauricenaclia apatris* **sp. nov.**, and *Melanonaclia ranomafana* **sp. nov.** Additionally, five new synonyms are established: *Thyrosticta incerta* **syn. nov.**, *Thyrosticta melanisa* **syn. nov.**, *Thyrosticta angustipennis* **syn. nov.**, *Dysauxes subfenestrata* **syn. nov.**, *Tritonaclia inauramacula* **syn. nov.** In total, 30 valid species are covered in this paper. The morphology of the reviewed taxa is elaborated and illustrated, including genitalia of both sexes, and eggs, and determination keys to the genera are provided. The distribution, elevational ranges, and preferred vegetation types are provided for all examined species. We also gathered all available (though still scarce) data on their biology, including first observations of flowers nectaring.

KEY WORDS

determination key; eggs; molecular; morphology; new genus; new species; phylogeny; redescription; SEM; species delimitation

INTRODUCTION

The Madagascan lineage of the erebid tribe Syntomini, comprising around 100 species (Viette 1990) deriving from a single ancestor (Przybyłowicz et al. 2019), is the largest known evolutionary radiation of Macroheterocera in the island (Lees and Minet 2022). This group constitutes a suitable object for future studies of evolutionary processes in Madagascan insects, e.g. those determining local endemism (Wiorek et al. 2021). The most recent comprehensive monograph of the group was published by Griveaud in 1964 and comprised 15 genera (of which 11 were established in that work), However, their diagnoses were based on general descriptions of selected morphological characters, rather than explicit diagnostic definitions based on the indication of autapomorphies and other characters distinguishing them from other genera. The two largest genera, *Maculonaclia* Griveaud, 1964 and *Thyrosticta* Hampson, 1898, comprise 30 and 23 species respectively. These genera are highly variable morphologically, and even a superficial comparison of the species raises doubts about the monophyly of the genera, and their polyphyletic character was also confirmed by our initial molecular results (Przybyłowicz et al. 2019). Thus, the group demands a modern systematic revision, based on an integrative approach.

After the monograph on Madagascan Syntomini (treated therein as “Amatidae”) (Griveaud 1964), a series of further contributions to the group was published (Griveaud 1966, 1969, [1971], [1973], [1974], Viette, 1987). However, these works comprised only descriptions of new species and some previously unknown males and females, with no updates to the systematics. This is overdue, as e.g. the description of the male of *Melanonaclia perplexa* Griveaud, 1964 in Griveaud (1969) reveals it to possess genitalia not matching the diagnosis of the genus in which it was placed. Additionally, the elaboration of the group by Pierre Griveaud was done mostly based on the specimens currently deposited in Muséum national d'Histoire naturelle, Paris, France, and Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar, with the inclusion of some materials from Natural History Museum, London, UK. However, specimens of Madagascan Syntomini can be found also in other collections, and a significant amount of further materials has been collected since 1964. Among these specimens, there are males and females of species for which one of the sexes remained unknown. A satisfactory modern study would provide a more complex and accurate description of the morphological diversity of the group, with the indication of reliable apomorphies of taxa. Also, these materials, including specimens gathered in new fieldwork up to at least 2020, provide much further data on species occurrences, thus contributing to a better knowledge on the distribution of each species, but also on the biology and ecology of the group, for which

Griveaud (1964) presented next to no data. Striking lacunae include early stages and foodplants of the group.

Historic summary of *Thyrosticta* and *Melanonaclia*

The genus *Thyrosticta* was established by Hampson (1898), with its diagnosis based solely on the general morphology of labial palpi, tibial spurs, and wing venation, and comprising a few species of Madagascan Syntomini later partly moved to different genera (Griveaud 1964). Currently, the genus *Thyrosticta* comprises 23 species (Viette 1990), of which 14 were described in Griveaud (1964), and four in Griveaud (1969). Griveaud (1964), apparently considering the high morphological diversity of the genus arranged by him, established seven "sections" of *Thyrosticta*, based mostly on the morphology of the antennae and genitalia (however, often misinterpreted), but decided to maintain them in one genus, even though all the other genera, except the very diverse *Maculonaclia*, comprise from one to eight species (Griveaud 1964, Viette 1990).

The genus *Melanonaclia* Griveaud, 1964 originally comprised six species (including three described by Griveaud 1964) with dark brown to almost black general body colouration, white wings pattern and yellow or white marks on the body. It was originally defined based on a number of morphological characters. However, some of them were partly misinterpreted, e.g. the shape of the antennae.

This paper continues a series of articles concerning the re-evaluation of the biodiversity of Madagascan Syntomini (Przybyłowicz et al. 2019, 2021, Przybyłowicz and Wiorek 2023, Wiorek et al. 2021), and here we focus on reviewing the genera *Thyrosticta* and *Melanonaclia* within an integrative taxonomy framework and include some details on early stages and adult biology.

MATERIALS AND METHODS

Acronyms of collections

ISEA PAS – Institute of Systematics and Evolution of Animals Polish Academy of Sciences, Kraków, Poland;
ANHRT – African Natural History Research Trust, Leominster, UK;
CEP-MZUJ – Zoological Museum of the Jagiellonian University, Kraków, Poland;
MfN – Museum für Naturkunde, Berlin, Germany;
MNHN – Muséum national d'Histoire naturelle, Paris, France;
NHMUK – Natural History Museum, London, UK;
NMP – Národní Muzeum, Prague, Czech Republic;
NRM – Naturhistoriska riksmuseet, Stockholm, Sweden;
PZBT – Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar;
SGN – Senckenberg Naturmuseum, Frankfurt am Main, Germany;
SMNS – Staatliches Museum für Naturkunde, Stuttgart, Germany;
coll. P. Basquin – private collection of Patrick Basquin France;

Other abbreviations

Sc – subcostal vein
Rs – radial sector
R1-R5 – radial veins
M1-M3 – medial veins
CuA1-CuA2 – cubital veins
1A+2A, 3A – anal veins
DC – discal cell

ML – Maximum Likelihood
BI – Bayesian Inference

PN – "Parc National", National Park
RS – "Réserve Spéciale", Special Reserve
RN – "Route Nationale", National Road

MW – Marcin Wiorek

DL – David C. Lees
NW – Niklas Wahlberg
ŁP – Łukasz Przybyłowicz

Study area

The area of the study covers Madagascar and the adjacent islands of Nosy Be and Nosy Boraha (= fr. Île Sainte-Marie / Sainte Marie de Madagascar).

Materials and sampling methods

The study is based on both freshly collected and museum specimens.

The specimens collected during the trips in 2018, 2019 and 2020 were obtained based on the research permits from Direction Generale de l'Environment et des Forets and Direction de la Gestion des Ressources Naturelles Renouvelables et des Ecosystemes. These individuals were caught predominantly by day, but also with the use of automatic light traps provided with UV or visible light sources, and sporadically with Malaise traps. Because of the characteristic activity pattern and behaviour of Madagascan Syntomini (see Wiorek et al. 2021), the most efficient method is diurnal collecting with an entomological net, focused on the individuals sitting on uppers surfaces of leaves or occasionally flying along the vegetation margins, e.g. forest edges along a path. For further description of the method see Przybyłowicz et al. (2021). The collected individuals were killed with ethyl acetate, pinned on entomological pins, and subsequently spread, after leg sampling for the molecular study.

The museum materials comprise specimens deposited in the collections of: ISEA PAS, ANHRT, CEP-MZUJ, MfN, MNHN, NHMUK, NMP, NRM, PZBT, SGN, and SMNS.

The study was designed to be based on the primary materials only, including the specimens available to P. Griveaud and collected by him and other French and Malagasy collectors of his times, and also the materials obtained later, after the series of papers on Madagascan Syntomini was published (Griveaud 1964, 1966, 1969, [1971], [1973], [1974], Viette, 1987). In total, 1402 specimens representing all species from the reviewed genera *Thyrosticta* and *Melanonaclia*, identified by MW to species level, were included in the study (Tab. S1). Additionally, in the study were included 35 observations of Madagascan Syntomini from iNaturalist, provided with pictures allowing for undoubted identification of the individuals to species level (Tab. S1).

Morphological study

Each specimen intended for further morphological research was spread (if applicable) and photographed with the use of a Canon EOS 70D camera, provided with a macro lens EF 50 mm, before further examination. Additional pictures of body details were taken using a stereoscope microscope Leica S9i system, integrated with the LasX software, allowing for stacking. The pictures of type specimens housed in MNHN were taken by M. Depraetere (2018) and are available in the Insects - Lepidoptera (EL) database of MNHN, on https://science.mnhn.fr/institution/mnhn/collection/el/item/search . The pictures of types deposited in NHMUK are courtesy of the Trustees of the Natural History Museum, unless indicated otherwise. The identity of all mentioned specimens was confirmed by MW in the collections.

The genitalia descriptions provided by Griveaud (1964, 1969) very often lack an explicit mention of important details, and the vesica of the male genitalia, potentially bearing taxonomically significant characters, usually is uneverted in the original slides by P. Griveaud, housed in MNHN. Additionally, we already find the genitalia drawings in Griveaud (1964, 1969) sometimes very different from reality (see Wiorek et al. 2021). Thus, we decided to include a comprehensive male and female genitalia redescription in the paper.

Genitalia dissection and preparation was done with the standard method of abdomen maceration in 10% NaOH solution in a water bath. The dissection was conducted in glycerine, with water used for rinsing and a water solution of chlorazol black for staining. Prepared and stained genitalia were mounted in glycerine on labelled microscope slides, without coverslips to maintain the possible anatomical (3D) arrangement of the genitalia. Photographs of the genitalia were taken with the same stereoscope microscope as mentioned above. The male genitalia were photographed from the front, back and side (if their shape allowed such an arrangement), the phallus from the right and left side, and the female genitalia from the dorsal and ventral side, allowing for more detailed visualisation of morphological characters. After photographing, the genitalia were mounted on microscope slides in Euparal.

Eggs laid by the females collected in the field and placed in plastic vials were left to dry on the vial walls and then stored in a freezer at -20°C. For visualisation with SEM photography, up to three eggs from a single female were rehydrated overnight in a tube with distilled water, to regain their spherical shape. Then, using the tip of a thin pin under a binocular microscope, the eggs were gently cleaned from particles like scales or dust. Subsequently, for dehydration required for SEM preparations, the eggs were immersed in three ethanol solutions of increasing concentration, up to 70% in the last one. Further, the eggs were left to evaporate residual alcohol and placed on carbon discs. As a result of dehydration in alcohol, an egg collapses inwards on the side opposite to the micropylar area, allowing for secure attachment to the disc with the concave part, usually without significant distortion of the egg shape, and good exposure of the micropylar area. Also, the eggs retrieved from abdomens during genitalia dissection were used for SEM visualisation. Examining the eggs of *Thyrosticta minuta* (Boisduval, 1833), obtained in both ways, we verified that NaOH maceration of the abdomen does not affect the exochorion structure of the eggs in the abdomen.

For visualisation of the wing venation, we prepared wings slides following the protocol by Banasiak (2015), with slight modifications.

For SEM visualisation of morphological details, relevant body parts were torn off from dried specimens and placed on carbon discs. Wing scales were sampled with a fine entomological pin, except for the cases of entire wing surface visualisation. The preparations were further coated with gold. SEM pictures were taken with the use of HITACHI SU8600 Ultrahigh-Resolution Scanning Electron Microscope in the Laboratory of Scanning Electron Microscopy and Microanalysis of the Institute of Geological Sciences, Jagiellonian University, Kraków (Poland).

For general morphological terminology, we follow Miller (1991), and the terms used to describe the head and thorax are explained in Figure 1. The terminology for the wing venation also follows Miller (1991) (Fig. 2), while the comparison with the system used by Griveaud (1964) is presented in Table 1. However, the reduction of the forewing radial veins to four – and in rare cases to three – present in some Madagascan Syntomini, is difficult to interpret in terms of homology. Therefore, we treated it as a loss among R2, R3, and R4, taking into account the side-most position of R1 and R5, and thus their presumed consistent presence across the group (see also Holloway 1988). Additionally, for the hindwing, we modified the terminology by Miller (1991), following the Arctiinae-specific approach by Jacobson and Weller (2002), and treated the first vein along the costal margin as fused Sc+Rs+M1, and anal veins as 1A+2A, and 3A (see also the remark in Tab. 1) (Fig. 2).

For the forewing pattern terminology (Fig. 2), characterised below, we adapted and modified the system proposed by Obrazstov (1966), already implemented in studies on Syntomini (Ignatyev and Zolotuhin 2006, Przybyłowicz and Tarcz 2015 – but see the different approach in Ignatev et al. 2023).

Table 1. Wings venation terminology used in this study, with a comparison of different systems proposed in the literature.

Forewing		Hindwing		
Griveaud (1964)	Miller (1991)	Griveaud (1964)	Miller (1991)	Jacobs and Weller (2002)
12	Sc	not annotated, presumably treated as lost	Sc+R*	lost/fused*
11	R1	7	Rs	Rs+M1*
10	R2	6	M1	
9	R3	5	M2	M2
8	R4	4	M3	M3
7	R5	3	CuA1	CuA1
6	M1	2	CuA2	CuA2
5	M2	1**	2A	1A+2A
4	M3		3A	3A
3	CuA1	*According to Jacobs and Weller (2002), the lack of Sc+R results from fusion rather than loss (see also Holloway 1988, Kitching and Rawlins [1999]), and as such, i.e. fused Sc+Rs+M1, is treated in Przybyłowicz (2019) and here. **See discussion.		
2	CuA2			
1	1A+2A			

In general, the forewing pattern (Fig. 2) consists of three groups of blotches, located in the basal, medial, and distal portions of the wing: i) basal blotches: fm_1 - along costal margin, including Sc; fm_2 - in the basal portion of DC; m_1 – between the basal portion of DC hind margin and 1A+2A; am_1 – below 1A+2A, including the hind margin; ii) medial blotches: m_2 – in the distal portion of DC, between R and DC hind margin, sometimes including also Sc; fm_3 – between DC hind margin and CuA2; m_3 – between CuA2 and 1A+2A; iii) distal blotches: m_4 – between R5 and M1; am_4 – between M1 and M2; m_5 – between M2 and M3; m_6 – between

M3 and CuA1. The colouration of these groups adopted in Figure 2 corresponds with the Arctiinae forewing groundplan proposed by Gawne and Nijhout (2020).

The hindwing pattern consists of a single basal blotch, and distal blotch or blotches (Fig. 2), which can be connected in different ways, up to complete fusion into one, large blotch covering most of the wing surface (see Obrazstov 1966).

The terminology for genitalia in general follows Koda (1987), with the terms explained in Figure 3. For eggs descriptions we follow Peterson (1964) and Döring (1955), as implemented in Korycinska (2012), for spermatophores we applied the terminology by Mann (1984), explained in Figure 4, and for scales morphology – by Kristensen and Simonsen [1999].

Molecular study

For the molecular study, two legs of each specimen were sampled and stored in a plastic tube at -20°C, or processed immediately after sampling. For the genomic DNA extraction, the NucleoSpin Tissue kit (Macherey-Nagel, Germany) was used following the manufacturer's protocol. Up to eight molecular markers, the same as used in Przybyłowicz et al. (2019, 2021), were amplified, using the primers by Wahlberg and Wheat (2008), following the protocols used in Zenker et al. (2017). Sanger sequencing of successful PCR products was either commissioned to Macrogen Europe (Amsterdam, the Netherlands) or done at the Institute of Systematics and Evolution of Animals Polish Academy of Sciences (Kraków), using BrilliantDye Terminator v.3.1 kit (NimagGen, the Netherlands), and ABI Prism 3130xl sequencing machine. Obtained sequences were compared with the relevant chromatograms and manually aligned to reference sequences using the BioEdit program (Hall 1999). Ambiguous sites were encoded according to IUPAC nucleotide codes. Such curated sequences were stored and managed with the VoSeq database (Peña and Malm 2012). The sequences obtained in this study are deposited in GenBank (Tab. S2) [the sequences, which did not obtain accession numbers yet are marked with X]. In the analyses we also used sequences published in Przybyłowicz et al. (2019, 2021), and Wiorek et al. (2021). All samples used in the molecular study are listed in Table S2. Part of the specimens included in the papers by Przybyłowicz et al. (2019, 2021), deposited in NHMUK, were reidentified by MW (Tab. 2).

Table 2. Samples used in Przybyłowicz et al. (2019, 2021) reidentified in this study.

Sample code	Species identification in Przybyłowicz et al. (2019, 2021)	Species identification in this study
DL1860	Genus indet. spS4	*Toulgoetinaclia obliquipuncta*
DL1801	*Thyrosticta* spS2	*Melanonaclia toulgoeti*
DL1769	*Thyrosticta trimacula*	*Melanonaclia ranomafana* **sp. nov.**
DL1770	*Tenuinaclia* sp1	*Mortinaclia perplexa* **comb. nov.**
DL1792	Genus indet spS1	*Mauricenaclia peyrierasi* **comb. nov.**
DL1795	*Dubianaclia* sp7	*Thyrosticta sylvicolens*
DL1810	*Dubianaclia* sp14	*Dubianaclia amplificata*
DL1811	*Thyrosticta* cf. *minuta*	*Mauricenaclia bruneata* **comb. nov.**

Phylogenetic analyses conducted within the ML framework were done in IQ-TREE (Nguyen et al. 2015) on the web server (Trifinopoulos et al. 2016). The dataset was partitioned by gene fragment (i.e. 11 partitions) and the best substitution model for each partition was found using the model-finding tool implemented in IQ-TREE (Kalyaanamoorthy et al. 2017). Support of nodes was checked with Ultrafast Bootstrap (Hoang et al. 2017) and SH-like approximate likelihood test (Guindon et al. 2010), both with 1000 replicates. Additionally, an RAxML analysis (Stamatakis 2014) was conducted on CIPRES. The analyses within the BI framework were done using MrBayes (Ronquist et al. 2012) on CIPRES, with two independent runs of 10 million generations, each with four chains, sampled every 1000 generations, with a 25% burn-in.

Subsequently, to explore the potential cases of cryptic species observed in the topologies of the obtained trees, species delimitation analyses were conducted on the DNA barcode region (COI-begin), and also nuclear regions EF1a-begin and GAPDH. We used one cluster-based method – Automatic Barcode Gap Discovery (ABGD) (Puillandre et al. 2012), available on the server https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html , and one tree-based method – the ML implementation of Poisson Tree Processes (PTP) (Zhang et al. 2013). For the input parameters of the ABGD analyses see File S1. Input trees for the PTP analyses were constructed in IQ-TREE (Nguyen et al. 2015).

The results of the Bayesian implementation of PTP (bPTP) were rejected due to irrelevant outputs, arranging the specimens into a high number of single-sample "species" with very poor support.

Species distribution analyses

Label data from all specimens housed in the examined collections were gathered (Tab. S1), and a list of all collecting localities was prepared. The localities without originally indicated geographic coordinates were geolocalised based on Dorr (1997), Viette (1991), and Moat and Smith (2007), using Google Maps (Tab. S3). Records from the same place, e.g. a few spots located several hundred meters apart in the same forest patch, for mapping purposes were assigned to one point. The elevation data were taken predominantly from the original labels, taking into account the high probability of considerable errors in the secondary determination of the elevation, as many of the localities could be geolocalised only approximately. We used Google Earth to obtain these data for only a few species, clearly missing label data from the specimens collected in low elevations. Distributional analyses were conducted in QGIS software. The classification of the remaining primary vegetation of Madagascar follows Du Puy and Moat (1996), with some additions after Moat and Smith (2007). The data on 2000-2020 deforestation were taken from LOFM (2022). The names of protected areas follow Goodman et al. (2018).

Etymology of the new generic names

The new genera introduced in the paper are named after the characters from "The Penguins of Madagascar" television series: Skipper, Kowalski, Rico, Private, Julien, Mort, and Maurice. The second part of the generic names refers to the convention of using the stem "naclia" provided with various prefixes in naming the genera of Madagascan Syntomini. Therefore, the name *Mauricenaclia* refers to the name Maurice, and not to the island of Mauritius.

RESULTS

Phylogenetic relationships

The analyses conducted on the dataset composed of up to eight molecular markers, with ML (IQTREE (Fig. 5A-B) and RAxML (Fig. S1)) and BI (MrBayes, Fig. S2) approaches are in general congruent with each other. The overall topology is similar to the results of Przybyłowicz et al. (2019). Our trees differ only in the position of the "*Balacra*" and "*Thyretes* + *Pseudothyretes*" clades; the topology of the Madagascan clade is identical, and its monophyletic character is sustained. Our results show with high support that the genera *Thyrosticta* and *Melanonclia – sensu* Griveaud (1964) – are polyphyletic. The majority of the morphological "sections" of *Thyrosticta*, proposed by Griveaud (1964), constitute separate, monophyletic clades, raised here to generic level (see Systematics). The only exception is the "group of *Thyrosticta trimacula*", from which *T. bimacula* Griveaud, 1964 forms its own, monotypic lineage, and *Thyrosticta trimacula* (Mabille, [1879]) belongs to the genus *Melanonaclia*. The majority of species of the genus *Melanonaclia* form a monophyletic clade; only *Melanonaclia perplexa* belongs to a separate, not closely related lineage, additionally forming a cryptic species complex (see below).

In the Madagascan clade, *Toulgoetinaclia obliquipuncta* (Rothschild, 1924) forms a well supported lineage sister to all remaining taxa, which are arranged in four main clades (Fig. 5A-B).

The first clade comprises two genera: *Julienaclia* **gen. nov.** (the former "group of *Thyrosticta pauliani*"), represented by one of its two species, *J. pauliani* (Griveaud, 1964) **comb. nov.**, sister with a very high support to *Kowalskinaclia* **gen. nov.**, (the former "group of *Thyrosticta vieui*"), with all three species included. The biggest difference in the topology between the tree obtained with IQ-TREE (Fig. 5A) and the two others (Figs S1, S2), is the placement of the single *Kowalskinaclia vieui* (Griveaud, 1964) **comb. nov.** specimen DL_14R-218. In the latter, it is arranged together with the specimens of *Kowalskinaclia dilata* (Griveaud, 1964) **comb. nov.**, however in all the analyses its placement has very low support values (see also Systematics).

The second clade, sister to *Julienaclia* **gen. nov.** + *Kowalskinaclia* **gen. nov.** with a very high support, is the genus *Melanonaclia* in its reviewed shape (Fig. 5A), represented by five species out of seven.

Going down the tree (Fig. 5B), we find the third clade, sister to the two above-mentioned and enjoying 100% support, composed of: i) *Mortinaclia* **gen. nov.**, a "monotypic" genus comprising only *Melanonaclia perplexa* (but being an unresolved species complex); ii) *Micronaclia* cf. *imaitsia*; and iii) the monotypic *Riconaclia* **gen. nov.**, with *R. bimacula* **comb. nov.**, being sister (however with low support), to iv) *Skippernaclia* **gen. nov.** (the former "group of *Thyrosticta lacrimata*"), represented by all species except *Skippernaclia leesi* **sp. nov.**, which was unavailable for molecular study. The topology of our trees (Fig. 5B, Figs S1, S2) suggests an unclear taxonomic status of *Skippernaclia ankaratra* (Griveaud, 1964) **comb. nov.** and *S. vestigii* (Griveaud, 1964) **comb. nov.**, but this results from the scarcity and poor quality of molecular data obtained from the only available specimen of the latter species, rather than their conspecificity (see Systematics). Further in the same clade fall *Maculonaclia leopardina* (Rothschild, 1911) and *Privatenaclia* **gen. nov.** (the former "group of *Thyrosticta triangulifera*"), with all three species included.

In the bottom of the tree (Fig. 5B) we find the fourth clade, which is sister to all the above described ones, albeit with low support, formed by: i) *Tritonaclia* species, placed there with very low support, ii) *Thyrosticta sylvicolens* (Butler, 1878), the type species of the genus, now becoming monotypic, sister with low support to iii) the genus *Dubianaclia* Griveaud, 1964. The last group in that clade, sister to *T. sylvicolens* + *Dubianaclia* with very good support values, is iv) the "*Dysauxes*" clade (see Przybyłowicz et al. 2021). It comprises: *Mauricenaclia* **gen. nov.** (the former "group of *Thyrosticta minuta*"), with only *Mauricenaclia raharizonina* (Griveaud, 1964) **comb. nov.** missing in the analyses, the African species *Pseudonaclia puella* (Boisduval, 1847) (the type species of a polyphyletic genus, which comprises also some species belonging to the "*Amata* clade" (Przybyłowicz et al. 2019)), and the genus *Dysauxes* Hübner, [1819], including both the Palaearctic species, and *D. florida* de Joannis, 1906 from Mauritius. The Mauritian species is sustained as the basal lineage to all remaining *Dysauxes* species, and the topology of the "*Dysauxes* clade" differs from the results of Przybyłowicz et al. (2021) in *P. puella* being sister directly to *Dysauxes*, with none of *Mauricenaclia* **gen. nov.** species placed in between.

Species delimitation analyses

The presence of potential cryptic species complexes within some of the reviewed taxa, suggested by the tree topology (Fig. 5A-B), is supported by the results of both the cluster-based (ABGD) and tree-based (PTP) species delimitation analyses (Fig. 5A-B). The results of the ABGD analyses for each gene region are shown in Figures S3-S7, and outputs of the PTP analyses are included in File S1. The ABGD analysis for the DNA barcode region of COI gene indicated the intraspecific gap at the p-value around 0.03-0.04.

Potential cryptic species were found within: *Kowalskinaclia cowani* (Griveaud, 1964) **comb. nov.**, the above-mentioned case of *Kowalskinaclia vieui* **comb. nov.**, *Melanonaclia luctuosa* (Oberthür, [1911]), *M. trimacula* **comb. nov.** (Fig. 5A), *Mortinaclia perplexa* **comb. nov.** and *Mauricenaclia minuta* **comb. nov.** (Fig. 5B). The best supported is the case of the *M. minuta* **comb. nov.** lineage represented by the sample DL_02-325 (Fig. 5B, see Systematics), which appears as a separate species in all analyses based on both mitochondrial and nuclear markers (Figs S3-S7, File S1). However, for any of the cases listed above, except *M. perplexa* **comb. nov.**, we could not find morphological characters defining the potentially new species (see Systematics).

General morphological results

The reviewed taxa are highly diverse morphologically, both in form and colouration. However, we were able to find diagnostic characters for all new genera described here (see Systematics). Additionally, we identified a number of additional characters, which are predominantly stable at the intrageneric level, and their combination varies at the intergeneric level, providing additional traits to define the genera. These characters are described below and partly summarised in Table 3.

Antennae. Antennae, which were one of the key characters in the classification proposed by Griveaud (1964), vary from bipectinate, through serrate to piliform (Tab. 3, Figs 6-8). Bipectinate antennae in both sexes are present in *Julienaclia* **gen. nov.** (Fig. 7A-B). In the genera *Thyrosticta* and *Kowalskinaclia* **gen. nov.**, the antennae in males are bipectinate (Figs 6, 7C), whilst in females - piliform in the former genus, and slightly serrate in the latter (Fig. 6D). In the remaining genera: *Melanonaclia*, *Skippernaclia* **gen. nov.**, *Privatenaclia* **gen. nov.**, *Riconaclia* **gen. nov.**, *Mauricenaclia* **gen. nov.**, and *Mortinaclia* **gen. nov.**, the antennae are piliform in both sexes (Figs 7E-H, 8A-F). The only exception is the male of *Mauricenaclia peyrierasi* (Griveaud, 1969) **comb. nov.**, possessing slightly serrate antennae (Fig. 8G).

Differently expressed sexual dimorphism in the structure of the antennae is present in all genera. In *Julienaclia* **gen. nov.** the pectination in the female is less prominent (Fig. 7B). In the genera with piliform antennae, their ventral side is densely covered with short setae and part of antennomeres in females is provided with a pair of longer and thicker setae oriented downwards, which in males are less numerous and less prominent, or even absent - except for the terminal portion of the antennae, always provided with such distinct setae in both sexes (Figs 7E-H, 8A-F).

Table 3. Additional morphological characters defining the genera covered in the paper, "+" – presence, "-" – absence.

Character/genus	Antennae	Male foreleg scale tuft	Additional hindleg tibial spurs	Forewing radial veins	Female ventral pheromone glands
Thyrosticta	sexually dimorphic	-	1	4	+
Skippernaclia **gen. nov.**	piliform	+	0	4/3*	+
Kowalskinaclia **gen. nov.**	sexually dimorphic	-	2	5	+
Privatenaclia **gen. nov.**	piliform	+	0	4	+
Julienaclia **gen. nov.**	bipectinate	-	2	5	+
Riconaclia **gen. nov.**	piliform	+	0	4	+
Mauricenaclia **gen. nov.**	serrate or piliform	-	0/1*	4	-
Melanonaclia	piliform	+/-*	0/1*	5	-
Mortinaclia **gen. nov.**	piliform	-	1	4	-

* characters variable among species within the genus, see text.

Foreleg scales brush. In males of some species, a pencil-like tuft of elongate scales was detected along the posteroventral surface of the foreleg coxa (Figs 9-12). This structure is either present in all species of a genus or completely absent (Tab. 3). The exception is *Melanonaclia lugens* (Oberthür, 1893), which is the only species of its genus devoid of the tuft (and the morphology of that structure varies in the genus, see below).

The tuft originates posteriorly at the foreleg base (Fig. 9) and normally is hardly visible or invisible in the specimens spread with the legs arranged in anatomical position (Fig. 9D, F) – sometimes, it is additionally located in a longitudinal cavity of the coxa. It probably can be unfolded in the shape of a pompom-like brush, and as such was preserved in two specimens of *Skippernaclia lacrimata* (Griveaud, 1964) **comb. nov.** (Fig. 9E). In most cases, the scales forming the tuft are yellow to almost creamy, hair-like (Fig. 9A-E), cylindrical, pointed at the tip and empty inside, with the walls formed by a dense meshwork, with numerous holes, and sometimes with plaques (Figs 10, 11A-B). Only in *Melanonaclia toulgoeti* Griveaud, 1964 and *Melanonaclia nigra* (Griveaud, 1964) the scales are distinctly widened, ribbon-like, and seemingly less porous (Figs 9F, 11C-F, 12).

The function of the tuft needs further research; SEM visualisation did not reveal any crystal-like structures resembling potential pheromone-transfer-particles (PTPs) on the scales surface, the presence of which would indicate for the scent function (but see discussion).

Additional hindleg tibial spurs. Another genus-specific character is the presence and number of additional hindleg tibial spurs, varying from absent, through single one, to two (Tab. 3, Fig. 13). The only exceptions are *Melanonaclia lugens*, *M. toulgoeti*, *Mauricenaclia minuta* **comb. nov.**, and *M. rothschildi* (Griveaud, 1964) **comb. nov.**, which have no additional spurs, in contrary to other species in their genera, which possess a single one.

Wings shape and venation. The shape of the wings is generally genus-specific, with rather low intrageneric variation, except in *Melanonaclia* (Figs 14-17).

The forewing is usually regularly subtriangular, with well defined tornus (Figs 14-15), except *Skippernaclia* **gen. nov.** (Fig. 14A-B) and *Riconaclia* **gen. nov.** (Fig. 14C), in which the forewing is narrowed, elongate and slightly rounded. The outer margin is usually convex, only in *Julienaclia* **gen. nov.** (Fig. 14D), the female of *Melanonaclia nigra* (Fig. 14E, G) and the male of *M. toulgoeti* (Fig. 14H) provided with a differently expressed, shallow incision in the subtornal area. The forewing venation is also generally uniform, except for the number of radial veins, which varies from five to four (Tab. 3, Figs 14-15). Additionally, in *Skippernaclia vestigii* **comb. nov.** occurs reduction to three radial veins (see Systematics). However, this character should be considered with caution, as anomalies and even intraindividual asymmetry were found in some species (Figs 14A-B, E-F, 15F-G, see also Systematics).

The hind wing shape varies from subtrapezoidal, to subtriangular and elongate suboval, and is usually uniform within the genus, except *Melanonaclia* (Figs 16-17). The veins Sc+Rs+M1 are generally fused (Tab. 1, Figs 2, 16-17), but in some species an indistinct bifurcation can occur in the very terminal portion (Figs 16A-B, 17A-B, E-F). Additionally, the presence of a small cell in the proximobasal portion of DC (Figs 2, 16-17) was recorded. The extent of fusion of the basal portion of M2 and M3 also seems to be a genus-specific character, at least in some cases. These two veins are almost completely not stalked to stalked at most in 1/3 of their length in *Mauricenaclia* **gen. nov.** (Fig. 17D), and almost completely stalked (over 2/3 of their length) in *Kowalskinaclia* **gen. nov.** (Fig. 17A), *Privatenaclia* **gen. nov.** (Fig. 17C) and *Riconaclia* **gen. nov.** (Fig. 16C). In the remaining genera, M2 and M3 are stalked in around 1/2 of their length (Figs 16-17). The presence of both hindwing anal veins (1A+2A and 3A) appears to be stable, except *Mauricenaclia minuta* **comb. nov.** (Fig. 17D-E), but – similarly to the variation in forewing radial veins – should be treated with caution (see discussion).

Wing scales modifications. The reviewed taxa exhibit different forms of wing scale modifications (Figs 18-25), of which the most common is semi-transparency of blotches. This phenomenon is based on the reduction of the scale size on the blotches, both on the upper- and underside of the wing (Fig. 18A-B). The semi-transparent blotches are never devoid of scales, which differ from slightly narrowed (Figs 18A, 19A-B) to distinctly shortened and "deformed", although maintaining the arrangement of ridge-lamellae and microribs (Fig. 19C-F).

A peculiar exception are male hindwings of *Mauricenaclia minuta* **comb. nov.** (Fig. 18C-D), *M. octopunctata* (Rothschild, 1924) **comb. nov.** (Fig. 18E-F) and *M. peyrierasi* **comb. nov.** (Fig. 18G-H), in which the modified, narrowed scales are present only on the upperside, whilst the underside is covered with regular ones (see also remarks for the genus in Systematics). Additionally, the latter species possess fully developed, but completely transparent scales on the part of the hindwing upperside (Fig. 18G) and also on the forewing underside (Fig. 22C, F), which to our best knowledge is unique among all Madagascan Syntomini.

Blotches semi-transparency is more common and distinct in the forewing, but it is differently expressed among the genera, and partly species-specific. The only genus with a complete lack of semi-transparency is *Skippernaclia* **gen. nov.** Moderate semi-transparency of the forewing is present in *Thyrosticta* and *Kowalskinaclia* **gen. nov.**, and of both wing pairs – in *Riconaclia* **gen. nov.** The genera *Privatenaclia* **gen. nov.**, *Julienaclia* **gen. nov.**, *Mauricenaclia* **gen. nov.** and *Melanonaclia* have distinctly semi-transparent fore wing blotches, and the three latter genera – also the hind wing blotches. However, the hind wing blotches are species-specific: in the species of *Julienaclia* **gen. nov.** and *Melanonaclia*, with yellow hindwing colouration, the semi-transparency is completely absent. Finally, in the genus *Mortinaclia* **gen. nov.** both the fore- and hindwing blotches are always distinctly semi-transparent (see Systematics and relevant figures therein).

Other than the semi-transparent blotches, males of some species possess a longitudinal narrow streak of reduced, pale yellow to creamy scales, located above or on both sides of the 1A+2A vein. This structure is always absent in females (Figs 20, 21). Such an area was detected in *Privatenaclia seguyi* (Griveaud, 1964) **comb. nov.** (Fig. 20 A-B, absent in the remaining two species of the genus), *Riconaclia bimacula* **comb. nov.** (Fig. 20C), *Melanonaclia trimacula* **comb. nov.** (Fig. 20D), *M. luctuosa* (Fig. 20E, absent in the other species of the genus), and *Mortinaclia* **gen. nov.** (Fig. 20F). In the latter genus, the streak additionally shimmers lilac when set at a certain angle (Fig. 20F). Scales forming the streak in *P. seguyi* **comb. nov.** (Fig. 21), in general shape and size, are similar to those covering the semi-transparent forewing blotches (Fig. 19C-F) but differ from them in possessing numerous holes.

Further, the males of *Mauricenaclia minuta* **comb. nov.**, *M. octopunctata* **comb. nov.**, and *M. peyrierasi* **comb. nov.** in the forewing underside, below DC hind margin and CuA1, have a field composed of a few types of morphologically different scales, of ochraceous to pale grey colouration, with slight reflective properties (Figs 22-25). In *M. octopunctata* **comb. nov.** the area viewed from a certain angle has a metallic sheen, blue in the central part, passing through green to purple in the outer part (Fig. 22B, E). That effect was not observed in the two remaining species discussed in this paragraph. *Mauricenaclia minuta* **comb. nov.** along CuA2 has a suboval area of distinctly different, shiny, subrectangular and elongate scales (Fig. 22A, D, 23), which are only slightly narrowed basally and roundly incised along the terminal margin (Fig. 23B-C). The longitudinal ridges are parallel to each other and rarely anastomosing, formed by overlapping ridge-lamellas, with the interridge areas provided with very indistinct microribs, which seem to be fused with the background, and provided with numerous grain-like and irregular flake-like protrusions (Fig. 23D). In *M. octopunctata* **comb. nov.** and *M. peyrierasi* **comb. nov.** a similar but less distinct, suboval field of scales is present, located along 1A+2A (Fig. 22 B-C, E-F). In *M. octopunctata* it is formed by short scales, rounded in the basal portion and subrectangular terminally, with rarely anastomosing longitudinal ridges, similar to those in *M. minuta*. However, in contrary to the latter species, the inter-ridge areas in *M. octopunctata* are provided with distinct, bow-like micro ribs, some of them interrupted in the central part, transversely extended and terminated in the interridge area (Fig. 24). The analogical portion of the forewing underside in *M. peyrierasi* **comb. nov.** is composed of completely transparent scales (Fig. 22F), which gives the field a pearl-grey, slightly shiny and “oily” appearance (Fig. 22C, see also the relevant figures in Systematics). The scales are of a shape and size similar to those of *M. octopunctata* **comb. nov.**, but distinctly incised at the pedicel, with the microribs arranged into a herringbone pattern rather than arched, and their transverse protrusions are longer than in *M. octopunctata* and fused with the next microribs, not terminated in the interridge area (Fig. 25).

Finally, among the reviewed taxa, the most distinct and unique wing scale modifications are present in the male of *Melanonaclia nigra* (Figs 26-27). In the basal portion of its forewing underside, above 1A+2A, it has a longitudinal streak of ochraceous, elongate and erect, spine-like scales (Fig. 26A, C), which are empty inside, with the walls formed by a dense meshwork (Fig. 26D-F). On the hindwing upperside, around the area of DC, there is an irregular field of sooty black, “oily” shiny scales (Fig. 26B), which are enlarged and arranged almost upright, leaning one on another (Fig. 27A). The SEM visualisation of these scales revealed them to be rather solid inside than meshy, with numerous holes in the walls, some of which contain crystal-like structures. It can be hypothesised that the crystal-like particles are PTPs, and the modified scales of the forewing underside and hindwing upperside together form an androconium (see discussion).

Female abdomen. In all genera covered in this paper, the 8th tergite of the female abdomen is reduced to a narrow, bar-like to rib-like plaque, laterally fused with the lateral arms of lamella postvaginalis and transforming into apophyses anteriores (Figs 3D-E, 28A), and located inside the abdomen, ventroterminally to the 7th tergite (Fig. 28A-B). The 7th sternite is elongate and often provided with a transverse, groove-like cavity, in a non-descaled abdomen looking like it is composed of two segments (Fig. 28C-D).

Female ventral pheromone glands. The presence or absence of the ventral pheromone glands is another genus-specific character (Tab. 3). The shape and size of both dorsal and ventral glands are highly variable, even at the intraspecific level, but some genus-specific characters can be identified as well, especially in the proportion of the length of the dorsal and ventral glands (Fig. 29, see Systematics).

Eggs. Eggs of four species of Madagascan Syntomini are described for the first time.

Kowalskinaclia vieui **comb. nov.** egg first description (laid by the female MAD_060) (Fig. 30) Subspherical, diameter around 0.56 mm. Entire egg surface covered with cellular-type exochorion sculpture, with the cells separated by well defined, narrow ribs. Micropylar plate in form of shallow, indistinct depression on dorsal pole, with 3-4 micropyles. Micropylar rosette composed of 6-7 subtrapezoidal or subrhomboidal, elongate, wedge-shaped cells, with angular outer margins. Micropylar zone composed of 10-11, penta- to heptagonal cells, with dominance of hexagonal ones. The remaining surface not differing distinctly from the micropylar zone, with rhomboidal to heptagonal cells. Aeropyles absent in micropylar zone, appearing in the outer corners of the cells forming the first ring around micropylar zone, and present in entire remaining surface, only in the cell corners, in the form of small holes, surrounded by subtriangular to round ring, not protruding over the ribs edges.

Privatenaclia seguyi **comb. nov.** egg first description (dissected from the abdomen of the female DL_2973) (Fig. 31).

Subspherical, diameter around 0.65 mm. Only the dorsal pole covered with cellular-type exochorion sculpture, with cells separated by well defined, narrow ribs. Micropylar plate in form of shallow, indistinct depression on dorsal pole, micropyles unavailable. Micropylar rosette composed of seven elongate, petaloid cells with rounded outer margin, separated by well defined, narrow ribs. Micropylar zone composed of 11 penta- to heptagonal, irregular cells of similar size. Around micropylar zone two additional rings of cells, not differing from micropylar zone, without aeropyles, gradually disappearing on the outside. The remaining surface without cell-like sculpture, but densely covered with irregularly scattered aeropyles in the form of small, round holes, located at the bottom of small, subtriangular to round well-like rings. Some of the rings connected in pairs by straight, indistinct ribs.

Mauricenaclia minuta **comb. nov.** egg first description (dissected from the abdomen of the female DL_02-325, and laid by the female MAD_299) (Fig. 32).

Subspherical, diameter around 0.63 mm. Entire egg surface covered with cellular-type exochorion sculpture, with the cells separated by well defined, narrow ribs. Micropylar plate in form of well defined depression on dorsal pole, in the form of irregular, six-pointed star, with micropyles located in its outer corners. Micropylar rosette composed of 7-8 subtrapezoidal or subrhomboidal (mostly pentagonal), elongate, wedge-shaped cells, with angular outer margins. Micropylar zone composed of around 15-16 irregular, mostly narrow and elongate penta-hexagonal cells. The remaining surface not differing distinctly from the micropylar zone, covered with rhomboidal to heptagonal cells, but regular, not elongate. Aeropyles absent in micropylar zone, in the remaining area numerous, in the form of small, dot-like holes, surrounded by not prominent, subtriangular to round well-like rings, located mostly also along cell walls, but also in the corners. Part of the lateral surface of the eggs (oriented with the dorsal pole up) both laid by the female and retrieved from the abdomen, seems to be partially exfoliated to some extent and densely covered with small holes and narrow grooves of unknown origin, located mostly along the cell margins, but also within the cells.

Mauricenaclia octopunctata **comb. nov.** egg first description (dissected from the abdomen of the female DL_02-26) (Fig. 33).

Subspherical, diameter around 0.63 mm. Entire egg surface covered with cellular-type exochorion sculpture, with the cells separated by well defined, narrow ribs. Micropylar plate in form of shallow, indistinct depression on dorsal pole, micropyles unavailable. Micropylar rosette composed of 8 elongate, regularly petaloid cells. Micropylar zone composed of 12 elongate and narrow, irregular, subtrapezoidal to subrectangular cells. The remaining surface not differing distinctly from the micropylar zone, covered with relatively large, irregular, predominantly hexagonal cells, with only some penta- and heptagonal ones. Aeropyles absent in micropylar zone, in the remaining area very few and indistinct, hardly visible, in the form of small, dot-like holes, not surrounded by any additional ring-like structure, located not only in cell corners, but also along their walls.

Distribution

In total, the specimens of the species covered in this study were collected or recorded in 191 localities (Fig. 34, Tab. S3).

We were unable to d\s only a few following localities from the labels: i) “Antsianaka” – according to Viette (1991), located in the area E of the Lake Alaotra, thus plausibly within the current area of PN Zahamena; ii) “Sahajinga, N. Ouest Behanana” – plausibly misspelt “Sahajinja” and/or “Bealanana”, there are a few places named Sahajinja, in different parts of Madagascar; iii) “Ankandro” – an unidentified Catala’s collecting locality; iv – “Ambinanirano [or Ambinanirana], Kieca” – perhaps misspelling.

Additionally, single specimens are labelled very generally, with “Nord et Centre de Madagascar”, “Plantations du Sambirano” and “Tamatave et forêts d'Alahakato” - the latter perhaps can be misspelt “Alakato” (Dorr, 1997).

Additionally, three localities: Antananarivo, Fianarantsoa, and Vondrozo are in some cases doubtful, considering the specimen's origin (from collectors: Le Moult, Brothers Perrôt, and Lamberton), and the overall distribution of the species in question. In the case of the insects collected in “Fianarantsoa” by Brothers Edouard and Benoni Perrôt, already Alluaud (1903: 641) found them unreliable and indicated, that they “actually come from the region of Kioko (or Ankioko), a village located two days’ walk to the east from Fianarantsoa, on the old

Mananjary trail, in the middle of the Tanala forest, a region which has absolutely no connection with the surroundings of Fianarantsoa". Additionally, the materials from the Perrôts' collecting are often labelled with long collecting time, comprising even a few months ("semestre" / "trimestre"). In the case of M. Charles Lamberton and Eugène Le Moult, it is not clear if they collected the specimens themselves in the field; Le Moult appears not to have even visited Madagascar. More likely, they amassed or bought material collected by others. The majority of the specimens of Madagascan Syntomini collected by Lamberton are labelled as Southern Madagascar ("Sud de Madagascar"), and even those with more precise locality share the same date of receipt, 04.1922 ("Reçu de M. Lamberton en avril 1922"). It has been already verified that the collecting localities of Lamberton's specimens are in some cases unreliable regarding the actual species ranges (Viette 1962, see also Wiorek et al. 2021). Finally, all the specimens by Le Moult are labelled with "Antananarivo", the capital city of Madagascar, likely merely reflecting where collected specimens were traded from. Indeed, during the few decades of the French entomologists' presence in Madagascar (early 1950s-1970s), only one species of Madagascan Syntomini, *Melanonaclia trimacula* **comb. nov.**, was actually recorded from Antananarivo (Tab. S1, see also Systematics).

Systematics

Genus *Thyrosticta* Hampson, 1898

Type species: *Naclia quadrimacula* Mabille, [1879]: 85, by original designation, a junior subjective synonym of *Pseudonaclia sylvicolens* Butler, 1878 (Figs 35-39A)

Thyrosticta quadrimacula Griveaud 1964: 84, pl. I, fig. 53.
Thyrosticta sylvicolens Viette 1990: 169.

Pseudonaclia sylvicolens Butler, 1878: 293, holotype: ♂, NHMUK, NHMUK010620992 (Fig. 35A);
= *Naclia quadrimacula* Mabille, [1879]: 85, holotype: ♂, NHMUK, NHMUK010620991 (Fig. 35B), recognised by Viette and Fletcher (1968);
= *Naclia perpetua* Oberthür, 1893: 3-4, pl. I, fig. 6, holotype: ♀, NHMUK, NHMUK010620987 (Fig. 35C);
= *Naclia quadrimacula* var. *confluens* Oberthür, 1893: 3, pl. 1, fig. 10, holotype: ♀, NHMUK, NHMUK010621036 (Fig. 35D);
= *quadrimacula* ab. *holoxantha* Zerny, 1912: 37;
= *Naclia quadrimacula* Oberthür, 1893: 2-3, pl. I, fig. 9, non Mabille, [1879] (see: Zerny 1912);
= ab. 1 *confluens* Hampson, 1898: 131;
= ab. 2 *quadrimacula* Hampson, 1898: 131.

Material. 75 specimens (ISEA PAS - 1 ♂; MNHN - 16 ♂♂, 7 ♀♀; NHMUK - 7 ♂♂, 13 ♀♀; PZBT - 21 ♂♂, 10 ♀♀) (Tab. S1)

Diagnosis. Male antennae distinctly bipectinate (Fig. 35) (in Griveaud 1964 inconsistently stated either as bipectinate or quadripectinate), with the flagellomeres symmetrical on both sides of the antenna, and a flagellomere around 4x longer than its shaft (Fig. 6A-B). The most similar bipectinate antennae, with a similar proportion of dimensions, are present in *Vadonaclia marginepuncta* Griveaud, 1964 - however, in that species, the flagellomeres are asymmetrical, in the basal portion of the antenna around 2x longer on the outer side than on the inner side, and equal in the terminal portion. In the species of *Dubianaclia*, which have bipectinate antennae, flagellomeres are at most 1.5-2x longer than the rami (and some *Dubianaclia* species have piliform antennae in both sexes).

In the male genitalia (Fig. 36): gnathos in the form of well sclerotised plaque, entering uncus basoventrally, see redescription below.

In the female genitalia (Fig. 37): shape of the signum, composed of two pairs of pouch-like cavities covered with spine-like scobinations, see redescription below.

Thyrosticta sylvicolens superficially is the most similar to the species from the genus *Dubianaclia*, to which is also sister according to our molecular results (Fig. 5B). However, it lacks the terminal black ring on the abdomen, characteristic to *Dubianaclia*, having instead differently expressed dorsal row of ochraceous-brown blotches (Fig. 35).

The species can be further defined by the following set of morphological characters: Pencil-like tuft behind male foreleg coxa absent (present in *Dubianaclia*); hindleg tibia with a single additional spur; forewing as in Griveaud (1964: Fig. 192) regularly subtriangular, not elongate, with hind and outer margins of approximately equal length, 1A+2A terminated at the well defined tornus, four radial veins; forewing blotches: basal: fused fm_2+m_1 - elongate and comprising the wing base (in *Dubianaclia* separated from the wing base by a narrow stripe of brown scales), medial: fused $m_2+fm_3+m_3$, distal: m_4, fused m_5+m_6, slightly semi-transparent blotches present; hindwing almost like in Griveaud (1964: Fig. 192, but both 1A+2A and 3A present), subtrapezoidal to suboval, costal margin straight, slightly arched medially; Sc+Rs+M1 straight, fused, M2 and M3 stalked in around basal 1/4 of their length; Hindwing with one large medial pale yellow blotch without semi-transparency;

In the male genitalia (Fig. 36), described and illustrated here correctly for the first time, the terminal part of valva is narrowed and hook-like (similarly as in part of *Dubianaclia* species), claw-like arms of tegumen and curved hook on vesica absent (whilst present in majority of *Dubianaclia* species).

Based on a number of characters mentioned above, and especially the male antennae being unique among all Madagascan Syntomini we decide to keep it as a separate, monotypic genus.

Taxonomic note. The name *quadrimacula* was introduced first by Boisduval *in museo* (Oberthür 1893), which is supported by a handwritten label characteristic for specimens from the Boisduval's collection, attached to the specimen deposited in NHMUK (NHMUK010620991) (Fig. 35B), and this specimen was recognized as the holotype of *Naclia quadrimacula* by Viette and Fletcher (1968).

Griveaud (1964) indicated that the name *quadrimacula* was published by Mabille in April 1878, and thus it would have priority before the name *sylvicolens*, published by Butler in October 1878. Although the date 15 April 1878 is indeed given in the foreword of Mabille's work (Fig. 38A), the fascicle of the Bulletin for the year 1878 (the third volume) was published in April 1879, as indicated on the wrapper (Fig. 38B). Thus, the name *sylvicolens*, published in October 1878 (Fig. 38C), has priority over *quadrimacula*.

Analyses of the type specimens of *Naclia perpetua* and *Naclia quadrimacula* var. *confluens* revealed no morphological differences from *Pseudonaclia sylvicolens* and thus we maintain these taxa as junior subjective synonyms of the latter, as proposed by Hampson (1898).

The taxon interpreted by Hampson (1898) and Zerny (1912) as "*Naclia quadrimacula* Oberthür, 1893, non Mabille, [1879]", according to the information stated in the Oberthür's original work (1893), was perhaps intended to be a redescription of the species originally described by Mabille [1879] but based on a larger number of specimens in better condition. However, Hampson (1898) utilised this name to classify one of two "aberrations" of the species proposed by him – the one with the abdomen devoid of the dorsal stripe.

The name *quadrimacula* ab. *holoxantha* was most probably introduced by Zerny (1912) as a *nomen novum* for the form "*confluens*" (referred to as "ab.", not "var." originally described by Oberthür, 1893), but without any comment or justification. However, Seitz (1930) interprets *holoxantha* as a form separate from *confluens* and characterised by the enlarged forewing blotches, providing illustrations of both of them.

Male genitalia redescription (Fig. 36)

Tegumen moderately sclerotised, narrow, subdorsally with deep U-shaped concavity of anterior margin, widening laterally, then again narrowing towards vinculum, with which is incompletely fused; uncus moderately sclerotised, basal portion flattened dorsoventrally, of rhomboidal shape, bent downwards, terminal portion narrowed and flattened laterally, forming beak-shaped cavity open ventrally, with pointed tip; sublateral arms of tegumen originating medially on its posterior surface, moderately sclerotised, oriented upwards, fused with membrane protruding along dorsal surface of tegumen, covered with minute scobinations; gnathos originating in the cavity at uncus base, widening into arrowhead-shape, moderately sclerotised plate, with two longitudinal, sublateral, heavier sclerotised ribs; vinculum moderately sclerotised, very narrow, laterally reaching slightly above basodorsal part of valva, junction with tegumen membranous; saccus wide and short, flattened dorsoventrally and oriented backwards, open at the base, in a form of subtriangular pocket; valva elongate, reaching beyond uncus; basal 2/3 subtrapezoidal, rapidly narrowing terminally into claw-like tip, distinctly curved inwards and pointed; costal margin straight, slightly rolled up ventrally forming a rib; sacculus in basal portion sinuous, with distinct cavity, remaining portion straight, towards terminal narrowing, covered with elongate, erect, dense setae; ventral side of the claw-like tip with a few minute scobinations and a few setae, shorter than those on sacculus; outer surface of valva covered with minute, rounded, slightly protruding scobinations; phallus elongate, straight and tubular, very slightly narrowing towards tip, weakly sclerotised, except for longitudinal plate in terminal portion on right wall; vesica membranous, distinctly elongate, protruding leftwards, at right angle to phallus, then behind membranous diverticulum again curved leftwards, diverticulum dorsally with narrow, longitudinal cornutus in form of a fused, subtriangular, tooth-like protrusions forming saw-like plaque.

Remarks: Griveaud (1964) does not provide the code numbers of *T. sylvicolens* genitalia slides, which were described and depicted in the paper. The slide labelled as a male of *T. sylvicolens* in the MNHN collection has the number 262, and the male specimen of undoubtedly *T. sylvicolens*, labelled with the corresponding number and without abdomen, is deposited in the collection of PZBT. However, that slide, matching the drawing in Griveaud (1964), apparently was not made of that PZBT specimen, as all other males examined by us possess the distinct, hook-like terminal protrusion on the valva.

Female genitalia redescription (Fig. 37)

Anal papilla subrectangular, densely covered with minute scobinations, with sparse, elongate setae of different lengths, more dense laterally on dorsal side; narrow and elongate, lobate membranous protrusions, parallel to each other located between ventral margins of papillae, in the terminal portion densely covered with minute scobinations; apophysis posterioris slightly longer than anal papilla, moderately sclerotized straight, terminally flattened into a leaf-shaped protrusion; apophysis anterioris of around 1/2 of the length of anterioris, straight and needle-like, originating from well developed, subrectangular lobe; dorsal pheromone glands in form of two tapes located dorsomedially, shorter than anal papilla, narrow and of uniform width; ventral pheromone glands in form of very short terminally broadened protrusions, located lateroventrally; 7th sternite moderately sclerotised, enlarged, and laterally extended to the abdomen terminal margin, embracing 8th sternite around; 8th sternite reduced to well sclerotised, narrow and elongate, subtrapezoidal lamella antevaginalis, directed slightly rightwards, medially densely covered with minute, elongate, spine-like scobinations and resembling the cat tongue surface, terminal margin with small U-shaped incision, distally concave into small cavity and laterally extending into basoventral arms of apophysis anterioris; 8th tergite transformed into moderately sclerotised, narrow plaque, sublaterally with rib-like proximal margin, lateroterminally widening towards the base of apophysis anterioris; ostium bursae large, well sclerotised, suboval and right-skewed, forming a prominent but weakly sclerotised cavity; antrum well sclerotised, narrow, tubular, slightly arched and reaching to basal margin of 7th sternite, provided with longitudinal ribs; ductus bursae originating rightwards at right angle from terminal portion of antrum, narrow and tubular, entirely membranous, with longitudinal plicae, smoothly transforming into subconical basal portion of corpus bursae; corpus bursae regularly suboval, pouch-like and not elongate, covered with longitudinal plicae and small scobinations; medioventrally with two signa, in 1/3 and 2/3 of the length of corpus bursae, of equal size, each in the form of a pair of longitudinally elongate, suboval invaginations arranged symmetrically to each other along the main axis of corpus bursae, covered with tiny, tooth-like protrusions; ductus seminalis membranous, tubular and very narrow, originating at the fusion of antrum and ductus bursae, from the right wall.

Immature stages. Unknown.

Biology. Individuals are collected by netting by day, while there is no data on attraction to light. Specimens were collected from February to April and from August to November. In the corpus bursae of a single female (MNHN, EL82750), collected on 22-29.11.1971, one collum was found. Associated with evergreen, humid forest, mostly at mid but also low elevation.

Distribution (Fig. 39A). Eastern Madagascar, in the regions of: Sava (Anjanaharibe), Alaotra-Mangoro (Befody, south to Analamazaotra Reserve), Atsinanana (Brickaville, 50 km W of Mahanoro), Vatovavy Fitovinany (Ranomafana PN, including ValBio Centre), Matsiatra Ambony (Vohiparara, Ifanadiana, Fianarantsoa(?)), Atsimo-Atsinanana (Madiorano), Anosy (near Tolanaro, Anosyennes Mountains). From around 50 up to 1600 m elevation.

The record from Fianarantsoa by Brothers Perrôt, however not remote from other localities, needs to be confirmed (see Results). Most of the localities are within large and protected patches of forests, and only some are currently devoid of primary vegetation (LOFM 2022).

Skippernaclia **gen. nov.**

Type species: *Thyrosticta lacrimata* Griveaud, 1964

Diagnosis. In the female abdomen, the junction between the 6th and 7th sternites is lateroterminally provided with semicircular, pouch-like cavities (Fig. 40). Additionally, the corresponding area of the 7th sternite is provided laterobasally with shallow cavities covered with scales (see below). Somehow similar structures are present in the genus *Melanonaclia* (in the sense defined below in this paper), but of different shape, varying among species from subtrapezoidal to rounded, and located on the extension of the differently expressed groove running along the sternite lateral margins, which is absent in *Skippernaclia* **gen. nov.** In *Kowalskinaclia* **gen. nov.** there are also present lateral cavities, which are located terminally on the 7th sternite, not on its basal margin.

In the male genitalia (Figs 41-43): proximal margin of tegumen dorsomedially with small, subtriangular, dorsoventrally flattened shield-like protrusion oriented forwards, parallel to dorsomedial surface of tegumen; tegumen very narrow laterally and prominent dorsomedially, elongate subtrapezoidal, protruding, medially wider than the length of the uncus itself; vesica terminally with a few irregular diverticula, of which one always roundly terminated and provided with a bunch (not a row) of extremely elongate, prominent and heavily sclerotised, spine-like cornuti.

In the female genitalia (Figs 44-47): corpus bursae in the apical portion provided with single, distinct, heavily sclerotised, clamp-like curved plaque, with differently expressed spine-like and claw-like protrusions of species-specific arrangement. Somehow similar single basal plaque is present in the genus *Tenuinaclia* Griveaud, 1964, but of a completely different shape, either short and suboval (in *T. andapa* Griveaud, 1964 and *T. oberthueri* (Rothschild, 1911)), or distinctly elongate and narrowed medially, with short transverse protrusion (in *T. melancholica* Le Cerf, 1921) (Griveaud 1964).

Remarks. The “Group of *T. lacrimata*”, treated by Griveaud (1964) as the “second section” of *Thyrosticta* was characterised based on the male antennae and genitalia (Griveaud 1964), but neglecting some distinct, unique traits.

The genus can be further defined by the following set of characters: small moths with the colouration uniformly ochraceous brown to dark brown / almost black, with such unicolourous abdomen and legs, and wing blotches and body pattern from pale yellow to intensively ochraceous-orange (Fig. 48). The most similar species from other genera of

Madagascan Syntomini are discussed in the species diagnoses below. Antennae piliform in both sexes, ventrally densely covered with very short erect setae, with a very subtle sexual dimorphism - in the females each antennomere is provided with a pair of longer and thicker setae, absent in the male (Fig. 7G); the pencil-like tuft of scales behind the male foreleg coxa present, consisting of very thin, pale yellow to creamy-whitish scales (Fig. 9E); additional hindleg tibial spurs absent (Fig. 13A); forewing narrowed but not distinctly elongate, hind margin smoothly transforming into the slightly longer outer margin, without distinctly angular tornus, venation with at most four radial veins (see also the remarks for *S. lacrimata* **comb. nov.** and *S. vestigii* **comb. nov.**), DC outer margin medially slightly reduced, laterally on both edges formed by styli from which originate veins M1 and M2, respectively (Fig. 14A-B). Forewing pattern: basal and medial blotches differently expressed in *S. vestigii* **comb. nov.** and in the remaining species, distal: fused m_4+am_4+m_5+m_6, sometimes am_4 missing, semi-transparency absent. Hindwing elongate, with costal and hind margins almost parallel to each other, Sc+Rs+M1 straight, fused but sometimes slightly bifurcated in very terminal portion (Fig. 16A-B), M2+M3 basally stalked along around 1/2 of their length, 3A present; hindwing pattern: one large basomedial blotch, or two smaller blotches, fused by a narrow stripe, semi-transparency absent;

In the male genitalia, sublateral arms of tegumen absent (Figs 41-43);

In the female genitalia, ventral pheromone glands present, 2x longer than dorsal ones (Figs 44-47).

Skippernaclia **species determination key based on adult characters**

1. Hindwing with two yellow blotches, one in basal and one in distal portion, completely separated, or fused by a narrow streak, forewing with one basal and one medial blotch, separated from each other, or at most fused by a narrow streak (Fig. 48A-I, K-L).....................................2

- Hindwing with a single, large, yellow medial blotch, forewing with basal and medial blotches fused into one, large longitudinal blotch covering basal 1/2 of the wing (Fig. 48J)..*S. vestigii* **comb. nov.**

2. Forewing blotches m_5 and m_6 of equal size, fused into regular, 8-shaped blotch (Fig. 48K-L)...*S. leesi* **sp. nov.**

- Fore wing blotch m_5 smaller than m_6, fused into irregular, subtrapezoidal to subtriangular blotch, which can be fused with or separated from blotch m_4 (i.e. blotch am_4 can be present or absent) (Fig. 48A-I).....................................*S. ankaratra* **comb. nov.** / *S. lacrimata* **comb. nov.***

*diagnostic characters of these two species, indicated by Griveaud (1964), appear to create a continuous variation, making them superficially indistinguishable (see remarks for *S. lacrimata* **comb. nov.**).

***Skippernaclia* species determination key based on male genitalia**

Remarks. The male of *S. leesi* **sp. nov.** remains unknown.

1. Terminal portion of vesica with a bunch on narrow and elongate spines, at their base distinctly bent downwards, arranged at right angle to the main axis of vesica (Fig. 41)..*S. lacrimata* **comb. nov.**

- Terminal portion of vesica with a bunch on narrow, elongate, straight spines, protruding forwards and parallel to the main axis of vesica (Figs 42-43)..*S. ankaratra* **comb. nov.** / *S. vestigii* **comb. nov.***

*In the materials available for our study, the genitalia of these two species are indistinguishable, especially since the only preparation of the male of *S. vestigii* **comb. nov.** (Fig. 43), deposited in MNHN (P. Griveaud slide No. 431), has uneverted vesica.

***Skippernaclia* species determination key based on female genitalia**

1. Basal signum on corpus bursae arranged horizontally and located laterally, clasping corpus bursae below the junction with ductus bursae (Fig. 44)..........................*S. lacrimata* **comb. nov.**

- Basal signum on corpus bursae arranged vertically, located in the apical portion of corpus bursae, above the junction with ductus bursae (Figs 45-47)...2

2. Basal signum located apically and not extended laterally on either side of corpus bursae, in the form of a rib, medially without any protrusion, on one end with three short, straight spine-like protrusions, on the other end with single, elongate, claw-like spine (Fig. 47)...*S. leesi* **sp. nov.**

- Basal signum extended laterally on the left wall of corpus bursae (Figs 45-46)..3

3. Basal signum elongate, rib-like, shorter arm located at the apical portion of corpus bursae, widened and palm-like, provided with a row of four straight spines of different lengths, arranged from the shortest to the longest one; the opposed arm reaching to 1/2 of the length of corpus bursae, in terminal portion provided with a few small, tooth-like protrusions of different sizes (Fig. 46)...*S. vestigii* **comb. nov.**

- Basal signum in the form of well sclerotised plaque, not a rib, laterally reaching up to 1/2 of the length of corpus bursae, entirely covered with spine-like protrusions of different lengths, arranged in groups separated by small plain areas; lateroterminal portion in some specimens weakly sclerotised, transforming into a field covered with small scobinations (Fig. 45)...*S. ankaratra* **comb. nov.**

Skippernaclia lacrimata **comb. nov.** (Figs 39 B, D, 41, 44, 48A-D)
Thyrosticta lacrimata Griveaud, 1964: 87, pl. I, fig. 54; Viette 1990: 169.
Holotype: ♂, MNHN, EL65165 (Fig. 48A), P. Griveaud slide No. 264 (Fig. 41F-G), by original designation.

Material. Four specimens (MNHN - 2 ♂♂, 1 ♀; NHMUK - 1 ♂) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys.
Forewing pattern is identical in *S. lacrimata* **comb. nov.** and *S. ankaratra* **comb. nov.**: basal blotches: fused fm_2 and m_1 (indistinct), medial: m_2 only, distal: m_4+am_4+m_5+m_6 fused into sinuous stripe, or am_4 missing (Fig. 48A-D).

Among all other Syntomini species, superficially the most similar to *S. lacrimata* **comb. nov.** (and *S. ankaratra* **comb. nov.**) are: *Maculonaclia altitudina* Griveaud, 1964 and *Maculonaclia brevipenis* Griveaud, 1964, but contrary to all *Skippernaclia* **gen. nov.** species, the former possess two medial blotches in the forewing, the second of which is located below DC hind margin, and is narrow and elongate, streak-like, and the latter has no basal blotch of the forewing, and small, dot-like second medial blotch. Additionally, both species have the shape of genitalia completely different from *Skippernaclia* (Griveaud 1964).

Taxonomic note. Our research revealed *Skippernaclia lacrimata* **comb. nov.** and *S. ankaratra* **comb. nov.** to be superficially indistinguishable, but well defined by the shape of genitalia (Figs 41, 42, 44, 45).

The ochraceous-yellow marks on the head and thorax, indicated by Griveaud (1964) to be completely absent in *S. ankaratra* **comb. nov.** and present in *S. lacrimata* **comb. nov.**, appear to vary across both species from well developed, through reduced to absent, and - for example - all three paratypes of *S. ankaratra* **comb. nov.** (deposited in MNHN), with the forewing shape matching the holotype, in fact, do possess yellow blotches on the tegulae. Additionally, the forewing distal blotches, indicated by Griveaud (1964) to form a continuous streak in *S. lacrimata* **comb. nov.** and two separate blotches in *S. ankaratra* **comb. nov.**, are also variable, and based on the genitalia, we have found specimens of *S. lacrimata* **comb. nov.** with an "*ankaratra*-like" forewing pattern.

Moreover, based on the results of our morphological and molecular research, the female allotype (MNHN, EL65166) of *S. lacrimata* **comb. nov.** (Fig. 48F) is not conspecific with the male holotype (MNHN, EL65165) (Fig. 48A). Designation of the allotype done by Griveaud (1964) was arbitrary, as that specimen was collected at different times, and in an unknown locality. The male specimen from Marojejy (CLV_3 - EL83636, Fig. 48C)) analysed by us, undoubtedly belonging to *S. lacrimata* **comb. nov.** based on the genitalia, in our molecular results (Fig. 5B) turned out to be conspecific with the female specimen (CLV_7 - EL83635, Fig. 48B) collected in the same locality and at the same time. The genitalia of that *S. lacrimata* **comb. nov.** female (Fig. 44) differ from those of the allotype of its species (Fig. 45E-F), described by Griveaud (1964). Further, the "allotype" specimen of *S. lacrimata* **comb. nov.** appeared to belong to *S. ankaratra* **comb. nov.** (Fig. 45A-D) (see diagnosis of the species below). Thus, here we describe the female of *S. lacrimata* **comb. nov.** correctly for the first time.

Male genitalia redescription (Fig. 41)

Tegumen moderately narrow and elongate, subtrapezoidal, U-shaped, lateral arms completely fused with vinculum; uncus multidimensional, lateral margins in proximal half convex, remaining portion flattened dorsoventrally and dorsally provided with longitudinal rib, distal portion narrowed laterally into claw-like protrusion, terminated with small, pointed hook, dorsal and lateral surfaces covered with sparse, erect setae of varying lengths;

vinculum very narrow, V-shaped; saccus well developed, subconical; juxta well developed, in form of moderately sclerotised ring with moderately wide walls, located medially in the apparatus, with irregular margins and V-shaped incision frontally on ventral wall;

valva narrow and elongate, of the length approximately equal to uncus, basal portion irregularly subtriangular and flat, terminal portion narrow, claw-like and three-dimensional, basally on ventral side with bulbous protrusion; costal margin basically straight, slightly sinuous; basal half of sacculus elongate subtriangular, remaining portion straight; both outer and ventral surface of valva covered with sparse, erect setae of different lengths, denser along terminal part of sacculus; phallus tubular, moderately sclerotised, slightly wider in basal portion, indistinctly bent downwards; vesica slightly bent upwards, basal half of the length of phallus, tubular and entirely membranous, terminal half basally on ventral wall provided with small, irregular, well sclerotised plaque, bulbous widened, with a few diverticula, armed with differently expressed sclerotisations; the longest diverticulum located on ventral side tubular, with longitudinal plicae, terminally with around 7 elongate spines, bent downwards; on the right side a very narrow, tubular diverticulum, slightly shorter and with no sclerotisations; medial diverticulum shorter that the two above described, tubular, in terminal part conically narrowing, with dull tip, basally with irregular, angular, curved and well sclerotised plaques; the shortest diverticulum on dorsal wall, provided with irregular sclerotisation;

Female genitalia description (Fig. 44)

Anal papilla subtrapezoidal, moderately sclerotised, terminal margin slightly concave , covered with dense, minute scobinations, and sparse, elongate, erect setae; apophysis posterioris of the length of anal papilla, well sclerotized, straight, slightly sinuous, needle-like; apophysis anterioris of similar length, needle-like; dorsal pheromone glands in form of two separate very narrow and elongate, slightly twisted and narrowing towards the tip, not ramifying membranous tapes; ventral pheromone glands opening lateroventrally, of similar structure but significantly longer; ostium bursae very distinct and well sclerotised, broad and flattened dorsoventrally, semilunar in cross section; sternite 7th wide, moderately sclerotised, covered with dense scobinations, terminal margin folded inwards, basal margin sublaterally slightly curved inwards and densely covered with hard to remove scales; antrum well developed and moderately sclerotised, subtriangular, flattened dorsoventrally and narrowing towards the end, funnel-like; ductus bursae broad, flattened, in terminal portion distinctly curved, dorsolateral wall along its entire length heavily sclerotised, ventrolateral wall completely membranous; corpus bursae basally with bulbous entrance, separated from remaining portion by constriction, remaining part elongate and narrow, regularly subovate, membranous, with dense longitudinal plicae; signum very distinct, in form of horizontal, elongate clamp on the right wall of basal bulbous part of corpus bursae, forming unclosed ring around it, terminally on both ends widened into suboval plaques ventrally provided with 5-6 prominent, straight, claw-like spines on each side, oriented inwards, but not touching each other apically, however distinctly narrowing the tract lumen; on left wall of corpus bursae, in 1/4 and 1/2 of its length, two additional, subrhomboidal signa, consisting of main, medial, horizontal row of a few straight, short spines oriented inwards, and two additional, arched rows of less distinct spines, one above and one below the medial one; ductus seminalis very narrow and elongate, twisted, originating from a distinct, subconical, membranous and plicated diverticulum, located basally on the left side of corpus burse, right below the clamp-like signum; further portion of ductus seminalis provided with elongate, tubular, membranous bulla seminalis.

Immature stages. Unknown.

Biology. The freshly collected specimens available to our study (CLV_7 - EL83635, CLV_3 - EL83636, and NHMUK015109728, Fig. 48B-D) were collected with UV light traps. Individuals undoubtedly belonging to *S. lacrimata* **comb. nov.** were collected in February and October, respectively. Additionally, the remaining, indistinguishable specimens of *S. ankaratra* **comb. nov.** / *S. lacrimata* **comb. nov.** available to our study were recorded in February, March, May, October, and November. In the corpus bursae of one female (CLV_7 - EL83635), collected on 10.02.2018, a single collum was recorded (Fig. 44).

In Marojejy the species is associated with evergreen, lower montane humid forest. Ambatondrazaka (the holotype collecting locality) is currently covered with secondary vegetation (LOFM 2022). For the further comment see the information for *S. ankaratra* **comb. nov.** below.

Distribution (Fig. 39B, D). Northern east of Madagascar, the regions of Alaotra-Mangoro (Ambatondrazaka) and Sava (Marojejy). From around 1040 up to 1320 m elevation.

Skippernaclia ankaratra **comb. nov.** (Figs 39C, D, 42, 45, 48E-I)
Thyrosticta ankaratra Griveaud, 1964: 87, pl. I, fig. 55; Viette 1990: 169.
Holotype: ♂, MNHN, EL65167 (Fig. 48E), by original designation.

Material. Seven specimens (ISEA PAS - 4 ♀♀; MNHN - 2 ♂, 1 ♀) (Tab. S1)
Additionally, 17 unidentified specimens of *S. lacrimata* **comb. nov.** / *S. ankaratra* **comb. nov.** (MNHN - 3 ♂♂, 3 ♀♀; NHMUK - 1 ♀; PZBT - 5 ♂♂, 5 ♀♀) (Tab. S1).

Diagnosis. The species is superficially indistinguishable from *S. lacrimata* **comb. nov.**, but clear diagnostic characters present in the genitalia are provided in the determination keys.

Although the male genitalia in the general appearance are very similar to *S. lacrimata* **comb. nov.**, with clear differences present only in the vesica, the vinculum of *S. ankaratra* **comb. nov.** seems to be basally curved backwards more distinctly than in *S. lacrimata* **comb. nov.** (Figs 41, 42).

Taxonomic note. For the general comments, see the remarks for *S. lacrimata* **comb. nov.** above.

The male holotype of *S. ankaratra* **comb. nov.** (MNHN, EL65167) has not been dissected and still has the abdomen (Fig. 48E). We did not find the specimen from which the *S. ankaratra* **comb. nov.** male genitalia preparation (P. Griveaud slide No. 266) was made, neither in MNHN nor in PZBT. Thus, although the existence of a species separate from *S. lacrimata* is confirmed by the morphology of the genitalia (Figs 41, 42, 44, 45) and molecular results (Fig. 5B), further research is required to verify the taxonomic status of the holotype of *S. ankaratra* **comb. nov.**, considering the superficial indiscernibility from *S. lacrimata* **comb. nov.**, and lack of confirmation in a genitalia dissection.

We decide to assign to *S. ankaratra* **comb. nov.** the female specimen (MNHN, EL65166) designated by Griveaud (1964) to be the allotype of *S. lacrimata* **comb. nov.** (Fig. 48F), which appeared to be not conspecific with the male holotype (Fig. 48A) (see the remarks for *S. lacrimata* **comb. nov.** above). The female specimen of *S. lacrimata* **comb. nov.** (CLV_7 - EL83635, Fig. 48B), available to our molecular and morphological study, and undoubtedly conspecific with the male of *S. lacrimata* **comb. nov.** (CLV_3 - EL83636, Figs 5B, 48C), has a horizontally arranged signum (Fig. 44), which is unique among all *Skippernaclia* species. Thus, we conclude that the “allotype” of *S. lacrimata* **comb. nov.**, with horizontally arranged signum (Fig. 45E-F) is conspecific with the four female specimens of *S. ankaratra* **comb. nov.** examined by us (Fig. 5B, 48G-I). Although we did not have a male of *S. ankaratra* **comb. nov.** available for our molecular study to verify their conspecifity molecularly, this approach is supported also by the distribution of the collecting localities, and more parsimonious than establishing a new species.

Thus, below we describe the female of *S. ankaratra* **comb. nov.** for the first time.

Male genitalia redescription (Fig. 42)

Tegumen vert narrow laterally, medially forming prominent, protruding, subtrapezoidal plate, narrowing towards uncus base, and longer than uncus itself, U-shaped, completely fused with vinculum; uncus basally narrow and membranous in submedian portion, on lateral margins with narrow longitudinal rib on each side; remaining portion, dorsoventrally flattened, dorsally provided with longitudinal rib, terminal portion gradually narrowing towards small, pointed hook, dorsal and lateral surfaces covered with sparse, erect setae of varying lengths; vinculum very narrow, V-shaped, basally moderately curved backwards; saccus well developed, in a form of elongate, pointed, subconical protrusion oriented downwards and slightly backwards; juxta well developed, in form of moderately sclerotised ring with moderately wide walls, located medially in the apparatus, ventral portion elongated downwards and reaching sacculi, with subtriangular incision on distal margin;

valva narrow and elongate, of the length approximately equal to uncus, basal portion irregularly subtriangular and flat, with both margins narrowly folded inwards, terminal portion narrow, claw-like, basoventrally provided with bulbous protrusion; costal margin straight, slightly arched basally and terminally, medially with bulbous protrusion; basal 2/3 of sacculus sinuous, slightly convex, remaining portion straight; both outer and ventral surface of valva covered with sparse, erect setae of different lengths, denser along terminal part of sacculus; phallus tubular, moderately sclerotised, indistinctly bent downwards; vesica slightly longer than phallus, in basal half tubular and membranous, terminal half distinctly bent upwards, forming slightly broadened, multidimensional pouch provided with irregular, well slcerotised plaques, terminally with a membranous, club-like diverticulum covered with prominent, elongate, straight and heavily sclerotised cornuti, longer in distal portion and shorter basally;

First female description (Fig. 48G-I)

Head. Proboscis well developed, dark brown; head entirely dark ochraceous brown to almost black, below eye along frons small subrectangular greyish area devoid of scales; labial palpus three-segmented, narrow, straight, porrect, concolorous with head, 1st palpomere ventrally with elongate scales; antennae piliform, ochraceous brown, ventrally densely covered with short, erect setae;

Thorax. Patagia, tegulae, thorax and pleurites entirely dark ochraceous brown to almost black, tegulae terminally with elongate and piliform scales;

Legs. Entirely ochraceous brown; additional tooth on clave absent; arolium present; tarsi lateroventrally with rows of spine-like, ochraceous setae; foreleg: tibia of around 3/4 of femur length, epiphysis present, ochraceous brown, of around 2/3 of tibia length; tibia and 1st tarsomere together longer than femur; midleg: tibia with one pair of ochraceous brown terminal spurs of equal length; hindleg: tibia with one pair of ochraceous brown terminal spurs, of equal length;

Abdomen. Entirely ochraceous brown, only terminal sternite sublaterally with indistinct admixture of a few paler, ochraceous-orangish scales; distal margins of terminal tergite and sternite with elongate scales, but sternite without any distinct incision;

Forewing. Elongate and narrow, subtriangular, background ochraceous brown with three ochraceous-orangish blotches of different shape and size: one in basal, one in medial and one in distal portions; basal blotch (fm1) subtrapezoidal, slightly elongate, reaching to around 1/3 of wing length, from R, reaching beyond 1A+2A but terminated before wing hind margin; medial blotch (m2) subtrapezoidal to subsquare, in DC, from R to DC outer margin; distal blotch (fused m_4, am_4, m_5, and m_6) narrow, between R and CuA1, in form of narrow, sinusoidal streak of irregular width, am_4 portion projected towards wing central portion, m_5 and m_6 portions towards wing outer margin; underside as upperside, but the basal blotch extended outwards, and touching the medial blotch; basally with a group of pale yellow to almost creamy scales oriented towards costal margin and forming retinaculum subdorsale; cilia ochraceous brown, in basal portion of wing hind margin row of elongate and piliform scales concolorous with wing background;

Hindwing. Elongate, suboval, reaching to 2/3 of forewing length; background ochraceous brown, with two fused ochraceous-orangish blotches; basal blotch from wing base to 1/3 of its length, including basal portion of wing hind margin, inner margin sharply constricted to narrow ochraceous orangish stripe along DC hind margin, fusing with distal blotch; distal blotch from Sc+Rs+M1 to CuA1, irregular; underside as upperside; cilia concolorous with wing pattern, longer in basodistal margin; Sc+Rs+M1 completely fused, M2 and M3 stalked in the basal 1/2 of their length; frenulum present;

Female genitalia first description (Fig. 45)

Anal papilla subtrapezoidal, moderately sclerotised, covered with moderately dense, soft, erect setae of equal length; apophysis posterioris slightly longer than anal papilla, weakly sclerotized, basal half subtriangular, terminal half needle-like; apophysis anterioris of similar length, needle-like; dorsal pheromone glands in form of two elongate, narrow, straight membranous tapes; ventral pheromone glands similar to dorsal but almost 2x longer and terminally curly; ostium bursae membranous, with lateral projections of subtriangular shape, very wide; sternite 8th narrow, membranous; antrum well developed, wide, around 2x longer than wide, flattened dorsoventrally, plain, moderately sclerotized, and slightly constricted in medial portion; ductus bursae wide, flattened dorsoventrally, moderately sclerotised, twisted and slightly narrowing towards end, terminal portion bent rightwards and downwards, covered with longitudinal plicae; corpus bursae elongate, subovate, membranous, densely plicate; signum in form of well sclerotised, prominent longitudinal plate, between left side of terminal portion of ductus bursae and diverticulum, extended towards basal 1/3 of corpus bursae, in medial and terminal portions covered ventrally with claw like, slightly curved spines; in 2/3 of corpus bursae additional small plate provided with a row of distinct spines; ductus seminalis narrow, membranous, originating terminally from laterobasal, distinct conical diverticulum bent anteriorly.

Immature stages. Unknown.

Biology. Adults are collected by netting by day; there is no data on attraction to light. Individuals undoubtedly belonging to *S. ankaratra* **comb. nov.** were recorded in May, November and December (for the information of the uncertain *S. ankaratra* **comb. nov.** / *S. lacrimata* **comb. nov.** specimens see above). In the corpus bursae of one female (DL_06-051), collected on 08.11.2006, six complete spermatophores (i.e. colla with still attached corpora, Fig. 4) were recorded. Additionally, in two other females (MAD_108 and MAD_110), collected on 07.12.2019, around 3-5 colla were recorded in each (Fig. 45D). The species is associated with evergreen, mid elevation humid forest.

Distribution (Fig. 39C-D). The specimens undoubtedly representing *S. ankaratra* **comb. nov.** were collected in the central east of Madagascar, in the regions of: Alaotra-Mangoro (Zahamena), Analamanga (N from Mandraka Park, Ampolomita, Antananarivo(?)) and Amoron'i Mania (Ambositra, along RN7 towards Ambohimanga Sud (Fig. 39C). From around 1235 to 1310 m elevation.

The remaining, superficially indistinguishable specimens of *S. ankaratra* **comb. nov.** and *S. lacrimata* **comb. nov.** were collected in the north and central Madagascar, in the regions of: Sava (Marojejy) and Analamanga (Lake Mantasoa, La Mandraka, Ampolomita, and Antananarivo(?)) (Fig. 39D). From 1250 up to 1700 m elevation.

Remarks. The ranges of *S. lacrimata* **comb. nov.** and *S. ankaratra* **comb. nov.** in the context of the distribution of the remaining, indeterminate specimens (Fig. 39B-D) suggest the former to be distributed in the northern east, and the latter in the central east of Madagascar, with sympatric occurrence in the region of Alaotra-Mangoro. As mentioned, the record from Antananarivo (Le Moult), although not distant from the other two localities in Analamanga, must be regarded with scepticism.

The areas of Ampolomita and Ambositra are already devoid of primary vegetation. Additionally, the area around Mandraka Park was intensively and almost completely deforested in the last two decades, as for Ambositra, which was almost completely devoid of the remnants of forest vegetation (LOFM 2022).

The data for *S. ankaratra* **comb. nov.** and *S. lacrimata* **comb. nov.** taken together suggest the species to be bivoltine, with one generation appearing in February-May, and the second in October-December. However, both species are small and rather cryptically coloured, thus easy to overlook, and their potential seasonality may be the result of collectors' activity, which demands further research.

Skippernaclia vestigii **comb. nov.** (Fig. 39E, 43, 46, 48J)
Thyrosticta vestigii Griveaud, 1964: 89, pl. I, fig. 56; Viette 1990: 170.
Holotype: ♂, MNHN, EL65168, by original designation.

Material. Five specimens (ISEA PAS - 1♀; MNHN - 2 ♂♂; PZBT - 2 ♂♂) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. Forewing pattern: basal blotches (seemingly $fm_2+m_1+am_1$) completely fused with medial blotches (seemingly $m_2+fm_3+m_3$) into one large, longitudinal blotch, distal: $m_4+am_4+m_5+m_6$ fused into an hour-glass shaped blotch, posterobasally connected with the basal blotch by a very indistinct, narrow stripe (see Wiorek et al. 2021).

Immature stages. Unknown.

Biology. Adults are collected by netting by day; there is no data on attraction to light. Recorded in May, October and December. Associated with evergreen, mid elevation humid forest (see Wiorek et al. 2021).

Distribution. Endemic to Ambohitantely RS (Fig. 39E). Around 1550-1600 m elevation.

Remarks. The female of the species was described for the first time in Wiorek et al. (2021). That single female specimen available to our morphological study (Fig. 48J) has three radial veins in both forewings, which potentially could be an apomorphy of the species, but it requires verification in a longer series of specimens.

Skippernaclia leesi Wiorek, 2024 **sp. nov.** (Figs 39F, 47, 48K-L)
Type locality: Ambohitsitondroinan'i Mahalevona, Masoala National Park.
Holotype: ♀, NHMUK, NHMUK015109746, genitalia slide NHMUK [to be provided later].
ZooBank [to be provided later].

Material. The holotype is the only known specimen (Tab. S1).

Diagnosis. the diagnostic characters are provided in the determination keys. Fore wing pattern: basal blotch: m_1 only, medial: m_2 only, distal: m_4, fused m_5+m_6.

Unfortunately, the only specimen of the species was not available for molecular study, but the shape of the signum in the female genitalia (Fig. 47) is clearly distinct from the superficially most similar species *S. lacrimata* **comb. nov.** and *S. ankaratra* **comb. nov.** (Figs 44, 45). To the contrary, in the shape of the signum, *S. leesi* **sp. nov.** resembles most closely *S. vestigii* **comb. nov.**, from which it is superficially completely different (Fig. 48). Thus, the new species is well supported morphologically.

Description (Fig. 48K-L)
Head. Proboscis well developed, dark brown; head entirely ochraceous brown; labial palpus three-segmented, narrow, straight, porrect, concolorous with head; 1st palpomere ventrally with elongate scales; antennae piliform, ochraceous brown, ventrally densely covered with short, erect setae;
Thorax. Patagia, tegulae, thorax and pleurites entirely dark ochraceous brown to almost black; tegulae terminally with dense tuft of ochraceous brown piliform scales;
Legs. Entirely ochraceous brown; additional tooth on clave absent; arolium present; tarsi lateroventrally with rows of spine-like, ochraceous setae; foreleg: tibia of around 3/4 of femur length, epiphysis present, ochraceous brown, of around 2/3 of tibia length; midleg: tibia with one pair of ochraceous brown terminal spurs of equal length; hindleg: tibia with one pair of ochraceous brown terminal spurs, of equal length (additional spurs absent);
Abdomen. Entirely ochraceous brown;

Forewing. Elongate, subtriangular, background ochraceous brown with four ochraceous-orangish blotches of different shape and size: one in basal, one in medial, and two in distal portions; basal blotch (fm$_1$) subtrapezoidal to suboval, from R and reaching slightly beyond 1A+2A, terminated before wing hind margin; medial blotch (m$_2$) subsquare, in DC, from Sc to DC outer margin; first distal blotch (m$_4$) suboval, between R and M1; second distal blotch (fused m$_5$ and m$_6$) 8-shaped, between M2 and CuA1, slightly constricted along M3, both portions of similar size; underside as upperside, but the basal blotch extended outwards and reaching at least half the wing, not touching medial blotch; basally with a group of pale yellow to almost creamy scales oriented towards costal margin and forming retinaculum subdorsale; cilia ochraceous brown, in basal portion of wing hind margin row of elongate and piliform scales concolorous with wing background; distal blotches less rounded, rather subrectangular in shape;

Hindwing. Elongate, suboval, reaching to 2/3 of forewing length; background ochraceous brown, with two fused ochraceous-orangish blotches; basal blotch from wing base to 1/3 of its length, including basal portion of wing hind margin, inner margin sharply constricted to narrow and short ochraceous orangish stripe along DC hind margin, fusing with distal blotch; distal blotch irregular, from Sc+Rs+M1 to CuA1; underside as upperside; cilia concolorous with wing pattern, longer in basodistal margin; Sc+Rs+M1 completely fused, M2 and M3 stalked in the basal 1/2 of their length; frenulum present;

Female genitalia description (Fig. 47)

Anal papilla subtrapezoidal, weakly sclerotised except for margins, covered with erect setae, much denser at margins; dorsal pheromone glands well developed, in form of narrow, elongate, twisted, rarely anastomosing membranous tubes; ventral pheromone glands of similar shape, slightly shorter; apophyses straight and narrow, needle-like; posteriores as long as papillae anales, anteriores shorter, of around half the length of posteriores; ostium bursae membranous, with lateral projections of subtriangular shape; antrum well developed, flattened dorsoventrally, wide and around 2x longer than wide, membranous; 7th segment wide, membranous; ductus bursae membranous, of the width of atrium and similarly flattened, dorsal wall with sclerotised plaque, ventral wall plain, membranous, terminally provided with prominent, longitudinal, parallel plicae; corpus bursae membranous, elongate, entirely covered with distinct plicae forming longitudinal, parallel ridges; signum singular, prominent, in a form of a strongly sclerotised, narrow, elongate, buckle-like plaque with tips slightly bent downwards, located at basal portion of corpus bursae; medial portion of signum straight, left tip terminated with a narrow plate, ventrally with four short spine-like protrusions, and a few minor scobinations, right tip terminated with a single, elongate, claw-like spine; below the signum, on the left wall of corpus bursae, in its basal 1/5 and 2/5 two indistinct sets of a few tiny spine-like scobinations; ductus seminalis narrow, originating from terminal portion of small, narrow, outstanding diverticulum covered with plicae, opposite to ductus bursae.

Immature stages. Unknown.

Biology. The only known specimen (Fig. 48K-L) was collected on December 28, 1993, at around 11:00 - 12:00 am. Associated with evergreen, mid elevation humid forest.

Distribution. The species is known only from its type locality (Fig. 39F), around 1210 m elevation.

Remarks. The only locality of the species is still located within a large and undisturbed forest patch, located within Masoala PN, and currently not endangered with deforestation.

Etymology. We dedicate this species to Dr David C. Lees, our collaborator and colleague, in recognition of his significant contributions to the research on Madagascan Syntomini he has made during the three decades of research in Madagascar.

Kowalskinaclia **gen. nov.**

Type species: *Thyrosticta vieui* Griveaud, 1964

Diagnosis. In the female abdomen, 7th sternite lateroterminally with longitudinal, subrounded cavities, parallel to its lateral margins. Similar structures, but differently expressed and located, are present in *Skippernaclia* **gen. nov.** and in *Melanonaclia*.

In the male genitalia (Figs 49-51): saccus completely reduced, basal portion of the right wall of vesica provided with short, straight, protruding tubular diverticulum.

In the female genitalia (Figs 52-53): corpus bursae on the right side provided with diverticulum not extending above the main part of corpus bursae, ventrally provided with differently expressed, irregular fields covered with dense, short spines; left wall of corpus bursae with single signum in the form of broad, horizontal plaque provided with prominent spines.

Remarks. The "Group of *T. vieui*", treated by Griveaud (1964) as the "fourth section" of *Thyrosticta* was characterised based on the antennae (but very generally) and the characters of the male genitalia (Griveaud 1964).

This genus can be further defined by the following set of morphological characters: medium sized moths, body colouration with high intraspecific variation, generally dark ochraceous brown with pale yellow to ochraceous-orange pattern, the abdomen uniformly dark brown or with pale yellow terminal margins of segments (Figs 54-55); antennae distinctly sexually dimorphic - in the male bipectinate, each ramus dorsoterminally provided with a single thick, elongate, distinct seta, and dorsally with additional two, less prominent ones (Figs 6C, 7C), in the female slightly serrate, each antennomere ventrally with a small oblique lobe, on both lateral margins provided with three thick, erect setae, the longest one on the outer angle of the lobe (Figs 6D, 7D); brush-like tuft behind male foreleg coxa absent; hind leg tibia with additional pair of spurs, located in 3/4 of tibia length (Fig. 13F); forewing regularly subtriangular, not elongate, with hind and outer margins of approximately equal length, 1A+2A terminated at the well-defined tornus, five radial veins, lateral portions of DC outer margin formed by short styli (Fig. 15A); forewing pattern (Figs 54-55): basal blotches: absent in *K. cowani* **comb. nov.** and "black" morphotype of *K. dilata* **comb. nov.** (see Wiorek et al. 2021), in *K. vieui* **comb. nov.** and "yellow" morphotype of *K. dilata* **comb. nov.** - fm_2; medial blotches: m_2 and m_3, distal blotches: m_4, fused m_5+m_6, semi-transparency present; hind wing elongate, costal margin straight, slightly arched basomedially, hind margin basally with distinct, rounded protrusion reaching to 1/2 of the wing length, followed by indistinct medial incision; Sc+Rs+M1 straight, fused but can be slightly bifurcated in the very terminal portion, M2 and M3 stalked in around basal 3/4 of their length, 3A present (Fig. 17A); hindwing with one medial pale yellow blotch, of species-specific shape, semi-transparency absent (Figs 54-55);

The male genitalia, except vesica, are indistinguishable among the species, suboval, small and simple, valvae relatively short, terminated with tiny claw-like hook and not reaching beyond the tegumen, phallus short, tubular and basally distinctly curved upwards, vesica of species-specific shape and sclerotisations (described below) (Figs 49-51).

In the female genitalia ventral pheromone glands present, slightly more prominent that the dorsal ones (Figs 52-53).

***Kowalskinaclia* gen. nov. species determination key based on adult characters**

1. Tegulae ochraceous brown; hindwing with a large yellow blotch, regularly suboval or only slightly incised laterally, at the wing margins (Fig. 55)..............................*K. cowani* **comb. nov.**

- Tegulae pale yellow; hindwing with a large yellow blotch, medially provided with distinct protrusion, which is usually not wider than 1/3 of the wing width (Fig. 54)................................2

2. The medial protrusion of the hindwing blotch broad, regularly suboval, in the shape of half of an ellipse (Fig. 54A-C)...*K. dilata* **comb. nov.**

- The medial protrusion of the hindwing narrow and elongate, with parallel margins and rounded tip (Fig. 54D-I)..*K. vieui* **comb. nov.**

***Kowalskinaclia* gen. nov. species determination key based on male genitalia**

1. The basal diverticulum of vesica elongate and straight, terminally obliquely cut and provided with a longitudinal row of elongate cornuti (Fig. 51D-F)...........................*K. cowani* **comb. nov.**

- The basal diverticulum of vesica short and curved, covered with small scobinations or very short cornuti, that are irregularly distributed and not arranged in a row......................................2

2. Left wall of vesica on the opposite site to the base of diverticulum covered with an irregular field of short, subtriangular toot-like protrusions (Fig. 49C-D)....................*K. dilata* **comb. nov.**

- Left wall of vesica completely plane on the opposite site to the base of diverticulum...*K. vieui* **comb. nov.**

***Kowalskinaclia* gen. nov. species determination key based on female genitalia**

Remarks. The female of *K. dilata* **comb. nov.** remains formally undescribed (but see the remarks for the species).

1. Diverticulum of corpus bursae short, subconical, oriented horizontally and in terminal portion covered with short spine-like protrusions (Fig. 53)...................................*K. cowani* **comb. nov.**

- Diverticulum of corpus bursae elongate, tubular, basally directed obliquely downwards and in around 1/2 of its length turned upwards, terminal portion laterally with a field of spine-like protrusions, terminally plane (Fig.52)...*K. vieui* **comb. nov.**

Kowalskinaclia dilata **comb. nov.** (Figs 49, 54A-C, 56A)
Thyrosticta dilata Griveaud, 1964: 92, pl. I, fig. 60; Viette 1990: 169.
Holotype: ♂, MNHN, EL65153, by original designation .

Material. 58 specimens (ANHRT - 3 ♂♂; ISEA PAS - 45 ♂♂; MNHN - 3 ♂♂; PZBT - 7 ♂♂) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys.

Superficially, the most similar to *K. dilata* **comb. nov.** (and to *K. vieui* **comb. nov.**) are some species of the genus *Maculonaclia*, especially *M. ankasoka* Griveaud, 1964, *M. elongata* Griveaud, 1964, *M. lambertoni* Griveaud, 1964, *M. leopardina* and *M. tenera* (Mabille, [1879]). However, they have different wing patterns, especially in the hindwing, which either has two small blotches, or one arched stripe - only *M. elongata* has the hindwing very similar to *K. dilata* **comb. nov.** and *K. vieui* **comb. nov.**, but in the forewing it has a large basal yellow blotch. Additionally, all these species listed above have a well developed saccus in the male genitalia.

Immature stages. Unknown.

Biology. Adults are collected by netting by day, and also regularly attracted to UV and visible light at night. Recorded from February to May, in July, and from October to December. Copulation was observed in July at night (Fig. 57). Associated with evergreen, mid elevation humid forest.

Distribution (Fig. 56A) This species so far was known only from Ambohitantely RS in the Central Plateau of Madagascar (Griveaud 1964, Wiorek et al. 2021). Recently, in the collection of ANHRT we found two specimens (ANHRT 00215262, ANHRT 00215260) collected in Andasibe PN in eastern Madagascar. From around 930 (Andasibe) to 1530-1600 (Ambohitantely) m elevation.

Remarks. The male genitalia (Fig. 49) were redescribed in Wiorek et al. (2021). The female has never been collected and thus remains formally undescribed. However, a couple *in copula* were photographed by Len de Beer in Ambohitantely on July 4, 2023 (Fig. 57) (https://www.inaturalist.org/observations/171368012). Based on the photograph, the female differs from the male in its less prominent antennae, similarly to the remaining two species of the genus. The forewing pattern and uniformly black colouration of the abdomen suggest it to represent the "black" morphotype of the species (Wiorek et al. 2021). However, the presence of both colour morphs in females needs to be verified.

The lack of female specimens in the analysed materials may suggest that only males of *K. dilata* **comb. nov.** are attracted to light.

Both localities of the species are within protected areas – RS Ambohitantely and PN Andasibe, however the former is endangered by fires of the grasslands surrounding the Reserve.

Kowalskinaclia vieui **comb. nov.** (Figs 7C-D, 50, 52, 54D-I, 56B-D)
Thyrosticta vieui Griveaud, 1964: 91, Pl. I, Fig. 59; Viette 1990: 170.
Holotype: ♂, MNHN, EL65171, by original designation.

Material. 233 specimens (ISEA PAS - 5 ♂♂, 1 ♀; MNHN - 155 ♂♂, 1 ♀; NHMUK – 8 ♂♂; PZBT - 58 ♂♂, 3 ♀♀, 1 ex sex unknown; SMNS - 1 ex. sex unknown) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. For additional remarks see also the diagnosis of *K. dilata* **comb. nov.**

Male genitalia redescription (Fig. 50)
Tegumen roundly U-shaped, broad subdorsally and narrowing laterally, completely fused with vinculum, laterally with slightly bent outwards, forming round convexity, that is more distinct than in the other species of the genus; uncus elongate, slightly bent downwards, basal portion flattened dorsoventrally and of uniform width, then narrowing towards flattened laterally, beak-shaped terminal portion with pointed tip; uncus laterally covered with erect setae of different length, denser in the basal part; vinculum very narrow, roundly U-shaped;
saccus almost absent, in form of very indistinct medial widening of vinculum; valva elongate, shorter than uncus, wide basally and narrowing around the half of its length towards rounded apex, costal margin convex in basal 1/3, with claw-like protrusion very slightly bent inwards at the end; sacculus straight in basal half, remaining portion arched; costal margin and terminal half of sacculus covered with minute sculpture, entire margins covered with sparse, erect setae of different length denser in terminal portion; phallus moderately elongate, tubular, of uniform width, distinctly curved upwards, membranous or with very weak sclerotisation in terminal

part; vesica basally membranous, only with a small field of minute scobinations on bottom wall, remaining portion entirely covered with dense, well sclerotised, minute scobinations; at the base on the right side short, tubular, roundly terminated diverticulum, bent upwards and covered with minute scobinations and short, spine-like protrusions, most densely in the terminal portion; Remarks: In one specimen (EL75951) the basal, wider part of valva is longer, the narrow terminal portion is shorter, and claw-like tip of costal margin is missing - however, there is no difference in the shape and sculpture of vesica.

First female description (Fig. 54E)

Head. Proboscis well developed; frons pale yellow; vertex medially ochraceous brown with admixture of a few pale yellow scales in the central portion behind scapi, laterally pale yellow; postocular area pale yellow, in the bottom part with a narrow ochraceous brown blotch along distal margin; labial palpus three-segmented, elongate, narrow, porrect, covered with mixture of pale yellow and ochraceous brown scales, 1st palpomere ventrally with elongate pale yellow scales oriented downwards, 2nd palpomere ochraceous with yellow admixture ventrally, 3rd palpomere ochraceous with yellow tip; antennae slightly serrate, each antennomere ventrally with heart-shaped protrusion projected downwards, dorsally pale yellow, with terminal 1/3 ochraceous brown, ventrally densely covered with short, erect setae, additionally each antennomere with a pair of longer setae, on each lateral margin; scapus pale yellow, with subdorsal, ochraceous brown blotch (Fig. 7D).

Thorax. Patagia entirely ochraceous brown with elongate scales; tegulae pale yellow, only basally with admixture of ochraceous brown scales, terminal portion with pale yellow elongate scales; mesothorax ochraceous brown, laterally with elongate and piliform scales, medially with pale yellow blotch; metathorax pale yellow, partially worn; metascutum ochraceous brown, laterally with piliform scales; pleurites partially worn, with ochraceous brown scales and pale yellow blotches at wing bases;

Legs. Mostly pale yellow, with some ochraceous brown marks; additional tooth on clave present; arolium present; tarsi lateroventrally with rows of spine-like, ochraceous setae;

foreleg: tibia of around 2/3 of femur length, epiphysis present, pale yellow, of 3/4 of tibia length; tibia and 1st tarsomere together of the length of femur; midleg: tibia with one pair of pale yellow terminal spurs, distal one slightly longer; hindleg: tibia with one pair of pale yellow terminal spurs, inner one slightly longer; one additional pair of pale yellow spurs in 3/4 of tibia length, shorter than the terminal ones and similarly of unequal length;

Abdomen. Ochraceous brown with pale yellow marks: tergites 1st – 6th ochraceous brown, with narrow pale yellow terminal margin; 7th tergite ochraceous brown, and terminal margin covered with elongate pale yellow scales; sternites and lateral portion of abdomen with identical pattern as tergites, including lack of yellow margin on 7th segment; 7th sternite terminally without any distinct incision;

Forewing. Elongate, subtriangular, background ochraceous brown with five pale yellow to very pale yellow, almost creamy blotches of different shape and size, partially semi-transparent: one in basal portion, and two in medial and distal portions; basal blotch (fm_1) irregular, elongate, slightly fusiform, from below costa to basal portion to DC hind margin, pale yellow, not semi-transparent; first medial blotch (m_2) elongate, suboval, in DC, from Sc to DC outer margin; more intensive yellow and regular scales along Sc, R and DC hind margin, medial portion semi-transparent, covered with smaller and scarce pale yellow scales; second medial blotch (m_3) subsquare, from below DC hind margin and CuA2, to slightly beyond 1A+2A, pale yellow, medially slightly semi-transparent, with smaller and scarce scales; First distal blotch (m_4) irregularly suboval, between R and M1, pale yellow to almost creamy, emarginated with regular scales, medially semi-transparent, with smaller and scarce scales; second distal blotch (fused m_5 and m_6) irregularly subtriangular to 8-shaped, portion between M2 and M3 smaller and narrower, widening beyond M3 and reaching CuA1, semi-transparent, similarly as the above described; underside as upperside, but fm1 elongate towards wing base, and posterior portion of m3, below 1A+2A elongate towards wing base, but covered by the hindwing; additionally, below fm1 retinaculum subdorsale in form of tuft of pale yellow, elongate scales; cilia ochraceous brown; in basal portion of wing hind margin row of elongate and piliform ochraceous brown scales;

Hindwing. Elongate, subtriangular, reaching to 1/2 of forewing length; along costal margin ochraceous brown stripe reaching to 2/3 of wing length; basal portion with pale yellow blotch, in posterior part of the wing reaching to tornus, in anterior portion with two protrusion, one smaller towards costal margin in 2/3 of wing length and second larger, narrow and elongate, deeply incising outer ochraceous brown zone; underside as upperside, cilia concolorous with wing pattern, longer in basal portion of hind margin; Sc+Rs+M1 completely fused, M2 and M3 stalked in the basal 2/3;

Female genitalia first description (Fig. 52)

Anal papilla subtrapezoidal to subrectangular, moderately sclerotised, covered with indistinct scobinations and sparse, erect setae of equal lengths; terminal margins with more prominent, dense scobinations and dense setae of different lengths; apophysis posterioris slightly longer than anal papilla, weakly sclerotized, needle-like, straight; apophysis anterioris much shorter than anterioris, moderately sclerotised, narrow, needle-like and straight; dorsal pheromone glands in form of two separately opened, short, narrow, tubular, straight and not anastomosing tapes of similar lengths; ventral pheromone glands of the similar shape but slightly more developed; 7th sternite weakly sclerotised, sublaterally on terminal margin with irregular to round, prominent cavities covered with scales, lamella antevaginal moderately sclerotised, in form of subrectangular plate; 8th sternite membranous, covered with minute scobinations more dense on membranous medial portion forming lamella postvaginalis; ostium bursae wide but short, semilunar, moderately sclerotised; antrum fused with ductus bursae, wide and flattened dorsoventrally, very slightly narrowing, ventral wall and lateral margins of dorsal wall moderately sclerotised; corpus bursae suboval, membranous, with indistinct, minute scobinations; in basal portion of ventral wall indistinct, moderately sclerotised, granular scobinations; signum in the terminal portion of dorsal wall, in form of transverse, narrow and elongate, moderately to well sclerotised plate in terminal 2/3 of bursa length, along margins covered with straight, spine-like protrusions directed inwards corpus bursae, but slightly bent towards outer margins of the plate; ductus seminalis narrow, originating terminally from a very distinct, wide, tubular, membranous appendix bursae, originating on the left side of the basal portion of corpus bursae, directed downwards and in half of its length bent upwards, making the entire bursa looking like consisting of two chambers of almost equal size; on dorsal, right and ventral walls partly covered with irregular fields of numerous, moderately sclerotised spine-like protrusions.

Immature stages. Unknown, except for the egg described here for the first time.

Biology. Adults are collected by netting by day, and also attracted to light at night, reported all year round. Associated with evergreen humid forest, mostly at mid, but also low elevation. The Ankarafantsika locality (Fig. 56B, see below) differs from the other parts of the species range in the type of primary vegetation, with the presence of marshlands, mangroves and dry, deciduous western forest.

Distribution (Fig. 56B-C). Mainly central east of Madagascar. Our molecular results suggest *K. vieui* **comb. nov.** to be a complex of two cryptic species (Fig. 5A), which corresponds also with its distribution (but see below). The main range of the complex appears to be divided into two allopatric units (Fig. 56C): “northern”, represented in the tree by the specimens MAD_132 and MAD_004 (Fig. 5A), in the regions of Alaotra-Mangoro (Andranomalaza south to Lakato and Beparasy, including Ankasoka, where the holotype of *K. vieui* **comb. nov.** was collected), Analamanga (Analavory south to Lac Mantasoa) and Vakinankaratra (Andranotobaka), and “southern”, represented in the tree by the specimen DL_14R-218 (Figs 5A, 54F), in the regions of Amoron'i Mania (near RN 7, between Ambalamanakana and Ambatofitorahana) and Matsiatra Ambony (Tsarafidy-Ankafina and Ranomafana). Additionally, single specimens were collected in: Diana (Beangona Ambevy), Analanjirofo (Ambohitsitondroin' Mahalavona) and Boeny (Ankarafantsika). From around 1040 to 1700 m elevation.

Remarks. The molecular results, however mitochondrial only and not nuclear (Figs S3-S6, File S1), suggest *K. vieui* **comb. nov.** to be a cryptic species complex. Although, in the limited set of specimens available for our analyses we did not find any morphological characters allowing for unambiguous diagnosis and description of a potentially new species. The specimen DL_14R-218 (Fig. 54F), representing the presumed new species, has the lateral diverticulum in the vesica completely devoid of cornuti, which could be potentially a species specific character, but the other specimens vary in the extent of cornuti coverage. Thus, a larger number of specimens is necessary to analyse this variation.

In this context, the taxonomic status of the specimens collected in the localities distant from the main species range (Ankarafantsika, Beangona Ambevy, Ambohitsitondroin’ Mahalavona) should be verified as well.

Kowalskinaclia vieui **comb. nov.**, in contrast to *K. dilata* **comb. nov.**, does not seem to have discrete morphotypes (Fig. 54D-I). The general colouration of the yellow parts of the body varies continuously from intensively, almost ochraceous-orange to very pale, almost creamy-white. In the total number of specimens included in the study, we found only single ones with i) extremely reduced body pattern, i.e. entirely brown abdomen and reduced forewing pattern, from the lack of the basal blotch, up to no blotches at all (Fig. 54H), ii) the narrow protrusion of the hindwing medial blotch separated from the blotch and forming a separate strike (Fig. 54G), iii) slightly reduced forewing pattern, with smaller blotches, or iv) extremely developed forewing pattern, with basal, m_2 and m_3 connected with each other by narrow yellow stripes, and m_4 narrowly elongate towards m_5+m_6. A single specimen of the latter form, deposited in NHMUK (NHMUK010621702, Fig.54I) and labelled as “paratype” most probably was intended by Griveaud to be described as a new species, “*Thyrosticta quadrata*” in lit., which, however, did not happen.

Considering the number of specimens deposited in the analysed collections, this species is one of the most commonly collected Madagascan Syntomini. The highest numbers of specimens were collected in March and November; however, this can reflect the collectors activity and not necessarily the seasonal peaks of abundance. Females appear to be collected sporadically, as we found only five specimens. This suggests that males are more active than females, similarly as in *K. dilata* **comb. nov.**

The localities of the "southern" population (Fig. 56D), representing the presumed separate species, were either already devoid of primary vegetation, or largely deforested in the last few decades. This includes a complete 2015-2019 deforestation of the area west of Ranomafana PN (LOFM 2022), where the specimen DL_14R-218 was collected. In the "northern" population, the localities south from Anjozorobe Angavo Protected Area are most vulnerable, also largely deforested in the last two decades (LOFM 2022).

Kowalskinaclia cowani **comb. nov.** (Figs 51, 53, 55, 58)

Thyrosticta cowani Griveaud, 1964: 93, Pl. I, Fig. 62; Viette 1990: 169.

Holotype: ♂, MNHN, EL65155 (Fig. 55A), P. Griveaud slide No. 240 (Fig. 51E), by original designation.

= *Thyrosticta incerta* Griveaud, 1964 **syn. nov.**

Thyrosticta incerta Griveaud, 1964: 93, Pl. I, Fig. 61; Viette 1990: 169.

Holotype: ♂ MNHN, EL65154 (Fig. 55B), P. Griveaud slide No. 238 (Fig. 51F), by original designation.

Material. 91 specimens (ISEA PAS - 9 ♂♂, 4 ♀♀; MNHN - 31 ♂♂, 3 ♀♀; NHMUK - 1 ♂; PZBT - 37 ♂♂, 2 ♀♀, 3 exx. sex unknown; SGN - 1 ♂) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. The individuals with fully developed forewing pattern (Fig.55) are superficially similar to the same species as listed above for *K. dilata* **comb. nov.** and *K. vieui* **comb. nov.** Additionally, the individuals without the blotch m_3 and of ochraceous-orangish colouration (Fig. 55I), resemble *Tsirananaclia tripunctata* Griveaud, 1964. However, the latter differs in irregular margins of the hindwing medial yellow blotch (which are smooth in *K. cowani* **comb. nov.**).

Individuals with the completely reduced forewing pattern (Fig. 55K-L) are the most similar to other Madagascan Syntomini with brown-black forewing and medially yellow hindwing, i.e. *Maculonaclia griveaudi* Viette, 1987, *M. nigrita* Griveaud, 1964, and all three species from the genus *Micronaclia* Griveaud, 1964. However, both these *Maculonaclia* species have elongate and narrowed forewings, and differently expressed hindwing patterns. *Micronaclia* species are distinctly smaller and differ from *K. cowani* **comb. nov.** in the well developed saccus in the male genitalia.

Taxonomic note. Griveaud (1964) described the form with completely dark brown forewing (without pattern) as a separate species - *Thyrosticta incerta* Griveaud, 1964, represented only by the male holotype (Fig. 55B) and defined by the supposed differences in the genitalia. However, our reanalysis of the original male genitalia slides of *K. cowani* **comb. nov.** (slide P. Griveaud No. 240, made of the holotype EL65155) (Fig. 51E) and *T. incerta* (slide P. Griveaud No. 238, made of the holotype EL65154) (Fig. 51F), deposited in MNHN, led to the conclusion that the differences between them indicated by Griveaud (1964) result from misinterpretation of artefacts created during preparation. In the slide of *Thyrosticta cowani*, the vesica is completely uneverted (Fig. 51E), whilst in the preparation made of the only known specimen of *Thyrosticta incerta*, the vesica is everted only partially and clearly torn in such a way, that the cornuti seem to create a dorsal row (Fig. 51F). In the series of male genitalia preparations with properly everted vesica made by us, we also did not find any variation in genitalia, regardless of the high variation of the forewing pattern. Thus, we interpret *Thyrosticta incerta* as a junior subjective synonym of *Kowalskinaclia cowani* **comb. nov.**

Male genitalia redescription (Fig. 51)

Tegumem U-shaped, broad dorsally and narrowing laterally, completely fused with vinculum; uncus elongate, slightly bent downwards, wider basally and narrowing towards flattened laterally, beak-shaped terminal portion with pointed tip, medially covered with erect setae of different lengths; vinculum very narrow, roundly U-shaped; saccus very small, in a form of indistinct broadening of vinculum; valva elongate, shorter than uncus, wide basally and rapidly narrowing towards claw-like apex; costal margin shallowly concave; sacculus sinuous, medially convex, then incised and straight further on, covered with minute sculpture; both margins covered with sparse, erect setae of different length; outer surface of valva covered with minute, rounded, slightly outstanding scobinations, more dense along costal margin and narrow terminal portion; phallus elongate, weakly sclerotised, slightly bent in half length, moderately narrowed in terminal portion; vesica membranous, at basal portion plain, with elongate, tubular, slightly narrowing, straight diverticulum protruding from the right wall, dorsally covered with minute scobinations, terminal portion narrowing obliquely and densely covered with spine-like sclerotisations of varying length; remaining portion of vesica tubular, membranous, slightly narrowing, covered with plicae and very dense minute scobinations, often imposing its full eversion.

Remarks. Genitalia are generally moderately sclerotised, but in some specimens almost membranous.

Female genitalia redescription (Fig. 53)

Anal papilla subsquare, weakly to moderately sclerotised, entirely covered with dense, minute scobinations and erect setae of different length, between ventrolateral margins two membranous conical protrusions covered with minute scobinations; anterodorsal, submarginal zone of each papilla with distinctly denser setation; apophysis posterioris slightly longer than anal papilla, sclerotized, needle-like, straight, slightly sinuous; apophysis anterioris of the length of anterioris, sclerotised, narrow, needle-like and straight; dorsal pheromone glands located submedially, in form of a pair of twisted, not anastomosing membranous tapes; ventral pheromone glands, of the similar shape and length but slightly broader, located sublaterally; 7th sternite membranous, covered with minute scobinations; lamella antevaginalis moderately sclerotised, heavier in medial and lateral portions, subtrapezoidal, shallowly incised medially; lamella postvaginalis in the form of membranous, pocket-like protrusion folded upwards; ostium bursae moderately wide, flattened dorsoventrally; antrum of uniform width, membranous to moderately sclerotised, laterally with longitudinal foldings; ductus bursae short, wider than antrum, bulbous and covered with wide plicae; corpus bursae suboval, not elongate, membranous, with plicae and indistinct, minute scobinations; in basal part on ventral wall longitudinal stripe of spine-like, straight, heavy sclerotised protrusion oriented inwards; signum in terminal 2/3 of the length of corpus bursae, in form of horizontal, elongate, heavily sclerotised narrow and elongate plaque of varying length, covered with elongate, straight spine-like protrusions directed inwards and bent in different directions; ductus seminalis narrow, tubular, originating from a distinct, tubular and slightly narrowing diverticulum of the length of half of corpus bursae, located in the basal portion of bursa, in terminal portion ventral walls densely covered with straight, heavily sclerotised spines directed inwards, lather then the additional zone of spines at the basoventral part of diverticulum.

Remarks. The specimens available for the study differ in the extent of sclerotisation of certain parts of genitalia. In antrum, ductus and diverticulum of a single specimen we found loose, moderately sclerotised straight spines, most probably deriving from diverticulum of the male vesica, torn off during copulation.

Immature stages. Unknown.

Biology. Adults are collected by netting by day, and also attracted to light at night. Recorded from August to April, with no seasonal pattern of morphotypes appearance. Associated with evergreen, low and mid elevation humid forests.

Distribution (Fig. 58). Central and southern east of Madagascar, disjunctive, with three separate areas of occurrence. The first one (northernmost) includes Alaotra-Mangoro (Ambatondrazaka south to Lakato); the second one includes Amoron'i Mania (Ambositra, along RN7), Matsiatra Ambony (Tsarafidy-Ankafina) and Vatovavy Fitovinany (PN Ranomafana); the third one (southernmost) includes Atsimo-Atsinanana (forêt de Befotaka) and Anosy (Anosyennes Mountains). From around 650 to 1600 m elevation.

Remarks. The species has a uniformly ochraceous-brown body (with only single specimens in MNHN observed to have ochraceous-orange admixture on tegula), with cuprous reflection on the legs. At the same time, it has one of the most variable forewing patterns among all Madagascan Syntomini. Two morphotypes can be distinguished, in the phylogenetic tree arranged into separate clades, and potentially belonging to separate species (Fig. 5A, Figs S3-S5). The first one ("white", where the holotype of the species belongs) has white and semi-transparent blotches on the forewing (Fig. 55A, C-F), and the other one ("orange") - ochraceous-orange ones, completely devoid of transparency (Fig. 55G-J). The pattern extends from the regular one, typical for the genus and consisting of two medial and two distal blotches (m_2, fm_3 and/or m_3, m_4 and m_5+m_6), through different extents of reduction, to a completely "melanistic" form, with uniformly dark brown forewing (see "*Thyrosticta incerta*" comment below) - which, however, seems to occur only in the "orange" morphotype (Fig. 55B, K-L). Most often reduced are the blotches m_3 and then m_4 (and the individuals without the latter never have the former). Also, the distributional pattern suggests allopatric occurrence of the two morphotypes, with the "white" one occurring in Alaotra-Mangoro, and the "orange" one in the remaining, southern part of the range (Fig. 58B).

Although the molecular results suggest the existence of two separate species, supported by the general morphology and distribution, we refrain here from describing the “orange” morphotype as a new species. First, we did not find any differences in the male or female genitalia of both forms. Secondly, in PZBT there are a few specimens collected in Tsarafidy (thus in the “orange” form range), possessing either white or “intermediate”, partly white / partly orange blotches (Fig. 55M). Thus, the issue demands further molecular and morphological research on a longer series of specimens from different localities, especially from SE Madagascar.

Privatenaclia **gen. nov.**

Type species: *Thyrosticta triangulifera* Griveaud, 1964

Diagnosis. In the male genitalia (Figs 59-61): uncus terminally in the form of proximally open tube, subtriangular in cross section, terminated with two ventral protrusions and dorsal claw-like hook. Tegumen sublaterally provided with straight, protruding, horizontal spine-like arms, reaching at most to 1/2 of the uncus length, parallel to the uncus and the dorsal plane of tegumen, and transverse to the plane of entire apparatus, indicated by the proximal margin of the tegumen. Similar arms are present in the males from i) the genus *Mortinaclia* **gen. nov.** (constituting an unresolved species complex described further in this paper), ii) part of the genus *Dubianaclia*, iii) the genus *Julienaclia* **gen. nov.**, and iv) in the genus *Stictonaclia* Hampson, 1898 (Griveaud 1964). However, in *Mortinaclia perplexa* **comb. nov.** and *Stictonaclia* these structures are much longer than uncus, and in *Dubianaclia* and *Julienaclia* they are shorter than uncus, and, respectively, hook-like and bent inwards. Additionally, in none of the mentioned taxa are the arms perpendicular to the tegumen. Vesica with distinct, well sclerotised, claw-like plaque located basoventrally and curved downwards.

In the female genitalia (Figs 62-63): conical, straight diverticulum oriented upwards, located basolaterally on the left wall of corpus bursae, entirely membranous or densely covered with minute scobinations. Similar basolateral diverticula are present in: i) *Maculonaclia ankasoka* - but located ventrally, not laterally, ii) the genus *Melanonaclia* (including the *Thyrosticta* species moved to it in this paper - see below) and in *Tenuinaclia oberthueri* - but provided with differently expressed sclerotised plaques, iii) *Kowalskinaclia* **gen. nov.** - but of pouch-like shape with numerous spines (described above in this paper), iv) *Toulgoetinaclia obliquipuncta* - which possess completely different shape of ductus bursae and signa of corpus bursae.

In the general appearance, somehow similar to *Privatenaclia* (Fig. 64A-F) are the species from the genus *Stictonaclia* (except *S. andriai* Griveaud, 1964 and *S. blandina* (Oberthür, 1893)). However, in all of these the hindwing has a single, large yellow blotch, sometimes provided with small brown dot, as opposed to two separate blotches in *P. seguyi* **comb. nov.** (Fig. 64A-C) and *P. ratovosoni* **comb. nov.** (Fig. 64D-E), and a single yellow blotch provided with a brown strike in *P. triangulifera* **comb. nov.** (Fig. 64F). Furthermore, *Stictonaclia* species usually possess the forewing hind margin basal blotch (am_1).

Remarks. The "Group of *T. triangulifera*", treated by Griveaud (1964) as the "fifth section" of *Thyrosticta* was characterised based on the male antennae and genitalia (Griveaud 1964).

This genus can be further defined by the following set of morphological characters: antennae in both sexes piliform (Fig. 7H), ventrally densely covered with short, erect setae, and each antennomere laterodorsally with a pair of thicker setae; brush-like tuft of scales behind the male foreleg coxa present (Fig. 9A); additional hindleg tibial spurs absent (Fig. 13B); forewing regularly subtriangular with hind and outer margin of similar lengths, tornus well defined, four radial veins (Fig. 15B); forewing always with five blotches: basal: fm_2 (but irregularly extended in *P. seguyi* **comb. nov.**), medial: m_2, m_3, distal: m_4, fused m_5+m_6, most of them distinctly semi-transparent, covered with sparse and smaller scales (Fig. 19C-F); hindwing relatively short and wide, subtrapezoidal in the general outline, costal margin arched, area above Sc+Rs+M1 relatively wide, basal portion of hind margin with distinct subrounded protrusion reaching beyond 1/2 of the wing length, remaining portion very slightly incised; Sc+Rs+M1 straight and completely fused, M2 and M3 stalked in around basal 2/3 of their length, 3A present (Fig. 17C); hindwing pattern with one basal and one distal blotch, separated from each other or fused, semi-transparent blotches absent.

In the female genitalia (Figs 62-63), ventral pheromone glands present, in shape and size similar to the dorsal ones; antrum and ductus bursae distinctly elongate and oriented leftwards, narrowing funnel-like and slightly twisted leftwards along its longitudinal axis, with membranous dorsal wall and well sclerotised, broadened plaque on ventral wall.

***Privatenaclia* gen. nov. species determination key based on adult characters**

1. Hindwing with basal and distal blotches distinctly fused together, so that the background forms an elongate and narrow, wedge-like blotch parallel to the costal margin (Fig. 64F)..*P. triangulifera* **comb. nov.**

- Hindwing with two well separated or only narrowly connected blotches.................................2

2. Basal blotch of the forewing regularly wedge-like subtrapezoidal, between Sc and DC hind margin (Fig. 64D-E)..*P. ratovosoni* **comb. nov.**

- Basal blotch of the forewing of irregular shape, reaching beyond Sc and DC hind margin (Fig. 64A-C)...*P. seguyi* **comb. nov.**

***Privatenaclia* gen. nov. species determination key based on male genitalia**

1. Valva with subtriangular tip, slightly curved inwards but not elongated into narrow hook-like protrusion, costal margin terminally with rounded protrusion followed by a shallow incision (Fig. 59C); vesica basoventrally with well sclerotised, flattened plate, basally distinctly curved downwards and terminated with prominent claw-like hook (Fig. 59D-F)..*P. seguyi* **comb. nov.**

- Valva terminally narrowed into differently expressed elongate claw-like tip, terminal portions of costal margin and sacculus symmetrical, without incisions; basoventral scletorisation in vesica distinctly curved backwards...2

2. Valva symmetrically leaf shaped, sacculus slightly more arched than costal margin, terminal hook-like tip indistinct (Fig. 60C)..*P. ratovosoni* **comb. nov.**

- Valva asymmetric, sacculus distinctly semicircular, terminal hook-like tip prominent (Fig. 61C)..*P. triangulifera* **comb. nov.**

Due to a very high similarity among the three known species (Figs 62-63) and availability of only single specimens for our study, it is impossible to provide a reliable determination key for the female genitalia.

Privatenaclia seguyi **comb. nov.** (Figs 59, 62, 64A-C, 65A)
Thyrosticta seguyi Griveaud, 1964: 97, pl. I, fig. 56; Viette 1990: 169.
Holotype: ♂, MNHN, EL65158, by original designation.

Material. 13 specimens (ISEA PAS - 8 ♂♂, 1 ♀♀; MNHN - 2 ♂♂; PZBT - 2 ♂♂) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys.
In the general appearance (Fig. 64), *P. seguyi* **comb. nov.** (and *P. ratovosoni* **comb. nov.**) is the most similar to *Melanonaclia trimacula* **comb. nov.**, *Melanonaclia ranomafana* **sp. nov.**, and *Julienaclia pauliani* **comb. nov.** (see below), especially in the hindwing pattern. However, they differ in the general patterns of the abdomen, in the arrangement of the forewing blotches, and - additionally - the male of *J. pauliani* **comb. nov.** has bipectinate antennae.

Male genitalia redescription (Fig. 59)
Tegumen moderately to heavily sclerotised, U-shaped, flat, wide apically and narrowing laterally towards vinculum, with which is incompletely fused and connected with membranes; uncus elongate, of the length of 2x width of tegumen, porrect and slightly directed downwards, in medial portion slightly incised dorsoventrally, basal half flattened dorsoventrally, remaining portion widening tubular towards the tip, subtriangular in cross section, apex dorsally with claw-like protrusion bent downwards, ventrally with distinct, submedian, rounded protrusion; sublateral arms of tegumen originating lateromedially on each side, straight, pointed, needle-like or slightly incised in terminal 2/3 and thus club-like, directed slightly upwards, of the length of 1/2 of uncus; vinculum U-shaped, narrow in basal half, terminal (lateral) portion with convex protrusion oriented backwards; saccus elongate, slightly bent backwards and narrowing towards tip that can be rounded or slightly pointed;
juxta well developed, in form of wide tube behind valvae, with a ventral, subrounded, bulbous protrusion entering between basal incision of sacculus; valva short, not reaching to uncus, irregularly subtrapezoidal, dully terminated; costal margin folded up ventrally, very slightly convex, almost straight (without basal rounded concavity), terminally rapidly narrowing and straight or in form of incision; sacculus basally shallowly concave, medially convex, terminal portion straight or with indistinct incision, folded inwards similarly like costal margin, fused with it in terminal portion of valva; both margins ventrally covered with sparse, elongate, erect, setae, some setae present also on outer surface along sacculus; terminal portion of sacculus with row of short, tooth-like protrusions, outer surface of valva covered with sparse, dot-like

scobinations; inner surface membranous; phallus moderately sclerotised, elongate, tubular, slightly bent upwards, basal tip rounded, ejaculatory duct opening membranous, located basodorsally; vesica membranous, basal portion of the width of phallus, plane, of 1/2 of phallus length, porrect; remaining portion bent rightwards, sclerotised, inside with well developed, heavily sclerotised longitudinal, claw-like plaque in membranous diverticulum, terminally covered with dense, short and erect spine-like protrusions; further portion of vesica in form of multidimensional diverticulum with a few cavities, dorsal side with indistinct, elongate, longitudinal, moderately sclerotised, rib-like plaque.

First female description (Fig. 64C)

Head. Proboscis well developed, black at base, medial portion brown, apex ochraceous; frons ochraceous yellow, with admixture of pale yellow scales on margins; vertex brown, laterally at margin small ochraceous yellow blotch; postocular area entirely ochraceous yellow to orangish; labial palpus three-segmented, porrect, distally slightly bent downwards (however this is unclear due to postmortal arrangement of the palpi), entirely ochraceous-brown, 1st palpomere ventrally with elongate scales oriented downwards; scapus and first three antennomeres brown, remaining portion of antennae unavailable;

Thorax. Patagia in submedial 1/3 ochraceous-brown, remaining portion ochraceous yellow to orangish; tegulae ochraceous yellow to orangish, in distal portion with piliform ochraceous scales; thorax medially worn of scales, laterally with ochraceous brown scales; pleurites ochraceous brown with small pale yellow blotch at hindwing base.

Legs. Available portions ochraceous brown with pale yellow marks; foreleg: ochraceous brown, frontal and lateral side of coxa pale yellow, distal portion of femur dorso-laterally with admixture of dark yellow-ochraceous scales, tibial epiphysis present, ochraceous brown, reaching to 3/4 of the length of tibia; tarsus ochraceous brown; midleg: coxa pale yellow, terminally pale ochraceous-brown, remaining portion of the leg unavailable; hindleg: coxa basally mix of ochraceous brown and pale yellow, terminally pale yellow, femur ochraceous brown, laterally on external side with pale yellow stripe, remaining portion of the leg unavailable;

Abdomen. Abdomen ochraceous-brown, tergite 1st and 2nd sublaterally yellow, 5th and 6th with very narrow, yellow anterior margin (which can be misattributed to posterior margin of tergites 4th and 5th), extending along lateral portions of each tergite; tergite 7th with comparatively wider yellow anterior margin, extended towards posterior portion of tergite – as a result tergite mostly yellow; sternites 2nd – 7th with extensive anteromedian yellow blotches, gradually diminishing towards posterior part of abdomen; sternite 7th with narrow, deep, U-shaped concavity in medial portion of terminal margin; lateral portion of abdomen with yellow blotches on each segment, forming longitudinal lateral stripes, however this is somewhat unclear due to the weak preservation of abdomen in the analysed specimen.

Forewing. Upperside background ochraceous-brown, with 6 yellow to semi-transparent blotches of different shape and size: two in basal portion, two in medial portion and two in distal portion; first basal blotch (fm$_1$) yellow to ochraceous yellow, in form of elongate rectangle, from between costal margin and Sc to hind margin of DC, fused with the second basal blotch; second basal blotch (m$_1$) in form of small, irregular stripe of yellow scales, mixed with ochraceous brown scales, more dense below DC hind margin;

first medial blotch (m$_2$) of irregular shape: rectangular portion from Sc to just below R with yellow to ochraceous-yellow regular scales, remaining portion subcircular to subtriangular, from below R and terminated before DC hind margin, semi-transparent, narrowly emarginated with yellow regular scales and medially covered with tiny, sparse concolorous scales; second medial blotch (m$_3$) irregular to slightly subtrapezoidal, originating in 1/4 of distance between DC hind margin and wing hind margin, outer margin with a small protrusion reaching slightly beyond CuA2, and posterior tip reaching slightly beyond 1A+2A; yellow, anterior portion medially semi-transparent, covered with sparse and smaller scales, remaining portion with regular scales; first distal blotch (m$_4$) between R and M1, suboval, emarginated with stripe of regular yellow scales, broader in the distal part; medially covered with small and sparse yellow scales; second distal blotch (fused m$_5$ and m$_6$) of irregular shape, from M2 towards wing outer margin, terminated before CuA1, portion between M2 and M3 (m$_5$) subrectangular, the second portion (m$_6$) subtriangular, along margins and vein M3 stripe of regular yellow scales, broadest in the outer tip; remaining portion with small, sparse yellow scales; underside similar to upperside, but: basal blotches fused and together extended towards medial part of the wing, making basal 1/4 of wing covered irregularly with yellow to pale yellow scales, partially extended into indistinct pale yellow streak along 1A+2A, reaching till half of the wing length; second medial and first distal blotches with more fuzzy and irregular margins; central portions of second medial and both distal blotches more densely covered with tiny pale yellow scales; cilia ochraceous, basally on hind margin row of yellow, elongate and piliform scales;

Hindwing. Subtriangular, elongate, reaching till about half of forewing, outer margin medially shallowly concave; background ochraceous-brown, with two yellow blotches; between costal margin and Sc+Rs+M1 pale yellow streak reaching to the second blotch, remaining portion of the margin pale ochraceous; basal blotch symmetrically pear-shaped, including wing hind margin, and reaching to its 2/3, with narrow ochraceous indentation at wing base; inner margin of the blotch basally along DC hind margin and medially along CuA2; second blotch in distal half of the wing, beyond DC, of irregular shape, from Sc+Rs+M1 towards M2 + M3 of regular width, from M2 + M3 widening into suboval blob, separated from outer margin by narrow ochraceous stripe, and internally emarginated by CuA1; underside as upperside, but yellow streak between costal margin and Sc+Rs+M1 reaching only to the half of the wing length; outer and hind margins with elongated scales; Sc+Rs+M1 bifurcated in terminal 2/3 of wing length, M2 + M3 bifurcated, frenulum present;

Female genitalia first description (Fig. 62)

Anal papilla rounded, moderately sclerotised, covered with minute scobinations and moderately dense, soft, erect setae of different length; apophysis posterioris equal to anal papilla, heavily sclerotized, sinuous, needle-like with rounded tip; apophysis anterioris of similar length and shape, medially bent upwards; dorsal pheromone glands in form of two submedial, elongate, narrow, curled membranous tapes of similar lengths, bi- or trifurcated in the half of their length. Ventral pheromone glands sublateral, not anastomosing, opening at ventral base of apophysis posterioris; ostium bursae wide, flattened dorsoventrally, outer margin medially shallowly incised; sternite 8th wide, membranous, sublaterally with moderately sclerotised elongate plate; antrum well developed, wide, around 2.5x longer than wide, flattened dorsoventrally and directed leftwards, ventral wall with longitudinal, heavily sclerotised plain plate; dorsal wall membranous, with narrow, sclerotised basal margin, processing into narrow, oblique, heavily sclerotised plate; ductus bursae moderately wide, flattened, oriented rightwards, membranous, covered with minute scobinations and folded into longitudinal plicae; corpus bursae elongate, of stomach-like shape, membranous, densely plicate, covered with minute sculpture; signum in form of two moderately sclerotised, transverse, suboval plates located in 1/3 and 2/3 of the corpus bursae length, with lateral margins covered with minute scobinations, medially with a row of tiny, short, spine-like protrusions; ductus seminalis narrow, membranous, originating terminally from laterobasal, distinct, moderately sclerotised, roof-shaped diverticulum of plane walls, located on the right wall of ductus bursae.

Immature stages. Unknown, except for the egg described here for the first time.

Biology. Adults are collected by netting by day; there is no information on attraction to light. Recorded from November to January. Associated with evergreen, mid elevation humid forest.

Distribution (Fig. 65A). Endemic to PN Marojejy, around 1200-1240 m elevation.

Remarks. The species occurs in the protected area, which experienced very little deforestation (LOFM 2022).

Privatenaclia ratovosoni **comb. nov.** (Figs 60, 63A-C, 64D-E, 65B-D)
Thyrosticta ratovosoni Griveaud, 1964: 97, Pl. I, Fig. 64; Viette 1990: 169.
Holotype: ♂, MNHN, EL65157, by original designation.

Material. 48 specimens (ISEA PAS - 1 ♂; MNHN - 22 ♂♂, 1 ♀, 1 ex. sex unknown; NHMUK - 1 ♂; PZBT - 7 ♂♂, 1 ♀, SMNS - 14 exx. sex unknown) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. The most superficially similar species are discussed in the diagnosis of *P. seguyi* **comb. nov.**

Male genitalia redescription (Fig. 60)

Tegumen moderately sclerotised, U-shaped, wide subdorsally, narrowing laterally, completely fused with vinculum; junction of tegumen and uncus with narrow, elongate, well developed sclerotisation; uncus elongate, of the length of two widths of tegumen, porrect and slightly directed downwards, basal half flattened dorsoventrally, remaining portion widening tubular towards the tip, subtriangular in cross section; apex dorsally with well sclerotised claw-like protrusion bent downwards, ventral wall terminally with small, subconical protrusion projected forwards; sublateral arm of tegumen originating lateromedially on each side, weakly sclerotised, in form of straight, pointed, needle-like protrusion directed slightly upwards, of the length of 1/2 of uncus; vinculum weakly to moderately sclerotised, narrow and U-shaped; saccus subtriangular, elongate and pointed, slightly bent dorsally; juxta well developed, moderately sclerotised, in form of wide tube behind valvae, with a ventral irregular protrusion entering between basal incision of sacculus; valva short, not reaching to uncus, leaf shaped, with pointed apex provided with short, claw-like tip oriented inwards; costal margin in basal portion with, rounded concavity, remaining portion slightly convex, almost straight, terminally narrowing toward the tip; entire margin folded up ventrally; sacculus basally and terminally shallowly concave, medially convex, folded inwards similarly like costal margin, fused with it in terminal portion of valva; both margins ventrally covered with sparse, elongate, erect setae; dorsally valva entirely devoid of setae and covered with minute sculpture; phallus moderately sclerotised, elongate, tubular, slightly bent upwards in terminal portion, basal tip rounded, ejaculatory duct opening membranous, located basodorsally; vesica membranous, basal portion of the width of phallus, and of 1/2 of phallus length, porrect; remaining part bent upwards, multidimensional, basal portion heavily sclerotised, transforming into well developed, irregular, L-shaped sclerotisation and membranous diverticulum, terminally covered with heavily sclerotised, dense scobinations; remaining portion above the sclerotisation and parallel to it, irregularly tubular, slightly widening, with a narrowed tip, on the right side laterodorsally with indistinct, elongate, longitudinal, moderately sclerotised, rib-like plaque.

First female description (Fig. 64E)

Head. Proboscis well developed, dark brown; frons ochraceous brown, laterally in medial portion with two pale yellow blotches; vertex ochraceous brown; postocular area pale yellow, but medially at the margin near eye small ochraceous brown blotch; labial palpus three-segmented, straight, porrect, entirely ochraceous brown, 1st palpomere ventrally with elongate scales oriented downwards; antennae filiform, entirely ochraceous brown including scapus, ventrally covered with short erect, pale setae;

Thorax. Patagia medially dark ochraceous brown, laterally with pale yellow margin; tegulae pale yellow, inner margin with elongate ochraceous brown scales, apex with tuft of ochraceous brown piliform scales; meso- and metathorax ochraceous brown, pleurites ochraceous brown;

Legs. Additional tooth on clave very small, in form of an indistinctive thorn on inner wall of clave; arolium present; foreleg: coxa pale yellow, remaining portion pale ochraceous brown, with admixture of pale yellow scales; epiphysis present, of the length of 2/3 of tibia, concolorous with the leg; tibia and 1st tarsomere longer than femur; midleg: coxa, trochanter and femur pale yellow, remaining portion pale ochraceous brown, but ventral surface of tarsus with marks of more intensive yellow; tibia with one pair of terminal ochraceous brown spurs, of equal length; hindleg: coxa, trochanter and femur pale yellow, tibia and tarsus dorsally ochraceous brown, ventrally yellow (more intensive than the basal parts of the leg); one pair of terminal spurs, of equal length; additional spurs absent;

Abdomen. Ochraceous brown, with some pale yellow marks laterally; 1st tergite ochraceous brown, sublaterally with two very indistinct, small pale yellow blotches; 2nd tergite entirely ochraceous brown; tergites 3rd – 8th medially ochraceous brown, laterally with differently expressed pale yellow blotch, with blurred inner margin; 8th tergite on terminal margin with elongate scales; 2nd sternite medially pale yellow, laterally pale ochraceous brown, sternites 3rd – 6th worn, with remnants of pale yellow scales; 7th sternite worn, ochraceous brown with admixture of pale yellow scales, medially with U-shaped incision; lateral part of the abdomen mostly unavailable, with partly visible mixture of ochraceous brown and pale yellow scales;

Forewing. Elongate, subtriangular, background ochraceous brown, with six pale yellow blotches of different shape and size, two in basal, medial and distal portion, part of them semi-transparent; first basal blotch (fm_1) elongate, subrectangular, along R stem, between Sc and basal portion of DC hind margin; second basal blotch (am_1) small and indistinct, elongate, along basal portion of wing hind margin; first medial blotch (m_2) of irregular leaf-like shape, anterior portion between Sc and R subrectangular with pale yellow regular scales, remaining portion in DC, widening beyond R, then narrowing towards sharp tip, in 1/2 of DC width, emarginated with regular pale yellow scales, medial portion semi-transparent, covered with mix of small and very small and scarce pale yellow scales; second medial blotch (m_3) below CuA1, round, semi-transparent, scales coverage as in DC portion of m_2 blotch; first distal blotch (m_4) irregularly suboval, pale yellow, semi-transparent as m_3;

Second distal blotch (fused m_5 and m_6), elongate, subrectangular, aslant towards wing outer margin, pale yellow, semi-transparent as above described blotches; underside as upperside, but fm1 elongate towards wing base, below that blotch retinaculum subdorsale, in the form of a tuft of elongate, pale yellow scales; semi-transparent coverage of the blotches identical as on upperside; M2 and M3 originating from single point at DC lower corner; cilia concolorous with the wing background, but along am1 row of elongate, pale yellow scales;

Hindwing. Subtriangular, elongate, reaching to 1/2 of forewing length, outer margin slightly concave medially; background ochraceous brown, like in male, with two pale yellow blotches; basal blotch pear-shaped, along wing basodistal margin, inner margin along DC hind margin and CuA2, with small, sharp ochraceous brown incision basally along 3A, and distally shallowly convex; distal blotch elongate, irregular, 8-shaped, constricted along stalked basal portion of M2+M3, and reaching to CuA1; Sc+Rs+M1 completely fused. M2 and M3 stalked in basal half of their length; underside as upperside, but in wing basal portion small irregular pale yellow blotch, continued by very narrow pale yellow strip along costal margin, reaching to 1/4 of wing length;

Remarks. The general body colouration and pattern are identical as in male.

Female genitalia first description (Fig. 63A-C)

Anal papilla subtrapezoidal, moderately sclerotised, covered with indistinct scobinations and sparse, erect setae of equal lengths, except for terminal margins with prominent, tiny scobinations and more dense setae of different length; apophysis posterioris of the length of anal papilla, moderately sclerotized, needle-like, straight, terminally slightly bent upwards; apophysis anterioris equal to anterioris, moderately sclerotised, narrow, needle-like and straight; dorsal pheromone glands in form of long, narrow, tubular, twisted and moderately anastomosing tapes of similar lengths, located submedially; ventral pheromone glands of the similar structure located sublaterally at the base of apophysis anterioris; 7th sternite weakly sclerotised, except for terminal margin forming a well sclerotised, concave ridge along ostium bursae; submedian portion of 8th sternite membranous, covered with minute scobinations and shallowly incised medially; lamella postvaginalis well sclerotised, in form of boat-shaped plaque above ostium bursae; ostium bursae wide, semilunar, well sclerotised; antrum well sclerotised, narrowing conically and bent rightwards; ductus bursae narrow, slightly sinuous, flattened dorsoventrally, membranous, directed rightwards, on the ventral wall with elongate, well sclerotised plaque, originating from antrum, on the dorsal wall in basal portion with moderately sclerotised granular sculpture; corpus bursae pear-shaped, membranous, with indistinct, minute scobinations and wide, indistinct plicae; signum on left side, in form of two weakly sclerotised plaques with tiny teeth-like protrusions, in 1/3 and 2/3 of the bursa length; ductus seminalis narrow, originating from a distinct, subconical, membranous appendix bursae covered with minute, indistinct scobinations, located in the basal left portion of bursa.

Immature stages. Unknown.

Biology. Adults are collected by netting by day; there is no information on attraction to light. Recorded from October to January, in March and August. Associated with evergreen, mid elevation humid forest.

Distribution. Central eastern Madagascar, in the region of Alaotra-Mangoro (Ankasoka, Maromitza Nature Reserve, Lakato). From around 1100 to 1150 m elevation.

Remarks. The highest number of specimens was collected from October to December, and only single individuals in the remaining months. This result, however, is likely biased by collector activity, and not seasonal abundance of the species. In Ankasoka and Lakato there are only small and fragmented patches of forest left (Fig. 65D).

Privatenaclia triangulifera **comb. nov.** (Figs 61, 63D, 64F, 65C)
Thyrosticta triangulifera Griveaud, 1964: 96, Pl. I, Fig. 63; Viette 1990: 170.
Holotype: ♂, MNHN, EL65156, by original designation.

Material. Six specimens (ISEA PAS - 1 ♂; MNHN - 3 ♂♂, 1 ♀; PZBT - 1 ♂) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. Superficially, the most similar are *Maculonaclia* species with the hindwing blotch in the form of an arched streak, on the outer margin provided with a small protrusion i.e. *M. ankasoka*, *M. dentata* Griveaud, 1964, *M. grjebinei* Griveaud, 1964, *M. itsikiorya* Griveaud, 1969, *M. lambertoni*, *M. sanctamaria* Griveaud, 1964, *M. tampoketsya* Griveaud, 1964, and *M. tenera*. However, none of them possesses the wedge-like forewing basal blotch characteristic of *P. triangulifera* **comb. nov.** (and *P. ratovosoni* **comb. nov.**, but see the diagnosis above) (Fig. 64D-F).

Male genitalia redescription (Fig. 61)
Tegumen moderately sclerotised, U-shaped, flat, with distinct ribs along margins, wide subdorsally and narrowing laterally towards vinculum, with which is incompletely fused and connected with membranes; uncus elongate, of the length of two widths of tegumen, porrect and slightly directed downwards, remaining portion widening tubular towards the tip, subtriangular in cross section, apex dorsally with claw-like protrusion bent downwards, ventrally with two small, rounded membranous protrusions; sublateral arms of tegumen originating lateromedially on each side, straight, pointed, needle-like, directed slightly upwards, of the length of 1/2 of uncus; vinculum U-shaped, narrow; saccus elongate, slightly bent backwards and narrowing towards rounded tip, with ribs along margins; juxta well developed, in form of wide tube behind valvae, with a ventral, rounded protrusion entering between basal incision of sacculus; valva short, not reaching to uncus, leaf-shaped, apex with elongate, claw-like protrusion bent inwards; costal margin sinuous, basally distinctly concave, in terminal 2/3 convex; terminal 1/3 of costal margin folded up ventrally; sacculus basally concave, remaining portion distinctly convex, folded inwards in terminal 1/3 similarly like costal margin,

fused with it in terminal portion of valva; both margins ventrally covered with sparse, elongate, erect setae, some setae present also on outer surface along sacculus; entire outer and terminal ventral surface of valva covered with sparse, dot-like scobinations; phallus moderately sclerotised, elongate, tubular, slightly bent upwards, basal tip rounded, ejaculatory duct opening membranous, located basodorsally; vesica membranous, basal portion of the width of phallus, plane, of 1/2 of phallus length, porrect; remaining portion bent rightwards, medially inside with well developed, heavily sclerotised longitudinal, irregular plaque; further portion of vesica in form of multidimensional diverticulum with a few cavities.

Immature stages. Unknown.

Biology. Individuals are attracted to light; there is no data on diurnal activity of the species. All specimens were collected in November. Associated with evergreen, mid elevation and lower montane evergreen forest.

Distribution (Fig. 65C). Endemic to Marojejy PN, around 1700-1875 m elevation.

Remarks. Similarly to *P. seguyi* **comb. nov.**, the species occurs in protected area with rather low deforestation pressure (LOFM 2022).

Julienaclia gen. nov.

Type species *Thyrosticta pauliani* Griveaud, 1964

Diagnosis. The two species of the genus, *J. pauliani* **comb. nov.** and *J. moerens* (Oberthür, [1911]) **comb. nov.** (see the Taxonomic note for the latter below) distinctly differ from each other in the general body colouration (Fig. 64G-L), but share the following characters, unique among all known Madagascan Syntomini: antennae bipectinate in both sexes (Fig. 7A-B) and sexually dimorphic, with rami shorter and less distinct in the female. Forewing outer margin wavy, with a shallow incision in subtornal area (Fig. 14D). A similar incision is present also in the genus *Melanonaclia*, but differently expressed, very distinct in *M. toulgoeti*, and hardly visible in *M. nigra* or *M. trimacula* **comb. nov.** (Figs 14E-F, H, 15F). Hindwing in both sexes distinctly subtrapezoidal, with the hind margin straight, reaching to around 2/3 of the length of costal margin and parallel to it, outer margin with prominent subrounded incision (Fig. 16E). Somehow similar hindwing shape is present in the male of *Dubianaclia amplificata* (Saalmüller, 1880), but this differs in venation (Griveaud 1964: Fig. 258f).

In the male, the 8th sternite distinctly subtrapezoidal, widening towards terminal margin, which is narrowly folded inwards and laterally narrowed and curved upwards, and forms a shield-like plaque covering basoventral portion of genitalia (vinculum and saccus) (Fig. 66);

In the male genitalia (Figs 67-68): valvae narrow, elongate and distinctly asymmetric, the right one broader and longer than the left one. A similar character can be found in the males belonging to the genus *Mortinaclia* **gen. nov.** (but constituting an unresolved species complex, see further in this paper), but the entire genitalia of that species, including valvae, have completely different shapes, and however they share the presence of additional arms on the tegumen, but of completely different shape (see the remarks for the genus *Privatenaclia* **gen. nov.** above).

In the female genitalia (Figs 69-70): corpus bursae with single, rounded signum located ventroterminally, and provided with short spine-like protrusions. A single signum is present also in the genus *Kowalskinaclia* **gen. nov.**, but of completely different shape and localisation (see the remarks for that genus above), and in *Tritonaclia stephania* (Oberthür, 1923), where it is located medially, and the ductus bursae in that species is short and distinctly widened.

Taxonomic note. The female of *Julienaclia pauliani* **comb. nov.**, described here for the first time (Fig. 64I), turned out to have genitalia (Fig. 69) very similar to *Melanonaclia moerens* (Oberthür, [1911]) (Fig. 70). At the same time, the males of *J. pauliani* **comb. nov.** and *Thyrosticta melanisa* Griveaud, 1969 share the distinctly asymmetric valvae (Figs 67-68), unique among all Madagascan Syntomini. These morphological observations led to the conclusion that *Thyrosticta melanisa* is conspecific with *M. moerens*, and congeneric with *J. pauliani* **comb. nov.** Thus, *M. moerens* is moved from the genus *Melanonaclia* to *Julienaclia* **gen. nov.**, and *T. melanisa* is treated as a junior subjective synonym of *M. moerens*.

Remarks. The "Group of *Thyrosticta pauliani*", treated by Griveaud (1964) as the "sixth section" of *Thyrosticta* and monotypic, was characterised based on the male antennae (erroneously interpreted as "quadripectinate", see the diagnosis above), presence of semi-transparent blotches on the forewing (distinct, but not unique among the species of *Thyrosticta*, see e.g. *Privatenaclia* **gen. nov.**) and the asymmetrical genitalia (Griveaud 1964).

This genus can be further defined by the following set of morphological characters: brush-like tuft of scales behind the male foreleg coxa absent; hindleg with additional pair of spurs in 3/4 of the tibia length; forewing upperside blotches: basal differently expressed (see the species remarks below), medial: m2, m3, distal: m4, fused m5+m6; hindwing with Sc+Rs+M1 completely fused, area above it narrow, M2 and M3 stalked in around basal 1/3 of their length, 3A present but almost along the basodistal margin (Fig. 16E); hindwing pattern species-specific (see below).

In the female genitalia, ventral pheromone glands present but much shorter and simpler than the dorsal ones, corpus bursae simple, without diverticula (Figs 69-70).

***Julienaclia* gen. nov. species determination key based on adult characters**

1. Body and wings dark ochraceous-brown, with white pattern, without yellow scales (Fig. 64J-L)..*J. moerens* **comb. nov.**

- Body and wings dark ochraceous-brown, with intensively yellow blotches on the wings and abdomen (Fig. 64G-I)...*J. pauliani* **comb. nov.**

***Julienaclia* gen. nov. species determination key based on male genitalia**

1. Lateral portions of tegumen and vinculum parallel to each other, apical part of tegumen flattened dorsoventrally, and the entire genitalia outline subrectangular; vesical basally with two lateral pouch-like diverticula, terminal portion of vesica plain and not divided into two arms (Fig. 67)..*J. pauliani* **comb. nov.**

- Lateral portions of tegumen slightly leaning towards each other, apical part of tegumen arched, and the entire genitalia outline suboval; vesica basally with two lateral pouch-like diverticula, terminal portion covered with minute scobinations and divided into two uneven arms (Fig. 68)..*J. moerens* **comb. nov.**

Genitalia of the females of the two *Julienaclia* **gen. nov.** species are indistinguishable in the materials available for this study, especially since there is only one, fixed preparation of *J. moerens* **comb. nov.**, deposited in MNHN (P. Griveaud slide No. 284) (Fig. 70).

Julienaclia pauliani **comb. nov.** (Figs 64G-I, 67, 69, 71A)
Thyrosticta pauliani Griveaud, 1964: 99, Pl. I, Fig. 66; Viette 1990: 169; Lees and Minet 2022: Fig. 9.70.

Material. 9 specimens (ISEA PAS - 1 ♂, 2 ♀♀; MNHN - 3 ♂♂, 1 ♀; NHMUK - 1 ♂; PZBT - 1 ♂) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. Forewing basal blotches: fm1 and m1, varying in size among individuals, the former one sometimes is almost absent.

Male genitalia redescription (Fig. 67)
Tegumen well sclerotised, rectangular, dorsal surface almost completely flattened dorsoventrally, anteromedian margin shallowly concave, lateral arms widely fused with vinculum; uncus basomedially with shallow rounded membranous area, broad, pentagonal, with lateral margins straight and parallel, then narrowing rapidly and fusing together at right angle at the tip; margins in terminal portion folded downwards, forming the base for the apical claw-like, bluntly terminated protrusion bent ventrally; dorsal surface covered with minute, dot-like, sparse scobinations, dorsally and along terminal 3/4 of margins with erect, elongate setae; sublateral arms of tegumen located laterally, spine like, pointed, oriented upwards at 45 degrees; vinculum narrow, subrectangular, slightly sinuous, with indistinct sublateral incisions, then sharply bent towards tegumen, in the inner corners with rounded incision and small subtriangular protrusion above it; vinculum lateral margins provided with distinct, flat subtriangular protrusions, apically on outer surface covered with sculpture, projected forwards (towards the abdomen tip); saccus wide basally, subtriangular, well sclerotised, especially along margins, narrowing towards dull termination and slightly bent backwards; juxta in form of moderately sclerotised, irregularly suboval to subtrapezoidal horizontal protrusion directed outwards, located at valvae base; valvae elongate, reaching to uncus base, bent upwards, basally tubular, remaining portion flattened dorsoventrally, distinctly asymmetrical; right valva at least 2x broader than the left one; in right valva costal margin straight, or with sinuous incision along the medial portion, with shallow incisions in 1/3 and 2/3 of its length, between incisions convex, terminally narrowing towards differently expressed, subtriangular, pointed tip, that is slightly bent upwards; sacculus basally very slightly convex, then incised in the basal half, remaining portion slightly convex, terminally narrowing; left valva narrower and slightly shorter than right

one, terminated with subtriangular tip, that is rather rounded and less pointed than in right valva; costal margin of similar shape to the right one, sacculus very slightly convex basally, then uniformly incised towards tip; both valvae on the basoventral surface possess subtriangular to saddle-shaped, horizontally oriented incision, reaching to around half of the valva width and opened outwards (towards vinculum), with the ventral/inner margin provided with small horizontal plate, protruding backwards (towards the base of the abdomen); outer surfaces of both valve covered with sparse, unevenly distributed, minute, dot-like scobinations and erect setae of different lengths, oriented in different directions; phallus very short, flattened laterally, broad in basal portion and narrowing towards vesica, coecum penis bulbous, roundly terminated, dorsobasally with elongate V-shaped cavity; vesica membranous, short, basally tubular, with one subhemispherical diverticulum on the left side, remaining portion in the form of tube, initially broad, then indistinctly twisted, narrowed, elongate, creased in the basal portion, and in terminal portion conically narrowing towards dull tip;

First female description (Fig. 64I)

Head. Proboscis well developed, ochraceous-brown; frons dark brown, with narrow, transverse, dark yellow, straight (or medially slightly arched towards vertex) stripe between eyes, that might be narrowly interrupted medially; vertex brown with yellow dot on lateral margin behind scapus; postocular area ochraceous-brown; maxillary palpi present, in form of ochraceous tufts of setae laterally to proboscis base, oriented aslant towards the proboscis; labial palpus three-segmented, straight, porrect, ochraceous brown, palpomere 3rd of 2/3 of the length of 2nd; antennae flattened dorso-ventrally, bipectinate, ochraceous brown except white scales dorsally at termination, each ramus ventrally covered with short, erect setae and with single seta on tip, longer than remaining;

Thorax. Patagia medially dark brown, laterally with yellow blotch; tegulae yellow, tip with piliform ochraceous scales; prothorax subdorsally from front coxa yellow; mesothorax dark brown, with two irregular yellow blotches in latero-median portion of mesoscutum; metathorax dark brown; pleurites ochraceous, with yellow blotches at wings bases;

Legs. Additional, minute tooth of claw present; arolium present; foreleg: ochraceous brown, coxa baso-laterally with tiny yellow dot, epiphysis present, reaching to 3/4 the length of tibia, ochraceous; tarsus ventrally with admixture of yellow scales, tibia + 1st tarsomere longer than femur; midleg: coxa ochraceous, remaining portion unavailable; hindleg: ochraceous, terminal portion of coxa and trochanter with pale yellow scales; tibia ochraceous, with one pair of pale yellow to creamy terminal spurs, inner one slightly longer, both shorter than tibia width;

additional pair of slightly shorter, pale yellow to creamy spurs in terminal 1/4 of tibia; tarsus ochraceous, ventrally with admixture of ochraceous-yellow scales, on ventral margins with row of elongate, ochraceous, spines projected downwards;

Abdomen. Abdomen with irregular pattern of dark brown and yellow scales; 1st tergite yellow, with anteromedian irregular, blurred ochraceous-brown blotch and posteromedial narrow, longitudinal oval ochraceous-brown spot; 2nd and 3rd tergites entirely ochraceous brown; 4th and 5th tergites yellow, with anteromedian, subrectangular ochraceous-brown blotches, on 4th narrowing rapidly into narrow longitudinal stripe on terminal margin, fusing with blotch on 5th, which terminates in 3/4 of tergite length; tergite 6th ochraceous brown, laterodistally with short narrow yellow stripes; tergite 7th ochraceous brown in basal half, in terminal half pale yellow; 2nd, 3rd and 4th sternites laterally ochraceous brown, medially with yellow blotch; 5th sternite brown, medially with a yellow stripe along terminal margin; 6th and 7th dark brown with yellow lateral margins; abdomen laterally partially deformed, visible portion yellow, with irregular brown blotches at intersegments 2nd - 5th, gradually diminishing in size.

Forewing. Upperside background ochraceous-brown, with 6 blotches of similar size: two in basal portion, two in medial portion and two in distal portion; basal two (fm_1 and m_1) yellow, subtriangular, close to each other, up to having slightly fused tips and forming one, sandglass-shape blotch with constriction at DC base hind margin; first basal blotch (am_1) from between costal margin and Sc, narrowing to DC hind margin and second one (m_1) from DC hind margin widening towards, but not touching 1A+2A; first medial blotch (m_2) rectangular, from Sc to hind margin of DC but terminated before it, between Sc and R with yellow scales, remaining portion semi-transparent, narrowly emarginated with single pale yellow regular scales and covered with tiny, sparse pale yellow to creamy scales; second medial blotch (m_3) irregular-subtrapezoidal, originating beyond DC hind margin, widening towards 1/2 of the distance between DC hind margin and 1A+2A, then narrowing and terminated beyond 1A+2A, yellow, in anterior portion partially semi-transparent, covered with smaller and sparse yellow scales; first distal blotch (m_4) between R5 and M1, subsquare, semi-transparent, narrowly emarginated with single pale yellow regular scales and covered with tiny, sparse creamy scales; second distal blotch (fused m_5 and m_6) subtrapezoidal, from M2 towards M3 of even width, from M3 slightly widening and terminated at CuA1, colouration and covering scales as in first distal blotch, with narrow stripe of pale yellow scales also along M3; underside similar to upperside, but basal blotches broadly fused in a transverse stripe; additional pale yellow stripe from second basal to second medial blotch, between 1A+2A and hind margin; smaller and sparse scales on the semi-transparent blotches similar as on upperside; cilia ochraceous brown, a row of piliform brown scales in postbasal portion of wing inner margin;

Hindwing. Subtriangular, elongate, reaching about half of forewing, outer margin sinusoidal, slightly incised in the posterior portion; basal portion yellow, between costal margin and Sc+Rs+M1 pale yellow, reaching 3/4 of costal and hind margins, in median portion above CuA1 forming a subrectangular projection towards outer ochraceous brown zone, and with indistinct ochraceous indentation at the base of wing; ochraceous subsquare median blotch from Sc+Rs+M1 to DC hind margin, and below CuA1 subtriangular ochraceous brown indentation of the outer zone towards medial portion of wing; underside as upperside, but subsquare medial blotch extended up to costal margin, and basal portion of costal margin (to the blotch) with pale yellow scales; Sc+Rs+M1 completely fused, M2 and M3 bifurcated in the terminal 2/3 of the wing; frenulum present.

Female genitalia first description (Fig. 69)

Anal papilla subtrapezoidal, moderately sclerotised, covered with minute scobinations and erect setae of different length, more dense along terminal margins; apophysis posterioris the length of anal papilla, heavily sclerotized, needle-like, sinuous with tip oriented inwards; apophysis anterioris around half the length of posterioris, heavily sclerotised, very narrow, needle-like and straight; dorsal pheromone glands in form of two long, narrow, twisted and anastomosing membranous tapes of similar lengths, located submedially; ventral pheromone glands much shorter, located sublaterally, in form of two long, narrow, moderately twisted and bifurcated or not anastomosing membranous tapes of similar lengths; 7th and 8th segments well sclerotised; 7th sternite wide, medially with deep U-shaped incision, along terminal margin with well sclerotised edge; 8th sternite (lamella postvaginalis) narrow, in terminal portion with distinct, outstanding convexity, medially provided with subtrapezoidal incision; posterior margin with prominent, sclerotised ridge, submedially provided with subtriangular outstanding protrusions, and narrowing towards ostium bursae; ostium bursae relatively narrow, in form of heavily sclerotized, suboval, slightly flattened dorsoventrally ring; antrum and ductus bursae fused, narrow, entirely membranous, covered with minute scobinations and oriented rightwards; corpus bursae in basal portion narrow, elongate and medially bent leftwards, then conically widening into pear-shape bursa, plicate with wide plicae and covered with minute sculpture; signum in terminal portion, almost on the bottom of bursa, in form of single, suboval to 8-shaped, strongly sclerotised plate covered with short, spine-like protrusions; ductus seminalis very narrow, originating at the bent in the very basal portion of bursa;

Remarks. The entire genitalia can have different extent of sclerotisation, and especially the protrusion on the terminal ridge of 8th sternite can be differently expressed.

Immature stages. Unknown.

Biology. Adults are collected by netting by day, flying actively around 1 pm.; there is no data on attraction to light. Recorded in October, and from December to March. In the corpus bursae of two females (DL_02-109 and MAD_209), collected on 19.01.2002 and 27.02.2020, one and two colla were recorded, respectively. Associated with deciduous, seasonally dry western forest and deciduous, dry southern forest and scrublands; the individuals were recorded both in dense forest and along paths.

Distribution (Fig. 71A). Along the southern and western coast of Madagascar, in the regions of: Androy (Ambovombe), Atsimo-Andrefana (Andranovory), Menabe (Kirindy forest, and the forest S of Befasy), Boeny (Tsingy de Namoroka PN). From around 70 to 500 m elevation.

Remarks. The southernmost localities are currently devoid of primary vegetation, and the forests in the area of Befasy have been almost completely cut in the last two decades.

Julienaclia moerens **comb. nov.** (Figs 64J-L, 68, 70, 71B, D)
Naclia moerens Oberthür, [1911]: 467-468, pl. 16, fig. 3.
Holotype: ♀, NHMUK, NHMUK010621037 (Fig. 64J), by monotypy.

Melanonaclia moerens Griveaud 1964: 72, Pl. I, Fig. 43; Viette 1990: 168.

= *Thyrosticta melanisa* Griveaud, 1969 **syn. nov.**
Thyrosticta melanisa Griveaud, 1969: 11, Pl. I, Fig. D; Viette 1990: 169.
Holotype: ♂, MNHN, EL65160 (Fig. 64L), P. Griveaud slide No. 578 (Fig. 68E-F), by original designation.

Material. 5 specimens (MNHN - 2 ♂♂; NHMUK - 1 ♀; PZBT - 2 ♀♀) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. This species has only a single blotch in the basal portion of the forewing (m_1), although in some specimens absent, whilst *J. pauliani* **comb. nov.** usually has two basal blotches (fm_1 and m_1).

Superficially the most similar species, also possessing bipectinate antennae, is *Vadonaclia marginepuncta*, but this has different shape of antennomeres (described in detail in the diagnosis of *T. sylvicolens*), orange-reddish marks on the vertex, patagia, tegulae, and a row of small pale blotches along the forewing outer margin, different shape of the hindwing, and differently shaped, symmetrical valvae in the male (Griveaud 1964).

Taxonomic note. This species so far has been known only from the female holotype deposited in NHMUK (NHMUK010621037) (Fig. 64J) and a single female specimen, dissected by Griveaud (1964). The latter specimen is deposited in PZBT (however without the label with the slide number), but the genitalia slide is in MNHN, P. Griveaud slide No. 284 (Fig. 70). Griveaud (1964) erroneously stated this species to have piliform antennae (“antennes simples”), which was the morphological characteristic of the genus *Melanonaclia*. In fact, both above-mentioned female specimens possess bipectinate antennae. Additionally, the similarity of the female genitalia of *J. pauliani* **comb. nov.** (described here for the first time) and “*Melanonaclia*” *moerens* (Figs 69-70) match the similarities between the male genitalia of *J. pauliani* **comb. nov.** and “*Thyrosticta” melanisa* (Figs 67-68).

Thus, we conclude that *T. melanisa* is conspecific with *M. moerens*, which is supported also by other morphological characters, and move it to the genus *Julienaclia* **gen. nov.**, as congeneric with “*Thyrosticta*” *pauliani*, the type species of the genus.

Male genitalia redescription (Fig. 68)

Tegumen well sclerotised, U-shaped, apically with widened anterior margin and distinct rounded incision in posterior margin, then sinuous, widened sublaterally, and narrowing towards vinculum, with which is completely fused; uncus distinct, folded downwards, basomedially with U-shaped membranous area, sclerotised only laterally, broad and tongue-shaped, flattened dorsoventrally, slightly narrowing medially, with margins terminally bent downwards, terminated with claw-like protrusion directed inwards; dorsally and along terminal 3/4 of margins covered with erect, elongate setae; sublateral arms of tegumen located sublaterally, spine like, pointed, oriented upwards at 45 degrees; vinculum narrow, broader than tegumen, subtrapezoidal; saccus wide basally, subtriangular, slightly bent backwards and roundly terminated; juxta in form of moderately sclerotised, irregularly suboval to subtrapezoidal horizontal plate, located at valvae base, entering into basal incision of sacculus; valva elongate, reaching to uncus base, bent upwards, basally tubular, remaining portion flattened dorsoventrally, distinctly asymmetrical; right valva at least 2x broader than the left one, costal margin sinuous, with shallow incisions in 1/3 and 2/3 of its length, between incisions convex, terminally narrowing towards pointed tip, slightly bent upwards; sacculus basally incised, then straight till 3/4 of valva length, terminally narrowing towards the tip; left valva tip not as pointed as in the right one; outer surfaces of both valve covered with sparse, unevenly distributed, minute, dot-like scobinations and erect setae of different lengths, oriented in different directions; phallus very short, flattened laterally, broad in basal portion and narrowing towards vesica, basal tip irregularly bulbous, ventrally with transverse rib-like crease, dorsolaterally on the left wall with subtriangular incision; vesica membranous, short, basally bulbous, with three plane, subhemispherical diverticula: two longer oriented leftwards and rightwards respectively, and one shorter protruding; remaining portion oriented upwards, tubular, elongate, covered with minute scobinations, dully terminated, basally on the right side with short, tubular, dully terminated diverticulum;

Immature stages. Unknown.

Biology. There is no data on diurnal / nocturnal activity of the species. The specimens were collected in October, December and January; the holotype of *Naclia moerens* is labelled as collected “between May and October”. All the localities where the species was collected are currently devoid of natural vegetation, and covered mostly with wooded grassland-bushland mosaic, with remnants of mangroves, western type coastal forest, deciduous seasonally dry western forest and evergreen humid forest low and mid elevation.

Distribution (Fig. 71B, D). Northern Madagascar, regions of: Antsiranana (Antsiranana, Beraty and the area of Beangona-Ambevy - “Andronomafana”) and Analanjirofo (Hiaraka). From around 250 to 1000 m elevation.

Remarks. The secondary forests in the western part of the species range (Beraty, Beangona-Ambevy) are already highly fragmented, with quite intensive patchy deforestation reported in the recent two decades in the former one (Fig. 71D).

Riconaclia **gen. nov.**

Type species: *Thyrosticta bimacula* Griveaud, 1964

Riconaclia bimacula **comb. nov.** (Figs 71C, 72A-C, 73, 74)
Thyrosticta bimacula Griveaud, 1964: 91, Pl. I, Fig. 58; Viette 1990: 169.
Holotype: ♂, MNHN, EL65170, P. Griveaud slide No. 397, by original designation.

Material. 10 specimens (ISEA PAS - 4 ♂♂, 2 ♀♀; MNHN - 1 ♂; NHMUK - 1 ♂; PZBT - 2 ♂♂) (Tab. S1).

Diagnosis. Forewing with basal blotch am1, and medial and distal blotches arranged in a longitudinal row, the latter consisting of the fused m_4+am_4+m_5, with m_6 always absent (Fig. 72A-C) - this arrangement and the lack of m6 with the presence of other distal blotches is unique among all Madagascan Syntomini.

In the male genitalia (Fig. 73), saccus distinctly shortened to subtrapezoidal protrusion of vinculum (but not completely reduced, as in the genus *Kowalskinaclia* **gen. nov.**); vesica in the terminal half distinctly bent upwards at an acute angle, outer wall densely ridged, entire vesica without sculpture, only in the terminal portion small, irregular, well sclerotised plaque.

In the female genitalia (Fig. 74), antrum and ductus bursae slightly spiral, distinctly oriented leftwards and arched backwards, thus extended significantly beyond the main vertical axis of the genitalia, entering laterally to the basal portion of corpus bursae, forming a very elongate, tubular diverticulum, oriented straight upwards.

The forewing pattern, and especially the structure of the genitalia differ distinctly from the two remaining species of the “*Thyrosticta trimacula* section”, in which the species was placed by Griveaud (1964), namely *T. trimacula* and *T. dujardini* Griveaud, 1969, as well as from the genus *Melanonaclia*, to which the two above mentioned species are moved here. Although the female genitalia of *R. bimacula* **comb. nov.** share with *Melanonaclia* the similarity of skewed ductus bursae provided with ventral sclerotisation, they have a different general form: i) in *R. bimacula* **comb. nov.** ductus bursae is narrower and the ventral sclerotisation occupies only around 1/3 of its width (and almost all ventral wall in *Melanonaclia*) (Fig. 74), ii) in *Melanonaclia* the basal diverticulum is not so prominent, and the basal portion of corpus bursae is provided with distinct, spined signa, completely absent in *R. bimacula*. In the male genitalia, *Melanonaclia* species share well developed, elongate uncus, almost absent in *R. bimacula* **comb. nov.**, and the vesica possesses a dorsal row of cornuti or at least scobinations, which are absent in *R. bimacula* **comb. nov.**, but instead the vesica is provided with terminal plaque.

These morphological findings are congruent with the molecular results, placing *R. bimacula* **comb. nov.** as a distinct lineage in the phylogenetic tree (Fig. 5B), not closely related to the other species of its "section", supporting its placement in a separate, monotypic genus.

Remarks. The species *Riconaclia bimacula* **comb. nov.** was included in the "Group of *Thyrosticta trimacula*", treated by Griveaud (1964) as the "third section" of *Thyrosticta*, and characterised by piliform antennae, well sclerotised male genitalia and "less than four blotches on the fore wing" (Griveaud 1964).

These characters, however, were treated superficially, and in such a general understanding are shared among many other Madagascan Syntomini, including other species of *Thyrosticta* (*sensu* Griveaud 1964). Additionally, the extent of the genitalia sclerotisation can vary among the individuals.

Here we move the species to its own monotypic genus, which can be further defined by the following set of morphological characters: antennae in both sexes piliform (Fig. 8A-B), ventrally densely covered by short, erect setae, with sexually dimorphic presence of a pair of elongate, thicker setae - on each antennomere in the female, and only on some antennomeres (except the terminal antennae portion) in the male; pencil-like tuft of scales behind the male foreleg coxa present (Fig. 9B); additional hindleg tibial spurs absent; forewing elongate and moderately narrowed, with the hind margin slightly longer than the outer margin, without distinct tornus, with four radial veins and DC outer margin in the medial portion moderately reduced (Fig. 14C); forewing blotches moderately semi-transparent; hindwing subtriangular, Sc+Rs+M1 completely fused, M2 and M3 largely stalked, 3A present (Fig. 16C-D); hindwing with one large medial blotch, in the male comprising the costal margin, in the female with narrow ochraceous brown stripe along the costal margin, medially provided with small, subtrapezoidal protrusion (see the description below).

In the female genitalia, ventral pheromone glands present, slightly longer than the dorsal ones (Figs 29B, 74).

Male genitalia redescription (Fig. 73)

Tegumen moderately to heavy sclerotised, U-shaped, broad subdorsally, with shallow incision laterally at uncus base, narrowing towards vinculum, with which is incompletely fused; uncus moderately to heavy sclerotised, base flattened dorsoventrally, remaining portion elongate, tear shaped, tubular, slightly narrowing laterally, with dorsal rib in terminal 1/3; apex with short, small claw-like protrusion oriented downwards; basal half dorsally and laterally covered with dense, elongate, erect setae; vinculum very narrow and almost membranous with weakly to moderately sclerotised rib forming the outer margin, lateroterminally slightly widened; saccus subtriangular to subtrapezoidal, short, roundly terminated; juxta well developed, moderately sclerotised, in form of a short and wide tube, situated in the basal incision of saccus, basoventrally with a sharp, subtriangular incision;

valva elongate, reaching beyond uncus; basal 2/3 irregularly subtrapezoidal, terminal portion claw-like, curved inwards and upwards, pointed; junction between valva and saccus broadly membranous; costal margin in basal portion straight, rolled up ventrally forming a rib, in the half of valva lengths with bulbous protrusion, then narrowed into the tip; sacculus sinuous, in basal 1/3 incised, then convex, medial 1/3 straight, terminal portion narrowed into the tip, from basal 1/3 to the tip covered with elongate, erect, setae of different lengths, and the outer surface covered with minute, sparse, dot-like scobinations; phallus elongate, straight and tubular, of uniform width, moderately sclerotised and slightly bent dorsally; basal tip rounded, with ejaculatory duct opening located basodorsally; vesica membranous, basal portion distinctly elongate, of the length of phallus, straight and pleated, terminal portion bent upwards, slightly more sclerotised, frontal surface with a few shallow, pocket-like diverticula oriented upwards; tip with irregular, well sclerotised plate, provided with elongate, claw-like spine oriented inwards and protruding leftwards; additionally, lateral wall in subterminal portion with indistinct, narrow and longitudinal, moderately developed sclerotisation.

First female description (Fig. 72C)

Head. Proboscis well developed, dark brown; head entirely ochraceous brown; labial palpus three-segmented, narrow, straight, porrect, slightly bent downwards, concolorous with head; antenna piliform, ochraceous brown, ventrally with two types of setae: dense, short, erect ones, and sparse, irregularly distributed distinctly longer setae.

Thorax. Patagia medially ochraceous brown, lateral third pale yellow; tegulae basomedially pale yellow, margins with elongate ochraceous brown scales, tip with tuft of ochraceous brown piliform scales; meso- and metathorax partly worn, ochraceous brown; pleurites ochraceous brown with pale yellow marks;

Legs. Mostly ochraceous brown, with some pale yellow marks; additional tooth on clave absent; arolium present; tarsi lateroventrally with rows of spine-like, ochraceous setae; foreleg: coxa ochraceous brown, frontally in terminal portion with pale yellow blotch; femur ochraceous brown, remaining portion unavailable; midleg: entirely ochraceous brown, tibia with one pair of concolorous terminal spurs of equal length; hindleg: entirely ochraceous brown, tibia with one pair of concolorous terminal spurs of equal length, no additional spurs;

Abdomen. Tergites yellow, submedially with irregular, ochraceous brown blotch with blurred margins, slightly narrower on 1st tergite, forming longitudinal stripe; sternites entirely ochraceous brown;

Forewing. Elongate, subtriangular, background dark brown with two yellow, not semi-transparent blotches of different shape and size: one in medial and one in distal portion of wing; basal blotch (am$_1$) yellow, narrow, elongate, between 1A+2A and dorsum, in basal half of wing; medial blotch (m$_2$) subtrapezoidal, in medial portion of DC, from R to Cu vein stems; distal blotch (fused m$_4$, am$_4$ and m$_5$) elongate, irregularly suboval, between R and M3; underside as upperside, but below 1A+2A and wing hind margin pale yellow stripe, from wing base to half of its length; below medial blotch (m$_2$) additional blotch (fm$_3$), well separated by ochraceous brown stripe along DC hind margin; cilia ochraceous brown, in basal portion of wing hind margin row of elongate and piliform pale yellow scales;

Hindwing. Elongate, suboval, reaching to 2/3 of forewing length; background ochraceous brown, with large yellow blotch medially; outer margin ochraceous brown, including entire costal margin and reaching to basal 1/3 of basodistal margin; in the medial portion of costal margin subtrapezoidal, pale ochraceous brown blotch, fused with the margin; underside as upperside, cilia concolorous with wing pattern, longer in basodistal margin; Sc+Rs+M1 completely fused, M2 and M3 stalked in the basal 3/4 of their length; frenulum present;

Remarks. The single female available to our study differs from the male in slightly larger wingspan, and some details in the pattern of wings and the abdomen. However, considering the variation within the series of four male specimens available to us, we cannot make any statements on sexual dimorphism, as these differences perhaps represent different possible states of continuous intraspecific variation. In the female described above, the forewing DC blotch does not reach behind the hind margin of the cell, whilst in all four male specimens the blotch is extended behind this margin. Secondly, the female possesses characteristic, ochraceous marking along the costa of the hindwing, that is completely absent in males. Finally, the female has longitudinal dorsal ochraceous brown stripe on tergites and entirely ochraceous brown sternites. Three out of four males have entirely yellow to orangish abdomen, with paler sternites. One male possesses a distinct, elongate, subdorsal stripe along the entire abdomen, and another one has such a stripe reaching only to the 5th tergite.

Female genitalia first description (Fig. 74)

Anal papilla subtrapezoidal, moderately sclerotised, entirely covered with minute scobinations and erect setae of different length, more dense along terminal margins; apophysis posterioris longer than anal papilla, sclerotized, needle-like, straight; apophysis anterioris around the half of the length of posteriores, sclerotised, narrow, needle-like and straight; dorsal and ventral pheromone glands well developed, if form of elongate, straight and bifurcated or not anastomosing membranous tapes of similar lengths; dorsal glands open narrowly at base of apophyses posterioris, ventral glands with much wider openings along lateroventral margin of papillae anales; 7th sternite weakly sclerotised, more intensively at terminal margin, forming a slightly concaved ridge along ostium bursae; 8th sternite (lamella postvaginalis) membranous, covered with minute scobinations and shallowly incised medially; ostium bursae wide, moderately sclerotised; antrum moderately sclerotised, narrowing conically and bent leftwards; ductus bursae narrow, curved rightwards into one helical turn, membranous, laterodorsally on the right wall with elongate, subrectangular, narrow, moderately sclerotised plaque, originating from antrum, terminated in 2/3 of the ductus length, terminally widened and provided with small granular scobinations; corpus bursae elongate, suboval, membranous, with indistinct, minute scobinations; signum on left side, in form of two horizontal, heavily sclerotised rows of short and straight spine-like protrusions, in 1/3 and 3/4 of the bursa length; ductus seminalis narrow, originating from a distinct, elongate diverticulum of the length almost equal to corpus bursae, located in the basal left portion of bursa, in medial portion on ventral wall provided with longitudinal sclerotisation in the form of small, elongate, suboval plaque.

Immature stages. Unknown.

Biology. Individuals are collected by netting by day and attracted to light at night. Recorded in October, November, January, March and April. In the corpus bursae of a single female (NHMUK015109726), collected on 08.11.1993, one complete spermatophore and three colla were found, indicating a recent mating. Associated with evergreen humid forest, mostly at mid, but also low elevation.

Distribution (Fig. 71C). Northern and central east of Madagascar, in the regions of Sava (Marojejy PN and Be Dinta), Analanjirofo (Ambohitsitondroin' Mahalavona), Alaotra-Mangoro (Zahamena, south to Lakato), Matsiatra Ambony (3.5 km SW of Vorondolo). From around 700 to 1700 m elevation.

Remarks. All localities are within larger forests patches being under different forms of protection - the only exception is Lakato, with only small fragments of forest left.

Mauricenaclia **gen. nov.**

Type species: *Syntomis minuta* Boisduval, 1833

In the general appearance, with characteristic ochraceous-rusty body colouration and the pattern of the wings and abdomen, the species of *Mauricenaclia* **gen. nov.** species superficially resemble the genus *Dysauxes*, and the African species *Pseudonaclia puella*. Both the taxa derive from the Madagascan evolutionary lineage of Syntomini, forming a monotypic "*Dysauxes* clade" together with *Mauricenaclia* **gen. nov.** (Fig. 5B, Przybyłowicz et al. 2019, 2021). Therefore, to correctly establish *Mauricenaclia* as a new genus and recognize its apomorphies, it was necessary to analyse also these closely related taxa.

The systematics of the Palaearctic species of *Dysauxes* based on morphology, including the genitalia description and illustration, was elaborated by Ignatyev and Zolotuhin (2006). Recently, the Mauritian endemic *Dysauxes florida* was confirmed to belong to the genus *Dysauxes* based on the molecular and morphological results (Przybyłowicz et al. 2021). The genitalia of both the male and female of *P. puella* have been unknown so far, thus we describe and illustrate them here for the first time.

Diagnosis. However, the species belonging to the "Group of *Thyrosticta minuta*", treated by Griveaud (1964) as the "seventh section" of *Thyrosticta*, form a monophyletic lineage in the phylogenetic tree (Fig. 5B) and are superficially similar to each other (Figs 72, 75-76), so it is difficult to indicate clear morphological apomorphies of the group.

The only diagnostic character shared by all *Mauricenaclia* **gen. nov.** species that we were able to identify is the combination of the shape of juxta and uncus in the male genitalia. The juxta consists of the medially located, well sclerotised tube, with the ventral arms forming a well sclerotised, U-shaped plaque arranged upside-down and entering between sacculi of the valvae. The uncus is differently expressed, flattened dorsoventrally (and additionally can be terminally bifurcated) or beak-shaped and flattened laterally, straight and of regular shape, and never distinctly widened dorsoventrally, nor tubular with a dorsal lobe-like protrusion.

Similar, U-shaped ventral arms of juxta are present in *Pseudonaclia puella* (Fig.86), an African species belonging to the same clade as *Mauricenaclia* **gen. nov.** (Fig. 5B, see also Przybyłowicz et al. 2021). However, that species has the medial portion of juxta in the form of subtriangular, transverse plaque, not a tube, and the uncus flattened laterally and medially widened dorsoventrally. Further, *Pseudonaclia puella* is distinct in i) prominent sublateral arms on the tegumen, absent in both *Mauricenaclia* **gen. nov.**, and *Dysauxes* (Ignatyev and Zolotuhin 2006, Przybyłowicz et al. 2021), and ii) uncus flattened laterally and in medial portion extended dorsoventrally, thus more similar to the unci of *Dysauxes* than *Mauricenaclia* **gen. nov.** (Ignatyev and Zolotuhin 2006, Przybyłowicz et al. 2021). Additionally, *P. puella* differs from the two remaining genera in some peculiarities of the wing venation, indicated in Przybyłowicz et al. (2021).

The shape and arrangement of juxta similar to those of *Mauricenaclia* **gen. nov.**, provided with ventral U-shaped plaque, is present also in the genus *Dysauxes* Hübner, [1819] (Ignatyev and Zolotuhin 2006, Przybyłowicz et al. 2021). However, that genus is characterised by different uncus, which is either bird-head-shaped, prominently flattened laterally and basally provided with a bulbous protrusion, very distinct in the majority of the species (Ignatyev and Zolotuhin 2006), or transformed into a sinuous, narrow tube, dorsally provided with a heart-shaped protrusion in *D. florida* (Przybyłowicz et al. 2021).

Even though *Mauricenaclia peyrierasi* **comb. nov.** (Fig. 76E-H) differs in many characters from the remaining species of the genus (see also the diagnosis of the species), and in the phylogenetic tree constitutes a lineage sister to all of them, it also shares the general similarity and several characters (e.g. wing scales modifications) with other *Mauricenaclia* species. Thus, establishing a separate, monotypic genus for this species within the well defined "*Dysauxes* clade" (Przybyłowicz et al. 2021) would be unnecessary. Additionally, removing it from the genus *Mauricenaclia* would not allow us to indicate any more distinct synapomorphies of the latter. Going further, the results of both molecular and morphological studies support the separateness of all three genera currently belonging to the "*Dysauxes* clade". Also, their geographical distribution, with *Mauricenaclia* **comb. nov.** present only in Madagascar, *Pseudonaclia puella* in Africa, and *Dysauxes* in Mauritius and the Palaearctic, support maintaining the systematics of the species in question arranged in three genera.

The genus *Mauricenaclia* can be additionally diagnosed with the following set of characters, which, however, are present in different subsets of the species and never in all of them: i) forewing in the basal portion of costal margin with short and narrow yellow streak, but absent in *M. peyrierasi* **comb. nov.**, *M. bruneata* (Griveaud, 1969) **comb. nov.** and *M. apatris*

sp. nov., and developed into V-shaped in *M. minuta* **comb. nov.** (Figs 72D-M, 75-76); ii) semi-transparency of the medial part of male hind wing (Fig. 18C-H), and presence of a blotch of transformed scales (Fig. 22) on the forewing underside (but only in *M. minuta* **comb. nov.**, *M. peyrierasi* **comb. nov.** and *M. octopunctata* **comb. nov.**) - somehow similar semi-transparency of the hindwing can be indicated in some species of the genus *Dysauxes*, but it is differently expressed: *Dysauxes parvigutta* (Christoph, 1899) and *D. famula* (Freyer, 1836) have smaller and scarce scales on both upper and underside of the hindwing; iii) hindwing outer margin either blurred and indistinct (in the male in *M. rothschildi* **comb. nov.** and *M. bruneata* **comb. nov.**), or very narrow (in the female of *M. rothschildi* **comb. nov.** and *M. bruneata* **comb. nov.** and in both sexes of *M. peyrierasi* **comb. nov.** and *M. octopunctata* **comb. nov.**) (Figs 72D-M, 75-76); iv) phallus proportionally short and wide, tubular and curved, with relatively short, pouch-like vesica densely covered with longitudinal plicae, directed at right angle to the phallus (except for *M. bruneata* **comb. nov.**, for which only a single preparation with uneverted vesica is available, and *M. peyrierasi* **comb. nov.**, with completely different shape of genitalia, described below) (Figs 77-85).

Among other Madagascan Syntomini, superficially the most similar to *Mauricenaclia* **gen. nov.** is *Toulgoetinaclia obliquipuncta*. This species is highly variable morphologically and also possesses the ochraceous abdomen with differently expressed brown dorsal blotches, and the individuals with fully developed forewing pattern resemble the most *M. minuta* **comb. nov.** and *M. raharizonina* **comb. nov.** However, *T. obliquipuncta* has bipectinate antennae and our molecular results place that species remotely from *Mauricenaclia*, in the lineage sister to all Madagascan Syntomini (Fig. 5A, Przybyłowicz et al. 2019).

Remarks. The genus can be further defined with the following set of morphological characters: medium sized moths, with characteristic, rusty-ochraceous to ochraceous-brown body colouration (Figs 72D-M, 75-76); antennae in both sexes piliform, consisting of relatively short, almost cube-shaped antennomeres, ventrally covered with short and dense, erect setae, with additional pair of thicker and longer setae on some antennomeres in the basal portion and each mere in the terminal portion (Fig. 8C-D) - the only exception is *M. peyrierasi* **comb. nov.**, with sexually dimorphic antennae, piliform in the female, and slightly serrate in the male, with each mere provided with a small lobe (Fig. 8G); brush-like tuft of scales behind the male foreleg coxa absent; hindleg with a single additional spur in the terminal portion of tibia (but absent in *M. minuta* **comb. nov.** and *M. rothschildi* **comb. nov.**)(Fig. 13D-E); forewing subtriangular, sexually dimorphic, in females more elongate, with the outer margin more distinctly longer than the hind margin - in males only slightly longer, tornus rounded, indistinct, subtornal area of the outer margin with a very shallow incision at the termination of CuA2, four radial veins, DC outer margin medially very slightly reduced (Fig. 15C-D); forewing with semi-transparent blotches present in all species, except *M. apatris* **sp. nov.**, basal: fm1, absent in some species, and extended, v-shaped in *M. minuta* **comb. nov.**, medial: m2 and m3, distal: m4, m5+m6; hindwing suboval, costal margin and Sc+Rs+M1 slightly arched, hind margin medially with small subrounded protrusion, basolaterally can be shallowly incised, Sc+Rs+M1 fused, M2 and M3 not stalked, or only in the very short basal portion, 3A absent, and CuA2 and 1A+2A at least partially reduced, in different arrangements (Fig. 17D-F).

In the female genitalia (Figs 87-93), dorsal pheromone glands highly variable among and within the species, ventral pheromone glands absent; 8th tergite reduced to very narrow and well sclerotised rib located below the terminal margin of the 7th tergite, laterally oriented downwards and fused with analogue lateral extension of similarly shaped lamella antevaginalis into distinctly elongate, V–shaped base of apophyses anterioris, especially well developed in and together forming a well sclerotised rim around the basal part of the genitalia. Similar arrangement of very narrow, rib-like plaques occurs also in other genera of Madagascan Syntomini, for example in *Riconaclia bimacula* **comb. nov.** (Fig. 74) but only in *Mauricenaclia* **gen. nov.** seems to form such a distinct V-shaped lateral branching.

As mentioned, the wings pattern of *M. peyrierasi* **comb. nov.**, *M. octopunctata* **comb. nov.**, *M. rothschildi* **comb. nov.**, and - to some extent - *M. bruneata* **comb. nov.** is one of the most sexually dimorphic among all Madagascan Syntomini. Such prominent differences can be indicated only in *Tritonaclia melania* (Oberthür, 1923), *Dubianaclia amplificata*, *D. quinquemacula* (Mabille, 1882) and *Melanonaclia nigra*.

***Mauricenaclia* species determination key based on adult characters**

1. Forewing uniformly pale ochraceous, with a few very indistinct, small, slightly darker blotches (Fig. 76I-K)..*M. apatris* **sp. nov.**

Forewing ochraceous brown, with pale yellow to creamy, partly semi-transparent blotches..2

2. Forewing base without pale yellow marking along costal margin and in female with two creamy white medial blotches (m_2 and m_3), of which the latter distinctly enlarged, in male with one medial blotch and with a suboval field of modified scales on the underside (Fig. 76E-H)..*M. peyrierasi* **comb. nov.**

- Pale yellow marking along the basal portion of forewing costal margin present..3

3. Basal marking of the forewing V-shaped, with one arm parallel to costal margin and the other directed towards wing medial part (Fig. 72D-M).......................................*M. minuta* **comb. nov.**

- Basal marking of the forewing in the form of single streak parallel to costal margin................4

4. Forewing second and third distal blotches (m_5 and m_6) suboval, of similar size, and well separated from each other by a narrow brown streak; hind wing ochraceous-tangerine-orange, not ochraceous-yellow, outer margin in the male very indistinct, almost absent, in the female ochraceous brown; forewing second medial blotch rounded, yellow-orangish (Fig. 76A-D)...*M. bruneata* **comb. nov.**

- Forewing second and third distal blotches (m_5 and m_6) fused together, with only a few dark scales along the vein M3...5

5. Hindwing yellow medial blotch with narrow, subrounded protrusion deeply incising the ochraceous brown outer margin, in such a way that its portion along the wing hind margin forms a distinct subtriangular indentation oriented towards wing medial part (Fig. 75A-C)...*M. raharizonina* **comb. nov.**

- Hind wing outer margin smooth, without distinct subtriangular indentation at the hind margin..6

6. Hindwing without semi-transparent portions, with clearly visible and well defined outer margin (Figs 75F-H, K-M)...
....male of *M. octopunctata* **comb. nov.** / *M. rothschildi* **comb. nov.***

- Hindwing with outer margin very narrow or indistinct, blurred and almost absent...................7

7. Hindwing ochraceous-yellow, along the outer margin blurred area of darker scales, gradually fading towards medial part of the wing; forewing underside without a suboval field of modified scales (Fig. 75D-E)...male of *M. rothschildi* **comb. nov.**

- Hindwing medially pale yellow, semi-transparent, outer margin very narrow, of regular scales, ochraceous brown, with yellow marking at basodistal margin (Fig. 75I-J); forewing underside with a suboval field of modified scales................................male of *M. octopunctata* **comb. nov.**

*females of these two species are indistinguishable based on external morphology, but possess clear diagnostic characters in the genitalia.

Mauricenaclia species determination key based on male genitalia

1. Uncus terminally divided into two subtriangular lobes..2

- Uncus terminally not divided..3

2. Uncus subsquare, broad and short, terminal subtriangular lobes extending beyond the lateral margins of the uncus (Fig. 82)..*M. octopunctata* **comb. nov.**

- Uncus narrow and elongate, subrectangular, terminal subtriangular lobes laterally not extending beyond the uncus outline (Fig. 80)..................................*M. raharizonina* **comb. nov.**

3. Valvae short, not narrowed, protruding horizontally, terminally arrowhead-shaped; phallus extremely elongate, in basal portion spirally coiled (Fig. 84)................*M. peyrierasi* **comb. nov.**

- Valvae elongate and narrowed terminally, oriented upwards and reaching beyond uncus; phallus regular, not coiled..4

4. Uncus broad and flattened, subtriangular, dorsally with differently expressed longitudinal groove, terminated with small, tooth-like protrusion (Figs 77-79).............*M. minuta* **comb. nov.**

- Uncus narrow and elongate, basolaterally with membranous, pouch-like protrusions (Figs 82, 85)...5

5. Entire phallus only slightly arched, narrowing towards the tip.........*M. rothschildi* **comb. nov.**

- Phallus basally distinctly curved downwards, remaining portion straight, not narrowing (Figs 83, 85)...*M. bruneata* **comb. nov.** / *M. apatris* **sp. nov.***

*the genitalia of these two species are difficult to provide reliable differences in the available materials. For *M. bruneata* **comb. nov.**, there is only one, original male genitalia preparation by Griveaud (Fig. 83), in very poor condition, and in the collections examined by us there are no more male specimens of this species, except for the holotype.

Mauricenaclia species determination key based on female genitalia

1. Ductus bursae very narrow extremely elongate and spirally coiled, around 5x longer than corpus bursae (Fig. 93)...*M. peyrierasi* **comb. nov.**

- Ductus bursae short, at most of the length equal to the length of corpus bursae...2

2. Terminal margin of the 7th sternite medially with distinct, subrounded incision; signum in form of two separate horizontal ribs of similar size (Figs 89-90, 92)...
..................*M. bruneata* **comb. nov.** / *M. raharizonina* **comb. nov.** / *M. rothschildi* **comb. nov.***

- Terminal margin of the 7th sternite medially with subtrapezoidal incision or slightly arched, without distinct incision; signum in form of two horizontal ribs of unequal size, fused at different extent, and located on an irregular, subtrapezoidal, hourglass-shaped or 8-shaped plaque..3

3. Terminal margin of the 7th sternite medially subovally arched, without deeper incision; plaque between signa usually plane, with granular scobinations and only sometimes with single, short spine-like protrusions (Fig. 91)...*M. octopunctata* **comb. nov.**

- Terminal margin of the 7th sternite medially slightly ventricose outwards, with subtrapezoidal incision of smooth angles; plaque between signa usually densely covered with vertical, subtriangular protrusions in the shape of shark teeth (Figs 87-88)..............*M. minuta* **comb. nov.**

* the female genitalia of these three species are indistinguishable, and the available materials are scarce, most of them being fixed microscope slides. However, the species are clearly different in the external characters.

Mauricenaclia minuta **comb. nov.** (Figs 72, 77-79, 87-88, 94)
Syntomis minuta Boisduval, 1833: 80-81, Pl. 11, Fig. 6.
Holotype: ♂, NHMUK, NHMUK013384798 (Fig. 72D), genitalia slide NHMUK010314359 (Fig. 77E-F), by monotypy.

Thyrosticta minuta Griveaud 1964: 100, Pl. I, Fig. 67; Viette 1990: 169.

= *Thyrosticta angustipennis* Le Cerf, 1921: 420 **syn. nov.**
Thyrosticta angustipennis (Griveaud 1964): 103, Pl. I, Fig. 68; Viette 1990: 169.
Holotype: ♀, MNHN, EL64491 (Fig. 72E).

= *Dysauxes subfenestrata* Aurivillius, [1900]: 245 **syn. nov.**
Lectotype: ♀, NRM (Fig. 72F), genitalia slide P194, Ł. Przybyłowicz 2011.

Material. 322 specimens (ISEA PAS - 7 ♂♂, 5 ♀♀; MNHN - 46 ♂♂, 62 ♀♀; NHMUK - 39 ♂♂, 108 ♀♀; NRM - 2 ♀♀; PZBT - 25 ♂♂, 25 ♀♀; SGN - 2♀♀; SMNS - 1 ex. sex unknown) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. Males of *M. minuta* **comb. nov.** have the suboval field of transformed, elongate, dark brown scales with golden reflection, on the forewing underside, crossed by CuA2 (Figs 22A, D, 23). A similar field, present in *M. peyrierasi* **comb. nov.** and *M. octopunctata* **comb. nov.**, is discussed above.

Superficially, the most similar species are: *Mauricenaclia raharizonina* **comb. nov.** and females of *M. rothschildi* **comb. nov.** and *M. octopunctata* **comb. nov.**, but they differ in the straight, not v-shaped basal streak of the forewing.

In the male genitalia, the species is unique in the flattened, subtriangular uncus.

Taxonomic note.

1) *Thyrosticta angustipennis* **syn. nov.** was described by Le Cerf (1921) based on a single female specimen, collected in Fianarantsoa and obtained from Lamberton in 1920 ("ex Lamberton (1920)") (Le Cerf 1921), thus as already mentioned, the locality is potentially not reliable. The holotype deposited in MNHN (EL64491, Fig. 72E), according to the attached handwritten label, was recognized in the collection by P. Viette in 09.1952. In the original description, Le Cerf (1921) did not mention the basically identical *Thyrosticta minuta*, described almost 80 years before (Boisuval 1833). Instead, he indicated the similarity of *T. angustipennis* to *Maculonaclia agatha* (Oberthür, 1893), referring to the catalogue of Hampson (1898), in which *M. agatha* was placed in the genus *Thyrosticta*. Since neither *T. minuta* nor *M. agatha* were illustrated in Hampson (1898), the description of *T. angustipennis* and comparison to a not very similar species, at the same time overlooking an identical one, suggests that Le Cerf did not know *T. minuta*. Thus, it can be assumed that his intention was not to describe a species different but generally similar to *T. minuta*. This is plausible also because the majority of the specimens of "*Thyrosticta minuta*" and "*Thyrosticta angustipennis*" deposited in MNHN, where Le Cerf was based, were collected by the French entomologists already after his death in 1945. We found only a single specimen collected by A. Mocquerys in 1898 (EL82655), which potentially could be available for Le Cerf - but no such specimens of *M. agatha*.

Griveaud (1964), although indicated the similarity of *T. minuta* and *T. angustipennis*, and for the latter mentioned even that "we would have been tempted to make it a subspecies", sustained both taxa as valid species. Moreover, he designated the male "Neallotype" (MNHN, EL65161) for *T. angustipennis*, "utilising" the taxon to raise the variation in the shape of the forewing basal streak and m3 blotch to a species-specific character, assigning the males with a v-shaped basal streak and horizontally elongate, L-shaped second medial blotch to *angustipennis* (Griveaud 1964). At the same time, he indicated that the females of both species are superficially indistinguishable from each other, and possible to tell apart based on the genitalia only (Griveaud 1964) - whilst the female holotype of *T. angustipennis* has not been dissected. In the male genitalia, Griveaud (1964) indicated the dorsal surface of the uncus to be provided with a ridge in *T. minuta*, and with a longitudinal cavity in *T. angustipennis*. In fact, in the preparations made by us, the uncus in the basal portion always has a ridge, terminated before the tip with a differently expressed, small tooth-like protrusion, which varies in size, and sometimes is very indistinct and invisible from central angles (Figs 77-79). In the female genitalia, according to Griveaud (1964), *T. minuta* would have an undivided signum of corpus bursae, and *T. angustipennis* - separated into two. However, we found that the shape of the signum is highly and continuously variable (Figs 87-88).

Thus, we find no morphological characters that would allow us to diagnose two separate species, and considering the doubts mentioned above, we treat *Thyrosticta angustipennis* as a junior subjective synonym of *Mauricenaclia minuta* **comb. nov.**

2) The two female specimens of "*Dysauxes subfenestrata*", found by ŁP in NRM, undoubtedly belong to *M. minuta* **comb. nov.**, and one of them is labelled as "type" (Fig. 72F-G). This is congruent with the information indicated in the original description by Aurivillius [1900], which reads "2♀♀. – Museum Hamburg et Holmiae." [i.e. Hamburg and Stockholm], and the description matches the appearance of *M. minuta* **comb. nov.** The second specimen mentioned by Aurivillius [1900], was either not deposited in Hamburg eventually (Aurivillius was a Swede, based in NRM), and then both specimens from NRM are the ones from the original description, or it went to Hamburg, and then most probably was destroyed during WWII (Martin Husemann, pers. comm.), and the second specimen from NRM does not belong to the original series.

The species *Dysauxes subfenestrata* Aurivillius, [1900] was synonymised with *Naclia lucia* Oberthür, 1893 by Hampson (1914). Further, Griveaud (1964) indicated *N. lucia* to be a synonym of *Maculonaclia muscella* (Mabille, 1884) - however without indicating it as "**syn. nov.**". It seems that Hampson did not see the original specimens, and his synonimisation was based on the "diagnosis" provided by Aurivillius [1900], indicating the similarities of *subfenestrata* to *Naclia lucia*. Further, Griveaud (1964) considered the species *subfenestrata* to be described from a single female specimen indicated as a "lectotype" deposited in NHMUK. However, Griveaud (1964) also apparently did not examine the original material, nor the primary description. The information about the "lectotype" deposition in NHMUK is difficult to explain, as Hampson (1914) indicated the "type" to be deposited in Stockholm - maybe

Griveaud (1964) assumed, that the specimen has to be in the London Museum, since the previous taxonomic act was done by Hampson, who was based there.

Interestingly, the species *Thyrosticta minuta* is listed in Aurivillius (1909), suggesting that it has been known to him. However, it is mentioned there from Andranohinaly in SW Madagascar, where *M. minuta* **comb. nov.** does not occur (see distribution). Additionally, the information that "in the female, the 1b blotch of the forewing is white, not yellow as in the male" suggests that Aurivillius (1909) misinterpreted specimens of *M. rothschildi* **comb. nov.** and / or *M. octopunctata* **comb. nov.** possessing that dimorphism in the forewing (and both occurring in SW Madagascar, see below) for *M. minuta* **comb. nov.** This can provide an argument, that the "true" *Thyrosticta minuta* was in fact unknown to Aurivillius, leading to the description of *Dysauxes subfenestrata*.

3) Our molecular results suggest *Mauricenaclia minuta* **comb. nov.** to be a complex of three cryptic species. The first one is represented in the tree by a single specimen DL_02-325 (Figs 72H, 87), sister to all remaining (Fig. 5B). It was collected in a relatively distant, seemingly allopatric locality in the western part of Madagascar (Fig. 94), in a patch of relictual western rainforest. Its distinctiveness is supported also in the results of species delimitation analyses, based on both mitochondrial and nuclear markers (Figs S3-S7, File S1). The two remaining potential cryptic species (Fig. 5B), although arranged into separate clades, seem to be sympatric in the northern east of Madagascar (Fig. 94, see distribution). Considering the above-described, wide intraspecific variation within *M. minuta* **comb. nov.**, we were unable to delineate any diagnostic, species-specific morphological characters. Thus, we refrain from describing the new species here, and the case requires further studies on a longer series of specimens from different parts of the island.

Male genitalia redescription (Figs 77-79)

Tegumen U-shaped, the proximal margin with distinct, differently expressed incision, that vary from smoothly U-shaped to more angular and subtrapezoidal, so that the entire tegumen is narrowed subdorsally, and widened sublaterally into two semilunar lobes of varying width; tegumen incompletely fused with vinculum; uncus flattened dorsoventrally, elongate and subtriangular, basomedially with moderately deep, V-shaped and narrow longitudinal groove, terminal portion curved ventrally, dully terminated; in terminal, subdorsal portion elongate, longitudinal, narrow, sharp rib; uncus dorsally and laterally covered with elongate, erect setae, more densely in basal portion; vinculum narrow, U-shaped, with lateroterminal margins bent into small, semilunar protrusion oriented sideways; in some specimens on proximal surface provided with very small and short claw-like spine oriented backwards. saccus well developed, of varying shape, from regularly subtriangular to narrower and spatulate, dully terminated, slightly bent backwards; juxta well developed, subtrapezoidal, located between basal part of valve, shifted backwards, with margins aligned to proximal margin of vinculum; composed of ventral, well sclerotised plate, flattened dorsoventrally and of irregular shape, with distal margin touching transtilla, short and medially slightly incised; proximal margin longer, rounded, medially with differently expressed incision: from complete lack in some specimens to well developed and dividing the margin into two sublateral lobes; laterally from the plate two narrow, well sclerotised protrusions, right one short, straight and directed slightly leftwards, left one sinuous and bent rightwards, reaching to the central axis of genitalia symmetry, dorsal part of juxta membranous; ventral arms of juxta in form of transverse, moderately sclerotised, U-shaped plaque turned upside-down; valva narrow and elongate, of the length approximately equal to uncus, claw-like, pointed, slightly bent inwards; costal margin basally with distinct subtriangular incision, followed by small convex protrusion, remaining portion straight, with narrowing at the apex; sacculus comprising of two sections, overlapping in the medial part of the valva; basal portion slightly incised, towards subtriangular protrusion, then curved towards inner surface of valva and continued as longitudinal, medial rib on the inner surface of valva, reaching to its apex; distal portion of sacculus originating in 1/3 of valva length, basally with rounded protrusion, remaining portion arched towards apex; outer surface of valva plane only in very basal portion, remaining part covered with sparse, irregularly distributed, rounded scobinations of different sizes, additionally along both margins sparse, short and erect setae, most dense on the subtriangular protrusion in basal part of sacculus;

phallus tubular, semicircularly bent downwards, slightly narrowing towards tip, well sclerotised; vesica short, in basal portion small diverticulum directed forwards, remaining part directed upwards, short, of around 1/2 of the length of phallus, membranous, tubular, densely plicated, covered with irregularly distributed, tiny, weakly sclerotised scobinations, on ventral wall provided with differently expressed, well sclerotised structure, usually in the form of elongate longitudinal plaque, medially provided with differently expressed protrusion in form of irregular, small, tooth-like spine, or small, semicylindrical or subrounded plaque;

Remarks. There is some variation in the male genitalia, however it does not match the external morphological variation, nor the molecular tree topology. The entire genitalia vary among individuals from moderately to strongly sclerotised, but the extent of sclerotisation is uniform in each specimen.

Female genitalia redescription (Figs 87-88)

Anal papilla subtrapezoidal, moderately sclerotised, touching each other laterally at the dorsal side, terminal edge folded inwards, dorsal surface and the folding covered with very dense, minute scobinations; dorsal surface also with elongate, erect setae of different length, more dense along margins; apophysis posterioris of the length of anal papilla, well sclerotized, straight, needle-like pointed; apophysis anterioris of the length and shape of anterioris, created by lateral junction of two narrow, heavily sclerotised ribs running dorsally and ventrally around the base of papilla; dorsal pheromone glands highly variable in shape, in form of two long, tubular tapes of different width, twisted and anastomosing in different ways, located dorsomedially; ventral pheromone glands absent; 7th sternite rather narrow, weakly sclerotised, plain, with wavy surface, covered with sparse minute scobinations, in some specimens more dense sublaterally, terminal margin rounded, very slightly incised; lamella antevaginalis in the form of narrow, well sclerotised rib along terminal margin of 8th sternite, medially roundly arched at different extent, in some specimens forming a full suboval ring around antrum, sublaterally slightly widening and running further, creating ventral arm of the basal portion of apophysis anterioris; lamella postvaginalis well sclerotized, covered with dense, minute scobinations and folded inwards creating subtriangular cavity, distal margin proceeding towards basal part of papillae anales, densely covered with minute scobinations, and forming two diverticulum-like membranous cavities; ostium bursae indistinct, suboval, membranous; antrum completely fused with ductus bursae; ductus bursae tubular, from plain to densely plicated, in some specimens on lateral walls provided with two small, subovally longitudinal and narrow, differently expressed, well sclerotised plaques, covered with short, tooth-like spines; remaining portion covered with dense, indistinct, minute scobinations, varying from suboval and entirely plain to kidney-shaped and very densely covered with narrow plicae; corpus bursae membranous; signum located basomedially on the right wall, highly variable in shape, but generally in form of two differently expressed, horizontal, narrow rows of short, toot-like spines oriented inwards, and located on well sclerotized plaque, 8-shaped to hourglass-shaped, of different proportions, and covered with distinct scobinations, or short, tooth like protrusions; ductus seminalis membranous, tubular and narrow, originating laterally at the junction of ductus bursae and basal part of corpus bursae.

Immature stages. Unknown, except for the egg described here for the first time.

Biology. Adults are collected by netting by day; there is no data on attraction to light. Recorded all year round. In the corpus bursae of the female from the “western clade” (DL_02-325), collected on 04.02.2002, around 6-8 spermatophores were found, two of which with remnants of corpora, suggesting recent mating, and remaining consisting of broken colla only. In two further female specimens (MAD_282, Figs 72K, 88D and EL8363, Fig. 88B), collected on 30.x.-3.xi.2017 and vi(?).1972 respectively, a single collum was found, stuck in the ductus bursae. In further two females (MAD_294 and EL82639, Fig. 88C), collected on 22.xii.1994 and viii.1973, four and around eight colla were found in the corpus bursae. Associated mostly with evergreen, low and mid elevation humid forests, but also in coastal forest (on Nosy Boraha) and deciduous, seasonally dry western forest. The species was recorded also in secondary habitats, like vanilla agroforest (MAD_287 and MAD_288), *tavy* (slash-and-burn agricultural technique) areas (MAD_296 – MAD_301), or woody fallows (MAD_282), and seems not to be strictly associated with forests. A single specimen (EL74877) was collected “sur *Cinchona succirubra*” (Rubiaceae), however without an indication if it was nectaring from this plant.

Distribution (Fig. 94). Almost in all Madagascar (including the islands Nosy Be and Nosy Boraha), except the southwest part. In the regions of: Diana (Antsiranana south to Mt. Betampona), Sava (Vohemar south to Antanandava), Sofia (Belalona, Manongarivo, 40 km N of Port Berg), Betsiboka (Maevatanana), Analanjirofo (Mahitsy-Arongana, south to Forêt de Kalalao on Nosy Beraha and Fenerive(?)), Atsinanana (Vallée Onibe, Fito, Andekaleka) Alaotra-Mangoro (Ambany tanana south to Route de Beparasy), Analamanga (Mananjara, Antananarivo(?)), Melaky (Ambahibe, Tsingy de Bemaraha), Menabe (Analamanitsy, Mahabo), Matsiatra Ambony (Ambalavao), Vatovavy Fitovinany (Mananjary, Fianarantsoa, Ranomafana PN), Atsimo-Atsinanana (Midongy du Sud). From around 25 to 1750 m elevation.

The first cryptic species (“western clade”), represented in the tree (Fig. 5B) by the specimen DL_02-325, was collected in Analamanitsy in Bemaraha PN; the second one, represented by the specimens MAD_020, DL1802 and MAD_282, was collected in eastern Madagascar, in Ranomafana PN, Feony-ala near Analamazoatra, and in Ambodiala, respectively; the third one, represented by the specimens MAD_260, MAD_287 and MAD_288 was collected in north east Madagascar, in PN Ankarana (the first one) and Andrakata (remaining two).

Remarks. With well over 300 specimens housed in different collections, *M. minuta* **comb. nov.** is one of the most commonly collected species of Madagascan Syntomini, and also one of the first described (Boisduval 1833). Part of the localities is outside protected areas and already devoid of primary vegetation The single specimens from Mananjara (Le Moult), Tananarive “ex Lamberton”, and Fenerive by brothers Perrôt, however plausible considering the species range, require verification. The first two localities are in central Madagascar, and the species has not been recorded from Ambohitantely RS, the most important remnant of forest in the area (see Wiorek et al. 2021).

Mauricenaclia raharizonina **comb. nov.** (Figs 75A-C, 80, 89, 95A-B).

Thyrosticta raharizonina Griveaud, 1964: 104, Pl. I, Fig. 70; Viette 1990: 169.

Holotype: ♂, MNHN, EL65141, by original designation.

Material.10 specimens (MfN - 1 ♂; MNHN - 1 ♂, 3 ♀♀; NHMUK - 1 ♀; NRM - 1 ex. sex unknown; PZBT - 3 ♂♂) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys.

Male genitalia redescription (Fig. 80)

Tegumen moderately sclerotised, U-shaped, uniformly very narrow, incompletely fused with vinculum; uncus basally almost membranous, with two parallel, lateral, well sclerotised ribs along margins, surrounded by membranes connecting it with tegumen; remaining portion of uncus moderately but uniformly sclerotised, flattened dorsoventrally, moderately convex longitudinally, with slightly irregular lateral margins, terminally bifurcated into two subtriangular, thick, claw-like protrusions oriented downwards and slightly outwards laterally, at the angle of around 90 degrees to each other; dorsally along margins covered with minute, sparse dot-like scobinations and elongate, erect setae oriented in different directions; vinculum moderately sclerotised, narrow, V-shaped; saccus narrow and short, subtriangular, oriented slightly backwards; juxta in dorsal portion forming narrow, well sclerotized ring, ventral portion developed as sclerotized, horseshoe-shape plaque opened anteriorly; valva distinctly elongate, reaching beyond uncus tip, arrowhead-shaped; costal margin uniformly convex, basally from 1/4 to 1/2 of its length with a tubular rib, which in the half of valva is transiting to the medial part of valva inner surface; remaining portion of costal margin with a folding directed inwards, terminated before the tip, that is pointed and bent inwards in claw-like form; sacculus in basal

1/3 straight, and parallel to each other in both valvae; remaining portion uniformly shallowly incised towards the apex, but comprising of two sections, overlapping in the medial part of the valva: basal portion in form of indistinct folding directed inwards and terminating in the medial portion of valva inner side, remaining portion starting with indistinct convex protrusion, then straight, arched towards the tip; outer surface of valva covered with unequally distributed, minute scobinations, most dense along terminal half of sacculus, that is also provided with elongate, erect setae of different lengths;

phallus elongate, straight and tubular, moderately sclerotised; vesica in basal portion membranous, tubular, plain, remaining portion bent downwards, approximately of the length of phallus, densely covered with elongate, parallel plicae, terminal 2/3 of frontal surface forming elongate, well sclerotised, straight and narrow rib-like plaque; terminal portion rounded, covered with dense, minute scobinations;

Female genitalia redescription (Fig. 89)

Anal papilla subrectangular to slightly subtrapezoidal, moderately sclerotised, terminal edge folded inwards, dorsal surface and the folding covered with dense, minute scobinations, along terminal margin row of small, grain-like protrusions; distal 1/3 and terminal margin with sparse, elongate, erect setae of different lengths, more dense on the terminal margin; apophysis posterioris around 1.5x longer than anal papilla, originating medially from its basal margin, moderately sclerotized, straight and needle-like; apophysis anterioris of around 2/3 of the length of anterioris, with prominent subtriangular basal portion, straight and narrowing towards dully termination; dorsal pheromone glands in form of two moderately elongate, narrow, not anastomosing, membranous tapes of similar lengths, located dorsomedially, in basal half slightly sinuous, in distal half straight, terminated with bent, club-like widening; ventral pheromone glands absent; 7th sternite subtrapezoidal, moderately sclerotised, basolaterally with shallow, longitudinal cavities, terminal margin with shallow, elongate and arched incision; lamella antevaginalis medially subovally convex, fused with ventral wall of ostium, lateral arms in form of narrow and well sclerotised, slightly convex bars, further transforming towards apophyses anterioris; 8th tergite (lamella postvaginalis) in the form of irregular, horizontally extended, membranous field covered with minute scobinations, mediodistally elongated into two small, membranous, pouch-like convex lobes; along basal margin provided with well sclerotised rib, laterally transforming into subtriangular base of apophyses anterioris; ostium bursae flattened dorsoventrally, forming a cup-shaped chamber with well sclerotised outer wall; antrum completely fused with ductus bursae, membranous, narrowly tubular, with longitudinal plicae, dorsolaterally covered with sparse, well sclerotised scobinations reaching to terminal margin of 7th sternite; basal portion of corpus bursae originating rightwards, in the form of short, membranous tube, then bent downwards and widening conically, covered with minute scobinations, and opening to the remaining portion of corpus bursae slightly basomedially rather than apically; remaining portion of corpus bursae almost spherical, membranous, covered with broad plicae, lateral wall medially with two narrow, horizontal signa; one located in basal 1/3 of corpus bursae, right below its conical basal portion, small, with a row of three small, well sclerotised subtriangular protrusions; another one in 2/3 of corpus bursae, longer and broader than the first one, provided with irregularly arranged, short, spine-like protrusions of different lengths; ductus seminalis originating dorsally at the fusion of ductus bursae with corpus bursae, directed posteriorly, basally subconical, with dense, well sclerotised scobinations, narrowing into tubular, very narrow and entirely membranous duct.

Immature stages. Unknown.

Biology. There is no data on diurnal / nocturnal activity of the species. The specimens were collected in December, January and March. Additionally, the two specimens collected by Voeltzkow (housed in NRM and MfN) are labelled with the month of collecting written in Roman numerals, which reads “February” or “November”. In the corpus bursae of a single female (EL82622, Fig. 75B), collected on 8-31.01.1974, two colla were found. Associated mostly with deciduous, dry southern forest and scrubland, but perhaps also with deciduous, seasonally dry western forest, currently still present east from Lambomakandro (see distribution).

Distribution (Fig. 95A-B). Mainly southwest of Madagascar, the region of Atsimo-Andrefana (Zombitsy and Lambomakandro, south to the area of Ankalirano). Also, a single specimen was collected in Diana (vallée de la Besanetribe). From around 200 to 1200 m elevation.

Remarks. The only species covered in this paper, which is distributed mainly in the south-western part of Madagascar. The single specimen from the north of Madagascar, however superficially raising no doubts, requires verification of its taxonomic status, especially considering the completely different type of vegetation in that area (low and mid elevation humid forests).

All localities in the main range of the species are currently outside any protected area and devoid of natural vegetation. Small fragments of forest are left only in Zombitsy and the area of Ankalinaro, however both have been almost completely deforested in the last two decades, and this pressure can be continuously present in the area (Fig. 95B).

Mauricenaclia rothschildi **comb. nov.** (Figs 75D-G, 81, 90, 95C, E).
Thyrosticta rothschildi Griveaud, 1964: 105, Pl. I, Fig. 71; Viette 1990: 169.
Holotype: ♂, MNHN, EL65142 (Fig. 72E).

Material. 51 specimens (ISEA PAS - 2 ♀♀; MNHN - 10 ♂♂; NHMUK - 3 ♂♂, 1 ♀; PZBT - 35 ♂♂) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. *Mauricenaclia rothschildi* **comb. nov.** has very characteristic, "warm" copper tint of the ochraceous background, with golden reflection.

The females of *M. rothschildi* **comb. nov.** and *M. octopunctata* **comb. nov.** are superficially indistinguishable from each other, and however Griveaud (1964) indicated the former to have generally larger and longer wings than the latter, the difference is not clearly visible in the analysed materials.

Male genitalia redescription (Fig. 81)

Tegumen narrow, U-shaped, moderately sclerotised, both margins provided with well sclerotised ribs; proximal margin medially concave, so that the tegumen is widening sublaterally; tegumen not fused with vinculum; uncus straight and elongate, beak-like, basally membranous, with narrow, well sclerotised lateral rib on each side, and laterally provided with pouch-like membranes; remaining portion well sclerotised, provided with dorsal longitudinal rib, slightly narrowing laterally towards the tip, ventrally in terminal portion roundly incised, terminated with pointed, claw-like protrusion; dorsal surface plain, lateral covered with distinct, grain-like scobinations, basolaterally with elongate, erect setae oriented sideways; vinculum well sclerotised, very narrow, with heavier sclerotised ribs along both margins, U-shaped, lateroterminally provided with small, slightly bent protrusion overlapping terminal ends of tegumen; saccus in form of subtriangular protrusion directed backwards, flattened dorsoventrally and of uniform width (not subconical as in *Mauricenaclia apatris* **sp. nov.**), dorsoterminally provided with tiny claw-like protrusion directed upwards (absent in *M. apatris* **sp. nov.**); juxta well developed, X-shape, with dorsal arms in form of ring-like, subrounded structure located centrally between tegumen and vinculum, dorsally membranous and slightly incised, sublaterally widened and well sclerotised, laterally on external walls with one well sclerotised, horizontal, subtriangular protrusion on each side (larger than in *M. apatris* **sp. nov.**), oriented towards valva base, giving the entire dorsal part of juxta subtriangular, horizontally elongate outline (in *M. apatris* of the shape of equilateral triangle); ventral arms of juxta well sclerotised, located basally between sacculi, in form of U-shaped plaque, turned upside-down, with distal margin forming V-shaped incision, apically transforming into much narrower, elongate, U-shaped incision, reaching almost to proximal margin (in *M. apatris* **sp. nov.** the apical portion is much wider and shorter); valva moderately narrow (but proportionally slightly broader than in *M. apatris* **sp. nov.**) and elongate, straight, slightly incised in the half of its length; basal portion irregularly subrtrapezoidal, terminal part elongate subtriangular, pointed apex slightly bent inwards; costal margin with inwards folding along its entire length, basally with shallow, straight incision, followed by subrounded protrusion, remaining portion straight to the apex; sacculus comprising of two sections, overlapping in the medial part of the valva; basal portion with rounded incision followed by distinct convex protrusion, subsequently transgressing towards ventral surface of valva; terminal part of sacculus originating slightly before 1/2 of valva length, basally with short and elongate, subrounded protrusion, remaining portion straight, narrowing terminally towards apex; dorsal surface covered with sparse scobination, more dense in terminal half of valva, forming saw-like rows along margins; ventral surface along margins and in terminal portions covered with sparse, elongate, erect setae of different lengths, more dense and forming distinct field on rounded protrusion of sacculus basal portion; phallus tubular, slightly narrowing towards apex, bent downwards, well sclerotised, especially ventrally; vesica short, of around 1/2 of the phallus length, tubular, basal 1/3 membranous and straight, remaining portion slightly bent, tubular, of uniform width, dully terminated, with a pair of parallel to each other, longitudinal, irregularly sclerotised, narrow, plaques without well defined margins.

Female genitalia redescription (Fig. 90)

Anal papilla subtrapezoidal, moderately sclerotised, touching each other laterally at the dorsal side, with dorsal surface covered with very dense, minute scobinations; dorsal surface and terminal margin also with sparse, elongate, erect, hair-like setae of different lengths; apophysis posterioris about 1.5x longer than anal papilla, well sclerotized, narrow and straight, needle-like pointed; apophysis anterioris slightly shorter than posterioris, of similar shape, created by lateral junction of two narrow, heavily sclerotised anterior margins of 8th sternite and tergite; dorsal pheromone glands in form of two long, narrow, twisted and anastomosing membranous tapes of similar lengths, located dorsomedially; ventral pheromone glands absent; 8th sternite medially weakly sclerotised, laterally transforming into well sclerotised, covered with irregularly distributed, minute scobinations; terminal margin medially with distinct, subtrapezoidal incision, along the margin well sclerotised, narrow rib extending laterally into the ventral arm of the basal portion of apophysis posterioris; lamella postvaginalis in the form of membrane densely covered with minute scobinations and forming subtriangular, well developed cavity folded inwards, along distal margin fused with membranous, diverticulum-like cavities densely covered with minute scobinations and connected to basal part of papillae anales; ostium bursae indistinct, suboval, membranous, located medially; antrum and ductus bursae completely fused, membranous, moderately elongate, narrow, tubular, covered with longitudinal plicae; corpus bursae in basal portion tubular and elongate, broader than ductus and of its length, membranous, plan to indistinctly plicated, covered with minute scobination, remaining portion suboval, covered with dense, indistinct, minute scobinations; signum located basally on the right side, in the form of two horizontal, narrow and elongate plaques, ventrally covered with small grain-like sculpture; ductus seminalis membranous, tubular and narrow, originating in the terminal portion of ductus bursae;

Immature stages. Unknown.

Biology. Adults are collected by netting by day; there is no data on attraction to light. Specimens undoubtedly belonging to the species (i.e. males and dissected / DNA barcoded females) were recorded in February, March, October and December. In MNHN, there is one specimen (EL74773, Fig. 75E) labelled with the month of collecting written in Roman numerals, which reads “February” or “November”. In the corpus bursae of a single female (DL_05-857, Figs 75F, collected on 24.12.2004, five colla were found. Associated mostly with deciduous, seasonally dry western forest and deciduous, dry southern forest and scrubland. In the area west of Tolanaro, the latter vegetation type meets the evergreen, humid forest, occurring also in Tsaratanana in the north (see distribution).

Distribution (Fig. 95C) The specimens undoubtedly belonging to the species were recorded mostly from southern and western Madagascar, but also from the northern part of the island, from the regions of: Sofia (Tsaratanana), Menabe (Kirindy forest), Atsimo-Andrefana (Lambomakandro and Andranovory), and Anosy (Tolanaro). From around 60 to 1440 m elevation.

Remarks. Our molecular and morphological results show that the specimen from Tsaratanana (DL_05-857, Fig. 75F) is conspecific with the one from Kirindy (MAD_212, Fig. 75G), despite the considerable distance of the first locality from the others. The three southernmost localities are outside any protected area, and already devoid of primary vegetation.

Mauricenaclia octopunctata **comb. nov.** (Figs 75H-M, 82, 91, 95D-E)
Thyrosticta octopunctata Rothschild, 1924: 306.
Thyrosticta octopunctata Griveaud 1964: 103, Pl. I, Fig. 69; Viette 1990: 169.
Holotype: ♀, NHMUK, NHMUK013384803 (Fig. 75H), slide NHMUK010314353, by original designation.

Material. 19 specimens (ISEA PAS - 3 ♂♂, 4 ♀♀; MNHN - 3 ♂♂; NHMUK - 4 ♂♂, 1 ♀; PZBT - 4 ♂♂) (Tab. S1).
Additionally, 77 unidentified females of *M. rothschildi* **comb. nov.** / *M. octopunctata* **comb. nov.** (MNHN - 23 ♀♀; NHMUK - 4 ♀♀; PZBT - 49 ♀♀, SGN - 1 ♀) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. See also the comments for *M. rothschildi* above.

Male genitalia redescription (Fig. 82)
Tegumen moderately sclerotised, distal margin rounded, U-shaped, proximal margin roundly V-shaped and protruding over proximal margin, so the entire tegumen is very narrow medially, in the apical portion, and then widening laterally towards vinculum, with which is not completely fused; uncus flattened dorsoventrally, in basal portion dorsal surface moderately sclerotised, ventral surface membranous, lateral margins with moderately sclerotised rib, basally curved inwards and fused in medial portion, forming M-shaped structure; terminal

portion moderately sclerotised, slightly widening towards tip, in terminal portion distinctly bifurcated into two pointed, claw-like protrusions bent outwards; dorsal and ventral side sublaterally covered with sparse, minute scobinations and provided with elongate, erect setae directed sideways; vinculum moderately sclerotised, very narrow, U-shaped, lateroterminally with small, slightly rounded protrusion directed sideways; saccus moderately sclerotised, small, in form of dorsoventrally flattened subtriangular protrusion; juxta in form of moderately sclerotised, roundly V-shaped plate with tip oriented upwards, entering between basal portion of sacculi; transtilla in form of irregular, ventrally flattened, moderately sclerotised ring, located distally between valvae base; valva elongate, laterally leaf-shaped, costal margin basally with deep subtriangular incision, remaining portion convex; sacculus in basal 1/3 straight, then sharply bent outwards at the angle of around 120 degrees; remaining portion comprising of two sections, overlapping in the medial part of the valva: basal portion in form of indistinct, narrow folding directed inwards and terminating in the medial portion of valva inner side; remaining portion starting with indistinct convex protrusion, and straight, slightly sinuous towards claw-like, bent inwards tip of the valva; outer surface of valva covered with unequally distributed minute scobinations, most dense along terminal half of sacculus; both margins, and also ventral part of the terminal portion of valva covered with elongate, erect setae of different lengths; phallus of moderate length, tubular, slightly narrowing towards the tip, bent downwards and slightly rightwards, distaloventral margin extended into elongated plate, at the base of which vesica originates; vesica short, in form of tubular, densely plicated elongate pouch, covered with irregularly distributed, minute scobinations, ventral portion slightly longer, in the form of small diverticulum.

Female genitalia redescription (Fig. 91)

Anal papilla subtrapezoidal, moderately sclerotised, covered with minute scobinations, along terminal margins with elongate, erect setae of different length, ventrolaterally fused with membranous, subtriangular protrusions very densely covered with minute scobinations; apophysis posterioris slightly longer than anal papilla, heavily sclerotized, straight, very narrow, needle-like, slightly sinuous; apophysis anterioris of the length of anterioris, or slightly shorter, heavily sclerotised, very narrow, needle-like and straight; dorsal pheromone glands in form of two long, narrow, sinuous but not twisted and not anastomosing membranous tapes of similar lengths, located submedially; ventral pheromone glands absent; 7th sternite uniformly moderately sclerotised (slightly heavier than remaining segments), plain, covered with minute scobinations, terminal margin medially shallowly incised, with row of sparse, elongate erect setae; lamella antevaginalis very indistinct, in the form of narrow and elongate, slightly arched, moderately sclerotised plate located medially along terminal margin of 7th sternite; lamella postvaginalis in the form of irregularly subtrapezoidal membranous field covered with dense, minute, very short erect setae, sublaterally provided with paired cavities, terminolaterally fused with protrusions of papillae; ostium bursae indistinct, relatively small and narrow, without incision; antrum short, entirely membranous, tubular, on right wall provided with dense, minute scobinations, and completely fused with ductus bursae; ductus bursae very narrow and elongate, tubular, entirely membranous, covered with longitudinal plicae; corpus bursae pear-shaped, of the length equal to ductus bursae, covered with dense, minute scobinations, and moderately dense plice; signum located medially on left wall of corpus bursae, in the form of a distinct plaque provided with two horizontal rows of claw-like spines of different lengths, basal one shorter than distal one; ductus seminalis very narrow and indistinct, membranous, originating at the very base of antrum, from the scobinated field.

Remarks. Plicae on ductus bursae are differently expressed among specimens and vary from very dense, distinct folding to almost plain, with slightly marked ridges. In some specimens scobinations on antrum are missing.

Immature stages. Unknown, except for the egg described here for the first time.

Biology. Adults are collected by netting by day; there is no data on attraction to light. Specimens undoubtedly belonging to the species were recorded from September to March Additionally, the remaining specimens - superficially indistinguishable females of *M. rothschildi* **comb. nov.** and *M. octopunctata* **comb. nov.** were collected in January, March, May, August, October and December. In the corpus bursae of a single female (DL_2966), collected on 04.12.2011, one collum was found. Associated with evergreen, humid forests at low and mid elevation, deciduous, seasonally dry western forest, and deciduous, dry southern forest and scrubland. A single individual (MA_16-6 - EL83628) was collected in a humid grassland environment in PN Tsingy de Namoroka, flying at day over the flowers of *Entada leptostachya* (Fabaceae) (Claire Villemant pers. comm.).

Distribution (Fig. 95D-E). The specimens undoubtedly belonging to the species were recorded along the western coast of Madagascar, in the regions of Diana (Antsiranana, south to Beraty and Andringitra), Boeny (Majunga, Ampijoroa, Namoroka), Menabe (Kirindy forest), Atsimo-Andrefana (Andranovory). From around 35 to 1000 m elevation.

Additionally, the remaining, indistinguishable females of *M. rothschildi* **comb. nov.** and *M. octopunctata* **comb. nov.** were collected exactly within the range of both species (Fig. 95E), in the regions of: Diana (Antsiranana south to Beraty, including southern part of Nosy Be island), Boeny (Ampijoroa and Lac d'Ampijoroa), Betsiboka (foret de Kasijy), Atsimo-Andrefana (Ankazoabo, Lambomakandro, Andanovory), Anosy (Tolanaro). Additionally, single specimens were collected in Alaotra-Mangoro (Beparasy and Route Lakato). Up to around 1000 m elevation.

Remarks. The taxonomic status of the specimens from Alaotra-Mangoro should be verified, taking into account the significant distance from other localities.

Around half of the localities of *M. octopunctata* **comb. nov.**, as well as the remaining specimens of *M. octopunctata* **comb. nov.** / *M. rothschildi* **comb. nov.**, are within protected areas. However, many of them are already devoid of primary vegetation, and some have been highly fragmented by very recent deforestation - especially in the Corridor Ankeniheny-Zahamena and around RS Manongarivo.

Mauricenaclia bruneata **comb. nov.** (Fig. 76A-D, 83, 92, 96)

Thyrosticta bruneata Griveaud, 1969: 15, Pl. I, Figs E-F; Viette 1990: 169.

Holotype: ♂, MNHN, EL65162 (Fig. 76A), by original designation.

Material. 13 specimens (MNHN - 2 ♂♂, 6 ♀♀; NHMUK - 1 ♀; PZBT - 4 ♀♀) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys.

Female genitalia redescription (Fig. 92).

Anal papilla subtrapezoidal, moderately sclerotised, touching each other laterally at the dorsal side, terminal edge folded inwards, dorsal surface and the folding covered with dense, minute scobinations; external portion with sparse, elongate, erect setae of different lengths, more dense on the terminal margin; apophysis posterioris slightly longer than anal papilla, originating medially from its basal margin, moderately sclerotized, straight and needle-like; apophysis anterioris of around 2/3 of the length of posterioris, of similar shape, without prominent basal portion; dorsal pheromone glands in form of two moderately elongate, narrow, straight membranous tapes of similar lengths, located dorsomedially, in terminal portion anastamosing into very short protrusions; ventral pheromone glands absent; 7th sternite subtrapezoidal, gradually heavier sclerotised towards terminal portion, terminal margin medially with shallow and elongate, arched incision; lamella antevaginalis moderately sclerotised, narrow and rib like, U-shaped, laterally transforming into apophyses anteriores; lamella postvaginalis in the form of weakly sclerotised field covered with minute scobinations, mediodistally elongated into two membranous, narrow, scobinated lobes, protruding basoventrally between anal papillae; 8th tergite in the form of very narrow, moderately sclerotised rib, laterally transforming into apophyses anterioris; ostium bursae in form of small, semicircular cavity; antrum completely fused with ductus bursae, narrow, tubular and covered with longitudinal plicae; ductus bursae tubular and spirally bent rightwards; corpus bursae membranous, in basal portion tubular and twisted, remaining portion pear-shaped, covered with dense, indistinct, minute scobinations; signum located on ventral wall, in the form of two narrow, horizontal, well sclerotised, rib-like plaques, one located in basal 1/3 of corpus bursae, provided with row of short, spine-like protrusions, another one in 2/3 of corpus bursae, shorter, provided with only single, medial, short spine-like protrusion; ductus seminalis membranous, tubular and very narrow, originating ventrally, approximately at half of ductus bursae length;

Immature stages. Unknown.

Biology. Adults are collected by netting by day; there is no data on attraction to light. Recorded in August, and from November to January. In the corpus bursae of a single female (EL74968, Fig. 76D), collected on 14-19.08.1973, three colla were recorded. Associated with evergreen, low elevation humid forest and deciduous, seasonally dry western forest (occurring in northern Diana and Sava).

Distribution (Fig. 96A). Northern east of Madagascar, the regions of: Diana (Antsiranana and foret d’Analamerana), Sava (Vohemar), and Analanjirofo (Maitsoarnogana). From around 60 to 675 m elevation.

Remarks. Half of the localities are not protected and currently devoid of natural vegetation, but the remaining two are within big, protected patches of forest.

Mauricenaclia peyrierasi **comb. nov.** (Figs 76E-H, 84, 93, 96B)

Thyrosticta peyrierasi Griveaud, 1969: 16, pl. I, figs G-H; Viette 1990: 169.

Holotype: ♂, MNHN, EL65143 (Fig. 76E), by original designation.

Material. 24 specimens (MNHN - 4 ♂♂, 5 ♀♀; NHMUK - 1 ♀; PZBT - 9 ♂♂, 3 ♀♀, SGN - 1 ♂, 1 ♀) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination key. Additionally, in the male genitalia the sclerotised plaque of the membrane below uncus forms with it a clasp-like structure (Fig. 84C). The sexual dimorphism of the forewing second medial blotch, however present in some form in other species of the genus (e.g. larger size in the female than in the male of *M. octopunctata* **comb. nov.**), in *M. peyrierasi* **comb. nov.** has the extreme form of the complete absence of the white second distal blotch in the male. Instead, this area of the wing is darker than the background, which might be connected with the presence of the transformed scales in this part of the wing on the underside. The male of this species is unique among all Madagascan Syntomini in having transparent scales both on the fore- and hindwing. The male hindwing colouration and pattern are very characteristic, basodistally with a yellow blotch, remaining portion of the wing pearl-grey-ochraceous (Fig. 76E-H).

Male genitalia redescription (Fig. 84)

Tegumen moderately sclerotised, U-shaped, medially on proximal margin with very deep and narrow, V-shaped incision, separating two rounded, distinct lobes, laterally narrowing towards complete fusion with vinculum; uncus straight, oriented forwards, well sclerotised, basally vide and then narrowing towards the tip in form of straight claw-like, pointed protrusion; in terminal 2/3 on the ventral side short, subtriangular protrusion oriented downwards; dorsally and laterally covered with erect setae of rather uniform lengths, more dense and thicker in the basal portion of uncus; scaphium in form of well sclerotised plate, terminally provided with subtriangular protrusion similar and falling in parallel to the one on uncus, and probably forming together a kind of a clasp; vinculum moderately sclerotised, very narrow, rather shallow, roundly U-shaped; saccus moderately sclerotised, very indistinct, almost absent, in form of elongate, rounded protrusion along vinculum; juxta well developed, divided into two sclerotized plates almost entirely separated by membranous zone: larger, well developed, in form of dully terminated conical structure, membranous dorsally and ventrally, and well sclerotised laterally, projected forwards, in basal part with elongate ventral wall, bent downwards and reaching ventral part; smaller, moderately sclerotised subtriangular plate folded downwards, apically roundly V-shaped, with tip entering between basal portion of sacculi; valva narrow and elongate, reaching beyond uncus tip, slightly incised in the half of its length, basal irregularly subrectangular, of uniform width, terminal part elongate, arrowhead-shaped, narrowing towards claw-like pointed, slightly bent inwards apex; costal margin sinuous, basally with convex protrusion, then roundly incised medially, followed by another convex protrusion, remaining portion straight towards apex; sacculus comprising of two sections, overlapping in the medial part of the valva: basal portion slightly incised, then with convex protrusion, terminated in the medial part of the valva, remaining portion basally slightly convex, then straight towards the apex; basal portion of the valva dorsally well sclerotised, with costal margin and saccus slightly bent inwards, and ventrally connected by a membrane; distal, arrowhead-shaped part of the valva uniformly well sclerotised dorsally and ventrally, forming a subtriangular cavity, with a longitudinal rib running medially on the ventral surface; outer surface of valva covered with sparse minute scobinations; both margins in the terminal half covered with elongate, erect setae of different lengths; phallus extremely elongate, basal portion narrow and tubular, in form of four-fold spiral, with ventral wall moderately sclerotised and dorsal wall membranous, basal tip dull, slightly broadened and club-like; main part of the uncus moderately sclerotised, in the basal portion ventrally broadened by convex protrusion; vesica unavailable.

Female genitalia redescription (Fig. 93)

Anal papilla subtrapezoidal, moderately sclerotised, touching each other laterally at the dorsal side, terminal edge folded inwards, dorsal surface and the folding covered with very dense, minute scobinations, terminal margin with elongate, erect, hair-like setae of different length; apophysis posterioris of the length of anal papilla, heavily sclerotized, straight, needle-like pointed; apophysis anterioris of the length and shape of anterioris, created by lateral junction of two narrow, heavily sclerotised ribs running dorsally and ventrally around the base of papilla; dorsal pheromone glands in form of two long, narrow, twisted and anastomosing membranous tapes of similar lengths, located dorsomedially; ventral pheromone glands absent; 7th sternite moderately sclerotised, plain, covered with sparse minute scobinations, anterior margin in medial portion with transverse, narrow, well sclerotised rib, sublaterally transforming into subrectangular, elongate, moderately sclerotised field with blurred margins, extending to lateral margin of the 7th sternite; posterior margin medially with distinct U-shaped incision, along the margin well sclerotised rib, sublaterally widening and running further, creating ventral arm of the basal portion of apophysis posterioris; lamella postvaginalis in the form of longitudinal, narrow and elongate, well sclerotised plate, laterally fused with terminal margin of 8th sternite, along distal margin fused with membranous structure densely covered with minute scobinations, medially folded into three small, diverticulum-like cavities; ostium bursae suboval, shifted leftwards in relation to the body axis, and surrounded by plane membrane; antrum short, directed slightly leftwards, moderately sclerotised, tubular, oval in cross section, with plane walls; on right wall provided with dense, minute scobinations, and completely fused with ductus bursae; ductus bursae very narrow and distinctly elongate, forming three-fold spiral, tubular, moderately sclerotised and gradually transforming into membranous along its length; external surface plain, ventral covered with longitudinal plicae and small and sparse, granular scobinations; corpus bursae membranous, in basal portion tubular and twisted, remaining portion pear-shaped, covered with dense, indistinct, minute scobinations; signum located in the basal portion of corpus bursae, in the form of two horizontal, narrow and elongate plaques, covered with short, subtriangular tooth-like spines directed outwards and leaning on each other; ductus seminalis membranous, tubular and narrow, originating in the basal part of corpus bursae.

Remarks. Plicae on ductus bursae are differently expressed in different specimens and vary from very dense, distinct folding to almost plain with slightly marked ridges. In some specimens scobinations on antrum are missing.

Immature stages. Unknown.

Biology. Adults are collected by netting by day; there is no data on attraction to light. Recorded from October to January, in May, July and August. Associated with evergreen, low and mid elevation humid forest.

Distribution (Fig. 96B). Northern east of Madagascar, in the regions of Sofia (Tsaratanana), Analanjirofo (Ambodivoanio and Antanambe), and Analamanga (La Mandraka). From around 20 up to 1630 m elevation.

Remarks. Only in Tsaratanana does the species occur in a large, protected patch of forest. The remaining localities are devoid of natural vegetation, with only small and sparse forest fragments left, and the area of La Mandraka was deforested recently (LOFM 2022).

Mauricenaclia apatris Wiorek, 2024 **sp. nov.** (Figs 76I-K, 85)
Holotype: ♂, MNHN, EL83055; Paratypes: 2♂♂, MNHN, EL81680 and EL81694.
ZooBank [to be provided later].

Material. The type series comprises the only known specimens (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. Superficially, the most similar Madagascan Syntomini are *Soganaclia roedereri* Griveaud, [1971] and *Soganaclia tsaratananae* Griveaud, [1971], with ochraceous and pale yellow body colouration. However, in these species the forewing is narrow and elongate, with the hind margin around 1.5x longer than the outer margin and entirely ochraceous, whilst in *M. apatris* **sp. nov.** it is regularly subtriangular, not elongate, and provided with small ochraceous-brown blotches (Fig. 76I-K). The pale yellow blotch of the hind wing of *S. roedereri* and *S. tsaratananae* is restricted to its basodistal portion, and located below DC hind margin and CuA1, and in *M. apatris* **sp. nov.** the blotch has the shape and colouration characteristic to some species of *Mauricenaclia* **gen. nov.**, i.e. more intensively coloured along the wing margin, and paler and blurred in the central portion of the wing. The forewing pattern consisting of darker blotches on a paler background is rare among Madagascan Syntomini, and except *M. apatris* **sp. nov.** present only in *Tsirananaclia milloti* Griveaud, 1964 and *Tsirananaclia sucini* Griveaud, 1964. However, these two species have much more prominent wing pattern, with narrow ochraceous brown stripes along all veins of fore and hind wing, whilst in *M. apatris* **sp. nov.** the forewing pattern consist only of a couple of indistinct blotches (Fig. 76I), in some specimens hardly visible (Fig. 76K).

In the male genitalia (Fig. 85), the species very closely resembles *Mauricenaclia rothschildi* **comb. nov.** (Fig. 81). However, these two species differ in the following characters: i) the shape of the lateroterminal, subtrapezoidal protrusion of vinculum, which is more angular in *M. apatris* **sp. nov.**, and devoid of the right angled terminal edge in *M. rothschildi* **comb. nov.**; ii) the shape of saccus, which in *M. rothschildi* **comb. nov.** is subtriangular, flattened dorsoventrally and dorsoterminally provided with a small claw-like, upward protrusion, whilst in *M. apatris* **sp. nov.** the saccus is subconical, not flattened, and missing any protrusions; iii) the shape of the subtriangular, ventrolateral protrusions of juxta, which are horizontally elongate in *M. rothschildi* **comb. nov.**, and in the shape of equilateral, not elongate triangle in *M. apatris* **sp. nov.** iv) the shape of the shield-like plaque formed by the ventral arms of juxta, the apical portion of which is much wider and shorter in *M. apatris* **sp. nov.**;

Description (Fig. 76I-K)

Head. Proboscis well developed, ochraceous brown; vertex partially worn, ochraceous, margins along eyes pale yellow, frons ochraceous, lateral margins with pale yellow scales, postocular are entirely pale yellow; labial palpus three-segmented, narrow, elongate, porrect, slightly bent upwards, partially worn, pale yellow with admixture of ochraceous scales on 3rd palpomere; 3rd palpomere approximately of equal length to 2nd; antennae piliform, scapus ochraceous, available portion of flagellum ochraceous dorsally, ventrally dark brown without scales, densely covered with short, erect setae;

Thorax. Partially worn; patagia, tegulae and thorax ochraceous, metathorax also with remnants of pale yellow scales; tegulae terminally with elongate and piliform ochraceous scales; pleurites worn, pale yellow;

Legs. Largely worn, with mixture of ochraceous and pale yellow; tarsi lateroventrally with rows of spine-like, ochraceous-yellow setae; foreleg: pale yellow, only tibia and tarsus dorsally ochraceous; tibia of around 1/2 of femur length, epiphysis present, ochraceous, covered with pale yellow scales, of the length of tibia; tibia and 1st tarsomere together of the length of femur; midleg: pale yellow, tibia dorsally ochraceous, with one pair of pale yellow terminal spurs of equal length; hindleg: pale yellow, tibia with one pair of pale yellow terminal spurs, of equal length and one pair of additional pale yellow spurs in 3/4 of tibia length, shorter than terminal ones;

Abdomen. Partly worn, entirely yellow;

Forewing. Subtriangular, background ochraceous with very indistinct, small, suboval blotches of darker, ochraceous brown scales: one in the lower part of basal wing portion (perhaps corresponding with blotch m_3, however not present in all specimens), one in medial portion, in DC (m_2), and two in distal wing portion (m_4 and m_5+m_6); underside as upperside, but the blotches almost invisible; cilia ochraceous, in basal portion of wing hind margin row of elongate and piliform scales concolorous with wing background; retinaculum present;

Hindwing. Suboval, reaching to 1/2 of forewing length; distal 1/3 ochraceous, forming terminal margin; yellow stripe along hind margin from wing base to tornus, of around 1/3 of wing width; remaining portion of wing basal part covered with pale yellow to creamy, sparse, differently expressed scales; underside as upperside, but in one specimens entire basal 2/3 of the wing with yellow scales; cilia concolorous with wing pattern, longer in basodistal margin; Sc+Rs+M1 completely fused, M2 and M3 stalked in the basal 1/3 of their length; frenulum present;

Male genitalia description (Fig. 85)

Tegumen moderately sclerotised, U-shaped, but the proximal margin V-shaped, medially with deep incision, so that the entire tegumen is very narrow subdorsally, and widening sublaterally into two narrow, semilunar lobes, slightly bent upwards and forming a shallow trough; tegumen completely fused with vinculum; uncus straight and elongate, beak-like, basally membranous with narrow, well sclerotised lateral rib on each side, remaining portion well sclerotised, slightly narrowing laterally towards the tip, terminated with pointed, claw-like protrusion; dorsal surface plain, lateral covered with distinct, grain-like scobinations, basolaterally with elongate, erect setae oriented sideways; vinculum well sclerotised, very narrow, shallow U-shaped, lateroterminally provided with differently expressed, small, irregularly subtrapezoidal protrusion directed backwards; saccus well sclerotised, in form of subtriangular, rounded protrusion oriented backwards; juxta well developed, X-shaped, with dorsal arms in form of ring-like structure located centrally between tegumen and vinculum, dorsally widened and membranous, remaining portion well sclerotised, ventrally with V-shaped incision, lateroventrally on external walls with one subtriangular protrusion on each side, oriented towards valva base; ventral arms well sclerotised, located basally between sacculi, in form of U-shaped plaque turned upside-down, apically with very deep incision, reaching to its proximal margin; valva narrow and elongate, of the length approximately equal to uncus, straight, claw-like and pointed, slightly incised in the half of its length, basal portion irregularly subrhomboidal, terminal part elongate subtriangular, pointed apex slightly bent inwards; costal margin basally with two small protrusions separated by subtriangular incision, remaining portion slightly sinuous towards apex; sacculus comprising of two sections, overlapping in the medial part of the valva: basal portion slightly concave, towards flattened subtriangular protrusion, curved towards inner surface of valva and terminated, remaining portion basally convex, then slightly incised, and terminal portion straight towards the apex; from around half of valva length both margins folded inwards and fused in terminal portion, forming an elongate, subtriangular cavity reaching to the apex; basal 1/3 of dorsal surface completely plain, remaining part, including folded inwards, covered with sparse, irregularly distributed, rounded scobinations and indistinct, sparse, short and erect setae; phallus tubular, of uniform width, slightly bent downwards, well sclerotised, especially in ventral part; vesica short, of around 1/2 of the length of phallus, tubular, basal 2/3 moderately sclerotised, densely plicated, covered with sparse, minute scobinations; terminal part membranous, dully terminated, with numerous diverticulum-like foldings;

Immature stages. Unknown.

Biology. Unknown.

Distribution. Madagascar. The exact collecting locality remains unknown (see remarks).

Remarks. All three specimens were found in MNHN in 2022, among undetermined materials from Madagascar, labelled only with handwritten "46" and "Soga" (Fig. 76I-K). These data indicate the specimens to be collected by Pierre Soga. He was a renowned Malagasy forester and collector (Lacroix and Viette 1998), and the number "46" refers most probably to his 46th collecting expedition or locality, rather than the year 1946. Soga was in his 70s, when one of the authors (DL) met him in Madagascar in 2004, thus he would be rather too young to be an active collector already in 1946. Lacroix and Viette (1998) indicate 1953 as his earliest collecting date. Unfortunately, there is no complete list of Soga's expeditions or collecting localities (Joël Minet, pers. comm.). Soga was collecting mostly in the mountainous areas of the island, especially in Tsaratanana in northern Madagascar (Lacroix and Viette 1998), thus the specimens of *M. apatris* **sp. nov.** might have been collected in one of the massifs, but reliable indication of the exact locality is impossible with the current data.

Etymology. From Greek *apatris* - "without homeland", for the unknown collecting locality of the specimens.

Pseudonaclia puella (Boisduval, 1847)
Naclia puella Boisduval, 1847: 596

Male genitalia first description (Fig. 86)
Tegumen subdorsally on anterior margin with distinct, club-like widened incision, sublaterally widening into subtrapezoidal plate, laterally on distal margin provided with prominent, elongate, narrow, claw-like, curved arms bent inwards, shorter than uncus and valve; junction with vinculum membranous; uncus narrow, flattened laterally, posterior portion extended dorsoventrally into claw-like termination, indistinctly incised at tip, covered with sparse, minute scobinations, without setae; vinculum narrow, U-shaped to slightly subtrapezoidal,

lateroterminally forming short, slightly curved arms overlapping terminal portion of tegumen; saccus well developed, subtriangular to slightly rounded, flattened dorsoventrally, oriented downwards and very slightly backwards; juxta in form of membranous to moderately sclerotised, subtriangular plaque, ventral arms in form of well sclerotised, U-shaped plaque oriented upside down between sacculi; valva elongate, of the length approximately equal to uncus, basal 1/3 widened and irregular, terminal 2/3 narrow, elongate, terminally pointed; costal margin with narrow folding inwards, basally rounded, then incised, remaining part convex, terminally bent upwards and terminated with pointed tip; basal portion of sacculus sinuous, medially roundly incised, parallel to each other in both valvae, then prominently rounded and transgressing on the valva inner surface, fusing with the folding of costal margin; remaining portion of sacculus originating in 1/3 of valva length, sinuous, medially with indistinct incision, terminally narrowed towards the tip; outer surface covered with small scobinations, sparse in basal 1/3 and dense in terminal 2/3 of valva, both margins rugged; along costal margin on the inner surface and terminally on outer surface elongate, erect setae of different lengths; phallus tubular, moderately sclerotised, straight, in basal portion slightly curved downwards; vesica of the length of phallus, divided into two pouch-like arms, basally at their branching provided with irregular, U-shaped sclerotisation; left arm shorter, reaching to around 2/3 of the entire vesica; the left arm irregular, pouch-like with very dense, longitudinal plicae, the right arm elongate, basally tubular, terminally club-like widened, plane, ventrally in terminal portion with narrow, irregular, longitudinal, moderately sclerotised plaque.

Female genitalia first description (Fig. 97)

Anal papilla flattened dorsoventrally and oriented transversely, kidney-shaped, terminal margin slightly folded inwards, in dorsal portion straight and parallel to each other in both papillae, in ventral portion slightly roundly incised; moderately sclerotised, covered with very dense minute scobinations, and elongate erect setae, denser along terminal margin; apophysis posterioris originating from a prominent, rounded lobe in the basal portion of anal papilla, narrowing subconically, well sclerotised and pointed, of the length approximately equal to anal papilla; apophysis anterioris well sclerotised, basally widened, of similar shape and size to posterioris; dorsal pheromone glands in form of very indistinct, transparent and hardly visible, tubular, twisted and anastomosing membranous tapes, connected with apophyses posterioris; ventral pheromone glands in form of single, submedial, shallow, membranous pouch; 7th sternite subrectangular, moderately sclerotised, lateromedially with subtrapezoidal convex protrusions, basal margin with very narrow, well sclerotised rib, terminal margin medially with rounded concavity; lamella antevaginalis in form of narrow, well sclerotised, subrectangular plaque, medially subovally convex around ostium, lateral arms of uniform width, further transforming towards apophyses anterioris; lamella postvaginalis in the form of small, weakly sclerotised ridge covered with short, thick setae, mediodistally transformed into rounded cavity located on the right side, behind ostium; 8th tergite in the form of moderately sclerotised, subrectangular plaque of uniform width, laterally transforming into base of apophyses anterioris; ostium bursae flattened dorsoventrally, suboval in cross section, very short, narrowing, cup-shaped at the bottom; antrum completely fused with ductus bursae, provided with elongate and narrow, well sclerotised plaque, with short basal portion located on dorsal wall, then twisted along right wall and transgressing on the ventral wall, terminally narrowed; posterior portion of ductus bursae elongate and tubular, approximately of the length of anterior portion, slightly twisted, covered with dense, minute scobinations and longitudinal plicae; corpus bursae kidney-shaped, with ventral wall almost straight, and dorsal wall roundly curved, covered with dense scobinations and longitudinal plicae; ventral wall medially with signum in form of two transverse, straight and narrow, well sclerotised ribs located in approximately 1/3 and 1/2 of the length of corpus bursae main part; ductus seminalis originating before the end of sclerotised part of ductus bursae, tubular, moderately sinuous and twisted.

Melanonaclia Griveaud, 1964

Type species: *Naclia luctuosa* Oberthür, [1911], Griveaud (1964): 66, by original designation.

Diagnosis. Large moths of dark brown to almost black body and wing colouration, with only yellow (and never white) markings on the body, and creamy-white and yellow semi-transparent wing blotches (Figs 98-100). In the female abdomen, the terminal segments usually are heavier sclerotised than the remaining part, and the 7th sternite laterally provided with differently expressed, longitudinal cavities, terminated with differently expressed laterobasal pouch-like cavities (Fig. 101). Similar, but differently expressed and located structures are present in *Skippernaclia* **gen. nov.** and *Kowalskinaclia* **gen. nov.** (see their diagnosis above).

In the female genitalia (Figs 102-108), basal portion of corpus bursae pouch like, in most of the species (except *M. nigra*, Fig.104 and *M. toulgoeti*, Fig. 105) provided with one or two prominent signa in form of flattened plaque, armoured with spine-like protrusion of different length.

Superficially the most similar to *Melanonaclia* are species from the genus *Tritonaclia* Hampson, 1898, sharing dark brown to black body colouration and wings background, with pale blotches. Although *Tritonaclia kefersteinii* (Butler, 1882) and *T. quinquepunctata* Griveaud, 1966. have yellow blotches on the abdomen, similarly as *Melanonaclia*, but they are arranged in lateral rows extending at least from the 2nd to 6th tergite, whilst in *Melanonaclia* the lateral abdominal blotches are present only in *M. luctuosa*, in the terminal portion, with an additional laterobasal blotch on each side in some specimens (probably only females) (Figs 98-99). Additionally, *T. kefersteinii* and *T. quinquepunctata* have the wing pattern consisting of more prominent, characteristic pale yellow-creamy blotches, none of which is semi-transparent, contrary to *Melanonaclia* (see also Przybyłowicz and Wiorek 2023). The remaining species of *Tritonaclia* on the abdomen have differently expressed ventral and lateral rows of 2-4 white blotches, whilst in *Melanonaclia* white blotches on the body are absent (except wings). Further, in all *Tritonaclia* species (except *T. kefersteinii*), the second distal blotch (m_5) is distinctly smaller than the third one (m_6), sometimes reduced to a minute dot, whilst in *Melanonaclia* m_5 and m_6 are of similar size and almost fused.

The male genitalia of *Tritonaclia* have lateral protrusions on the tegumen and additional, narrow and elongate process on the costal margin of valva (see Przybyłowicz and Wiorek 2023), both absent in *Melanonaclia* (Figs 109-114) The valva in *M. trimacula* **comb. nov.** is provided with a protrusion on costal margin (Fig. 113C), but in the form of short, and wide, subtriangular lobe.

Another species superficially similar to *Melanonaclia* is *Vadonaclia marginepuncta*. However, it has bipectinate antennae, absent in *Melanonaclia*, and orange-reddish body marks (see also the diagnosis of *T. sylvicolens* and *Julienaclia moerens* **comb. nov.**).

Remarks. The genus was characterised by Griveaud (1964) based on the presence of piliform antennae (which was untrue for "*Melanonaclia*" *moerens*, with bipectinate antennae, here excluded from the genus, see *Julienaclia* **gen. nov.**), lack of sublateral arms on the tegumen (but the male of "*Melanonaclia*" *perplexa* - unknown at the time and described later (Griveaud 1969) - does possess them), the shape of phallus, and the wing venation (which, however, is variable).

The genus can be further defined by the following set of morphological characters: antennae piliform in both sexes with very slight sexual dimorphism (Fig. 7E-F); brush-like tuft behind male foreleg coxa present (Fig. 9C), but in *M. toulgoeti* and *M. nigra* consisting of tape-like scales (Figs 9D, F, 11C-F, 12); Hind leg tibia with single additional spur (Fig. 13C) (except *M. lugens* and *M. toulgoeti*); forewing in most of the species regularly subtriangular (but variable in *M. toulgoeti* and *M. nigra*), not elongate, with hind and outer margins of approximately equal length, 1A+2A terminated at the well defined tornus, five radial veins (Figs 14E-H,15E-G); forewing blotches: basal am1 present in *M. trimacula* **comb. nov.** and *M. ranomafana* **sp. nov.**, remaining species with no basal blotch, medial: variable and partly species-specific, from only m_2 (always present), to fused m_2+fm_3+m_3, distal: m_4, fused m_5+m_6, semi-transparent blotches present; hindwing (Fig. 16F-H, 17G) variable among and sometimes also within species (see *M. nigra*, Fig, 16F-G) from subtriangular and subtrapezoidal to suboval and rounded, costal margin arched, Sc+Rs+M1 straight, completely fused, M2 and M3 stalked in around basal 1/3 to 1/2 of their length, 3A present; hindwing with one basal and on distal blotch, semi-transparent blotches present except *M. trimacula* **comb. nov.**, *M. dujardini* **comb. nov.** and *M. ranomafana* **sp. nov.**

The male genitalia variable among the species, with elongate and pointed valvae (except *M. luctuosa*), phallus tubular and elongate, vesica provided with a differently expressed, species-specific row of cornuti (except in *M. nigra* and *M. lugens*, where only scobinations present) (Figs 109-114).

In the female genitalia ventral pheromone glands absent.

Based on morphological and molecular results, *Melanonaclia moerens* is moved to *Julienaclia* **gen. nov.** (see above), and *Melanonaclia perplexa* to *Mortinaclia* **gen. nov.** (see below).

Melanonaclia species determination key based on adult characters

1. Wings with both pale yellow and white semi-transparent blotches..2

- Wings only with white semi-transparent blotches..4

2. Abdomen yellow, only dorsally with longitudinal row of differently expressed, irregular dark brown blotches and without lateral dark brown marks (Fig. 100E-G).....*M. dujardini* **comb. nov.**

- Abdomen yellow, dorsally and laterally with uniform, longitudinal dark brown stripes.. 3

3. Tergite 7th entirely dark brown (Fig. 100B).....................................*M. trimacula* **comb. nov.**

- Tergite 7th basolaterally with yellow marks (Fig. 100H).......................*M. ranomafana* **sp. nov.**

4. Abdomen entirely dark brown (Fig. 99A)...*M. nigra*

- Abdomen with yellow marks...5

5. Abdomen in lateroterminal portion with one or two yellow blotches on each side, ventrally without large suboval pale yellow blotch, foreleg coxa dark brown (Fig. 94A-D)...*M. luctuosa*

- Pale yellow ventral blotch on the abdomen present, foreleg coxa frontally with yellow blotch...6

6. Postocular area entirely yellow...*M. lugens*

- Postocular area entirely dark brown...*M. toulgoeti*

Melanonaclia species determination key based on male genitalia

1. Valva terminally not narrowed into claw-like protrusion but subrectangular, dully terminated, with terminal margin flat-cut at right angles to costal margin and sacculus (Fig. 109)...*M. luctuosa*

- Valva terminally narrowed into claw-like protrusion...2

2. Vesica no longer than 1/2 of the length of phallus, without longitudinal row of spines, in the terminal portion consisting of a few short diverticula...3

- Vesica longer than 1/2 of the phallus, tubular, without diverticula in terminal portion, provided with longitudinal row of spines...4

3. Vesica in terminal half ventrally with longitudinal, narrow, well sclerotised plaque (Fig. 110)...*M. lugens*

- Vesica without longitudinal plaque, but the dorsal diverticulum ventrally covered with a field of small, dense, subtriangular scobinations (Fig. 111)..*M. nigra*

4. Vesica basally with two small, rounded, pouch-like diverticula, terminal portion of vesica with around 15 prominent spines arranged in a row; costal margin of valva basally with subtriangular protrusion; saccus not elongate (Fig. 113)........................*M. trimacula* **comb. nov.**

- Vesica basally without diverticula, basal portion provided with several dozen of spines; saccus elongate, narrow and pointed...5

5. Spines on the vesica arranged in a narrow, longitudinal row (Fig.114)...*M. dujardini* **comb. nov.**

- Spines on the vesica distributed in an irregular field, in terminal 2/3 of its lengths distinctly widened; additionally, vesica in terminal portion densely covered with minute scobinations (Fig. 112)...*M. toulgoeti*

Melanonaclia species determination key based on female genitalia

1. Basal portion of corpus bursae completely membranous, without sclerotisations, or with one or two small, rounded plaques...2

- Basal portion of corpus bursae with prominent, well sclerotised, irregular plaques, completely flat, or provided with distinct, spine-like protrusions...3

2. Basal diverticulum of corpus bursae distinctly elongate, of around 2/3 of the length of corpus bursae and reaching till the medial portion of the 7th sternite; the 7th sternite basally distinctly widened, subtrapezoidal in the outline...*M. toulgoeti*

- Basal diverticulum of corpus short, reaching at most to the basal margin of the 7th sternite; the 7th sternite basally only slightly widened, subrectangular in the outline (Fig. 104)..*M. nigra*

3. Basal portion of corpus bursae with two well sclerotised plaques of irregular shape and ragged margins, one on ventral and one on lateral wall, each of them provided with a single, short. claw-like spine (Fig. 106)...*M. trimacula* **comb. nov.**

- Basal portion of corpus bursae with two well sclerotised plaques, at least one of them provided with prominent, claw-like spines..4

4. Both basal plaques of corpus bursae of similar size, kidney-shaped, along upper margin with two elongate, moderately curved spines, oriented slightly upwards and directed sideways into opposite directions (Fig. 102)...*M. luctuosa*

- Basal plaques of different sizes..5

5. One of the basal plaques distinctly extended laterally on the outer side, both plaques with prominent, straight spines oriented horizontally and directed sideways in opposite directions (Fig. 108)..*M. ranomafana* **sp. nov.**

- The basal plaque on the right wall reduced in size, provided with short and straight spine-like protrusions, the other plaque with prominent spines curved inwards, not straight and protruding laterally...6

6. The right basal plaque rounded (Fig. 103)...*M. lugens*

- The right basal plaque irregular, horizontally elongate (Fig. 107).........*M. dujardini* **comb. nov.**

Melanonaclia luctuosa (Oberthür, [1911]) (Figs 98A-D, 102, 109, 115A-B)
Holotype: ♂, NHMUK, NHMUK010621695 (Fig. 98A).
Naclia luctuosa Oberthür, [1911]: 467, pl. 16, fig. 4.
Melanonaclia luctuosa Griveaud 1964: 67, pl. I, fig. 39; Viette 1990: 168.

= *Tritonaclia inauramacula* Griveaud, 1964 **syn. nov.**
Holotype: ♀, MNHN, EL65140 (Fig. 98D).
Tritonaclia inauramacula Griveaud 1964: 80.

Material. 67 specimens (ISEA PAS - 6 ♀♀; MNHN - 11 ♂♂, 15 ♀♀; NHMUK - 5 ♂♂, 8 ♀♀; PZBT - 4 ♂♂, 18 ♀♀) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. Additionally, the postocular area is yellow.

Taxonomic note. *Melanonaclia luctuosa* was known to Griveaud (1964) only from the males, including the male holotype by Oberthür ([1911]), and superficially identical females were assigned to *Tritonaclia inauramacula*, following the classification proposed by him, based on wing venation (Griveaud 1964). Subsequently, the female of *M. luctuosa* was described by Griveaud (1969), based on the specimens collected in copula, and - erroneously as in the first description - by Przybyłowicz (2005). However, the analyses of the female genitalia of *M. luctuosa* (MNHN, P. Griveaud slide No. 579, Fig. 102D) and *T. inauramacula* (MNHN, P. Griveaud slide No. 276, Fig. 102E) revealed them to be identical and belonging to conspecific individuals. Thus, we treat *T. inauramacula* as a junior subjective synonym of *M. luctuosa*.

Results of our species delimitation analyses based on the DNA barcoding region (Fig. 5A, Figs S3-S5, File S1) suggest the specimen DL_2980 (from Ratsiaranana) to belong to a different species than the remaining two specimens, DL_SC3 and DL_SF11 (from Anjanaharibe Mt. and Vohitaly, respectively). However, the results are partly vague, as in the divisions into 34 initial partitions (Fig. S3) and 36 recursive partitions (Fig. S4) ABGD lumps together *M. luctuosa* and - undoubtedly separate species - *M. ranomafana* **sp. nov.**, whilst in the next step there are 39 recursive partitions (Fig. S5), in which *M. ranomafana* **sp. nov.** is treated separately, but also the *M. luctuosa* is divided as above. All three specimens in question are females, and we did not find any differences in their genitalia, nor any other potentially species-specific characters. Thus, we refrain from describing a new species, and the case demands further morphological and molecular research on a longer series of specimens of both sexes (as only a single male abdomen was available to our morphological study).

Male genitalia redescription (Fig. 109)

Tegumen U-shaped, distal margin dorsomedially with small subtriangular incision, separating two narrow, arched protrusions; proximal margin sublaterally with two narrow, elongate, subtrapezoidal protrusions; fusion with vinculum complete, but visible; uncus in basal margin connected with tegumen by membranous field, with basal portion widened, and medially with subtriangular incision, dividing it into two subtriangular lobes, laterally provided with narrow, membranous protrusions extending along tegumen and reaching to fusion with vinculum; remaining portion basally slightly constricted, spatula-like, dorsally flattened, narrow, terminally curved claw-like, with pointed tip; laterally covered with sparse, erect, elongate setae of different lengths, directed sideways; vinculum very narrow, subtrapezoidal to shallow U-shaped, lateroterminally slightly widened; forming arched, tubular protrusions overlapping lateroterminal portions of tegumen; saccus flattened dorsoventrally, along outer margin with well sclerotised narrow rib, basally wide and subtriangular, narrowing towards , spatula-like terminal protrusion, distinctly directed leftwards, terminated with subconical tip; juxta in form of horizontal, moderately sclerotised, elongate, subtrapezoidal plaque located medially, basoventrally provided with membranes fused with basodorsal portions of valvae ventral side; transtilla in form of moderately sclerotised, subtriangular, U-shaped plaque with tip oriented backwards and laterally bent downwards, located basally between sacculi; valva narrow and elongate, medially concaved, of the length approximately equal to uncus; basal half elongate, subtrapezoidal, terminal half irregularly subrectangular and curved inwards, terminally flat cut; costal margin in basal portion with shallow incision, medially with rounded protrusion and folded inwards into semicircular lobe, subsequently continued by well sclerotised longitudinal rib located medially along valva ventral side; remaining portion of costal margin slightly arched, terminally curved outwards, forming elongate, subtriangular protrusion; sacculus basally straight, in medial portion forming subtriangular protrusion inwards, fused with folding of costal margin, remaining portion straight, terminated with subtriangular protrusion, much smaller than the one on costal margin; terminal margin of valva straight, at right angles to costal margin and sacculus; outer surface in basal portion plain, medially irregularly, densely covered with minute scobinations, less dense in terminal portion; sacculus with three fields of erect, elongate setae oriented sideways, two elongate ones in basal and terminal portion, and narrow one in medial portion, separated from each other by plain field without setae; phallus tubular and elongate, basal portion slightly widened, uniformly well sclerotised, terminally slightly widened leftwards, with indistinct rounded protrusion on the left wall; vesica of around 2/3 of the length of phallus, divided by medial constriction into two portions: basal one entirely membranous, cylindrical, wide and directed slightly upwards; ventroterminally with originating terminal half, basally narrowed, then widening into irregular, weakly sclerotised, irregular pouch provided with five differently expressed, plain diverticula: basal one located dorsally, semicircular, in basal portion with moderately sclerotised, semilunular plaque of blurred margins; mediodorsal one short and narrow, dully terminated; lateroterminally on right wall two small, subspherical ones; basolaterally on left wall the largest one, elongate, subspherical, in terminal portion provided with row of four heavily sclerotised, elongate, needle-like cornuti of different lengths, and 5th alike cornutus separated from the remaining and located more basally in the ductus ejaculatorius;

Female genitalia redescription (Fig. 102)

Anal papilla subrectangular, moderately sclerotised, dorsally covered with sparse setae of different lengths, more dense along terminal margin; on ventral side between papillae narrow, lobate, membranous protrusions, parallel to each other; apophysis posterioris at least 1.5x longer than anal papilla, moderately sclerotized, slightly sinuous, needle-like; apophysis anterioris around 2/3 of the length of anterioris, thicker and more sclerotised, needle-like; dorsal pheromone glands in form of two long, wide, flattened, sinuous, membranous tapes located dorsomedially, in some cases ramifying in terminal portion; ventral pheromone glands absent; 7th sternite distinct, wide, in some specimens heavily sclerotised, plain, laterally on basal margin with distinct pouch-like cavity on each side, ventrally densely covered with scales, terminal margin medially distinctly incised; 7th tergite also wide and distinct, fusion of 7th sternite and 7th tergite without suture, but along it on the 7th sternite trough-like, longitudinal cavity; 8th tergite narrowed into elongate plaque, located terminally on the ventral side of tergite 7th; lamella postvaginalis in form of distinct, irregularly subtrapezoidal to semilunar plate, heavier sclerotised along terminal margin, forming sinuous ridge over dorsal margin of ostium bursae; ostium bursae very distinct, wide and elongate, semicircular in cross section, well sclerotised; antrum and ductus bursae indistinguishable, entire duct oriented rightwards, basally semicircular in cross section, then narrowing and flattened dorsoventrally, further twisted at around 90 degrees relative to its own axis, so that the terminal portion is flattened laterally, well sclerotised all along; basal portion of corpus bursae in form of relatively small, bulbous pouch, separated from remaining potion by distinct constriction and armed with prominent signa on dorsal and ventral wall, in form of well sclerotised, suboval plague, medially provided with elongate, narrow protrusion, from which origin two horizontal, elongate, pointed spines oriented sideways in opposite directions, and resembling bull horns; remaining portion membranous, slightly plicated, with very fine sculpture, regularly suboval; on ventral wall in 1/3 and 2/3 of its length narrow, horizontal signa, in form of semilunar plaque, along margin comb-like, provided with numerous small and short, subtriangular teeth; each signum additionally slightly clamp-like, with both ends curved inwards into the wall of corpus bursae; ductus seminalis membranous, tubular and narrow, originating form semiconical diverticulum directed rightwards and located in the upper part of the bulbous basal portion of corpus bursae, over the basal signa;

Remarks. Extent of sclerotisation varies among specimens, in some of them 7th tergite, 7th sternite, antrum and ductus bursae are very heavily sclerotised.

Immature stages. Unknown.

Biology. Individuals are collected by netting by day, and attracted to (actinic) light at night. Recorded all year round, except May and October. Associated with mostly low but also mid elevation evergreen, humid forests, including riparian, swampy habitats. Around half of the localities are along the eastern coast of Madagascar, which is currently devoid of primary vegetation and covered only with degraded humid forest.

Distribution (Fig. 115A-B). Northern Madagascar, mostly around Antongil Bay, regions of: Analanjirofo (south to Fenerive and Tampanambo), Sava (north to Maroambihy), Mahajanga (Belalono), Alaotra-Mangoro (Befody). The records from southern Madagascar, based on single, old specimens from Vondrozo ("Lamberton 1922") and Fianarantosa (unknown date and collector) are less reliable and require confirmation. From around 0 up to 1600 m elevation.

Melanonaclia lugens (Oberthür, 1893) (Figs 98E-H, 103, 110, 115C).

Lectotype: ♀, NHMUK, NHMUK010620990 (Fig. 98E), type designated by Oberthür (1893) *in museo*, as lectotype by Griveaud (1964).

Naclia lugens Oberthür, 1893: 7, Pl. 1, Fig. 14.

Melanonaclia lugens Griveaud 1964: 69, Pl. I, Fig. 41; Viette 1990: 168.

Material. 15 specimens (MNHN - 6 ♂♂, 3 ♀♀; NHMUK - 1 ♂, 2 ♀♀; PZBT - 3 ♀♀) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. Additionally, all coxa frontally with yellow blotch. In some specimens (female) small yellow blotch laterally at the base of the abdomen.

Male genitalia redescription (Fig. 110)

Tegumen moderately wide, roundly V-shaped, medially with two longitudinal, parallel, narrow, well sclerotised rib-like stripes; along proximal margin narrow, lobe-like, flat horizontal protrusion, laterally in terminal portion turning inwards and running along ventral margin; remaining portion of proximal margin terminated with small, semicircular protrusion directed backwards; distal margin medially with small, protruding subtriangular lobe; tegumen completely fused with vinculum; uncus basally Y-shaped, with two short arms directed towards each other and fused terminally, remaining portion narrow and tubular, claw-like, protruding and slightly curved downwards, tip cut diagonally and dorsally terminated with small, claw-like protrusion; laterally covered with sparse scobinations and elongate, erect setae; vinculum very narrow, U-shaped; saccus well developed, elongate subtriangular, pointed, oriented leftwards; juxta membranous, medially with two moderately sclerotised, vertically elongate plaques of irregular margin, located laterally on both sides of phallus; transtilla in form of suboval plaque, located basally between sacculi, covered with sparse minute scobinations; valva elongate, of the length approximately equal to uncus, basal 2/3 irregularly subtrapezoidal, remaining portion claw-like, pointed, distinctly curved inwards, directed upwards and towards each other at 45 degree angle; costal margin basally straight, slightly incised, in 2/3 of its length with subtriangular protrusion, then roundly narrowed into terminal, claw-like, slightly sinuous protrusion; sacculus basally shallowly incised, remaining portion slightly arched, parallel to each other in both valvae, in terminal 3/4 of its length forming subtriangular protrusion at the base of the claw-like tip; both valva margins folded inwards; outer surface of valva covered with irregularly distributed scobinations, terminal portion of sacculus and ventral surfaces terminally with sparse, erect setae of varying lengths; Phallus tubular, elongate and narrow, slightly curved upwards, uniformly moderately sclerotised, terminally with irregular, fuzzy margin, transgressing into very short, membranous terminal portion; vesica in total of 1/2 of the length of phallus, basal portion completely membranous, tubular and slightly narrowing, in around 1/3 of its length bent leftwards; terminal portion basally membranous, then with moderately sclerotised, irregular ring, transformed into narrow, well sclerotised longitudinal rib on the left wall; remaining part forming three diverticula; two dorsal horizontally parallel to each other, right one elongate and curved leftwards, membranous with very fine scobinations, narrowing and roundly terminated, left one cylindrical, shorter and broader than the previous one, creased, ventrally in medial portion provided with a few small, irregular, grain-like sclerites; below them third diverticulum, membranous, bent leftwards, of the shape similar to the upper right one, but shorter.

Female genitalia redescription (Fig. 103)

Anal papilla not extending over terminal margins of the abdomen, subtrapezoidal, subrectangular, moderately sclerotised, dorsally covered with sparse setae of different lengths, more dense along outer margins; on ventral side between papillae narrow, lobate membranous protrusions, parallel to each other; apophysis posterioris around 1.5-2x longer than anal papilla, moderately sclerotized, slightly sinuous, needle-like; apophysis anterioris around half of the length of anterioris, thicker and more sclerotised, needle-like, originating from well developed, sclerotised lobe; dorsal pheromone glands in form of two long, sinuous, tubular, membranous tapes located dorsomedially, club-like widened terminally, one of them bifurcated terminally into two short lobes; ventral pheromone glands absent; 7th sternite distinct and elongate but much narrower than 7th tergite, constituting only 1/3 of the circumference of the abdomen, moderately to well sclerotised, covered with dense minute scobinations; basal margin laterally with elongate, but narrow convex protrusion, above it along lateroterminal margin very indistinct, shallow cavity; terminal margin medially distinctly incised; 7th tergite distinct, elongate and widened, well sclerotised, covered with dense minute scobinations; fusion of 7th sternite and 7th tergite with heavier sclerotised rib; 8th tergite narrowed into an elongate, well sclerotised plaque, located along the ventral side of 7th tergite terminal margin, medially narrow, sublaterally widened into elongate, suboval lobe, terminated with apophysis posterioris; lamella postvaginalis well sclerotised, in form of bulbous plate, closing the lumen of ostium bursae; ostium bursae well sclerotised, elongate and narrow, semilunar; antrum straight, well sclerotised, narrowing dorsoventrally towards ductus bursae, both walls well sclerotised and plain; ductus bursae straight, around twice of the length of antrum, flattened dorsoventrally, of uniform width; dorsal wall membranous and plain; ventral wall medially with wide, longitudinal, well sclerotised plaque, entirely covered with dense, grain-like scobinations; corpus bursae suboval and elongate, membranous, with dense longitudinal plicae and very indistinct, dense scobinations; basally on dorsal wall round, heavily sclerotised plaque with three straight, distinct spines oriented inwards, one thick and long, and two small and short; on ventral wall in 1/5 and 1/3 of its length narrow, horizontal signa, seen from the side in form of semilunar plaque protruding inwards corpus bursae, along the margin comb-like, provided with numerous small and short subtriangular teeth; signum slightly clamp-like, with ends arched outwards into the wall of corpus bursae; ductus seminalis membranous, tubular and narrow, originating form diverticulum located basally and slightly leftwards on ventral wall of corpus bursae, next to terminal portion of ductus bursae, bulbous and narrowing subconically, medially on ventral wall provided with signum in form of very well sclerotised, irregular plaque with upper and lower edge bent outwards, medially with longitudinal protrusion, on both ends terminated with distinct, straight spines, directed upwards and downwards respectively;

Immature stages. Unknown.

Biology. Individuals are attracted to (actinic) light. Recorded from February to April, and in December. Associated with evergreen, humid forests at mid elevation, including riparian habitats.

Distribution (Fig. 115C). North and east of Madagascar, regions of: Sava (Anjanaharibe), Analanjirofo (Andranomaloto River), Alaotra-Mangoro (Beparasy). From around 750 to 1600 m elevation.

Remarks. The only known locality of the species in the central east of Madagascar (Beparasy) is already deforested (LOFM 2022).

Melanonaclia nigra Griveaud, 1964 (Figs 99A-D, 104, 111, 116A)
Holotype: ♀, MNHN, EL65134 (Fig. 99A), by original designation.
Melanonaclia nigra Griveaud 1964: 68, pl. I, fig. 40; Viette 1990: 168.

Material. 21 specimens (ISEA PAS - 1 ♂, 3 ♀♀; MNHN - 1 ♂, 2 ♀♀; NHMUK - 3 ♂♂, 2 ♀♀; NMP - 2 ♂♂, 3 ♀♀; PZBT - 2 ♂♂, 2 ♀♀) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. Additionally, the postocular area yellow and all coxa ochraceous brown (without yellow marks).

Male genitalia redescription (Fig. 111)
Tegumen U-shaped, wide apically and narrowing laterally, with two longitudinal, parallel, very narrow and well sclerotised rib-like stripes; proximal margin V-shaped, medially with rounded incision; fusion with vinculum incomplete; uncus narrow, protruding, claw-like curved downwards, terminated with small pointed hook, basally wide and completely membranous, remaining portion in form of subrectangular, elongate and slightly narrowing, well sclerotised plaque, proximally provided with subtriangular incision; uncus dorsally and laterally covered with sparse, erect setae of varying lengths, mostly directed sideways, some of them in basal portion very long, of the length of approximately 1/2 of uncus; vinculum very narrow, broad and shallow, V-shaped, lateroterminally slightly widened, forming small, subrounded protrusion at fusion with tegumen; saccus moderately long, narrow, flattened and distinctly directed leftwards, of uniform width and roundly terminated; juxta completely membranous, densely creased, with two subrectangular, moderately sclerotised fields on both sides of phallus; transtilla very narrow, in form of moderately sclerotised, vertical plaque bent halfpipe and open proximally, located basally between sacculi; valva elongate, of the length approximately equal to uncus, basal 2/3 irregularly subtrapezoidal, remaining portion claw-like, pointed, distinctly curved inwards, directed upwards and slightly towards each other; costal margin straight, only basally with shallow incision, followed by small protrusion; costal margin from around 1/3 of its length folded inwards, transformed towards subtrapeziodal, angular protrusion at the base of terminal claw-like portion of the valva; sacculus straight, in around 1/2 of its length with subrectangular incision, provided with heavily sclerotised, lobe-like protrusion fused with angular base of the terminal hook, deriving from the folding of costal margin; dorsal surface, except for the basal portion, covered with unevenly distributed scobinations, the most dense at the base of terminal hook; along both margins sparse, elongate, erect setae of varying lengths,

in the subrectangular incision of sacculus slightly thicker and denser, forming a brush-like set; terminal hook basodorsally covered with mixture of elongate and piliform scales, hard to remove; phallus tubular and elongate, basally slightly broader, uniformly moderately sclerotised, only very terminal portion membranous; coecum penis short, rounded; vesica in total of around 2/3 of the length of phallus, basal portion membranous and slightly bulbous, terminated with dorsal, irregular, moderately sclerotised plaque; remaining portion oriented leftwards and consisting of three diverticula; two on right sight, located one over another and basally fused, completely membranous, covered with sparse, fine scobinations, roundly terminated and slightly curved leftwards; third diverticulum twice as long as remaining two, tubular, membranous and slightly plicated, basolaterally on right wall with irregular, elongate field covered with dense, subtriangular, teeth-like scobinations; ductus ejaculatorius in the form of narrow, straight, weakly sclerotised tract, running inside slightly broader, membranous tube of around 1/2 of the length of phallus;

Remarks. The sclerotised part of juxta is fragile and thus easily tears off together with phallus, remaining attached to its terminal portion.

Female genitalia redescription (Fig. 104)

Anal papilla subtrapezoidal, moderately sclerotised, covered with dense, minute scobinations, and dorsally with sparse, erect setae of different lengths; on ventral side between papillae narrow, lobate, membranous protrusions, parallel to each other; apophysis posterioris around 1.5-2x longer than anal papilla, moderately sclerotized, slightly sinuous, needle-like; apophysis anterioris around half of the length of anterioris, thicker and more sclerotised, needle-like, originating from well developed, sclerotised lobe; dorsal pheromone glands in form of two moderately long, tubular, creased membranous tapes, located dorsomedially and not ramifying; ventral pheromone glands absent; 7th sternite irregularly subrectangular, elongate but much narrower than 7th tergite, constituting only around 1/3 - 1/4 of the circumference of the abdomen, moderately to well sclerotised, covered with dense minute scobinations; terminal margin medially with distinct, subtriangular incision, lateral margin with wide but shallow, trough-like cavity of uniform width, extended at the basal margin into short, subtrapezoidal, pocket-like invagination entering below proximal margin of 6th sternite; 7th tergite distinct, elongate and widened, subtrapezoidal, well sclerotised, covered with dense minute scobinations; terminal margins of 7th tergite and 7th sternite densely covered with elongate and piliform scales, hard to remove; 8th tergite narrowed into elongate, horizontal plaque with narrow, heavier sclerotised rib along basal margin, located along on the ventral side of

7th tergite terminal margin, medially narrow, sublaterally widened into elongate subtriangular lobe, terminated with apophysis posterioris; lamella postvaginalis basally membranous, horizontally creased, terminal margin developed into moderately sclerotised, subtrapezoidal horizontal plate densely covered with fine scobinations, closing the lumen of ostium bursae; ostium bursae well sclerotised, widened, laterally provided with narrow, lobate protrusion on each side, terminal margin medially roundly incised; antrum directed leftwards, well sclerotised, funnel-like; ductus bursae straight, directed leftwards, around twice of the length of antrum, flattened dorsoventrally, of uniform width, dorsal wall membranous and plain; ventral wall with well sclerotised plaque covered with dense, grain-like scobinations, terminated before the end of ductus; corpus bursae regularly suboval, membranous, with dense longitudinal plicae and very indistinct, dense scobinations; on ventral wall in 1/4 and 1/2 of its length narrow signa in form of horizontal, medially broadened, semilunar, comb-like plaque, along the margin provided with numerous small and short claw-like protrusions; ductus seminalis membranous, tubular and narrow, originating terminally from distinct diverticulum located basally and slightly leftwards on ventral wall of corpus bursae, next to terminal portion of ductus bursae, of the length varying among specimens, bulbous to slightly subconical, basomedially with small signum in form of rounded to suboval, moderately sclerotised plaque, that can be located on dorsal, ventral or on both walls.

Immature stages. Unknown

Biology. Individuals are collected by netting by day, while there is no data on attraction to light. Recorded from October to March and in May. Copulation was observed at dusk in specimens collected on 26.ii.1993. In the corpus bursae of a single female (DL_SG30), collected on 17.xii.2002, two colla were found. Associated with evergreen, humid forests, at low and mid elevation. A single individual was collected by DL nectaring on the flowers of Rubiaceae sp. in Maitsoarongana.

Distribution (Fig. 116A). North and east of Madagascar, regions of: Sava (north to Antsiranana, Marojejy PN), Analanjirofo (around Antongil Bay), Atsinanana (Andekaleka, Brickaville). From around 225 up to 1700 m elevation.

Melanonaclia toulgoeti Griveaud, 1964 (Figs 99E-H, 105, 112, 116B-C).
Holotype: ♂, MNHN, EL65136 (Fig. 99E), P. Griveaud slide No. 280, by original designation.
Melanonaclia toulgoeti Griveaud 1964: 70, pl. I, fig. 42; Viette 1990: 168.

Material. 35 specimens (ISEA PAS - 5 ♂♂, 9 ♀♀; MNHN - 1 ♂, 4 ♀♀; NHMUK - 7 ♂♂, 3 ♀♀; PZBT - 2 ♂♂, 1 ♀; SGN - 1 ♀; SMNS - 2 ♂♂) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. Additionally, in both sexes the forewing outer margin distinctly sinuous, medially incised, the deepest at the termination of CuA1. The incision is more distinct in the male, in which additionally the vein CuA1 originates in terminal 2/3 of DC hind margin (in 1/2 in the female), thus the wing possesses a large membranous field between DC hind margin, CuA1 and 1A+2A (Fig. 14H). The field tends to bent downwards, leading to a slight corrugation of the entire wing surface and a visual deepening of the outer margin incision in some spread specimens. In the male hindwing the dorsal surface of the area between costal margin, DC hind margin and CuA1 is covered with paler, ochraceous-greyish scales.

Male genitalia redescription (Fig. 112)
Tegumen U-shaped, sublaterally with round incision on proximal margin, further lateral portion narrowing towards incomplete fusion with vinculum; uncus very similar to that of *Melanonaclia nigra*, in basal portion connected with tegumen by narrow, completely membranous field, followed by subrectangular, elongate and slightly narrowing, well sclerotised plaque, medially on proximal margin with rounded incision, dividing the basal part into two subtriangular lobes; remaining portion of uncus claw-like, narrowed laterally, protruding and curved downwards, terminated with pointed tip; uncus dorsally and laterally covered with sparse, erect, elongate setae of slightly varying lengths, mostly directed sideways; vinculum very narrow, U-shaped, lateroterminally slightly widened; saccus elongate and slightly narrowing towards pointed tip, flattened and straight, distinctly directed leftwards; juxta completely membranous, densely creased, medially with two irregular sclerites on both sides of phallus; transtilla in form of moderately sclerotised, subtriangular, U-shaped plaque with tip oriented backwards and laterally bent downwards, located basally between sacculi; valva elongate, of the length approximately equal to uncus, basal half irregularly subrectangular, remaining portion beak-like and pointed, but shorter and not so narrow and claw-like as in the other species of the genus, curved inwards and directed upwards; costal margin basally straight,

in half of its length with semicircular incision; remaining portion rounded and incised towards the pointed tip, of the shape resembling birds head seen from side; sacculus basally with small incision, remaining portion arched towards the narrowed tip; both margins in terminal half folded inwards and fused together into protruding, subtriangular lobe in the half of valva length; dorsal surface, except for the basal portion, covered with unevenly distributed scobinations, along sacculus and in terminal portion of costal margin sparse, erect setae of varying lengths; phallus tubular and elongate, slightly widened subbasally, uniformly moderately sclerotised, only very terminal portion membranous; vesica very long, of around 1.5 of the length of phallus, basally completely membranous, tubular and straight, 1/3 of its length widened and distinctly bent leftwards, so the remaining 2/3 is parallel to phallus and directed backwards, slightly widened medially and narrowing terminally, covered with unevenly distributed and differently expressed, grain-like and subtriangular scobinations; in the right (outer) wall with longitudinal, elongate field of elongate, straight, heavily sclerotised spines oriented backwards (towards the base of vesica), of different lengths, much shorter in terminal portion;

Female genitalia redescription (Fig. 105)

Anal papilla relatively long and narrow comparing to other species of the genus, subtrapezoidal, covered with sparse, elongate setae of different lengths, rather regularly distributed in entire dorsal surface; on ventral side between papillae narrow and small, lobate membranous, protrusions, parallel to each other; apophysis posterioris of the length of anal papilla or slightly longer, moderately sclerotized, needle-like, straight or slightly curved; apophysis anterioris of the length and shape of anterioris, originating from well developed lobe; dorsal pheromone glands in form of two slightly sinuous, tubular membranous tapes located dorsomedially, of rather uniform width, in some specimens short and widened terminally, in others elongate and not widened; ventral pheromone glands absent; 7th sternite distinct and elongate, subtrapezoidal, much narrower than 7th tergite and constituting only 1/3-1/4 of the circumference of the abdomen, moderately to well sclerotised, covered with dense minute scobinations, basal margin laterally with elongate, shallow and wide, trough-like cavity, terminated with pouch like pocket of subtrapezoidal shape, invaginated below terminal margin of 6th sternite and reaching to around 1/3 of its length, inside densely covered with scales; terminal margin medially with distinct, narrow and deep incision of curved lateral margins, in some specimens with pointed tip; 7th tergite distinct, elongate and widened, well sclerotised, covered with dense minute scobinations; along fusion of 7th sternite and 7th tergite narrow, heavier sclerotised rib; 8th tergite distinctly narrowed into elongate, well sclerotised plaque with rib-like folding along basal margin, located ventrally along 7th terminal margin, medially narrow, sublaterally widened into elongate, subtriangular lobe, terminated with apophysis posterioris; lamella postvaginalis in form of relatively well sclerotised, horizontally densely creased plaque, covered with dense, minute scobinations, denser along terminal margin; ostium bursae relatively well sclerotised, elongate and narrow, semilunar; antrum well sclerotised, in basal portion wide, then funnel-like, narrowing dorsoventrally towards ductus bursae and in terminal portion distinctly directed rightwards in relation to the body axis; both walls well sclerotised and plain; ductus bursae straight, also directed rightwards, of around 1.5 of the length of antrum, flattened dorsoventrally, of uniform width, dorsal wall entirely membranous and plain, ventral wall with very narrow membranous lateral margins, medially with wide, well sclerotised plaque, covered with fine, irregular sculpture, and terminated before the end of ductus; corpus bursae suboval and elongate, membranous, with dense, longitudinal plicae and very indistinct, dense scobinations, on ventral wall in 1/4 and 1/2 of its length narrow, horizontal signa, in form of comb-like plaque protruding inwards corpus bursae, provided with numerous small and short subtriangular teeth; each signum slightly arched; ductus seminalis membranous, tubular and narrow, originating terminally from very prominent diverticulum located basomedially on ventral wall of corpus bursae; diverticulum only slightly shorter than main part of corpus bursae, oriented upwards, entering deep beneath 7th sternite, membranous and creased in the way resembling sponge mushroom; in basal portion tubular, terminally subconically narrowed, lateromedially on the right side with small, differently expressed signum of different shape, from irregularly suboval plaque provided with a few small and short spine-like protrusion, to single grain-like scobination;

Immature stages. Unknown.

Biology. Individuals are collected by netting at day and attracted to light. Recorded from November to April, and in September. In the corpus bursae of a single female (MAD_083), collected on 01.12.2019, one complete spermatophore and two colla were found. Associated with evergreen, humid forests, mostly at mid, but also at low elevation, including disturbed primary forests.

Distribution (Fig. 116B-C). North and central east of Madagascar, regions of: Analanjirofo (Maroantsetra), Alaotra-Mangoro (from Ambatondrazaka south to Sandrangato - Route d'Anosibe), Analamanga (La Mandraka and N from Mandraka Park). The records from

Antananarivo (Le Moult) are unlikely to be correct, because there is no evidence he collected in Madagascar himself. From around 65 up to 1310 m elevation.

Remarks. The main area of the species occurrence in central east of Madagascar has been intensively deforested in the last two decades (Fig. 116C).

Melanonaclia trimacula **comb. nov.** (Figs 100A-C, 106, 113, 117A-B)
Naclia trimacula Mabille, [1879]: 85.
Thyrosticta trimacula Griveaud 1964: 90, Pl. I, fig. 57; Viette 1990: 170.
Holotype: ♂, NHMUK, NHMUK013384731, slide NHMUK010314352, by monotypy(?), there is no direct designation in Mabille [1879], recognised by Griveaud (1964) and Viette and Fletcher (1968).

Material. 132 specimens (CEP-MZUJ - 1 ♂; ISEA PAS - 4 ♂♂, 14 ♀♀; MNHN - 21 ♂♂, 27 ♀♀; NHMUK - 13 ♂♂, 31 ♀♀; PZBT - 11 ♂♂, 10 ♀) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination key. The most similar species is *Melanonaclia ranomafana* **sp. nov.**, but it is always slightly larger and has yellow marks sublaterally on the terminal tergite (i.e. enlarged 7th in the female), and the terminal portion of abdomen in *M. trimacula* **comb. nov.** is entirely ochraceous brown. Further, *M. ranomafana* **sp. nov.** has an entirely yellow postocular area, or at least with admixture of yellow scales, which in *M. trimacula* **comb. nov.** it is always dark ochraceous brown. The next most similar species is *M. dujardini* **comb. nov.**, but it has only one, irregular yellow blotch in the hindwing (Fig. 110E-G). The other similar Madagascan Syntomini species are discussed in the diagnosis of *Privatenaclia seguyi* **comb. nov.** Among them, the most similar are some individuals of *Stictonaclia reducta* (Mabille, [1879]), but - similarly as *M. dujardini* **comb. nov.**, they have one, large yellow blotch in the hindwing (instead of two in *M. ranomafana* **sp. nov.** and *M. trimacula* **comb. nov.**), and different patterns of the abdomen.

Male genitalia redescription (Fig. 113)
Tegumen weakly to moderately sclerotised, V-shaped, apically wide, narrowing to the half of each arm, then of uniform width, completely fused with vinculum; proximal margin deeply

incised subdorsally; uncus moderately sclerotised, elongate and narrow, straight, claw-like, in terminal portion slightly bent ventrally; vinculum weakly sclerotised, almost membranous, very narrow, U-shaped; saccus subtriangular, wide basally, and slightly asymmetrically narrowing towards rounded tip; valva elongate, but not reaching beyond uncus, multidimensional; basal half subtrapezoidal, remaining portion divided into two lobes, one shorter and one longer, so the entire valva has the shape of crab claw; costal margin slightly concave, then forming heavily sclerotized subtriangular lobe reaching to the 2/3 of valva length; further part of costal margin forming incision between the two lobes, medially folded inwards, then transforming into dorsal rib of the saccular lobe; sacculus in basal portion straight, then slightly concave, terminal 1/3 slightly bent downwards and narrowing into claw-like lobe with pointed tip; costal margin and inner side of terminal portion of valvae covered with short, erect setae, outer surface along sacculus covered with minute, sparse scobinations; phallus membranous, elongate, wider at the base, then slightly narrowing, terminally slightly bent dorsally; vesica membranous, multidimensional, elongate, of 2/3 of the phallus length, straight, bent upwards at an acute angle and narrowing towards tip; on the right wall row with over a dozen of elongate, spine-like cornuti of varying length, directed downwards in different directions; at the base of vesica two short, subrounded diverticula oriented forward, and another diverticulum in 1/3 of vesica length, on left wall, slightly longer than basal two and bent downwards.

Female genitalia redescription (Fig. 106)

Anal papilla subtrapezoidal, weakly to moderately sclerotised, outer surface covered with sparse scobinations and setae, denser along margins; apophysis posterioris of 1.5 length of anal papilla, sclerotized, needle-like, straight, slightly sinuous; apophysis anterioris of 2/3 of length of posterioris, sclerotised, narrow, needle-like and straight; dorsal pheromone glands in form of two elongate, narrow, straight and not anastomosing membranous tubes, opening subdorsally; ventral pheromone glands absent; 7th tergite and sternite usually heavily sclerotised, but in some specimens almost completely membranous, plain, together in the shape of slightly conical collar; suture between terminal tergite and sternite sinuous, located on the ventral side of abdomen, in distinct, longitudinal, U-shaped cavity; distal margin of 7th sternite forming apprised ridge surrounding ostium bursae; lamella postvaginalis in form of membranous to moderately sclerotised, subtrapezoidal, wall-like plate at ventral side of papillae; ostium bursae wide, slightly flattened dorsoventrally;

antrum membranous to heavily sclerotised, funnel-shaped, narrowing towards ductus bursae; ductus bursae short, membranous, uniformly wide, in some specimens with indistinct sclerotisations; corpus bursae suboval, membranous, without plicae, on ventral side with pair of signa in form of horizontal, elongate, heavily sclerotised, narrow, semilunar plaques covered with row of short, tooth-like protrusions; ductus seminalis narrow, tubular, originating from distinct, bulbous diverticulum located at the right side in the basal portion of corpus bursae, with two patchy, flat, heavily sclerotised plaques of irregular shape, one on dorsal and one on ventral side, each with one straight, spine-like protrusion oriented inwards, in some specimens the two patches fused together into one, clamp-like plaque.

Immature stages. Unknown.

Biology. Adults are collected by netting at day, to Malaise traps, and rather sporadically attracted to light at night. Recorded from October to May; in PZBT there is one specimen with a hardly legible label, which reads “May” or “June”. In the corpus bursae of a single female (ISEZ-DNA_545), collected on 11.04.2018, two colla were recorded. Associated with evergreen, humid forests at mid elevation. The specimen from Sarodrano (see distribution) was collected in an area currently devoid of natural vegetation except with degraded southwestern dry spiny forest. The species was recorded both in forest habitats, including humid, enshadowed roadsides with grasses, shrubs and trees along an asphalt road in rainforest, as well as in completely secondary ones, like Parc Tsimbazaza in Antananarivo. A single individual was observed by DL nectaring at day on the flowers of *Psychotria* (*Mapourea*) sp. (Rubiaceae) (Fig. 118).

Distribution (Fig. 117A-B). Mainly central and southern east of Madagascar, regions of: Analamanga (Saha Forest Camp, south to Parc Tsimbazaza in Antananarivo, Alaotra-Mangoro (Eulopia Trail in Andasibe-Mantadia PN south to Beparasy), Amoron'i Mania (along Route Nationale 7), Matsiatra Ambony (from Ankafina-Tsarafisdy south to Mahasoabe), Vatovavy Fitovinany (Ranomafana PN, south to Ikongo), Ihorombe (Befarara), Anosy (foret d’Andranomangara). Additionally, the species was collected in Diana (Montagne d'Ambre - Les Roussettes) and Atsimo-Andrefana (Sarodrano). From around 900 up to 1750 m elevation.

Remarks. The taxonomic status of the specimens collected in the localities distant from the main range of the species - Montagne d’Ambre and Sarodrano - should be further verified, especially the latter one, considering the different type of vegetation in that part of the island.

The single specimen labelled as collected specifically in Tsimbazaza in Antananarivo on 22.v.1972 by A. Rakotoarisolo leaves no doubt. Most of the localities are already deforested, some of them very recently, and covered with secondary vegetation. Syntomines, though, have not been spotted at PBZT in more recent decades.

The ABGD analysis in the division into 39 recursive partitions (but not in 34 and 36, Figs S3-S5) indicates four specimens (DL_14Z-002, MAD_126, MAD_81 and MAD_130), forming a separate clade in the tree, as a potential separate species. However, this is not confirmed in ABGD analyses based on molecular markers (Figs S6-S7, nor in the PTP analysis (File S1), and we did not find any different, potentially species-specific morphological characters. Thus, we interpret the results as intraspecific variation with a geographical component, as the four specimens listed above were collected in the central part of the species range, and the remaining specimens, arranged in the second clade - in the southern part of the range (Fig. 117B).

Melanonaclia dujardini **comb. nov.** (Figs 100D-G, 107, 114, 117C)
Thyrosticta dujardini Griveaud, 1969: 10, Pl. I, Fig. C; Viette 1990: 169.
Holotype: ♀, MNHN, EL65172, by original designation.

Material. 6 specimens (MNHN - 1 ♂, 1♀; PZBT - 1 ♂, 3♀♀) (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. For further remarks see the diagnosis of *M. trimacula* **comb. nov.**

First male description (Fig. 100E)

Head. Proboscis well developed, ochraceous brown; frons, vertex and postocular area ochraceous brown, however vertex medially worn; labial palpus three-segmented, entirely ochraceous brown, elongate, straight, porrect, extending beyond frons for around 1/2 of its length; 2nd and 3rd palpomere approximately equal; antennae piliform, ochraceous brown, ventrally covered with short, erect setae, additionally each antennomere with longer seta on each lateral margins;

Thorax. Patagia medially ochraceous brown, laterally with small, pale yellow blotch; tegulae with mixture of yellow and pale yellow scales, tip with elongate and piliform ochraceous brown scales; meso- and metathorax partially worn, remaining scales ochraceous brown; pleurites pale ochraceous brown, with admixture of yellow scales at hindwing base;

Legs. Claws of all legs provided with minute, additional tooth; arolium present; foreleg: ochraceous brown, frontal surface of coxa pale yellow, tarsus ventrally pale ochraceous to yellowish; epiphysis present, pale yellow, of around 2/3 of tibia length, tibia and 1st tarsomere together of the length of femur; midleg: ochraceous brown, with tarsus as in foreleg; tibia with one pair of long terminal spurs, distal one slightly longer; hindleg: colouration as in fore- and midleg, but terminal portion of coxa frontally with pale yellow blotch; tibia with one pair of terminal spurs, distal one slightly longer; single, additional spur in 3/4 of tibia length, shorter than terminal ones;

Abdomen. Intensively yellow into orangish, dorsally with ochraceous brown marks; 1st tergite medially with trapezoidal dark ochraceous brown blotch, tergites 2nd and 3rd medially with longitudinal, narrow, irregular ochraceous brown blotch; tergites 4th and 5th dorsally with a few dark ochraceous brown scales in medial portion; tergites 6th and 7th entirely yellow; 8th tergite medially with brown longitudinal narrow stripe, terminated before terminal margin; terminal margin of 8th tergite with elongate, medially ochraceous brown, laterally yellow to orangish scales; sternites entirely pale yellow, paler than tergites; 8th sternite laterally in terminal portion with two ochraceous brown blotch on each side.

Forewing. Subtriangular, elongate; background very dark brown (but not black), with five blotches of different shape and size: two in basal portion, one in medial portion and two in distal potion; First basal blotch (fm_1) at the very base of the wing, intensively yellow, not to be misinterpreted as tegula extension; second basal blotch (am_1) below 1A+2A, touching wing hind margin, elongate, suboval to fusiform, in wing basal portion, yellow; medial blotch (fused m_2, m_3 and fm_3) large, irregular, pentagonal, in major in DC, from below R and exceeding DC hind margin, including the basal part of CuA2, pale yellow, in the anterior portion covered with mixture of regular and smaller, scarce scales, but in general not semi-transparent; first distal blotch (m_4) round, between R and M1, partially worn on both wings, with remnants of both regular and smaller, scarce, yellow scales; second distal blotch (fused m_5 and m_6) irregular, subtrapezoidal, between M2 and CuA1, portion between M2 and M3 (m_5) widening towards M3, portion between M3 and CuA1 (m_6) of uniform width, with both regular and smaller yellow scales; underside similar as upperside, but along hind margin, below the line going through terminal apex of medial blotch and further along CuA2, devoid of regular scales, and covered with very small, grain-like scales of very pale yellow, almost creamy colour; in basal portion of underside irregular blotch of pale yellow scales, with very narrow, pale yellow stripe fusing with medial blotch; medial and second distal blotches larger than on the upperside; all blotches densely covered with regular scales, thus the wing is not semi-transparent despite lower scales density on the upperside; cilia concolorous with the wing background, retinaculum present; Hindwing. Suboval, reaching half of the forewing length; basal portion with yellow blotch of irregular shape; outer zone with dark brown (but not black) margin, from around 1/2 of hind margin and 3/4 of costal margin; medial yellow blotch forming large, rounded protrusion towards outer margin; in basodistal wing portion outer margin reaching till around 1/3 of the wing width, with sharp tip protruding towards wing base; underside as upperside, but narrow ochraceous margin reaches till basal 1/3 of costal margin, and the basodistal portion of yellow blotch is covered with smaller, slightly elongate and scarcer yellow scales; M2 and M3 stalked in around 1/3 of their length; frenulum present.

Remarks. The male is generally similar to the female. The most distinct difference is lack of semitransparency in the male medial and second distal blotch. However, it should be noted that the species is known only from a few specimens.

Male genitalia description (Fig. 114)

Tegumen weakly sclerotised, almost membranous, with more distinctly sclerotised ribs along margins, U-shaped, very narrow, incompletely fused with vinculum; uncus basally membranous, with weakly sclerotised ribs on lateral margins; medial portion narrower, weakly sclerotised, straight, covered with long, hairy setae, terminal portion narrowed and slightly constricted ventrally towards hook-like apex bent downwards; vinculum weakly sclerotised, very narrow, U-shaped; saccus narrow and very long, spine like and asymmetrically directed leftwards; valva elongate, almost as long as uncus, narrowing towards sharp tip; costal margin in basal portion slightly folded inwards, in 1/3 of its length with rounded, shallow protrusion upwards, and subtriangular projection directed inwards; terminal half of costal margin covered with sparse, elongate, erect setae; sacculus sinuous, in its 1/2 with protrusion directed inwards and fused with the one of costal margin, making the terminal half of valva bent outwards, three dimensional and subtriangular in cross-section; valva in terminal half covered with setae, more distinct than these on costal margin; phallus weakly sclerotized, elongate, straight and tubular; vesica membranous, distinctly elongate, available portion with one short diverticulum; terminal portion with longitudinal, row of a few dozen cornuti in form of straight, well sclerotised spines, longer in terminal portion of vesica.

Immature stages. Unknown.

Biology. There is no data on diurnal / nocturnal activity of the species. Individuals were recorded from April to June, additionally the single specimen from Andekaleka has a hardly legible label, which probably reads "February". Associated with evergreen, humid forests at mid elevation.

Distribution (Fig. 117C). The species is known from two localities in the central east of Madagascar: Andekaleka in Atsinanana region and Beparasy in southern Alaotra Mangoro. From around 700 (Andekaleka) to 880 m (Route Beparasy) elevation.

Remarks. The area of Beparasy is currently covered with secondary vegetation, and the area of Andekaleka, located outside Zahamena Ankeniheny protected area, was affected with patchy deforestation in the last 10 years.

Melanonaclia ranomafana Wiorek and Przybyłowicz, 2024 **sp. nov.** (Figs 100H-J, 108, 117D)
TL: Ranomafana National Park.
Holotype: ♀, ISEA PAS, MAD_018; Paratypes: 2♀♀, ISEA PAS, MAD_019, and NHMUK, NHMUK [to be provided later].
ZooBank [to be provided later].

Material. The type series comprises the only known specimens (Tab. S1).

Diagnosis. The diagnostic characters are provided in the determination keys. The most similar species is *M. trimacula* **comb. nov.**, which is discussed above in the diagnosis of that species.

Description (Fig. 100H-J)
Head. Proboscis well developed, dark brown, almost black; head dark ochraceous-brown, including palpi and antennae, only postocular area in upper part with spot of pale yellow scales, and indistinct, narrow stripe of tiny yellow scales along posterior margin; labial palpi three-segmented, porrect and slightly curved downwards; antennae filiform, dark ochraceous-brown, covered with short, erect setae, more densely on ventral side, and distinctly outstanding at antennae tips.

Thorax. Patagia medially dark ochraceous-brown, laterally with yellow blotch, connected with the yellow blotch of postocular area; tegulae yellow, tip with elongate and filiform dark ochraceous-brown scales. Mesothorax and metathorax partially worn of scales, remaining portion mix of pale and dark ochraceous brown regular scales. Pleurites partially worn, with remnants of pale and dark ochraceous brown scales and tiny pale yellow blotch behind hind wing base.

Legs. Covered with mixture of pale and dark ochraceous-brown, with some pale yellow marks; tarsus ventrally on lateral margin with rows of ochraceous, spine-like setae; arolium present, additional tooth on clave present; foreleg: frontal surface of coxa pale yellow, trochanter and ventral side of tarsus with admixture of pale yellow scales, remaining portion ochraceous brown; tibia of 3/4 of the length of femur, epiphysis present, reaching 2/3 the length of tibia, emarginated with pale yellow scales; midleg: coxa frontally with pale yellow blotch and ventral side of tarsus with admixture of pale yellow scales, remaining parts ochraceous brown; tibia with one pair of ochraceous-brown terminal spurs of more or less equal length; hindleg: colouration as in midleg, additionally tibia with dorsal, irregular blotch of yellow scales; tibia with one pair of equal terminal spurs, and single additional spur of length comparable to terminal spurs, at terminal 3/4 of tibia length;

Abdomen. Pale yellow to yellow, with three ochraceous brown stripes, one dorsally and two laterally; terminal portion of abdomen dark ochraceous brown; 1st tergite medially with subtrapezoidal ochraceous brown blotch, sublaterally yellow, tergites 2nd - 6th medially with dorsal stripe formed by subsquare blotches of slightly irregular lateral margins, narrower than the blotch on 1st tergite, on some segments widening terminally, sublaterally yellow; tergite 7th similar to the preceding ones, but with broader basomedial blotch, basolaterally yellow blotch on each side, terminal half entirely ochraceous brown; sternites 2nd - 6th medially entirely pale yellow, laterally with small, ochraceous brown subrectangular blotches, sternite 7th ochraceous brown, sublaterally in basal part with small, indistinct pale yellow blotches, terminal margin medially with shallow U-shaped incision.

Forewing. Elongate, subtriangular, background dark ochraceous-brown but not black, with four pale yellow to semi-transparent blotches of different shape and size: the smallest one in basal portion, the largest, partially semi-transparent one in the medial portion and two partially semi-transparent in distal portion; basal blotch (am1) elongate, subtriangular, between 1A+2A and wing hind margin, reaching till 1/4 of the wing hind margin;

medial blotch (fused m_2, fm_3 and m_3) irregular, subrhomboidal, from R, widening towards DC hind margin, then narrowing and dully terminated before 1A+2A, portion in DC (m_2) along veins and inner margin with stripe of pale yellow regular scales, medially and along outer margin semi-transparent, covered with tiny and sparse pale yellow, almost creamy scales; portion below DC hind margin (fm$_3$ and m$_3$) less semi-transparent, entirely covered with smaller but regular pale yellow scales; first distal blotch (m$_4$) suboval, between R and M1, along veins with margins of regular pale yellow scales, wider along R, medially semi-transparent, covered with tiny and sparse pale yellow scales; second distal spot (fused m$_5$ and m$_6$) irregularly subtrapezoidal, between M2 and CuA1, portion between M2 and M3 with narrow stripe of regular pale yellow scales along entire margin (including M3 vein), the second portion between M3 and CuA1 with similar emargination, but wider along outer margin of the blotch; central part of both parts semi-transparent, with tiny, sparse, pale yellow, almost creamy scales; underside as upperside, with additional spot of elongate pale yellow scales in basal portion, below DC, forming retinaculum subdorsale;

Hindwing. Suboval, elongate, reaching till around half of forewing; background dark ochraceous brown, almost black, with two yellow blotches, one in basal and one in distal portion; basal blotch from wing base, irregular, reaching slightly beyond basodistal angle and 1/3 of costal margin, inner margin irregular, with subtriangular ochraceous brown indentation just below 3A; distal blotch irregularly subtrapezoidal, from 1/2 till 3/4 of wing length, slightly constricted on both sides in medial portion, with hind margin along CuA1; underside as upperside; Sc+Rs+M1 completely fused, M2 and M3 stalked in basal 1/3 of their length; frenulum present;

Remarks. The greatest difference between the specimens MAD_018 and MAD_019 is the shape of subtornal margin of medial blotch, which is smooth in the holotype while corrugated in MAD_019.

Female genitalia description (Fig. 108)

Anal papilla subtrapezoidal, weakly sclerotised, along margins covered with dense, short erect setae; apophysis posterioris equal to anal papilla, membranous, needle-like, slightly sinuous; apophysis anterioris of similar length and shape to posterioris; dorsal pheromone glands in form of two long, narrow, twisted and rarely anastomosing tapes, opened subdorsally; ventral pheromone glands absent; ostium bursae moderately wide, flattened dorsoventrally, semilunar; Sternites 7th and 8th weakly and evenly sclerotized, without distinct sculpture; antrum wide in basal portion, then narrowing, flattened dorsoventrally; ductus bursae moderately wide, flattened dorsoventrally, ventral wall with well sclerotised, plain plate slightly bent subdistally; corpus bursae two-part, with minute scobinations and distinct longitudinal plicae; main portion elongate, suboval, with signum located laterobasally on the left side of corpus bursae, in form of two transverse, narrow ridges, in medial portion distinctly extending inwards and covered with short, spine-like protrusions bent to the sides; basal diverticulum well developed, separated from corpus bursae by constriction, plain, directed upwards and narrowing towards tip, with additional two distinct signa opposite to each other on dorsal and ventral walls, in form of heavily sclerotised plates of irregular shape, with distinct, straight spine-like protrusions, two on dorsal and three on ventral plate; ductus seminalis narrow, membranous, originating from the tip of diverticulum.

Immature stages. Unknown.

Biology. The individuals are recorded at day, there is no information on attraction to light. The specimens were collected in June and August. Associated with evergreen, humid forests at mid elevation.

Distribution (Fig. 117D). Known only from PN Ranomafana, where it was collected in two localities: ValBio Centre and Sahamaloatra. From around 900 to 1000 m elevation.

Remarks. The two localities of the species are protected and do not seem to be endangered with imminent deforestation.

Etymology. From Ranomafana National Park, the locality where the species was collected.

Mortinaclia gen. nov.

Type species: *Melanonaclia perplexa* Griveaud, 1964

Melanonaclia perplexa Griveaud, 1964: 73, pl. I, fig. 44; Viette 1990: 168
Holotype: ♀, MNHN, EL65137 (Fig.119A), P. Griveaud slide No. 335 (Fig. 120A), by original designation.

Material. 25 specimens (ISEA PAS - 2 ♂♂; MNHN - 2 ♂♂, 5 ♀♀; NHMUK - 1 ♂, 1 ♀; PZBT - 4 ♂♂, 10 ♀♀) (Tab. S1).

Diagnosis. Small, dark brown to almost black moths, with white and pale creamy body coloration and semi-transparent wing blotches (Fig. 119). The pattern of the abdomen consists of creamy and white scales forming a medioventral suboval blotch, and laterodorsal blotches on the 1st segment and around 4th and 5th segment (Fig. 119B-D). The forewing is relatively short and wide, in the outline close to a right-angled triangle (Fig. 15H), and the hindwing is regularly suboval (Fig. 17H), reaching almost to the tornal portion of the forewing, giving the spread specimens a slightly "butterfly" appearance (Fig. 119).

In the female genitalia (Fig. 120), corpus bursae is basally provided with a signum in the form of a large, differently expressed irregular field covered with prominent, elongate spines.

The most similar, small and dark moths with white body and wing patterns belong to the genus *Tenuinaclia*. However, they have proportionally narrower, elongate wings, and the white blotches on the abdomen never extend to its dorsal surface. Additionally, *Tenuinaclia* species have only one small distal blotch in the hindwing, contrary to two blotches in *Mortinaclia* **gen. nov.**

Finally, in the general appearance, and especially wing pattern, *Mortinaclia* **gen. nov.** resembles some of *Melanonaclia* species (the genus in which it was previously placed), and *Tritonaclia* species. However, after the revision presented here, the genus *Melanonaclia* comprises only species characterised by the apomorphies provided above (see also the remarks for *Julienaclia moerens* **comb. nov.**, moved from *Melanonaclia*), with only yellow marks on the abdomen (Figs 98-100). In the genus *Tritonaclia* (except *T. kefersteinii* and *T. quinquepunctata* - see the diagnosis of *Melanonaclia*), the forewing blotch m_5 is also distinctly smaller than m6, and the abdomen has white pattern. However, *Tritonaclia* spp. are always much larger than *Mortinaclia* spp., and their abdominal pattern never extends distinctly on the dorsal surface.

Also the molecular results (Fig. 5B) support the movement of *Mortinaclia perplexa* **comb. nov.** to its own, monotypic genus.

Remarks. *Mortinaclia* **gen. nov.** can be further defined by the following set of morphological characters: antennae piliform in both sexes, slightly sexually dimorphic, in the females segments provided with a pair of more prominent setae (Fig. 8E-F); pencil-like tuft behind the male foreleg coxa absent; hindleg tibia of some specimens with a single, additional spur; forewing with four radial veins, 1A+2A terminated at the well defined tornus, M1 originating from a distinct stylus in the proximal corner of DC (Fig. 15H); forewing blotches: basal absent, medial: m_2 and m_3, distal: m_4, m_5 much smaller than m_6, and separated from each other by a narrow streak of ochraceous brown scales, all blotches semi-transparent; hindwing (Fig. 16H) suboval, costal margin slightly arched, hind margin slightly incised in the basal portion, Sc+Rs+M1 straight, completely fused, M2 and M3 stalked in around basal 1/3 of their length, 3A present; hindwing with one large basal and two smaller, rounded distal blotches of similar shape and size, all semi-transparent.

In the male genitalia (Fig. 120), sublateral arms of tegumen present, in the form of straight, narrow, slightly curved protrusion. In the female genitalia (Fig. 121) ventral pheromone glands absent.

Taxonomic note. Results of our morphological and molecular studies reveal *Mortinaclia perplexa* **comb. nov.** to be a complex of a few cryptic species, indistinguishable superficially, but clearly differing in the shape of both male and female genitalia. Due to the fact that the holotype of *M. perplexa* (Fig. 119) is a female (Griveaud 1964), and the male "neallotype" (MNHN, EL74609) was described a few years later from specimens collected in a different locality (Griveaud 1969), it is impossible to verify their conspecificity solely with morphological methods, and further molecular study is needed to contribute to the issue, on a larger number of specimens. The genitalia slide (MNHN, No. PG577) of the female specimen (MNHN, EL74610) collected in the same place as the male, and made "for verification of the female genitalia", as indicated in the label, (Fig. 120B) distinctly differs from the holotype (Fig. 120A) in the shape of the basal signum. Similar situation is in the males, and we found at least two different types of the genitalia (not shown), distinctly varying in the valvae shape. Thus, molecular analyses are necessary to match the males with the females. Since all known specimens of *M. perplexa* **comb. nov.** were collected in a few localities close to each other (see distribution), it seems that all potential cryptic species within *M. perplexa* **comb. nov.** are currently sympatric. Therefore, here we retain the genus monotypic, with only the female holotype undoubtedly representing *M. perplexa* **comb. nov.**

Immature stages. Unknown.

Biology. Adults were collected by day, while there is no data on attraction to light. Recorded in February, April, May, October, and November. In the corpus bursae of a single female (EL74948), collected on 15-20.11.1958, one or two colla were found (broken into pieces). Associated with evergreen, humid forests at low, mid and lower montane elevations, part of the localities is currently covered with secondary vegetation. In Masoala it was collected in highly disturbed primary riparian forest (DL_2985). The majority of the specimens were collected in November, possibly biased by the activity of a few collectors in the area in November 1967 and 1968 (Tab. S1), and not necessarily from seasonal species abundance. A single individual was observed at day on the flowers of *Cynanchum analamazaotrense* Choux (Apocynaceae: Asclepiadoideae) (iNaturalist observations: 38824345, 38824346, and 38824347 by the user sigrid_bt).

Distribution (Fig. 117E-D). The holotype of *Mortinaclia perplexa* **comb. nov.** was collected in Beondroka in Marojejy. The entire species complex occurs in the northern east of Madagascar, regions of: Diana (Montagne d'Ambre), Sofia (Belalona) and Sava (Vohemar, south to Antanandava – Antafononana River). From around 10 to 1200 m elevation.

Remarks. Except for PN Marojejy and PN Montagne d'Ambre, the localities are outside protected areas, and in some of them deforestation was recently reported (Fig. 117D).

DISCUSSION

The genera *Thyrosticta* and *Melanonaclia* as formerly constituted since Griveaud's time are here confirmed to be highly polyphyletic. They constitute nine separate evolutionary lineages, of which seven are here established as new genera, well supported both molecularly and morphologically. Phylogenetic trees (Fig. 5A-B, Figs S1-S2) already supported the monophyletic character of the Madagascan lineage of Syntomini (Przybyłowicz et al. 2019). Our tree is the most robust phylogeny of the group obtained so far. However, exact relationships within the group still demand further research on a larger dataset, comprising also the members of the genera absent in our study. This applies especially to the earliest diverging clade of Madagascan Syntomini, represented so far only by *Toulgoetinaclia octopunctata* (Przybyłowicz et al. 2019, 2021), which potentially will comprise more species. Elucidating that clade promised to shed light on the relationships between the Madagascan and African Syntomini, including members of the former subtribe Thyretiina (Thyretini *sensu* Przybyłowicz 2009), and especially the genera *Thyretes* and *Pseudothyretes*, which formed the sister lineage to Madagascan Syntomini in Przybyłowicz et al. (2019), but not in this study, in either case with low bootstrap values.

Our results reveal Madagascan Syntomini to be highly diverse genetically, with a few cases of potential cryptic species complexes, usually with well matching distributional patterns of populations, but no clear differences in the morphology (except in the case of the *Mortinaclia perplexa* **comb. nov.** species complex). The observed discongruence between molecular and morphological results, as well as between mitochondrial and nuclear genes (Figs S3-S7, File S1) can be an effect of different processes in the mitochondrial and nuclear genome evolution. However, in relatively shallow time-depth phylogenies the main source of such differences is incomplete lineage sorting (ILS), and not phenomena such as saturation (Maddison and Knowles 2006). ILS can cause an especially strong effect in relatively young yet highly diverse groups, originating from recent evolutionary radiations (e.g. Kozak et al. 2015). Since the entire tribe Syntomini evolved relatively recently, around 25 mya (Wahlberg et al. 2013), and the Madagascan lineage is perhaps much younger, even though it comprises already around 100 species, it can be hypothesised that ILS shaped the differences observed in the mitochondrial and nuclear genome.

In our study, we did not observe any unequivocal morphological differences within the potential cryptic species complexes, including the genitalia (except *Mortinaclia perplexa* **comb. nov.**, see below). On the one hand, this can result from the young evolutionary age of the lineages in question, which would not have enough time to accumulate morphological differences. On the other hand, there could be no selective pressure on the morphological structures, but e.g. on the mating system. Such a case of lepidopteran cryptic species separated by the different pheromonal communication schemes was described in Eriocraniidae (Lassance et al. 2019).

The only exception among the species studied here is in fact *M. perplexa* **comb. nov.** in which we found unambiguous differences in both male and female genitalia, but further molecular research is needed to match the sexes conspecifically. Another case of a seemingly truly separate species is the western lineage of *Mauricenaclia minuta* **comb. nov.**, whose distinctiveness is well supported in both mitochondrial and nuclear genes (Figs. S3-S7, File S1), and which is also well isolated and truly sympatric to other populations of *M. minuta*. However, the species is highly variable morphologically, impeding indication of any clear differences, especially having only two specimens available from the western population. A similar complex of cryptic species was recently found in the Palaearctic syntomine genus *Syntomis*, whose diversification was interpreted as a result of environmental and climate changes in the past, and morphological similarity is likely maintained as part of a mimicry system (Chiocchio et al. 2021). A similar interpretation can be proposed also in the case of Madagascan Syntomini. For example, the "western rainforest refugia mechanism" proposed by Vences et al. (2009) assumes that during the wet and warm periods of Pleistocene rainforest was extending from the east to the west of Madagascar. Nowadays the patches of the western rainforests are relics of those once widespread habitats, and so the western population of *M. minuta* could be relictual in nature. However, the results of population genetics research on mouse lemurs by Tiley et al. (2022) suggests that the dispersal from the eastern rainforest across the Central Highlands was possible also more recently, up to the recent Holocene, through riparian corridors. However, this is less plausible in the case of *M. minuta*, considering the deep genetic divergence of the western population, and no records of the species from the relictual forests of Central Highlands, especially RS Ambohitantely (see Wiorek et al. 2021).

Half of the potential cases of cryptic species complexes, i.e. *Kowalskinaclia cowani* **comb. nov.**, *K. vieui* **comb. nov.** and *Melanonaclia trimacula*, show very similar distributional patterns, with a clear partition into a "northern" and "southern" population (Figs. 56B-C, 58, 117A-B), and a potential barrier running along the Mangoro River watershed. This pattern corresponds relatively well with the centres of endemism north and south from the Mangoro River in the "watershed hypothesis" of microendemism, proposed by Wilmé et al. (2006). The river itself though does not seem to be an effective barrier for winged insects, which can fly or be transported by strong winds (in contrary to e.g. relatively well studied lemurs of chameleons, Pearson and Raxworthy 2009). However, the topography of river valleys surrounded by higher areas can play a role in the context of Quaternary climate changes and subsequent shifts of certain vegetation types up and downhill, leading e.g. to temporal fragmentation of once continuous low elevation forest into separated, higher elevation patches during dry periods (Vences et al. 2009). Since the speciation process is a continuum rather than a series of discrete events (de Queiroz 2007), the changes of climate and vegetation ranges could lead the mentioned species into the initial stages of vicariant speciation, which was interrupted by the subsequent fusion of the populations caused by further change of the climate conditions and vegetation ranges. In this context, the most interesting are the "intermediate" specimens of *K. cowani* **comb. nov.**, collected in the area of Tsarafidy (see Systematics), which potentially can be "hybrids" of the two morphotypes, and require further research.

Finally, it should be mentioned that the indication of potential cryptic species can result from the structure of our data. It has been shown that within large evolutionary radiations, like in the lemurs, (comparable in the number of species to Madagascan Syntomini), different lineages can have different diversification rates (Everson et al. 2023). In Lepidoptera, similar results were obtained for Heliconiini (Kozak et al. 2015), and such a pattern cannot be ruled out in Madagascan Syntomini. At the same time, the ABGD method searches for a universal value of p-distance indicating the gap between intra- and interspecific variation, which, however, can be different in the lineages evolving at different rates, and the method has been indicated as potentially sensitive to such scenarios (Puillandre et al. 2012).

In our morphological study, we based the apomorphies of the newly established genera mostly on the genitalic characters, as a fundamental approach. The genitalia of all but a few Madagascan species, including all type species of genera, were already known at least for one sex (Griveaud 1966, 1969, [1971], [1973], [1974], Wiorek et al. 2021), and the original slides are housed in MNHN, NHMUK and ISEA PAS. Additionally, here we describe the previously unknown male of one species and females of six species. That all allowed us for even more accurate morphological analyses, and to rule out that the type species of the newly established genera could be congeneric with the type species of any of the remaining genera, not covered in the paper. Currently only the females of *Kowalskinaclia dilata* **comb. nov.** (but see Systematics) and *Mauricenaclia apatris* **sp. nov.**, and the males of *Skippernaclia leesi* **sp. nov.** and *Melanonaclia ranomafana* **sp. nov.** remain unknown. On the one hand the general morphology of Madagascar Syntomini is highly diverse and complex, as shown in the morphological results, whilst some species are known from low numbers of specimens, sometimes only dissected and worn holotypes, which complicates access to adequate materials. On the other hand, genitalia can be analysed based on high quality photographs, and in most cases are in satisfactory condition (except for occasional preparation artefacts mentioned in the text).

Apart from the explicit morphological apomorphies indicated for each genus, we also identified several characters that revealed a uniform presence/absence pattern for the genus (with some exceptions in *Melanonaclia* and *Mauricenaclia* **gen. nov.**), whilst variable across genera. Most of the characters in Griveaud (1964) were not analysed at all, or elaborated only superficially, with e.g. the single wing venational groundplan attributed to the entire genus *Thyrosticta*.

Not only the classification of Syntomini has been an issue, but also higher classification of the superfamily Noctuoidea has for a long time been a riddle for taxonomists to solve, as accurately indicated by Nye (1975): “It is exceptional to find any two authors who use the same combination of subfamily names within the Noctuidae” [viz, the current Noctuoidea]. Also the classification within Arctiinae was a subject of scientific debates, with (e.g.) the tribe Syntomini included together with *Euchromia* (now in Arctiini: Euchromiina) into a single family “Amatidae” in the monograph by Griveaud (1964). Although recent papers have provided reliable molecular insights into the systematics of erebids (Zahiri et al. 2012) and syntomines in particular (Przybyłowicz et al. 2019), extensive morphological analyses, especially in understudied groups like Madagascan Syntomini, are crucial to provide a stable morphology-based taxonomy and classification of Arctiinae, and Noctuoidea in general.

The foreleg pencil-like tuft, located ventrally on the coxa, is to our best knowledge reported for the first time in Syntomini. A similar but differently expressed leg structures are present in males of other groups of Lepidoptera, e.g.: i) in the hindleg tibia of a few different taxa (genera to tribes) of Hesperiidae (Hernández-Roldán et al. 2014), and in some Hepialidae, in which the entire hindleg is transferred and lost its primary function (Birch and Poppy 1990); ii) in the fore-, mid-, or hindleg tibia of a few tribes of Geometridae: Larentiinae (Hashimoto 2021, Viidalepp 2011); iii) foreleg femur in Uraniidae (Lees 1992). The general morphological structure of the tufts observed in Madagascan Syntomini is very similar to those of Hesperiidae, in which they have been shown to be a scent organ (Hernández-Roldán et al. 2014). The same function Thus, the pencil-like tuft in Madagascan Syntomini also can be interpreted as a potential scent organ, especially as it is present only in males (thus androconial). However, this interpretation should be proposed with caution, since the similar structure mentioned in

Uraniidae has stridulatory function (Lees 1992), and in our SEM analyses no PTPs (see Kristensen and Simonsen [1999]) were identified on these scales.

In Lepidoptera, including Noctuoidea and specifically Arctiinae, different scent structures are present, but located predominantly in the abdomen, not in the legs (Birch et al. 1990). Arctiinae are especially well known for pharmacophagy, i.e. obtaining from plants toxic pyrrolizidine alkaloids (PAs) (Boppré and Monzón 2023), which are necessary for different processes, including pheromone synthesis (Boppré 1990, Lopez-Cacacho et al. 2024). Pharmacophagy has not been recorded in Syntomini so far (Zaspel et al. 2014), but this can result from the scarcity of observations of these moths in nature. Here we provide observations of nectaring in Madagascan Syntomini for the first time. Single individuals of a few species were observed nectaring or flying directly over the flowers of: *Psychotria* (*Mapourea*) sp. (Rubiaceae), *Cynanchum analamazaotrense* (Apocynaceae), *Entada leptostachya* (Fabaceae) and *Cinchona succirubra* (Rubiaceae) – however, the last observation should be treated with caution as it is not a native plant (see Systematics). All the listed plant families are known to contain different alkaloids. However, PAs are found mostly in Asteraceae and Boraginaceae (Gutiérrez-Grijalva et al. 2020). Thus, the issue demands further research in Madagascan Syntomini, especially that the group has generally vivid, aposematic body colouration, which in Arctiinae is often an advertisement of unpalatability / toxicity resulting from PA accumulation in the body (Boppré 1986).

Aside from genitalia and androconial characters, indication of apomorphies of the tribes currently recognized within Arctiinae is not trivial and it is often necessary to refer to very subtle characters (Jacobson and Weller 2002). There are a few seemingly unambiguous characters defining Syntomini (Kitching and Rawlins [1999]), also in larvae, which in Madagascan Syntomini are completely unknown. One of these characters is the fusion of hindwing veins Sc+Rs+M_1 (see Methods). However, the homology of the most proximal veins located along the hindwing costal margin still seems to be unresolved at the level of entire superfamily Noctuoidea (see Zahiri et al. 2012).

The scheme of hindwing venation used by Griveaud (1964) most probably is an implementation of the system used by Hampson (1898). However, Griveaud (1964) assumes the complete loss of the vein "8", i.e., Sc+R, and the veins "6" and "7" as fused Rs+M1, which conflicts with Jacobson and Weller (2002) (see Methods). The presence of an additional, small cell in the basal portion of DC, reported by us, supports the hypothesis that the front margin of DC is composed of the fusion of two veins, thus presumably Sc+R and Rs+M1. A similar structure, interpreted as an effect of fusion of veins and sometimes referred to as the precostal cell (Dupont et al. 2016), has been reported in other groups of moths such as Metarbelidae, Notodontidae, Drepanidae (Holloway 1986) or Lasiocampidae, where its presence was indicated as a diagnostic character of the genus *Haplopacha* (Dupont et al. 2016). However, according to our best knowledge, until now it has never been reported from Syntomini, nor from Arctiinae in general.

Furthermore, the interpretation of the hindwing anal veins in the general venation scheme figured by Griveaud (1964: Figs 2-4 and Fig. 9) is also unclear. Only in the genus *Euchromia* (currently in Arctiini) two anal veins are marked, indicated as 1a and 1b, thus following Hampson (1898). Considering our findings of the presence of two anal veins, 1A+2A and 3A, in all Madagascan Syntomini (but see *Mauricenaclia minuta*), the loss of the vein 2A (here 3A) indicated by Kitching and Rawlins ([1999]: 391) as one of the synapomorphies of Syntomini, is erroneous. In the Malagasy Region Syntomini lineage, the vein 3A seems to be reduced only in *Dysauxes florida* and *Pseudonaclia puella*, but outside the Malagasy Region retained in *D. famula* (Przybyłowicz et al. 2021). Thus, the issue demands verification in other Madagascan genera of Syntomini, and also in the remaining species of *Dysauxes*. Another apomorphy of Syntomini proposed by Kitching and Rawlins ([1999]: 391) is the loss of the hindwing frenulum in males. However, all species analysed here possess the functional retinaculum-frenulum wing coupling system. Thus, the only members of the Madagascan evolutionary lineage that lost the retinaculum (but never the frenulum) are *Dysauxes florida* and *Pseudonaclia puella*, and this should be considered as a secondary condition (see Przybyłowicz et al. 2021). These findings indicate, how still fragmentarily Syntomini are known in terms of morphology.

Finally concerning venation, as already mentioned, the variation in number of the forewing radial veins also raises questions about their homology. Griveaud (1964) did not comment on that issue, despite the presence of only four radial veins in majority of the genera established by him. Razowski (1971) interprets the presence of four radial veins in *Dysauxes ancilla* as a loss of the vein R4, and that interpretation was adopted in Przybyłowicz et al. (2021). In more recent publications concerning the general morphology of Arctiinae (Kitching and Rawlins [1999], Jacobson and Weller 2002) this issue is not addressed and demands further research. Additionally, we recorded a number of “anomalies” in both fore and hindwing venation: from distinct asymmetry in the form of presence of 3 or 4 radial veins in both forewings of a single individual, bifurcation of R2 or presence of an additional, indistinct 6th radial vein among R2-R4, to slight bifurcations in the terminal portion of the hindwing Sc+Rs+M_1 (Figs.). A significant variation in radial vein arrangement was reported also in the

Mauritian endemic *D. florida* and tentatively interpreted as a potential result of environmental stress, since such interpretation of this kind of variation has been proposed for *D. ancilla* (Betzholtz 2000). In any case, it seems that wing venation can be a relatively plastic character, demanding further research on its principles (see Przybyłowicz et al. 2021, and papers cited therein).

The pattern terminology for the forewing blotches used by us refers to the system proposed by Gawne and Nijhout (2020). However, that paper is based only on the analyses of species belonging to Arctiini, but it seems to be generally compatible with Syntomini as well, filling a significant knowledge gap, since the general groundplan have been so far elaborated e.g. for butterflies in general (Mazo-Vargas et al. 2022), for Zygaenidae (Nijhout [1999]) or Micropterigidae (Schachat and Brown 2016). In our opinion, the system proposed here best reflects the different locations and connections of spots in different species of Madagascan Syntomini, but especially the homology of basal forewing blotches requires further studies.

Another important morphological finding in this study is the different modifications of the forewing scales. The suboval blotches of modified scales in the forewing underside of *Mauricenaclia minuta* comb. nov, *M. octopunctata* comb. nov and *M. peyrierasi* comb. nov do not possess any holes or other structures on the scale surfaces, which would allow for pheromone release (Hall and Harvey 2002, Kristensen and Simonsen [1999], Pan et al. 2022). Additionally, their vivid, metallic iridescence suggests rather a visual signalling function, similarly as it was proposed for the transformed scales found in the genus *Haplopacha* of Lasiocampidae (Dupont et al. 2016). To the contrary, the scales of the streak located along the forewing hindmargin of *Privatenaclia seguyi* **comb. nov.** do possess holes on their surface, and the genus is devoid of a foreleg tuft (see above), thus the potential function of these scales may well also be androconial. The most unambiguous in this regard are the scales on the wings of *Melanonaclia nigra*. On the surface of black, enlarged scales in the central portion of hind wing upperside, numerous holes containing crystal-like PTPs were found. The scales of the basomedial portion of the forewing underside resemble in their shape and structure those forming the foreleg tuft. Thus, it can be hypothesised that these two types of scales together create an androconium, and are engaged in some kind of "contact behaviour", in Lepidoptera known e.g. in Danaidae (see Kristensen and Simonsen [1999]), during which the forewing underside scales take over and distribute the pheromones secreted from the hindwing upperside scales. Additionally, suboval fields of differently coloured scales are present also in the hindwing upperside of *Tritonaclia melania* and *T. tollini* (Keferstein, 1870), but their function still needs to be examined.

In this context, the ribbon-like shape of the scales forming the foreleg tuft in *Melanonaclia nigra* can be hypothesised to represent a secondary modification, resulting from the loss of their original function. Further, this potentially fits into some evolutionary trend present in the genus *Melanonaclia*, since *M. toulgoeti* also has ribbon like scales in the foreleg tuft, and *M. lugens* is completely devoid of that structure, but possesses a stripe of intensively yellow, modified scales along the forewing hind margin, which can potentially consist of scent scales.

Turning to female characters, in the abdomen, we find the 8th tergite to be reduced in size and integrated with the genitalia, whilst the 7th tergite is enlarged and provided with a transverse groove. This character is also worth analysing in other lineages of Syntomini and Arctiinae more widely, since generally the arrangement of the 8th tergite in female lepidopterans is variable and was already discussed (Kristensen [1999]).

The female genitalia also comprise a very important morphological character, namely the pheromone glands. The presence of the dorsal pheromone glands is one of the most unambiguous apomorphies of Arctiinae (Kitching and Rawlins [1999]: 389), and the ventral pheromone glands are specifically characteristic of Syntomini (cit). Thus, the lack of the latter structure in the genera *Mauricenaclia* **gen. nov.**, *Melanonaclia* and *Mortinaclia* **gen. nov.** should be considered as a secondary loss. The ventral pheromone glands fused into a single lobe are characteristic to the genera *Balacra*, *Melisa* and *Automolis* (Bendib and Minet 1998) of the former Thyretiina (Thyretini *sensu* Przybyłowicz 2009), which belong to the basal clade of Syntomini (Przybyłowicz et al. 2019). Two separate ventral pheromone glands, similar to those of Madagascan Syntomini, are present in the genus *Thyretes* (Bendib and Minet 1998), indicating close affinities between these two groups, as already indicated by the molecular results, placing the "*Thyretes* + *Pseudothyretes*" clade as sister to the Madagascan lineage of Syntomini (Przybyłowicz et al. 2019, but see the molecular results here).

Overall, the genera covered in our study are well defined both molecularly and morphologically, and the general appearance and certain morphological characters elaborated here are usually uniform within the genera. The most prominent exceptions are present in *Mauricenaclia* and *Melanonaclia* (Tab. 3), but the species belonging to them share the apomorphies of their genera and they form monophyletic clades (Fig. 5A-B).

However, we also observe some incongruences in the intrageneric relationships indicated by the molecular results, and those suggested by the general morphology, especially the most diverse genera *Melanonaclia* and *Mauricenaclia* **gen. nov.** For example, based solely on the female genitalia, *Melanonaclia nigra* (Fig. 104) and *M. toulgoeti* (Fig. 105) seem to be sister species, which could be supported by the ribbon-like shape of the scales forming the male foreleg tuft in these species. However, in the male genitalia, *M. nigra* (Fig. 111) resembles the most *M. lugens* (Fig. 110) rather than *M. toulgoeti* (Fig. 112). Finally, in the phylogenetic tree, *M. toulgoeti* is sister to the superficially different *M. trimacula* **comb. nov.**, and both are sister to *M. nigra* (Fig. 5A). Such incongruences are pervasive in the phylogenetic analyses, and are caused by numerous factors, causing the gene tree to differ from the actual species tree, e.g. the already mentioned ILS (Steenwyk et al. 2023). Future analyses based on a combination of molecular data, including the species missing in our dataset, and morphological characters matrix could help solve the unclear relationships in the genera in question.

Although usually more robust in the terms of the amount of data, molecular results should not be considered as more reliable in a case of incongruence with morphology; however, such an approach used to be implemented (Pisani et al. 2007). Such combined analyses, although bearing their own methodological limitations which can affect the results, usually allow for a reliable and more complex insight into the evolutionary history of a studied group (Keating et al. 2023).

Turning to colour patterning in general, comparing the general appearance of the examined species with their phylogenetic relationships suggests multiple, independent shifts between the black-white and black-yellow body pattern. It can be observed in the genera *Julienaclia* **gen. nov.** (one black-white and one black-yellow species) and *Melanonaclia* (four black-white and three black-yellow species) – in the latter genus, this shift could have appeared more than once, considering the tree topology (Fig. 5A-B, but see above). Additionally, *Mortinaclia perplexa* has the black-white body coloration, superficially resembling the genus *Melanonaclia*, in which it was previously placed. On the one hand, that pattern can result from the similar genetic background of the species belonging to the same evolutionary radiation, but on the other hand, some selective pressure can be present.

The black-white coloured species mentioned above occur generally only in the northern Madagascar, whilst the black-yellow ones are present in the central and southern part of the island (but not necessarily sympatrically). Additionally, the dark morphotype of *Kowalskinaclia cowani* **comb. nov.** (devoid of the forewing pattern) closely resembles other syntomine species from the genus *Micronaclia* and *Maculonaclia nigrita*, which occur in the same area. This may suggest presence of some mimicry rings within Madagascan Syntomini, since in lepidopterans with wings

(semi-)transparency the mimicry based on similar colouration was shown to be more important in co-mimicry than similar morphology (Corral-Lopez et al. 2021).

In Madagascan Syntomini the semi-transparency of wing blotches seems to be widespread, as among genera covered here only *Skippernaclia* **gen. nov.** is completely devoid of wings semi-transparency. However, as discussed above, there is no data on the potential accumulation of toxic or unpalatable substances by Madagascan Syntomini in their bodies. Thus, it is unknown if the potential mimicry would be Müllerian or Batesian in nature, and the issue requires further studies, as well as potentially involving other lepidopterans and even non-lepidopteran insects in that mimicry.

The immature stages of Madagascan Syntomini so far were completely unknown, except for the egg of *Maculonaclia* sp. illustrated in Przybyłowicz et al. (2021). Here we describe eggs of four species, belonging to three genera: *Kowalskinaclia vieui* **comb. nov.**, *Privatenaclia seguyi* **comb. nov.**, *Mauricenaclia minuta* **comb. nov.**, and *M. octopunctata* **comb. nov.** Despite the scarcity of materials, clear morphological differences among the eggs of different species can be observed e.g. in the extent of the egg surface sculpture (reduced in *P. seguyi* **comb. nov.**), and the aeropyle morphology (in *K. vieui* **comb. nov.** provided with distinct rings, absent in *Mauricenaclia* **gen. nov.** species). Additionally, the egg of *Dysauxes florida* from Mauritius was described and illustrated in Przybyłowicz et al. (2021). Interestingly, the egg surface of that species resembles the egg of *K. vieui* **comb. nov.**, rather than the closely related *Mauricenaclia* **gen. nov.** These results indicate the differences between genera or larger clades of Madagascan Syntomini, which needs to be further explored.

The remaining immature stages, i.e. larvae and pupae, astonishingly given the diversity and ubiquity of the group in native forests, remain unknown from the wild.

Indeed, the biology of Madagascan Syntomini has remained largely unknown, except for some general insights provided in Przybyłowicz et al. (2021) and Wiorek et al. (2021).

The biology of Palaearctic Syntomini species from the genera *Amata* and *Dysauxes* is well studied (e.g. Rammert 1987, Betzholtz 2002), including the elaboration of chemical bait lure for *Amata phegea* (Szanyi et al. 2022). However, the most diverse, tropical species of Syntomini are generally either unknown, or known only fragmentarily (Przybyłowicz 2009, Paśnik et al. 2023), with only single species being well elaborated in this regard (de Freina et al. 2020). In our study, we find most of the species to be associated with humid, evergreen forests of eastern Madagascar, which is congruent with the results by Lees et al. (1999).

All the species covered in the paper have well developed proboscis, but there are only a few observations or records of nectaring on exact plant species, discussed above. The larval food resources of Madagascan Syntomini are completely unknown. However, at least for the genus *Mauricenaclia* **gen. nov.**, we can hypothesise the larval ecology to be similar to that of the closely related genus *Dysauxes* and *Pseudonaclia puella*. Females of *D. ancilla* lay eggs randomly, without attaching them to any surface. The larvae demand a well developed layer of decaying oak leaves, which are one of their food substrates as well; however, certain species of herbaceous plants are necessary for their full development, of which the most important is *Pilosella officinarum* (= *Hieracium pilosella* in Betzholtz 2003a, b). In the case of *P. puella*, females lay eggs deep in the layer of leaf litter, and the larvae feed on decaying matter (Staude et al. 2023). In general, the larval diet consisting of algae, lichens, decaying matter etc. is well known in Syntomini (Kitching and Rawlins [1999]: 392, see also Przybyłowicz et al. 2021 for comments on *D. florida*).

The number of spermatophores or colla remnants recorded in corpus bursae of dissected females varied from one to around eight, and this indicates the presence of polyandry in Madagascan Syntomini, since a male is able to produce only a single spermatophore at a time. The collum of a spermatophore is not digested afterwards, thus the number of complete spermatophores and / or colla in the corpus bursae is a good indicator of the number of matings in the female (Mann 1984). Multiple matings involve different natural selection mechanisms and phenomena of evolutionary importance, such as sperm competition or sperm selection by the female (Blanco et al. 2009, LaMunyon and Eisner 1994). In *Utetheisa ornatrix* tiger moths (Arctiini) it has been shown that the female selects the sperm from the larger spermatophore, irrespective of body mass of the males it mated with (LaMunyon and Eisner 1994). In Syntomini, the males and females of *D. ancilla* were observed in the experimental conditions to be capable of multiple matings as well, and also in the field some females were observed to mate more than once (Betzholtz 2002).

Madagascan Syntomini seem to be generally rarely attracted to light, both UV and visible. Among the focal group of genera only *Kowalskinaclia dilata* **comb. nov.** is known to be an exception, coming to light in longer series of individuals (Wiorek et al. 2021). In our study we now record that behaviour in nine species, and it seems to be partly genus-specific, since present in *Riconaclia bimacula* **comb. nov.**, all three species of *Kowalskinaclia* **gen. nov.** and four out of seven *Melanonaclia* species.

The phenology and voltinism of the analysed species is difficult to assess based on the available data, since many records result from occasional, relatively short research trips ("missions") to certain parts of the island, conducted e.g. to different mountain massifs by Pierre Soga (Lacroix and Viette 1998). In general, Hilt et al. (2007) indicated no significant seasonality of species richness in Neotropical Arctiinae, but Maicher et al. (2018) obtained contradictory results from Mount Cameroon, i.e. in the Afrotropics. However, none of these studies was focused on Syntomini (absent in the Neotropics).

The environmental conditions during the year in humid, evergreen forests in the east of Madagascar can be – rather counterintuitively – highly unpredictable, causing also unpredictable fruiting and flowering, which leads to the development of different life histories in different groups of animals (Dewar and Richard 2007). Considering that the larvae of Madagascan Syntomini potentially can feed on decaying matter and non-vascular plants, it can be hypothesised that for their life success crucial are abiotic conditions, e.g. the optimal level of litter humidity. On the contrary, the success of adult Syntomini can depend on i.a. the availability of certain nectaring plants.

More distinct seasonality could be expected in those species inhabiting deciduous, seasonally dry forests of western Madagascar, with a more pronounced dry season lasting from around April to October-November, followed by a rainy season in the remaining months (Goodman et al. 2018). Indeed, *Julienaclia pauliani* **comb. nov.** and *Mauricenaclia raharizonina* **comb. nov.**, the two species predominantly connected with the dry habitats of western Madagascar, were collected in the months of the rainy season only. However, a strong sampling bias of collectors in the rainy season, when obtaining a larger diversity of specimens is possible overall, suggests that a phenologically stratified approach may be required.

The species covered in our study were collected or recorded from 191 localities across the entire island of Madagascar. The most explored places, i.e. the areas with the highest density of collecting localities, are in the east of Madagascar. These are (from N to S): Marojejy massif, Antongil Bay, the regions of Andasibe and Analamazoatra, and Ranomafana. In general, the best explored areas in the north and east of Madagascar are located within large national parks and other protected areas, whilst in the other parts of the islands the collecting localities are usually close to the main roads, e.g. in southwestern Madagascar along RN 7 between Sakaraha and Toliara (Tuléar) - see the distribution of *Mauricenaclia raharizonina* **comb. nov.**, *M. rothschildi* **comb. nov.** and *M. octopunctata* **comb. nov.** These sampling patterns observed in our data, as well as the distribution of sampling points, are congruent with the results of Iannella et al. (2019), based on the records from GBIF. This means that in general, Syntomini were recorded in the same places as other Lepidoptera of Madagascar, and the coverage of our study is relatively good (i.e. if any place in Madagascar Lepidoptera were collected, usually Syntomini were collected there too).

In general, as mentioned above, the majority of the species covered in the study occur in the east and central of Madagascar, i.e. along the longitudinal zone of humid, evergreen forests extending in that part of the island (Moat and Smith 2007). Only one genus, *Julienaclia* **gen. nov.** is associated typically with northern and western Madagascar, with a clear allopatric pattern of distribution of its two species (Fig. 71A-B). Among other genera, only *Mauricenaclia raharizonina* **comb. nov.**, *M. rothschildi* **comb. nov.** and *M. octopunctata* **comb. nov.** are distributed mostly in the south and along the west coast of Madagascar. The dry biotopes of Madagascar, although until recently considered a relic of the flora covering most of the island in the Paleogene (Wells 2003), in the light of recent results seem to be much younger, with the ancestors of some plants endemic to the dry biotopes appearing in Madagascar after Eocene, less than 34 mya (Ohba et al. 2016). The origin of the tropical rainforests in Madagascar has been dated for around 36 mya (Federman et al. 2015), thus around 10 million years before Syntomini evolved (Wahlberg et al. 2013). The highest diversity of Syntomini in the "eastern" forests of Madagascar may suggest this part of the island to be their centre of diversification, from which they may have dispersed westwards. However, the zoogeography of Madagascan Syntomini requires further research, in the context of the entire group.

The highest diversity of species (eight) is recorded from Marojejy, including two endemics of that locality: *Privatenaclia seguyi* **comb. nov.** and *P. triangulifera* **comb. nov.** Additionally, in our study we found four further species to be endemic to certain areas: *Skippernaclia vestigii* **comb. nov.** to Ambohitantely, *S. leesi* **sp. nov.** to Masoala, *Privatenaclia ratovosoni* **comb. nov.** to the Moramanga region, and *Melanonaclia ranomafana* **sp. nov.** to PN Ranomafana. Madagascar is well known for the local endemism patterns in the distribution of different groups, from which the best studied are perhaps lemurs and chameleons (Wilmé et al. 2006, Pearson and Raxworthy 2009) and in invertebrates an important example is the radiation of dung beetles (Knopp et al. 2011, Miraldo et al. 2011). Numerous mechanisms have been proposed to explain the diversity of distributional patterns observed in Madagascar (Vences et al. 2009), but they have been explored basically only in terrestrial vertebrates (Pearson and Raxworthy 2009). The processes that have shaped the distribution of Madagascan Syntomini still need to be elaborated. Recently, we identified RS Ambohitantely as a centre of local endemism of Syntomini in the Central Highlands of Madagascar (Wiorek et al. 2021), with eight recorded species (and five endemics), of which those occurring only there included *Skippernaclia vestigii* **comb. nov.** and *Kowalskinaclia dilata* **comb. nov.** However, here we find the latter species to occur also in PN Andasibe. This corresponds well with the hypothesis presented by Rakotondravony and Goodman (1998), that the forests of Ambohitantely and Anjozorobe (the latter located approximately halfway between Ambohitantely and Andasibe) might have been connected up to very recently, already in historical times. Further research involving population genetics would be needed in this case, considering the rather low dispersal ability of *K. dilata* **comb. nov.** through open habitats, inferred by us (Wiorek et al. 2021). It is the more interesting, that the contradictory results by Linares et al. (2009) showed the genus *Heteropsis* spp. (Satyrinae) in Ambohitantely to develop significant differences in COI sequence compared to other populations, suggesting rather a potential longlasting isolation.

Deforestation is one of the main threats to the preservation of the biodiversity of Madagascar, but also an important socio-economic problem (e.g. Vieilledent et al. 2020). In total, 80% of natural areas of Madagascar has been lost so far, including a 25% decrease of tree cover from 2000 only (Suzzi-Simmons 2023). For the majority of the species covered in our study, their ranges at least partly overlap the remaining large patches of already protected forest. Currently, the most threatened species seems to be *Privatenaclia ratovosoni* **comb. nov.**, occurring in the Moramanga region, which has been tremendously deforested in the last few decades (LOFM 2022). This is the more significant, in that all species of *Privatenaclia* **gen. nov.** are locally distributed endemics. Further, the most neglected and the least protected habitats in Madagascar are the western dry forests (Waeber et al. 2015). Here we report four Syntomini species to be associated with these dry biotopes. They occur e.g. in the area northeast of Toliara, which indeed is already almost completely devoid of natural vegetation (LOFM 2022). Moreover, deforestation threatens also the maintenance of genetic diversity of broadly distributed and thus – seemingly – directly less endangered species. For example, the area of occurrence of the southern population of *Kowalskinaclia vieui* **comb. nov.**, possibly constituting a separate cryptic species, is already deforested, and this genetic lineage can be irreversibly lost, considering the mentioned potential low abilities of the closely related *K. dilata* **comb. nov.** to thrive in open habitats.

Our results indicate that Madagascan Syntomini are a suitable system for further research on different aspects of evolutionary processes shaping the biodiversity of Madagascar. However, the group first demands a multifaceted research program, including systematic revision, to which this paper contributes.

CONCLUSION

The Madagascan Syntomini genera *Thyrosticta* and *Melanonaclia* are here elaborated molecularly and morphologically. They prove to be polyphyletic in the arrangement proposed by Griveaud (1964). Their species constitute nine distinct evolutionary lineages, of which seven are here established as new genera. Morphological analyses here facilitated identification of apomorphies for these genera, as well as providing a general elaboration of the morphology of the group, with identification of genus-specific characters neglected in the previous works. Immature stages remain unknown, except for the eggs of four species described here for the first time.

Results of our phylogenetic inferences, including species delimitation analyses, reveal presence of a few potential cryptic species complexes, but their elaboration of species level identities demands further research.

The already elaborated species are distributed across the entire island, with the majority of them being associated with humid, evergreen forests of eastern Madagascar (or nearby islands) at different elevations, and only a few occur in the dry habitats of southern and western Madagascar. Except for this general information on preferred biomes/habitats, knowledge of the biology of species in the radiation remains highly rudimentary. We gathered observations of nectaring in five species with indications of preference for Rubiaceae. The number of spermatophores or their remnants found in the dissected females indicates the presence of polyandry in Madagascan Syntomini. Some species are attracted to light, and this behaviour seems to be partly genus-specific. The biology of at least the species from *Mauricenaclia* **gen. nov.** can, however, be hypothesised to be similar to closely related *Pseudonaclia puella* and *Dysauxes* species. The chemical basis of possible aposematism remains unknown.

The majority of the species seem not to be directly endangered, but some of them are restricted to relatively small areas of occurrence, which have faced intensive deforestation in the last decades.

Further research including other genera of Madagascan Syntomini is necessary to elaborate the possible true diversity of the group in a comprehensive way.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY

Sequences obtained in this study are available in GenBank; sample codes and accession numbers of all used sequences are in Table S2. Label data from all specimens are in Table S1, and the coordinates of collecting localities – in Table S3. The details of phylogenetic and species delimitation analyses methods and results are in File S1, and Figures S1-S7.

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FIGURES

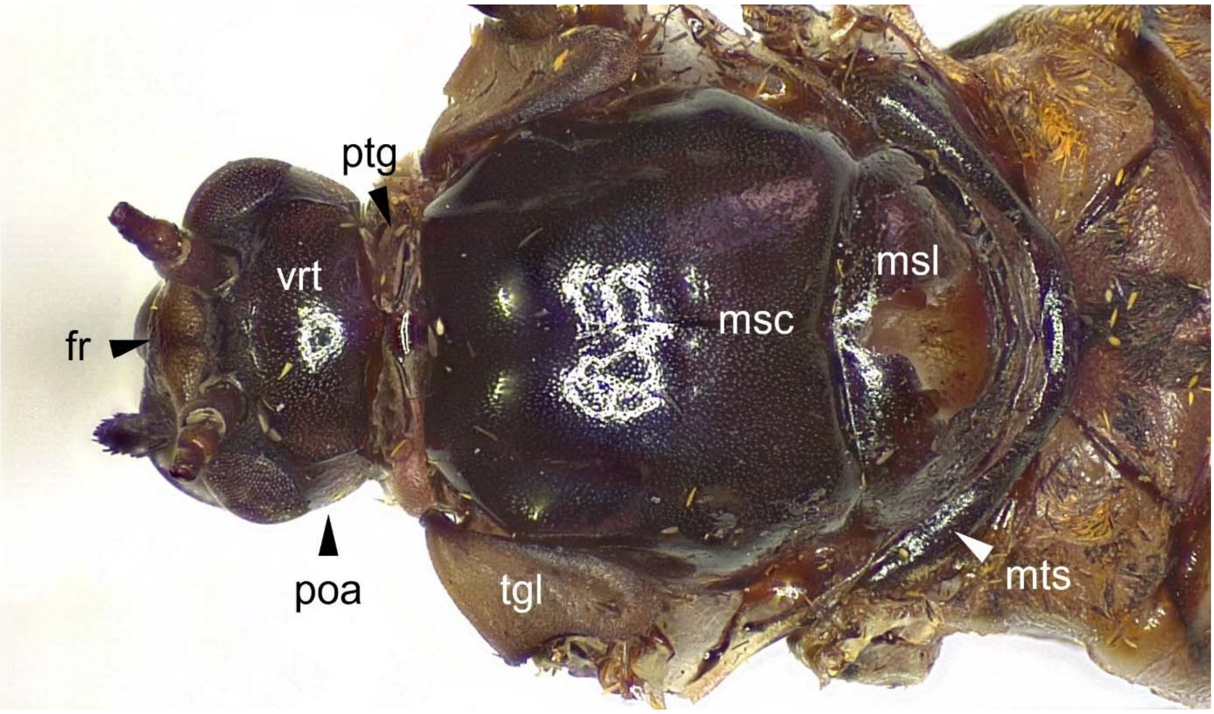


Figure 1. Head and thorax of Madagascan Syntomini: fr - frons, vrt - vertex, poa - postocular area, ptg - patagium, tgl - tegulum, msc - mesoscutum of mesothorax, msl - mesoscutellum of mesothorax, mts - metascutum of metathorax.

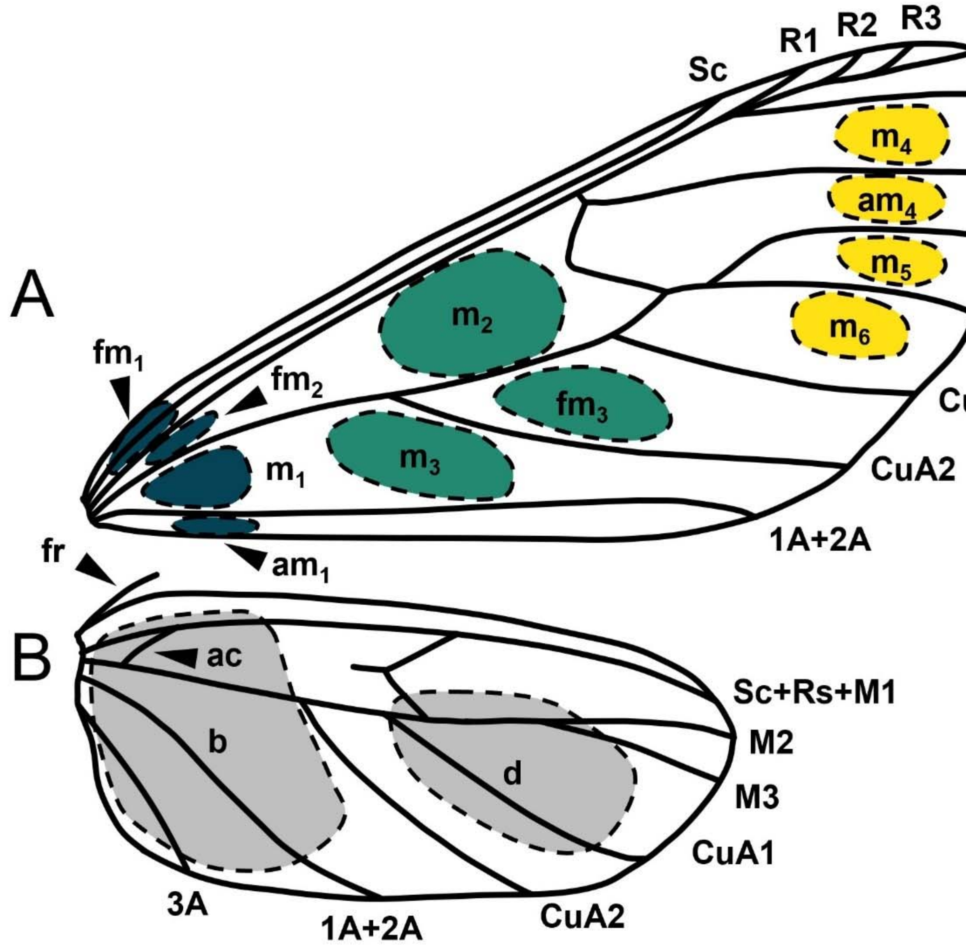


Figure 2. Wings venation and pattern of Madagascan Syntomini. A – forewing: Sc - subcostal vein, R1-R5 - radial veins, M1-M3 - medial veins, CuA1-CuA2 - cubital veins, 1A+2A - anal veins; fm$_1$ - first basal blotch, fm$_2$ - second basal blotch, m$_1$ - third basal blotch, am$_1$ - fourth basal blotch, m$_2$ - first medial blotch, fm$_3$ - second medial blotch, m$_3$ - third medial blotch, m$_4$ - first distal blotch, am$_4$ - second distal blotch, m$_2$ - third distal blotch, m$_6$ - fourth distal blotch; B – hindwing: Sc+Rs+M1 - fused subcostal, M2-M3 - medial veins, CuA1-CuA2 - cubital veins, 1A+2A, 3A - anal veins, ac - additional cell, fr - frenulum, b - basal blotch, d - distal blotch.

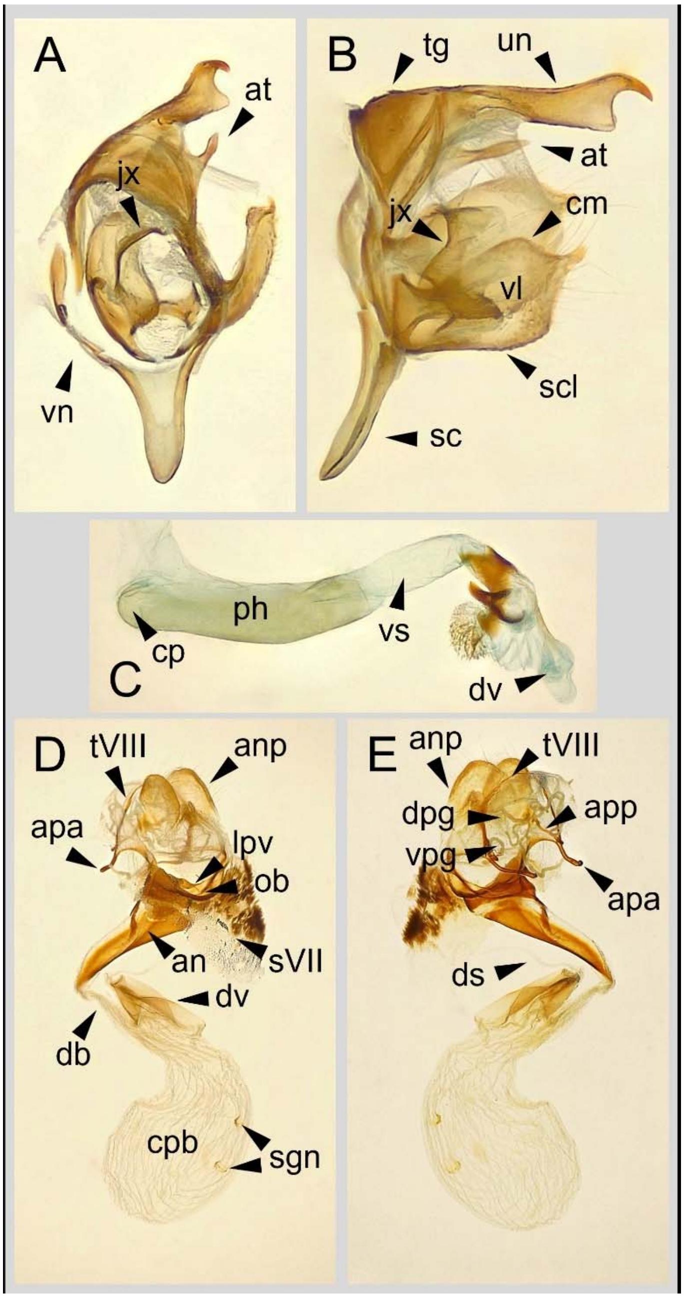


Figure 3. Genitalia of Madagascan Syntomini. A – male genitalia anterior side; B – male genitalia lateral side: un - uncus, tg - tegumen, at - sublateral, additional arms of tegumen, vn - vinculum, sc - saccus, jx - juxta, vl - valva, cm - costal margin of valva, scl - sacculus of valva; C – phallus with everted vesica: ph - phallus, cp - coecum penis, vs - vesica, dv - diverticulum; D – female genitalia ventral side; E – female genitalia dorsal side: anp - anal papilla, app - apophysis posterioris, apa - apophysis anterioris, dpg - dorsal pheromone glands, vpg - ventral pheromone glands, tVIII - 8th tergite, sVII - 7th sternite, lpv - lamella postvaginalis, ob - ostium bursae, an - antrum, db - ductus bursae, dv - diverticulum, cpb - corpus bursae, sgn - signa, ds - ductus seminalis.

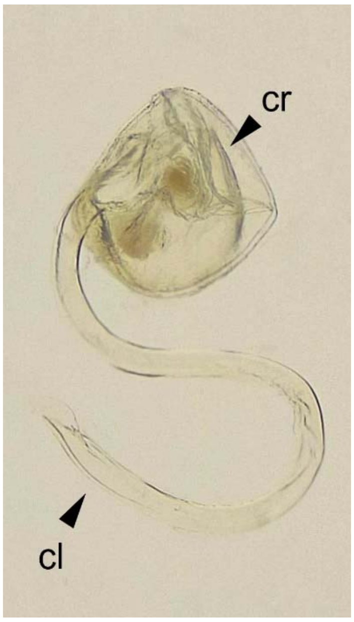


Figure 4. Spermatophore of *Skippernaclia ankaratra* **comb. nov.**: cr - corpus, cl - collum.

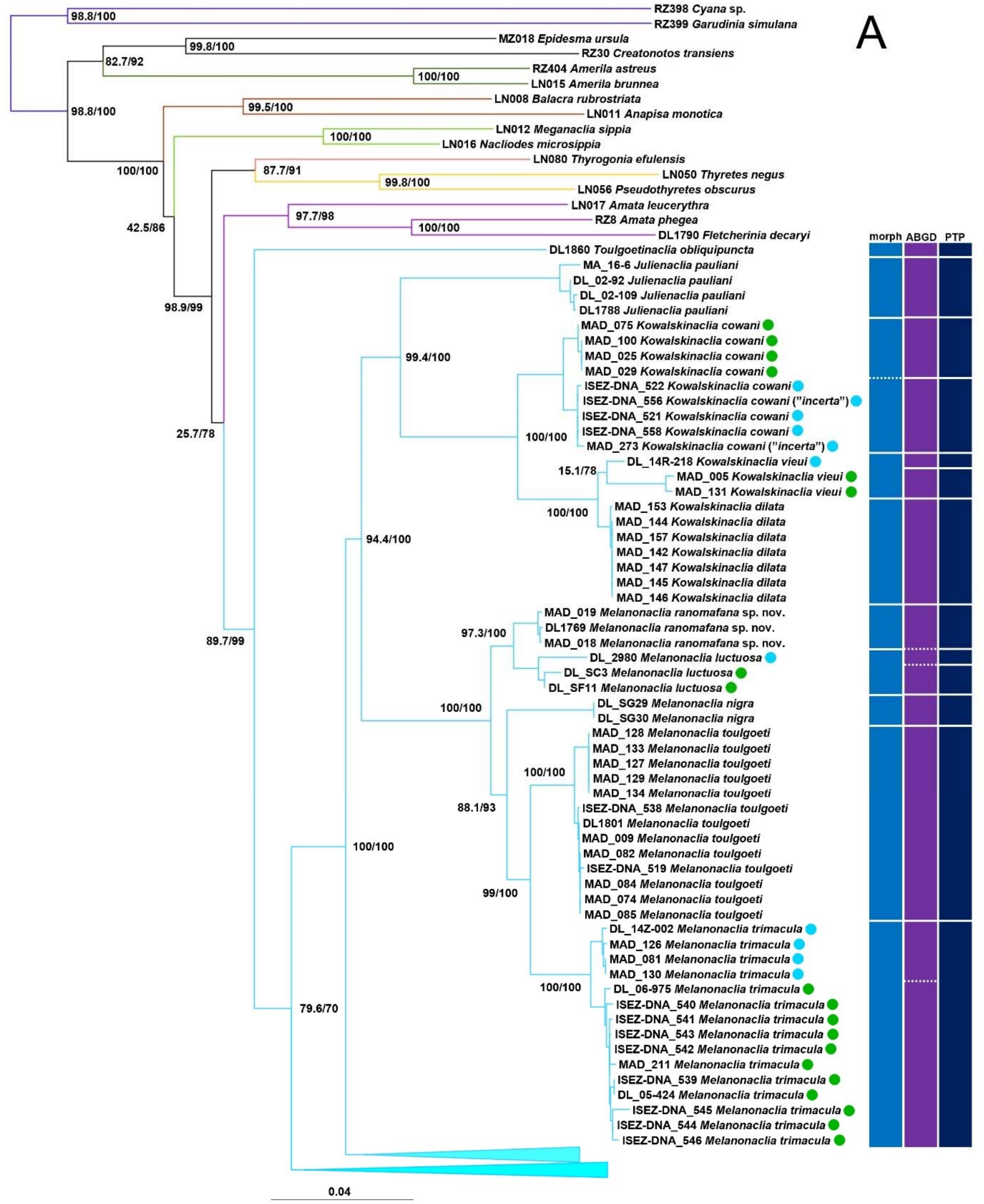


Figure 5A. (see caption below)

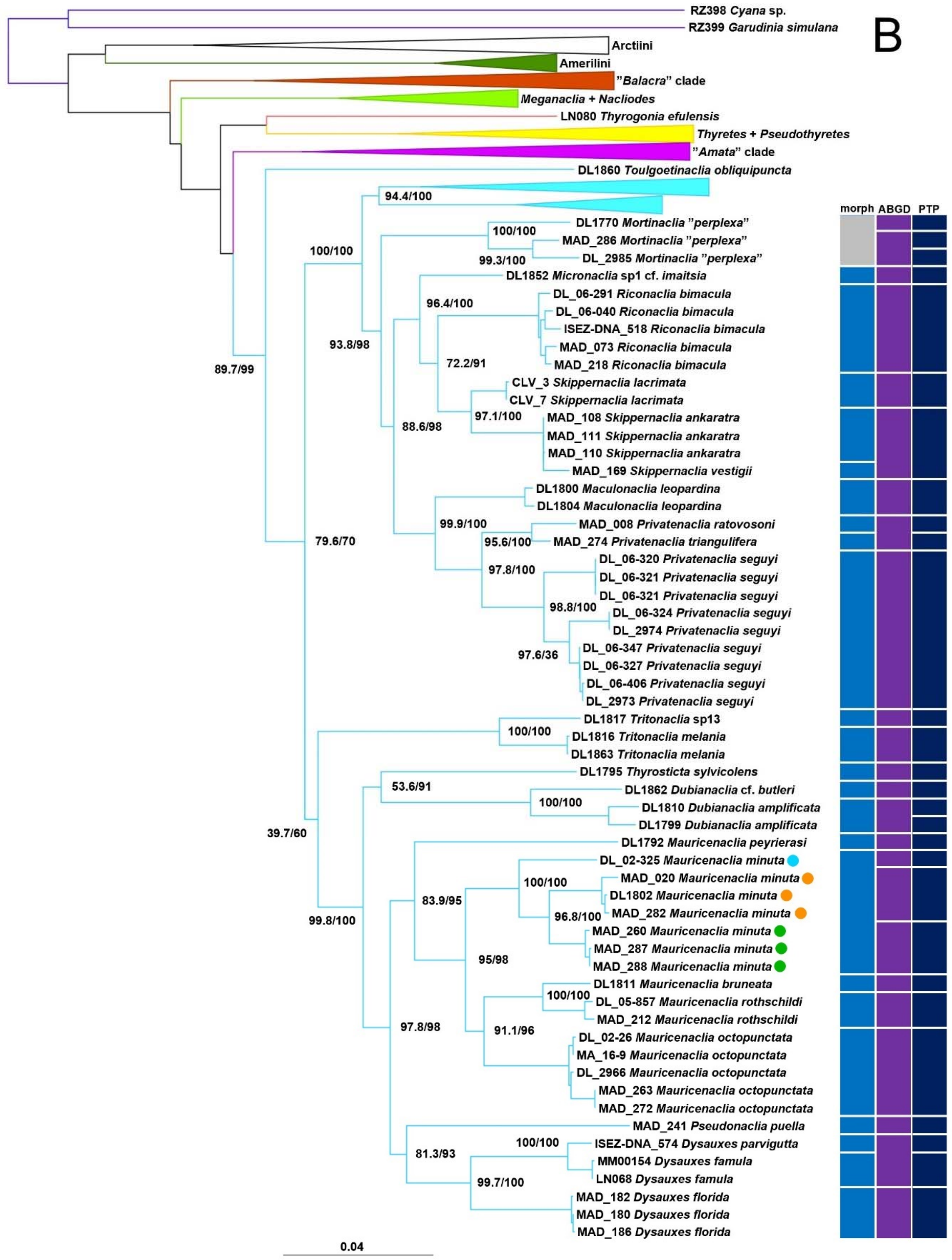


Figure 5A-B. Phylogenetic relationship of the taxa covered by the study, within the former genera *Thyrosticta* and *Melanonaclia* (*sensu* Griveaud 1964), based on ML analysis of all 8 markers dataset in IQ-TREE. Numbers at nodes represent SH-like/Ultrafast Bootstrap values. Colours of clades correspond with the trees in Przybyłowicz et al. (2019, 2021). Dots at sample names correspond with the illustrations of specimens and genitalia, and distributional maps of relevant, cryptic species complexes. The bar on the right shows the results of different species delimitation approaches: morph - based on morphological analyses, including genitalia, ABGD - Automatic Barcode Gap Discovery based on the barcode region of COI gene, PTP - Poisson Tree Processes, also based on the barcode region; dashed line indicates ambiguities in the delimitation results, grey colouration of the bar indicates insufficient data, see text.

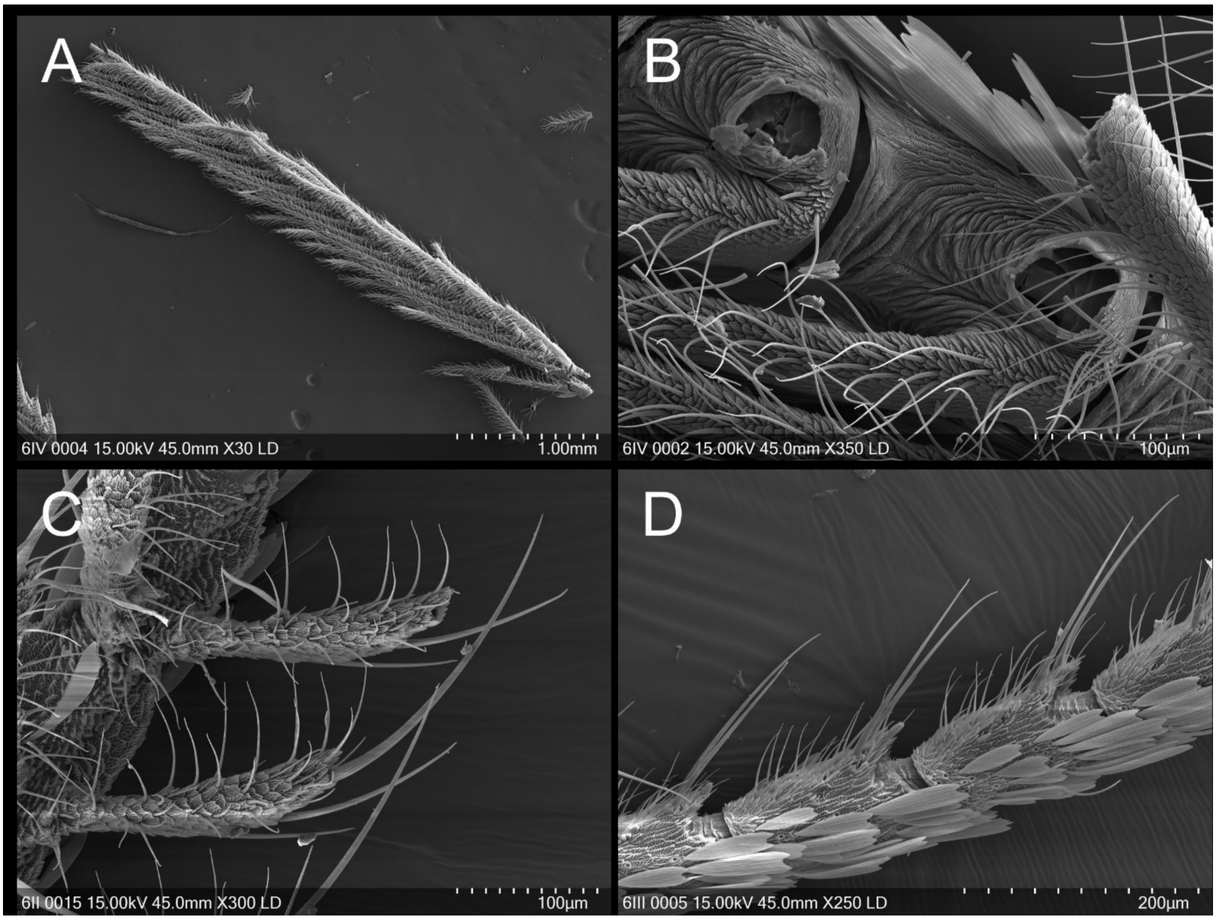


Figure 6. SEM pictures of the antennae of *Thyrosticta* and *Kowalskinaclia* **gen. nov.**:
A-B *T. sylvicolens* male; C – *K. dilata* **comb. nov.** male; D – *K. cowani* **comb. nov.** female.

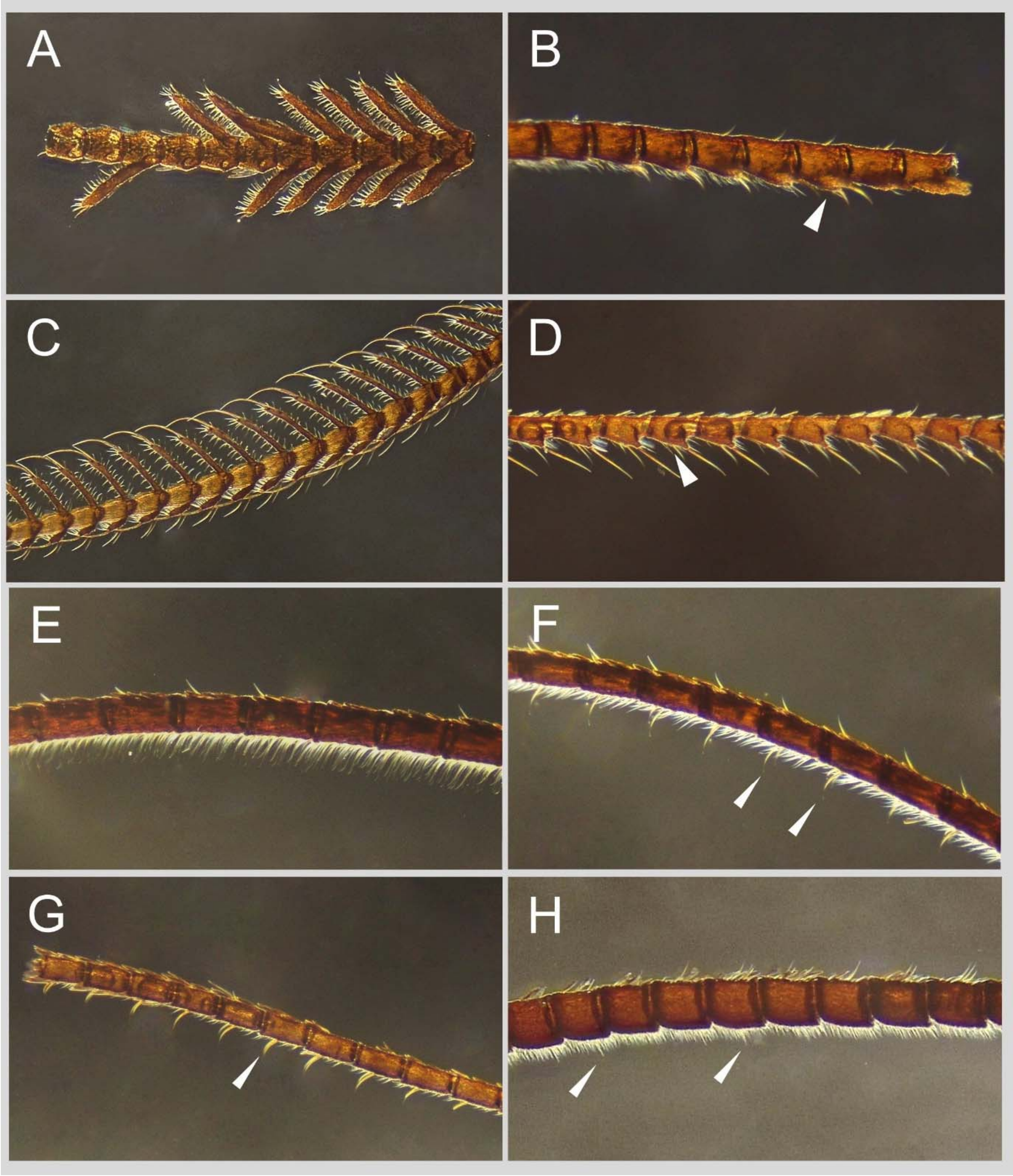


Figure 7. Morphology and sexual dimorphism of antennae of *Julienaclia* **gen. nov.**, *Kowalskinaclia* **gen. nov.**, *Melanonaclia*, *Skippernaclia* **gen. nov.**, and *Privatenaclia* **gen. nov.**: A – *J. pauliani* **comb. nov.** male; B - *J. pauliani* **comb. nov.** female; C – *K. dilata* **comb. nov.** male; D – *K. vieui* **comb. nov.** female; E – *M. trimacula* **comb. nov.** male; F – *M. trimacula* **comb. nov.** female; G – *S. lacrimata* **comb. nov.** female; H – *P. seguyi* **comb. nov.** male.

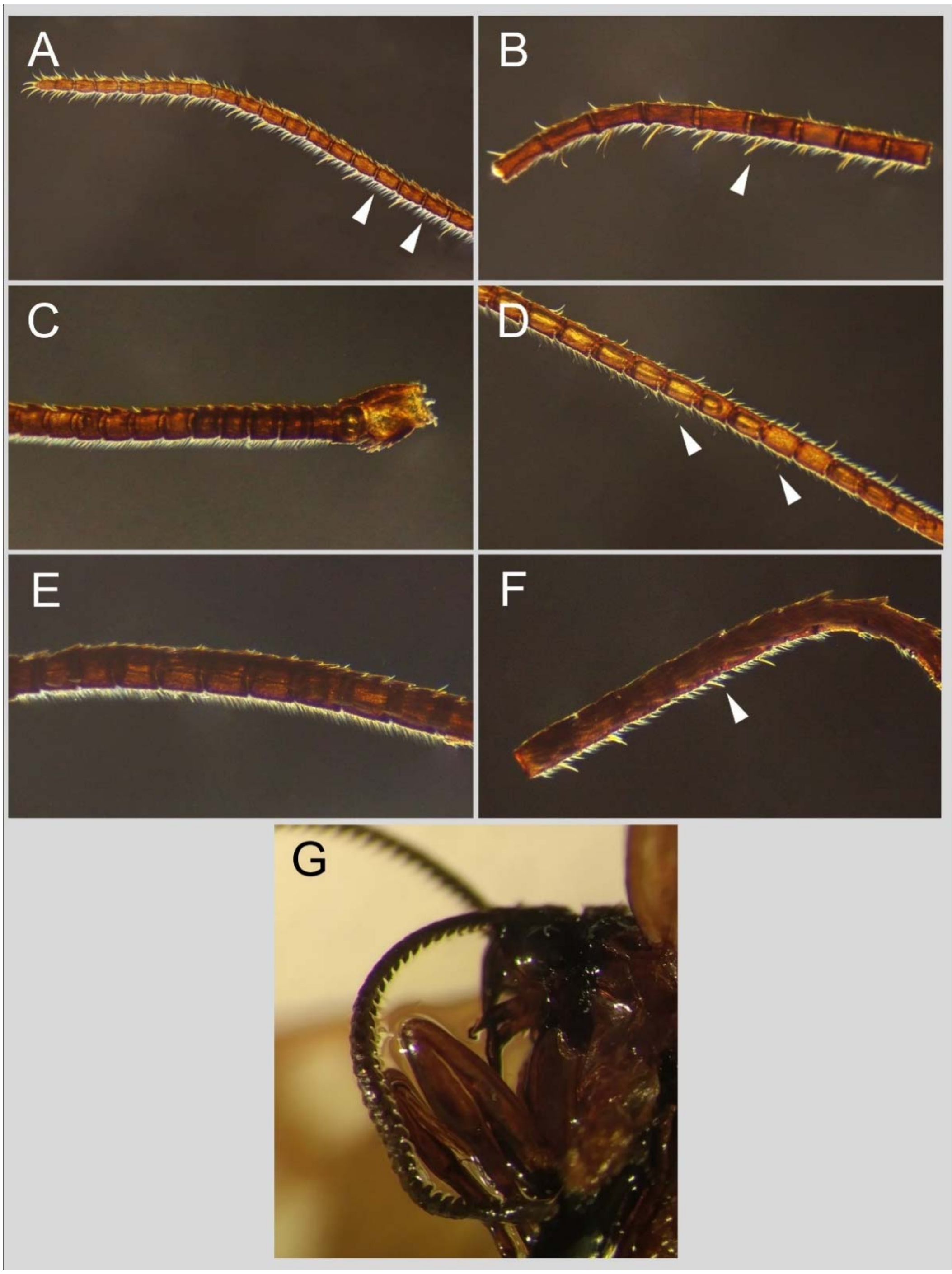


Figure 8. Morphology and sexual dimorphism of antennae of *Riconaclia* **gen. nov.**, *Mauricenaclia* **gen. nov.**, and *Mortinaclia* **gen. nov.**: A – *R. bimacula* **comb. nov.** male; B – *R. bimacula* **comb. nov.** female; C – *Mauricenaclia minuta* **comb. nov.** male; D – *Mauricenaclia minuta* **comb. nov.** female; E – *Mortinaclia perplexa* **comb. nov.** male; F – *Mortinaclia perplexa* **comb. nov.** female; G – *Mauricenaclia peyrierasi* **comb. nov.** male (holotype EL65143).

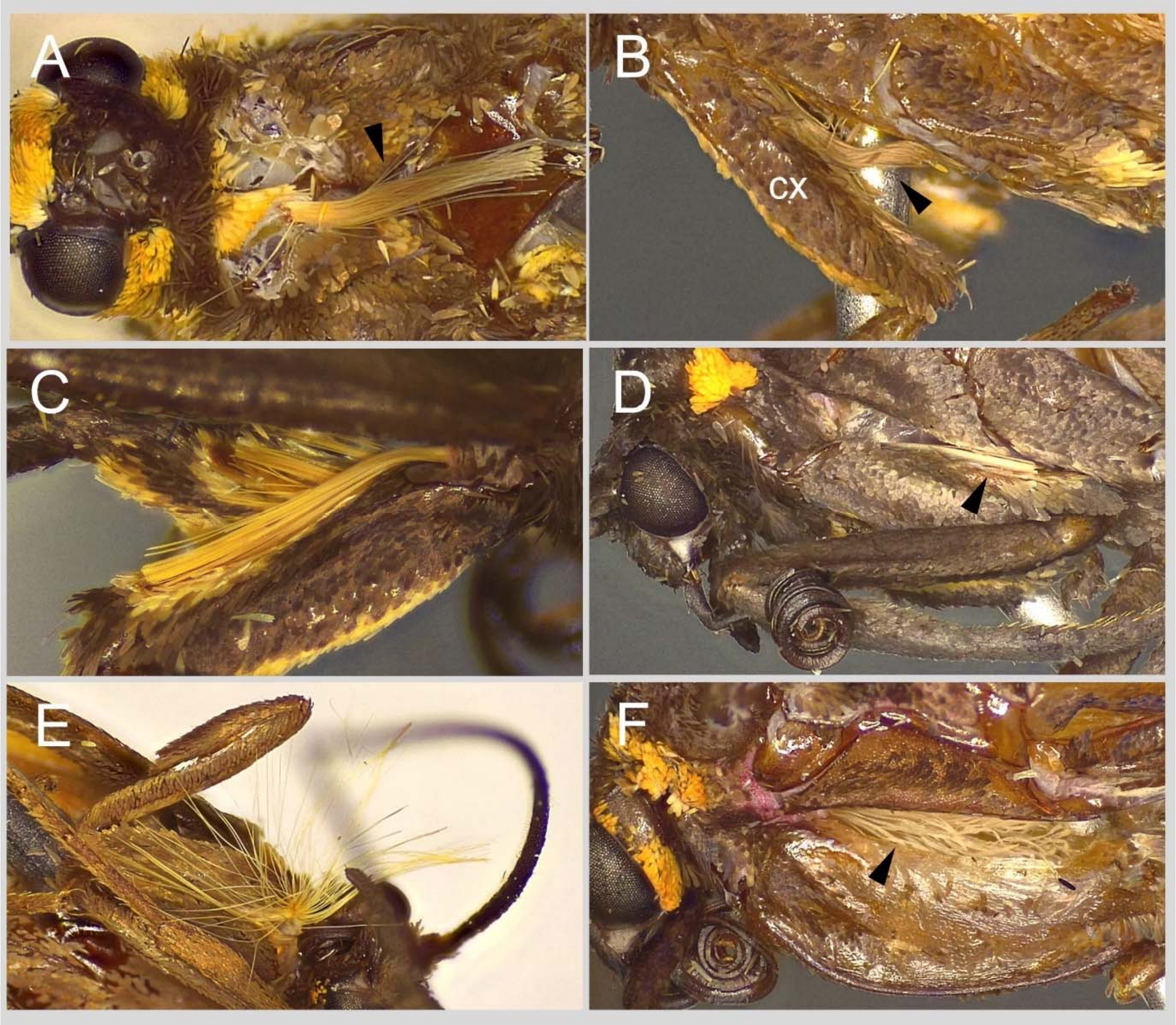


Figure 9. Male foreleg pencil-like scale tuft: A – *Privatenaclia seguyi* **comb. nov.**, both forelegs removed, arrowhead indicates the right tuft; B – *Riconaclia bimacula* **comb. nov.**, black arrowhead indicates the tuft, cx - coxa; C – *Melanonaclia trimacula* **comb. nov.**;
D – *Melanonaclia toulgoeti*, arrowhead indicates the tuft hidden behind the foreleg;
E – outstretched tuft in *Skippernaclia lacrimata* **comb. nov.**; F – *Melanonaclia nigra*, arrowhead indicates the tape-like scales of the tuft (see text).

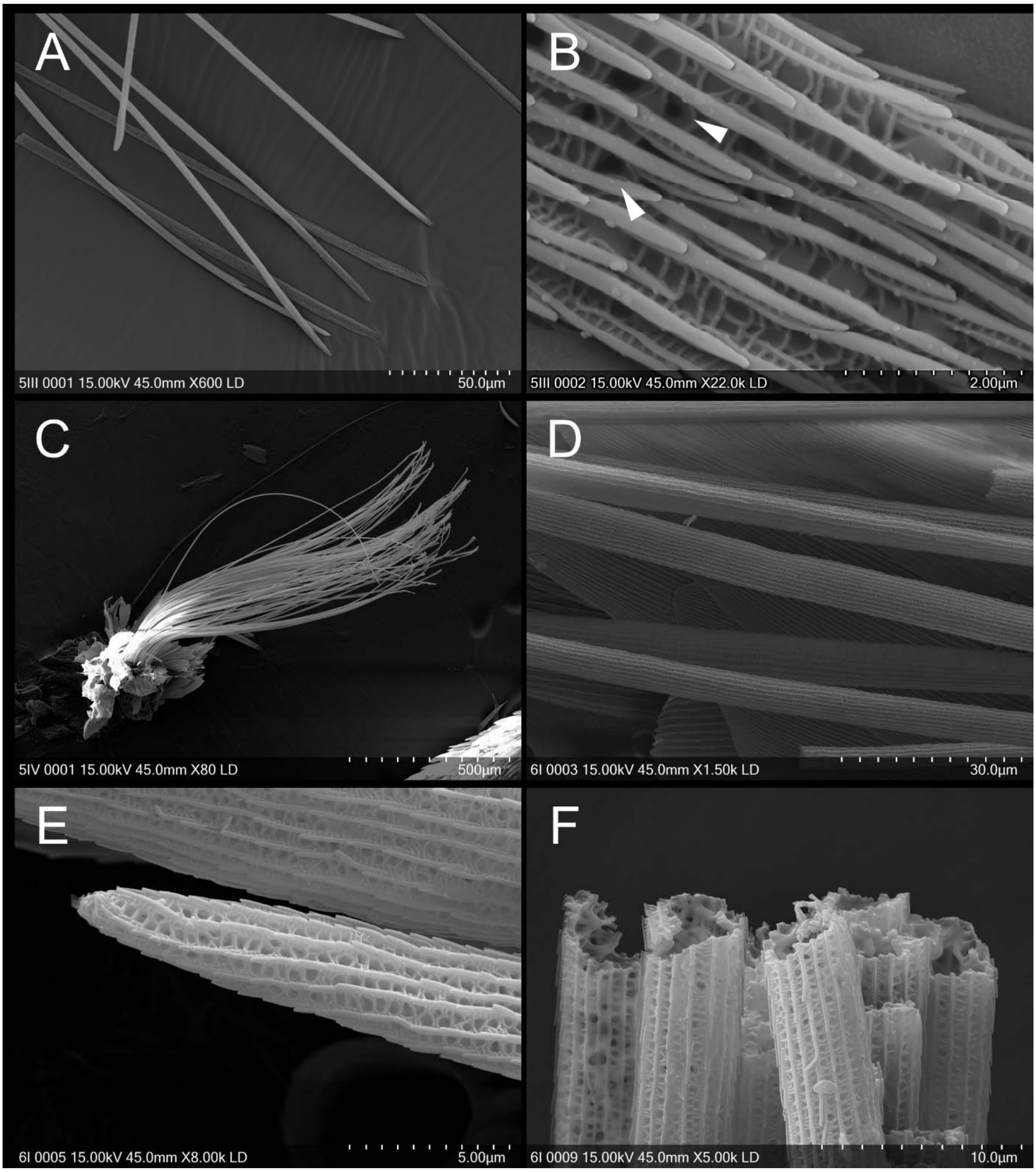


Figure 10. SEM pictures of male foreleg pencil-like scales tuft: A-B – *Skippernaclia lacrimata* **comb. nov.**; C – *Privatenaclia seguyi* **comb. nov.**; D-F – *Riconaclia bimacula* **comb. nov.**

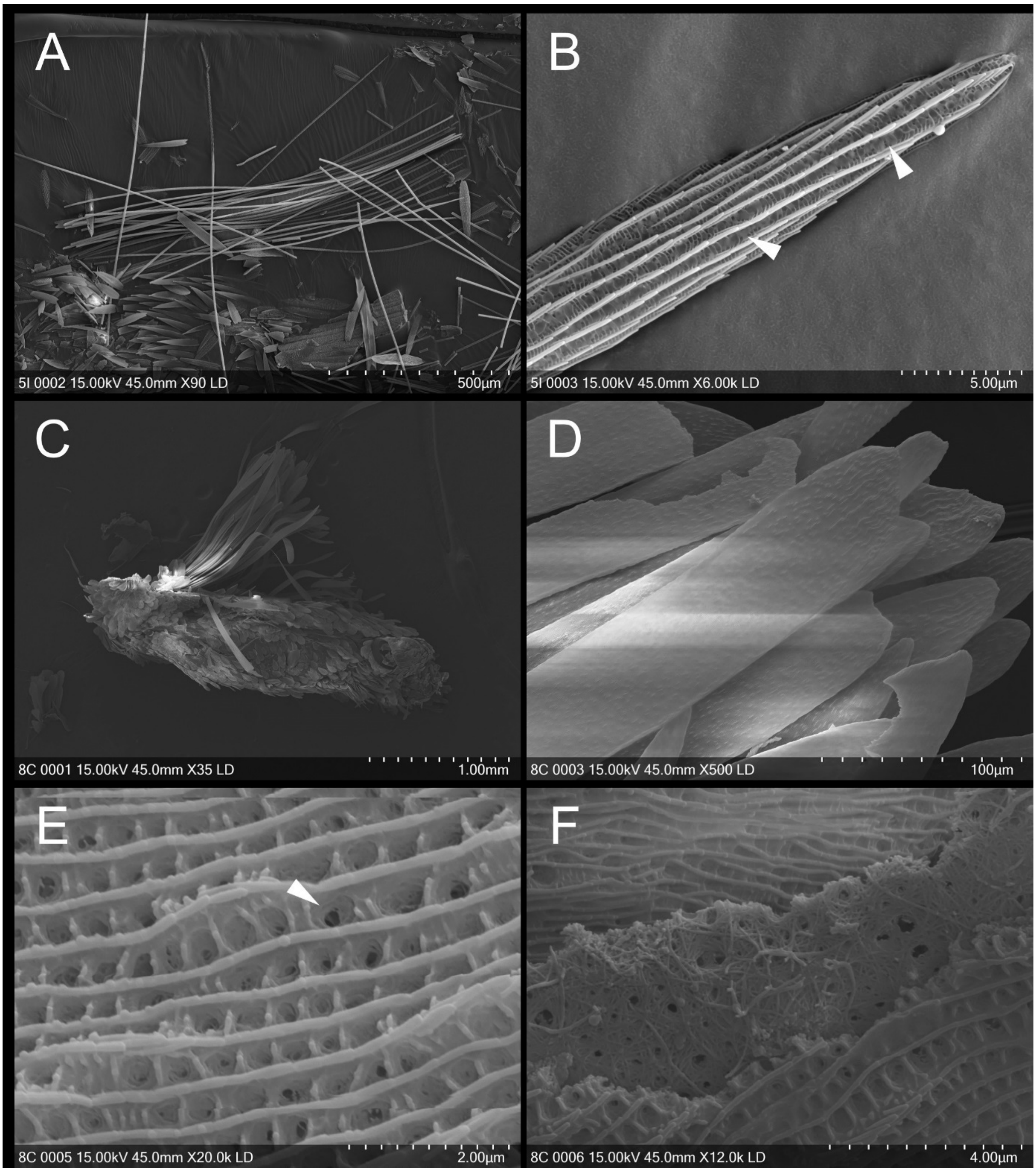


Figure 11. SEM pictures of male foreleg pencil-like scales tuft: A-B – *Melanonaclia trimacula* **comb. nov.**, arrowheads indicate inter-ridge plates; C-F – *Melanonaclia toulgoeti*.

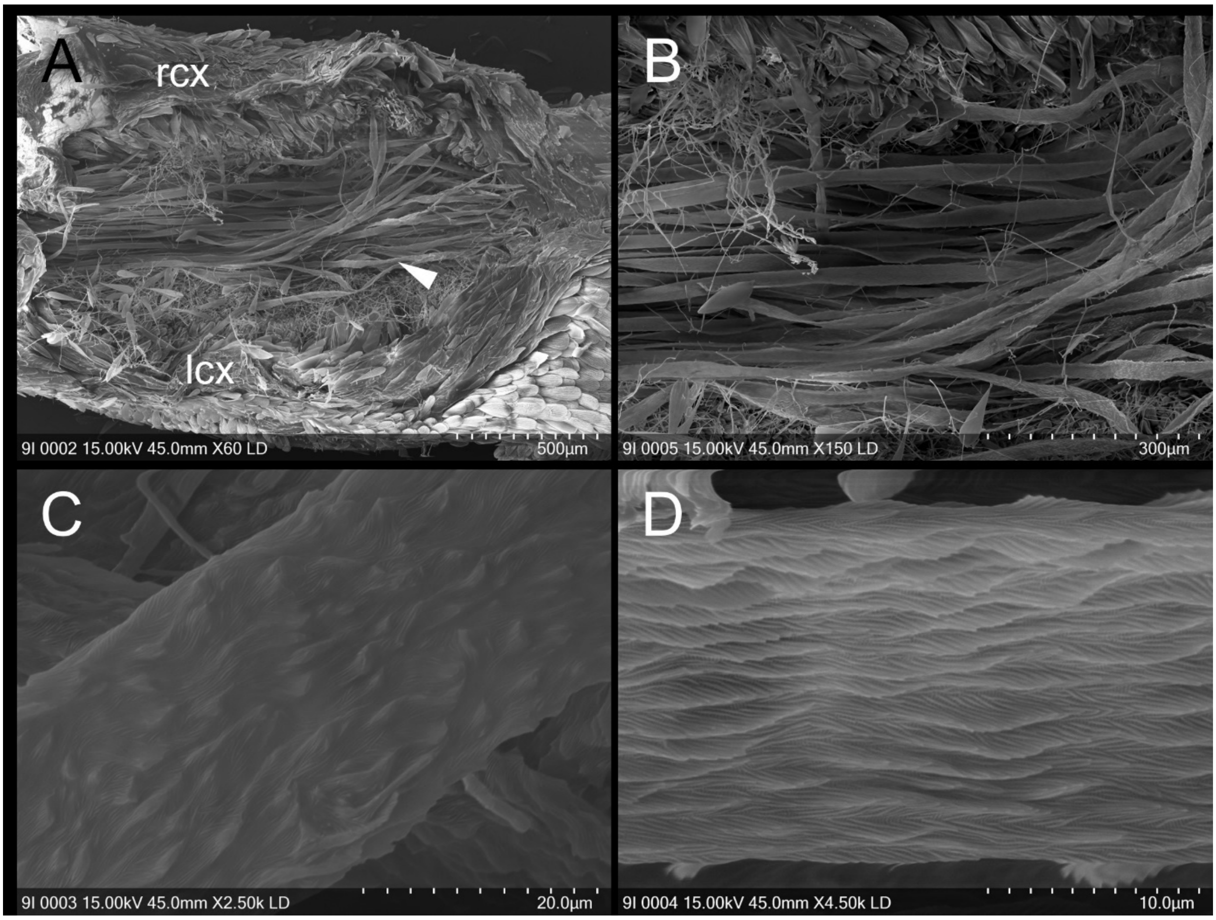


Figure 12. SEM pictures of male foreleg pencil-like scales tuft in *Melanonaclia nigra*:
A-B – general view of the structure (indicated with arrowhead) located in a cavity between coxa, rcx - right coxa, lcx - left coxa; C-D – surface of the tape-like scales forming the tuft in the species.

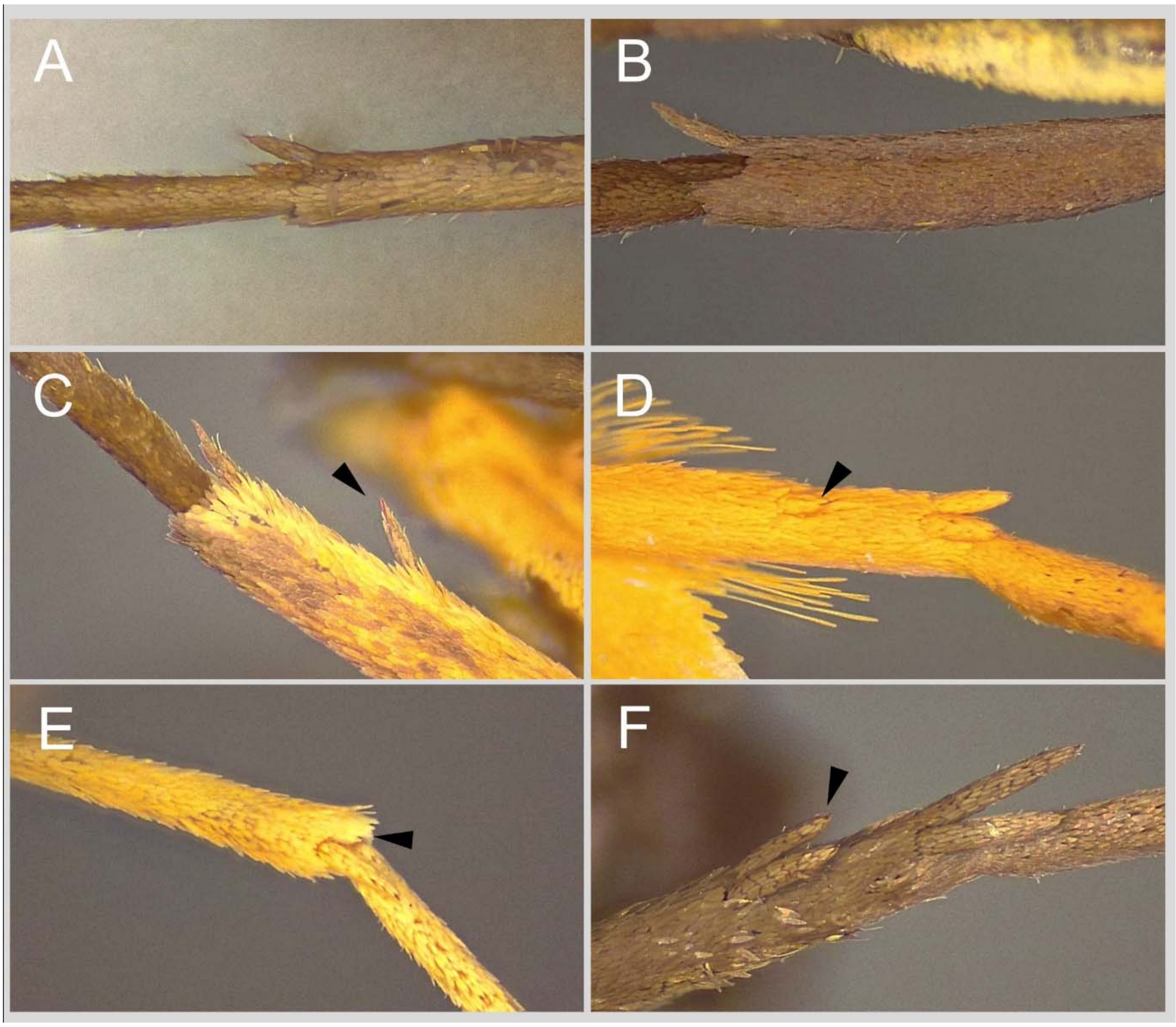


Figure 13. Hindleg tibial spurs: A – *Skippernaclia lacrimata* **comb. nov.** with no additional spurs; B – *Private seguyi* **comb. nov.** with no additional spurs; C – *Melanonaclia trimacula* **comb. nov.** with single additional spur; D – *Mauricenaclia octopunctata* **comb. nov.** with single additional spur; E – *Mauricenaclia raharizonina* **comb. nov.** with no additional spurs, in contrary to other species of the genus (see text), arrowhead indicates broken and missing terminal spur; F – *Kowalskinaclia cowani* **comb. nov.** with two additional spurs.

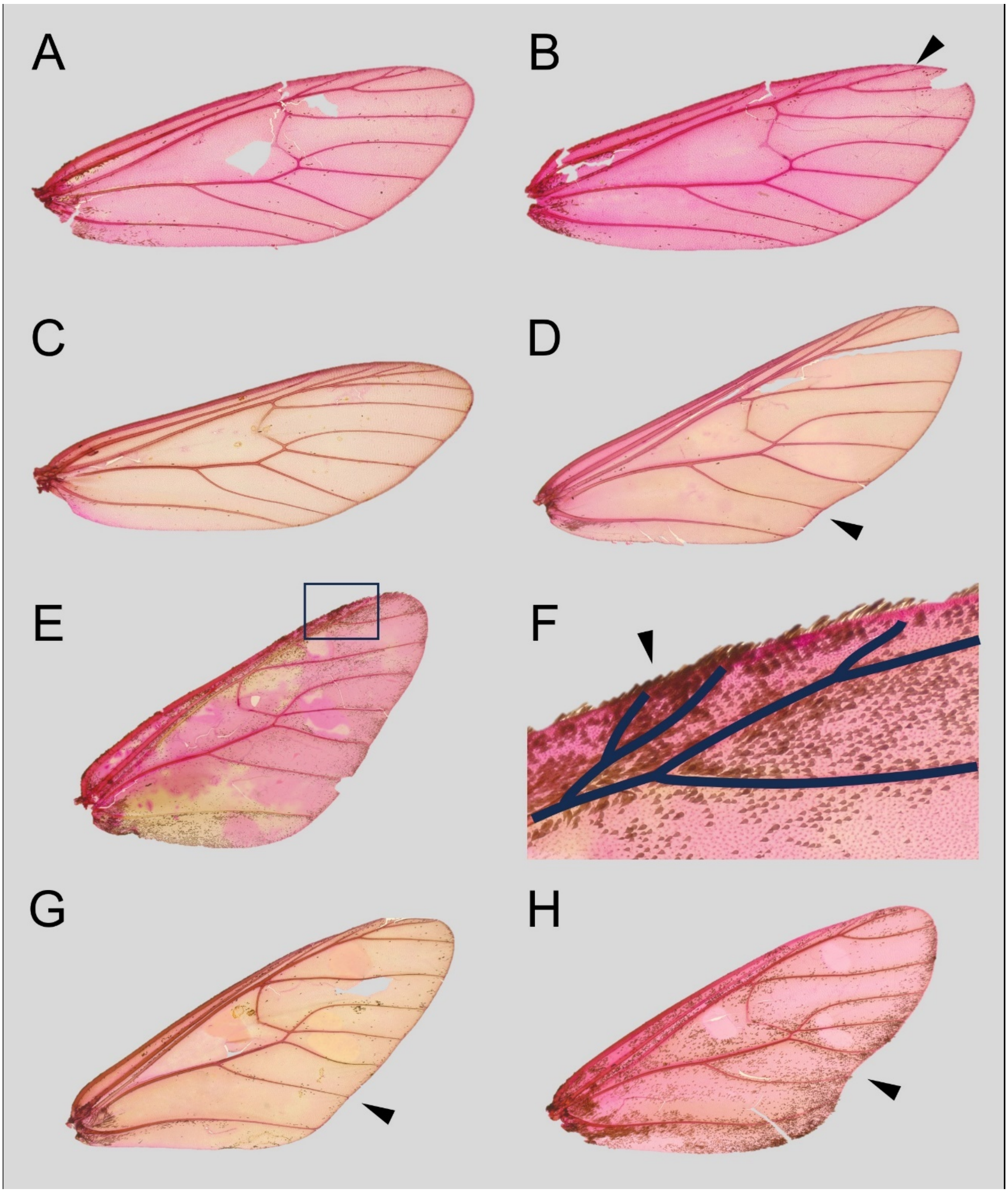


Figure 14. Forewing venation: A – *Skippernaclia lacrimata* **comb. nov.**, left wing of the specimen ISEA PAS, DL_06-051 with four radial veins; B – *Skippernaclia lacrimata* **comb. nov.**, right wing of the specimen DL_06-051 with three radial veins (arrowhead); C – *Riconaclia bimacula* **comb. nov.**; D – *Julienaclia pauliani* **comb. nov.**, arrowhead indicates incision in the subtornal area; E – *Melanonaclia nigra* male, frame indicates the area magnified in figure F; F – radial veins of *M. nigra* male, arrowhead indicates bifurcated vein R2; G – *M. nigra* female, arrowhead indicates indistinct incision in the subtornal area; H – *Melanonaclia toulgoeti* male, arrowhead indicates incision in the subtornal area.

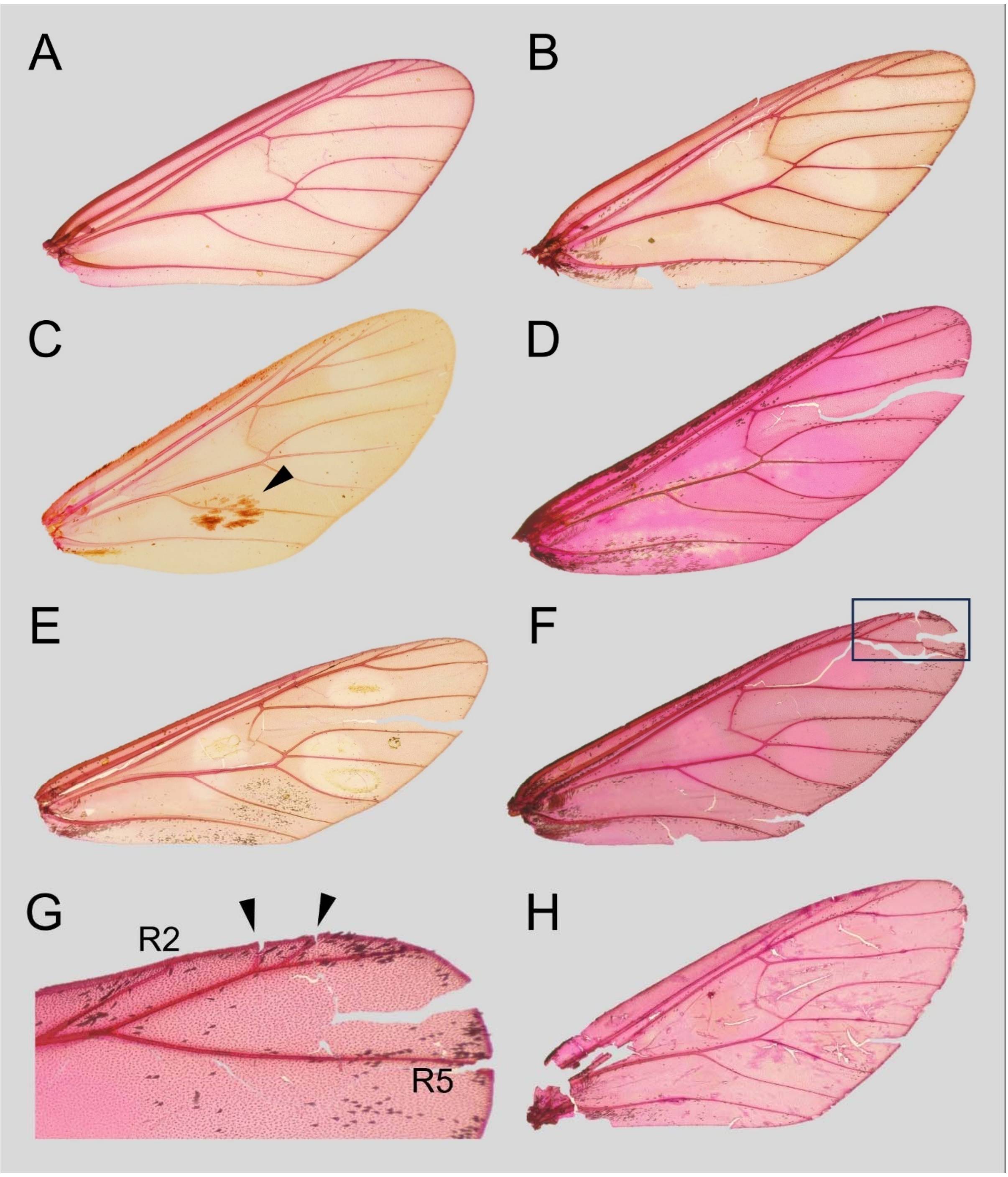


Figure 15. Forewing venation: A – *Kowalskinaclia dilata* **comb. nov.**, B – *Privatenaclia seguyi* **comb. nov.**, C – *Mauricenaclia minuta* **comb. nov.** male, arrowhead indicates the underside field of transformed scales; D – *Mauricenaclia minuta* **comb. nov.** female, note the difference in the wing width between the male and the female; E – *Melanonaclia trimacula* **comb. nov.** with regular, five radial veins (see text); F-G – *M. trimacula* with six radial veins, arrowheads indicate additional bifurcation in R3-R4; H – *Mortinaclia perplexa* **comb. nov.**

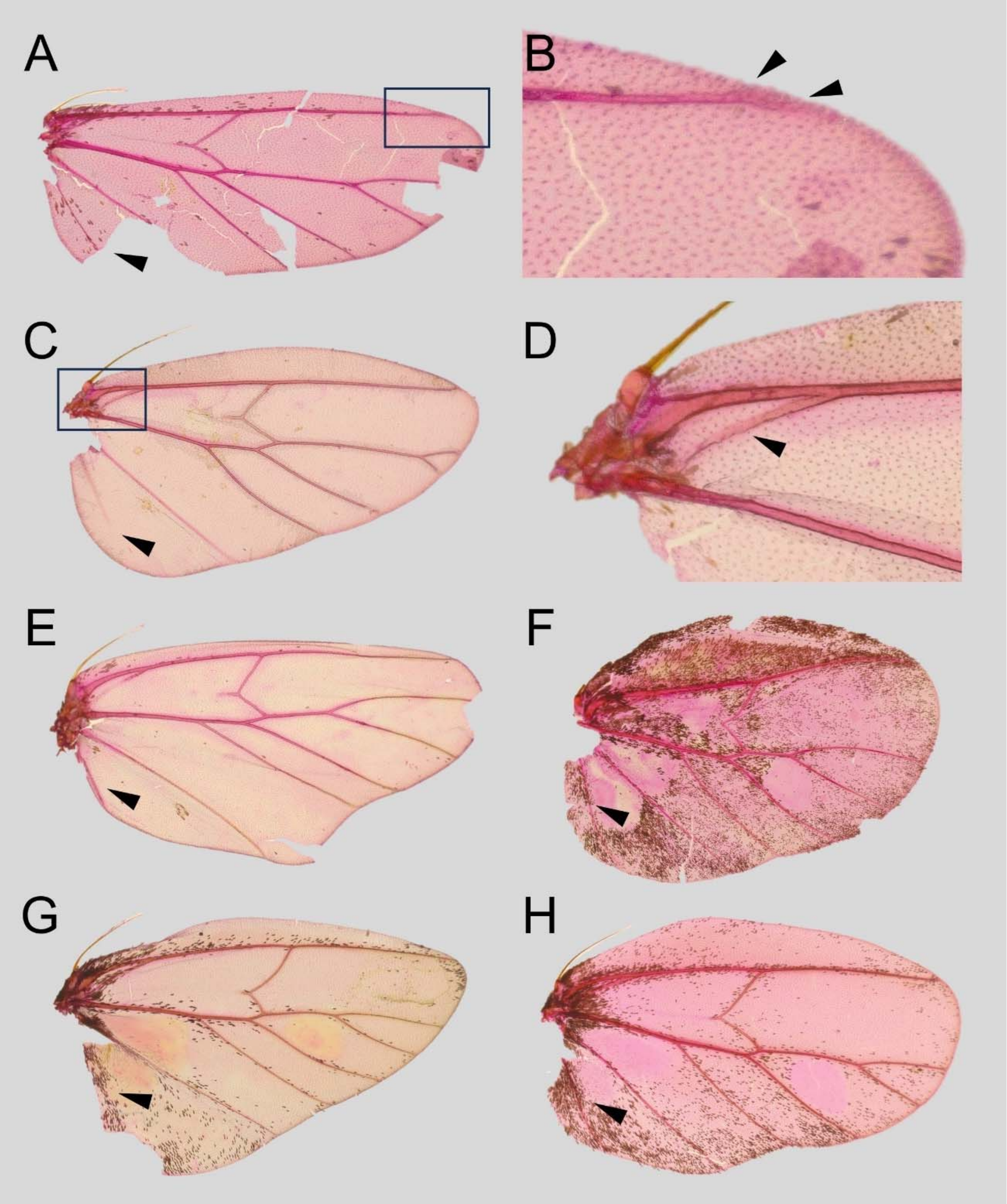


Figure 16. Hindwing venation: A – *Skippernaclia lacrimata* **comb. nov.**, vein 3A present (arrowhead), frame indicates area magnified in figure B; B – *S. lacrimata* **comb. nov.**, slight bifurcation of Sc+Rs+M1 in the terminal portion; C – *Riconaclia bimacula* **comb. nov.**, vein 3A present (arrowhead), frame indicates area magnified in figure D; D – *R. bimacula* **comb. nov.**, additional cell in the basal portion of DC (arrowhead); E – *Julienaclia pauliani* **comb. nov.**, vein 3A present (arrowhead); F – *Melanonaclia nigra* male, vein 3A present (arrowhead); G – *M. nigra* female, vein 3A present (arrowhead), note the sexual dimorphism of the hindwing in the species; H – *Melanonaclia toulgoeti* male, vein 3A present (arrowhead).

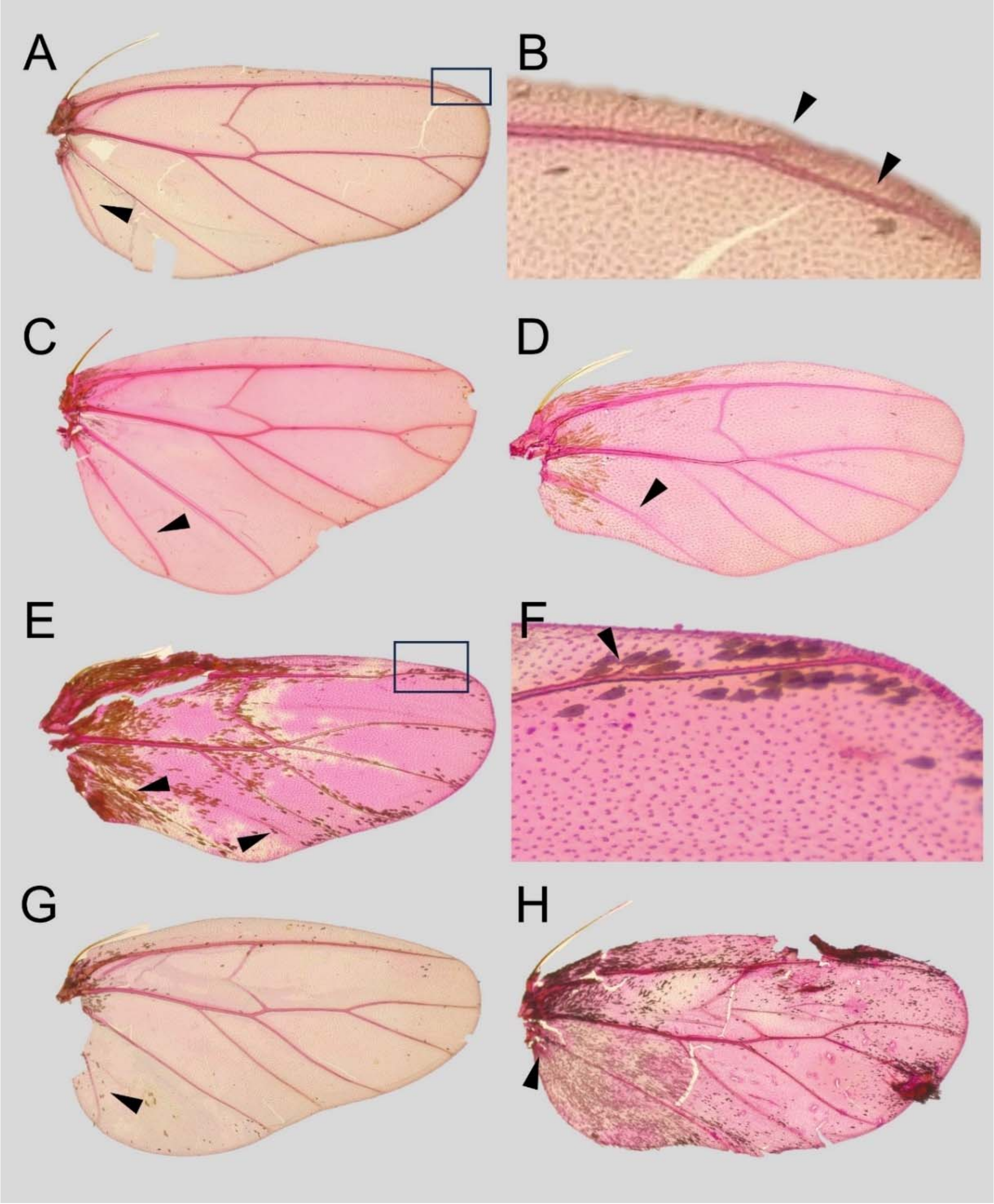


Figure 17. Hindwing venation: A – *Kowalskinaclia dilata* **comb. nov.**, vein 3A present (arrowhead), frame indicates area magnified in figure B; B – *K. dilata* **comb. nov.**, slight bifurcation of Sc+Rs+M1 in the terminal portion; C - *Privatenaclia seguyi* **comb. nov.**, vein 3A present (arrowhead); D - *Mauricenaclia minuta* **comb. nov.**, vein 1A+2A absent and 3A present (arrowhead); E – *M. minuta* **comb. nov.**, vein 1A+2A partly reduced and 3A present (arrowheads), frame indicates area magnified in figure F; F – *M. minuta* **comb. nov.**, slight bifurcation of Sc+Rs+M1 in the terminal portion; G – *Melanonaclia trimacula* **comb. nov.**, vein 3A present (arrowhead); H – *Mortinaclia perplexa* **comb. nov.**, with only basal portion of vein 3A remaining (arrowhead).

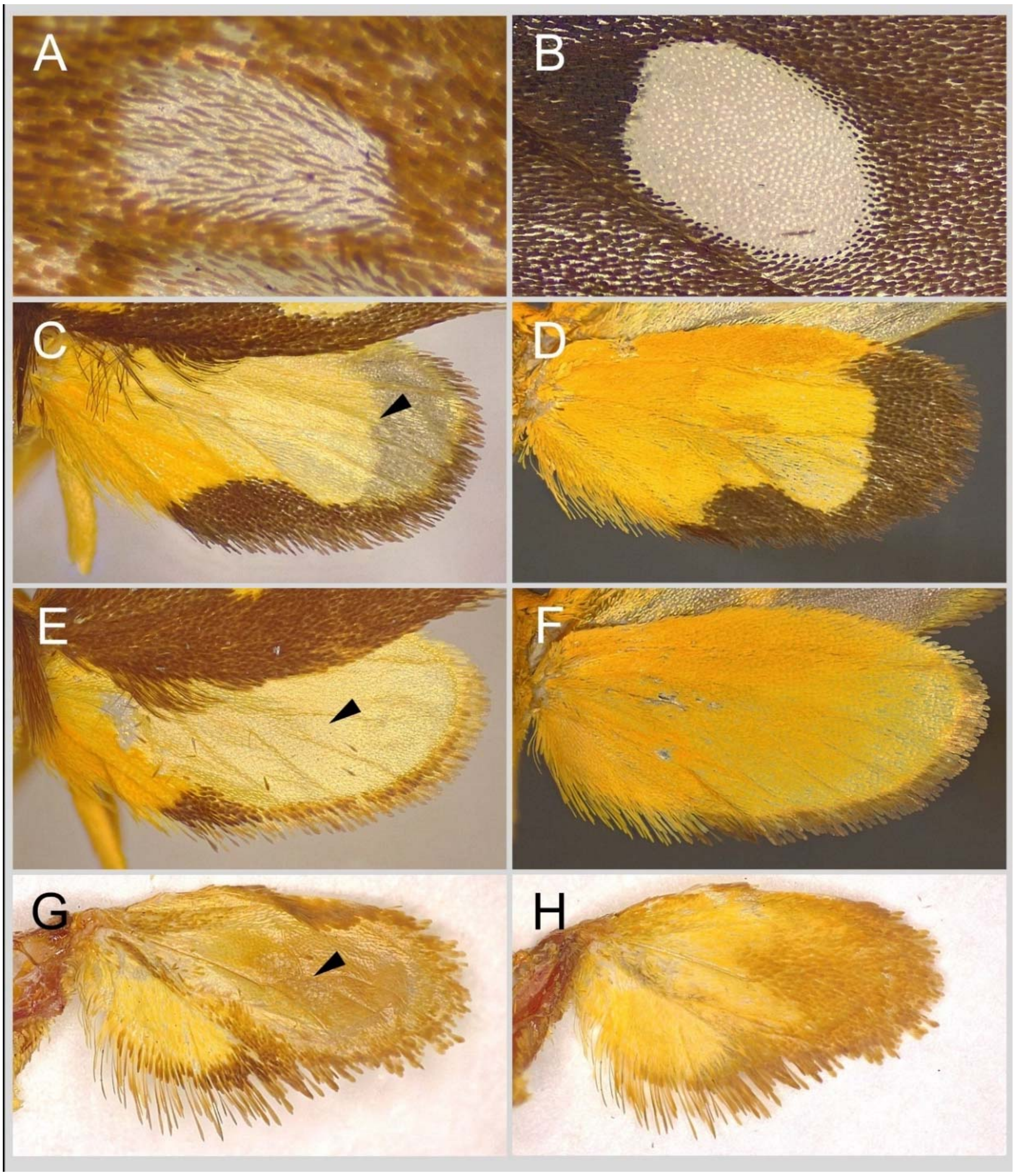


Figure 18. Wing scales modification: A – semi-transparent forewing blotch m5 (underside) in *Mauricenaclia peyrierasi* **comb. nov.**, with narrowed scales; B – semi-transparent hindwing distal blotch in *Melanonaclia nigra* (upperside) with scales reduced in size (see text); C – *Mauricenaclia minuta* **comb. nov.** hindwing upperside with reduced scales size in medial portion (arrowhead); D – *M. minuta* **comb. nov.** hindwing underside with regular scales; E – *Mauricenaclia octopunctata* **comb. nov.** hindwing upperside with reduced scales size in medial portion (arrowhead); F – *M. octopunctata* **comb. nov.** hindwing underside with regular scales; G – *Mauricenaclia peyrierasi* **comb. nov.** hindwing upperside with regular but completely transparent scales in medial portion (arrowhead); H – *M. peyrierasi* **comb. nov.** hindwing underside with regular scales.

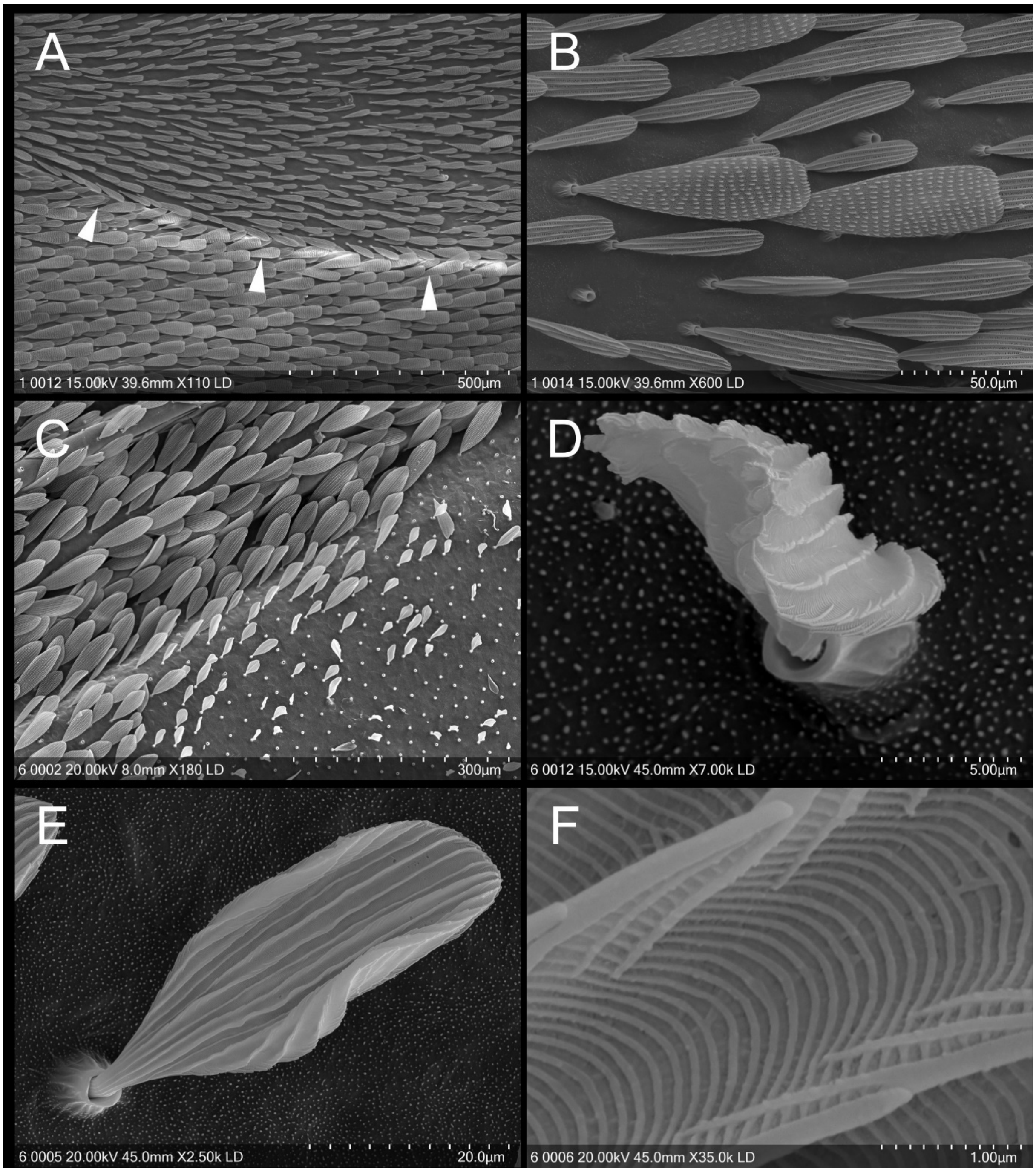


Figure 19. SEM pictures of scales covering semi-transparent blotches:

A – *Mauricenaclia minuta* **comb. nov.** forewing m_5+m_6 blotch, arrowheads indicate the transition between regular scales covering the wing background, and reduced scales covering the blotch; B – *M. minuta* **comb. nov.**, narrowed scales covering forewing m_5+m_6 blotch;

C – *Privatenaclia seguyi* **comb. nov.**, transition zone between regular scales covering the wing background, and reduced scales covering m_2 blotch; D-E – *P. seguyi* **comb. nov.**, reduced, “deformed” scales covering forewing blotch m_2; F – *P. seguyi* **comb. nov.**, magnification of the reduced scale covering forewing blotch m_2, with retained regular nanostructure.

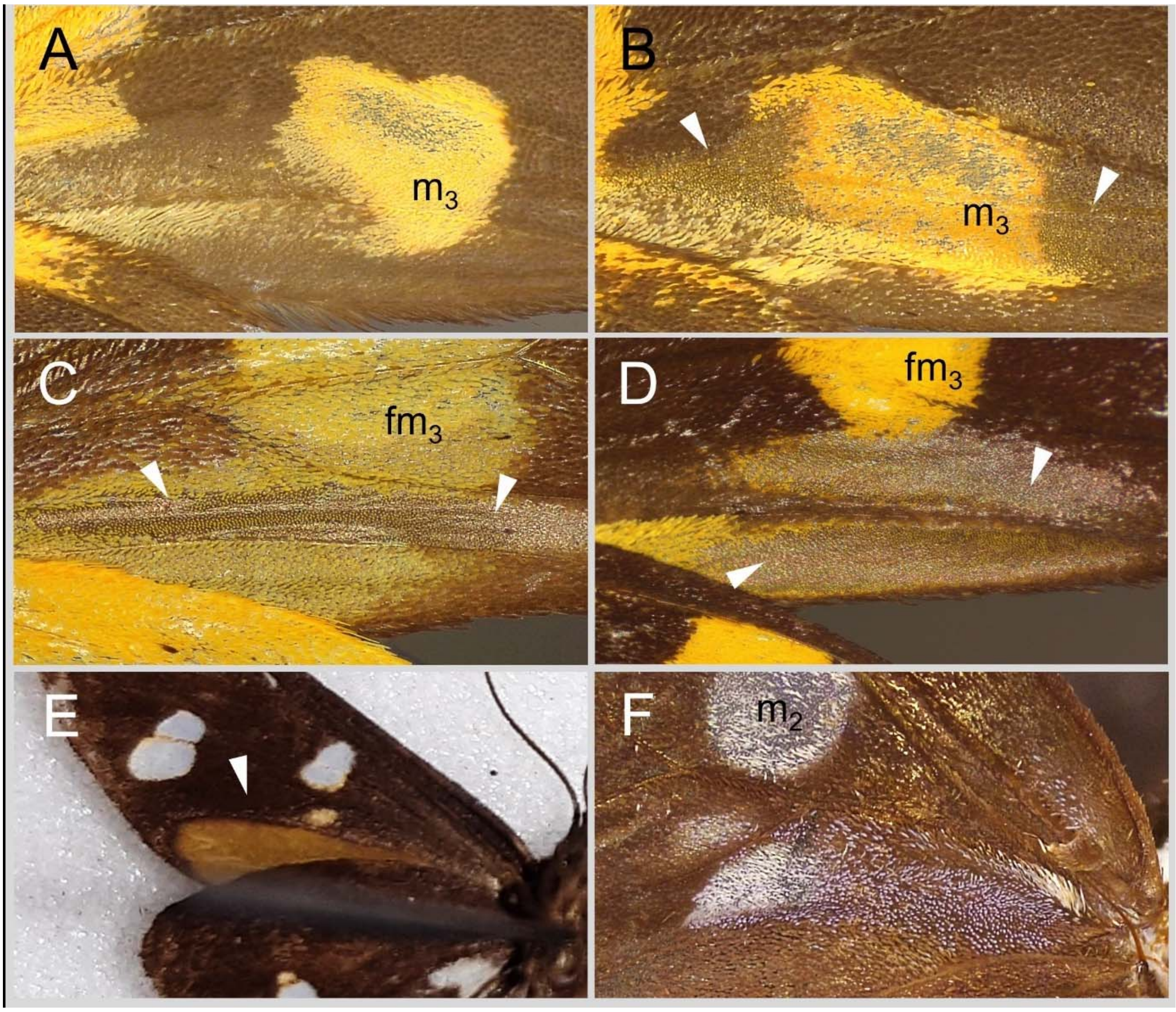


Figure 20. Streak of transformed, reduced scales along hind margin of forewing:

A – *Privatenaclia seguyi* **comb. nov.** female forewing underside without such a structure (see text), m_3 - forewing blotch m_3; B – *P. seguyi* **comb. nov.** male forewing underside with the streak (arrowheads), m_3 - forewing blotch m_3; C – *Riconaclia bimacula* **comb. nov.** male forewing underside with the streak (arrowheads), fm_3 - forewing blotch fm_3; D – *Melanonaclia trimacula* **comb. nov.** male forewing underside with the streak (arrowheads), fm_3 - forewing blotch fm_3; E – *Melanonaclia luctuosa* male forewing underside with the streak (arrowhead); F – *Mortinaclia perplexa* **comb. nov.** male forewing underside with the streak, note the lilac reflection of the structure, m_2 - forewing blotch m_2.

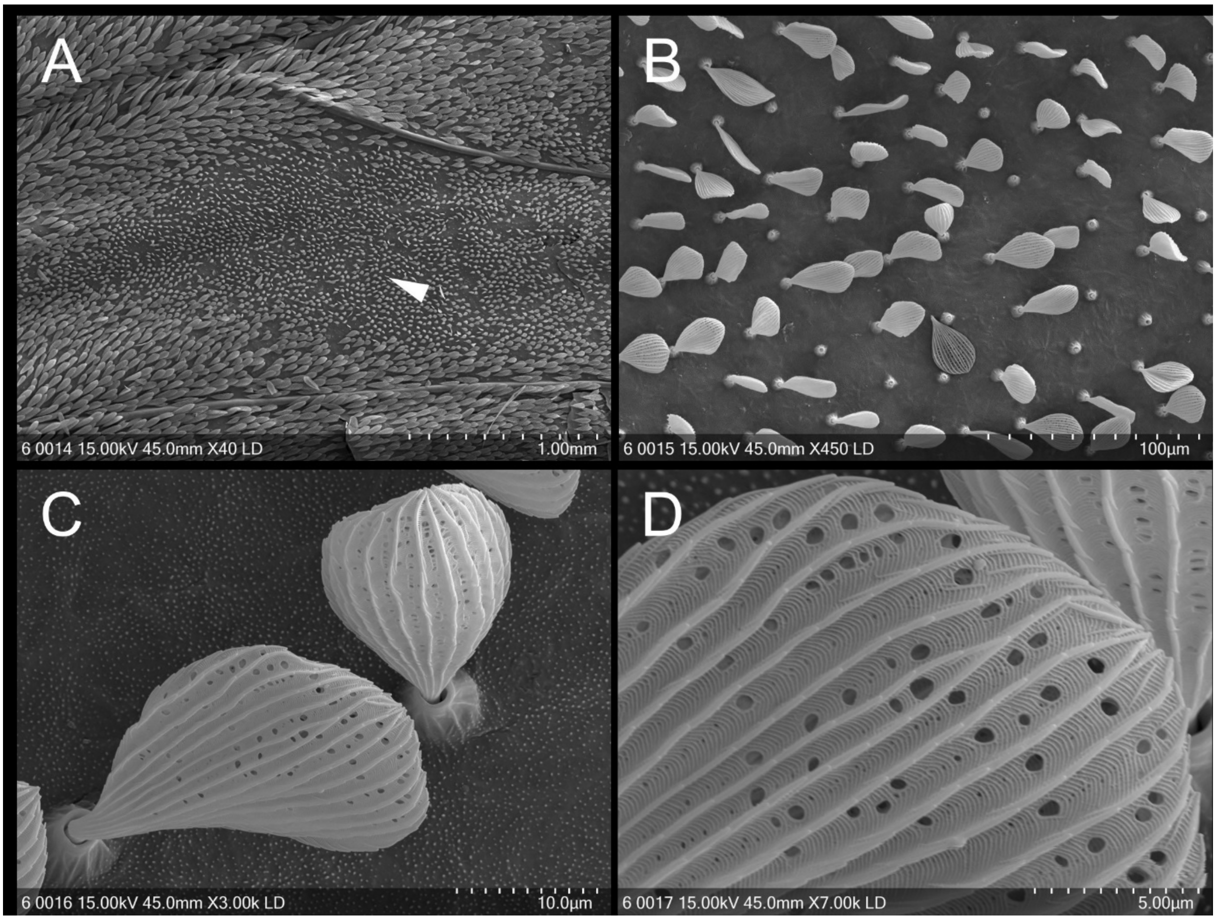


Figure 21. SEM pictures of scales covering the streak along the hind margin of the forewing in *Privatenaclia seguyi* **comb. nov.**: A – general view of the hind portion of the forewing, with the reduced scales streak indicated by arrowhead; B – magnification of the streak; C-D – structure of the reduced scales covering the streak, note numerous holes.

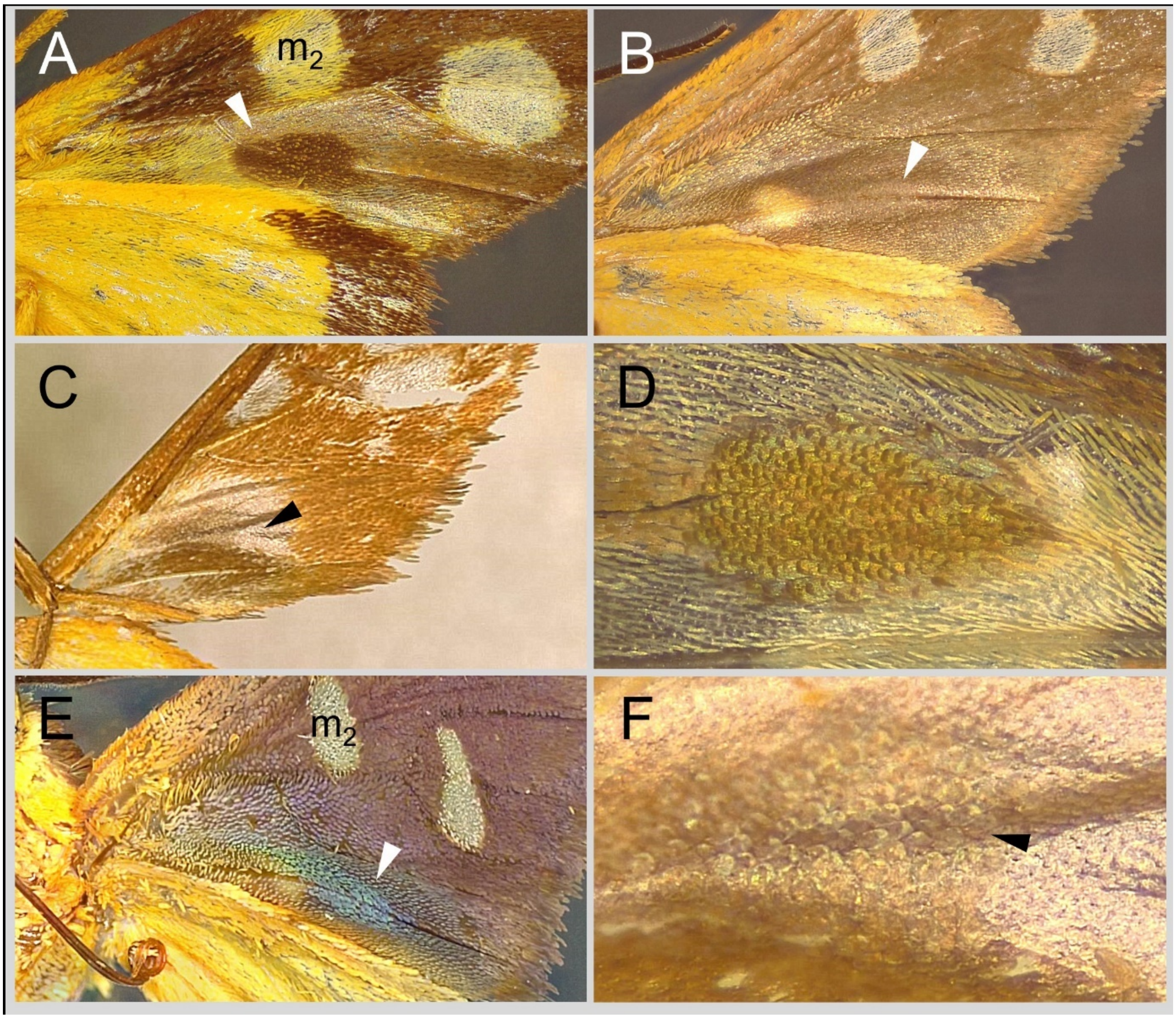


Figure 22. Transformed scales in the male forewing underside: A – *Mauricenaclia minuta* **comb. nov.**; B – *Mauricenaclia octopunctata* **comb. nov.**; C – *Mauricenaclia peyrierasi* **comb. nov.**; D – the central, suboval field of elongate scales in *M. minuta* **comb. nov.** (see text); E – the area of reduced scales in *M. octopunctata* **comb. nov.**, with the suboval field indicated by arrowhead (see text), note the metallic reflection of the area; F – regular, completely transparent scales (arrowhead) in the suboval field of *M. peyrierasi* **comb. nov.**

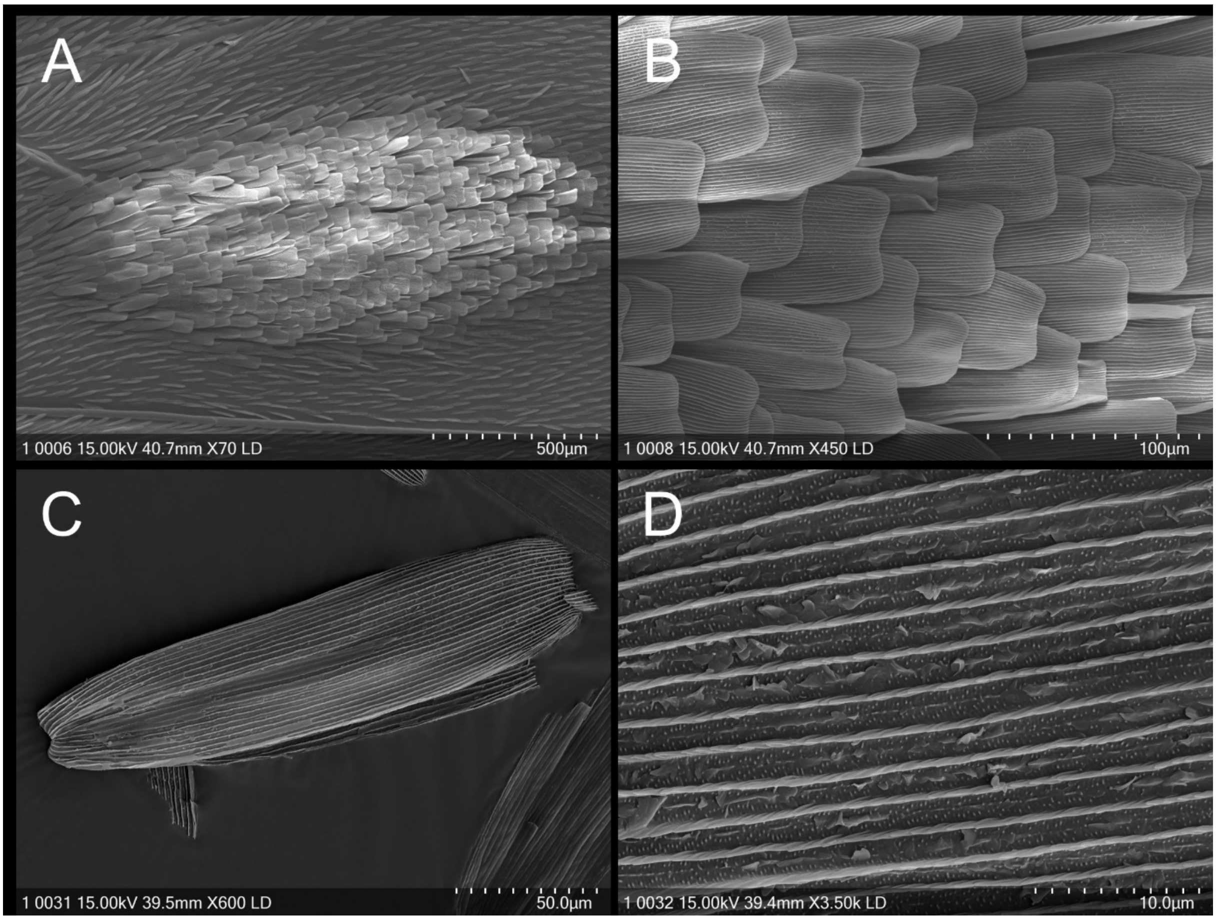


Figure 23. SEM pictures of the male forewing underside field of transformed scales in *Mauricenaclia minuta* **comb. nov.**: A-B – the general view; C – single scale from the field; D – magnification of the scale structure.

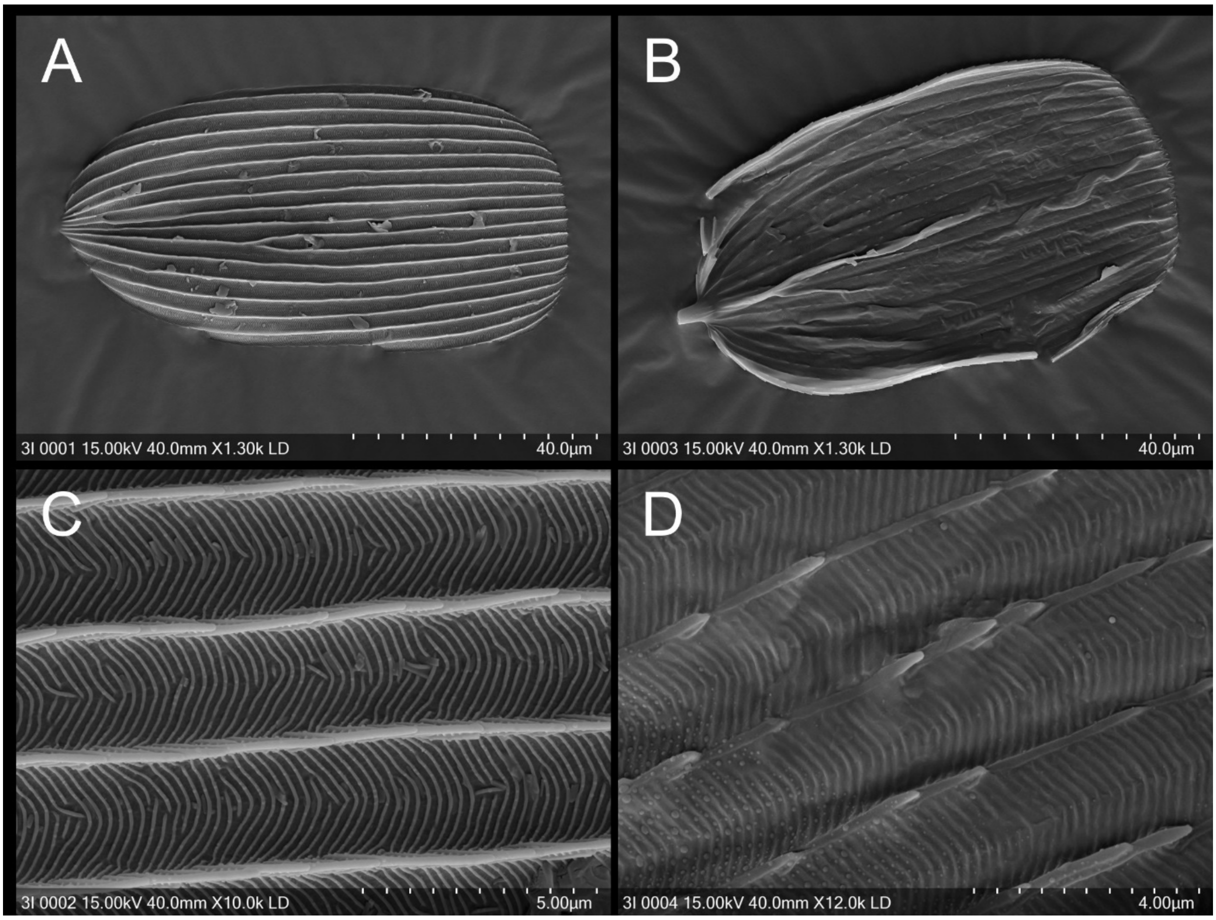


Figure 24. SEM pictures of the male forewing underside transformed scales of *Mauricenaclia octopunctata* **comb. nov.**: A – the outer side of scale; B – the back (wing) side of scale; C – magnification of the outer side structure; D – magnification of the back (wing) side structure.

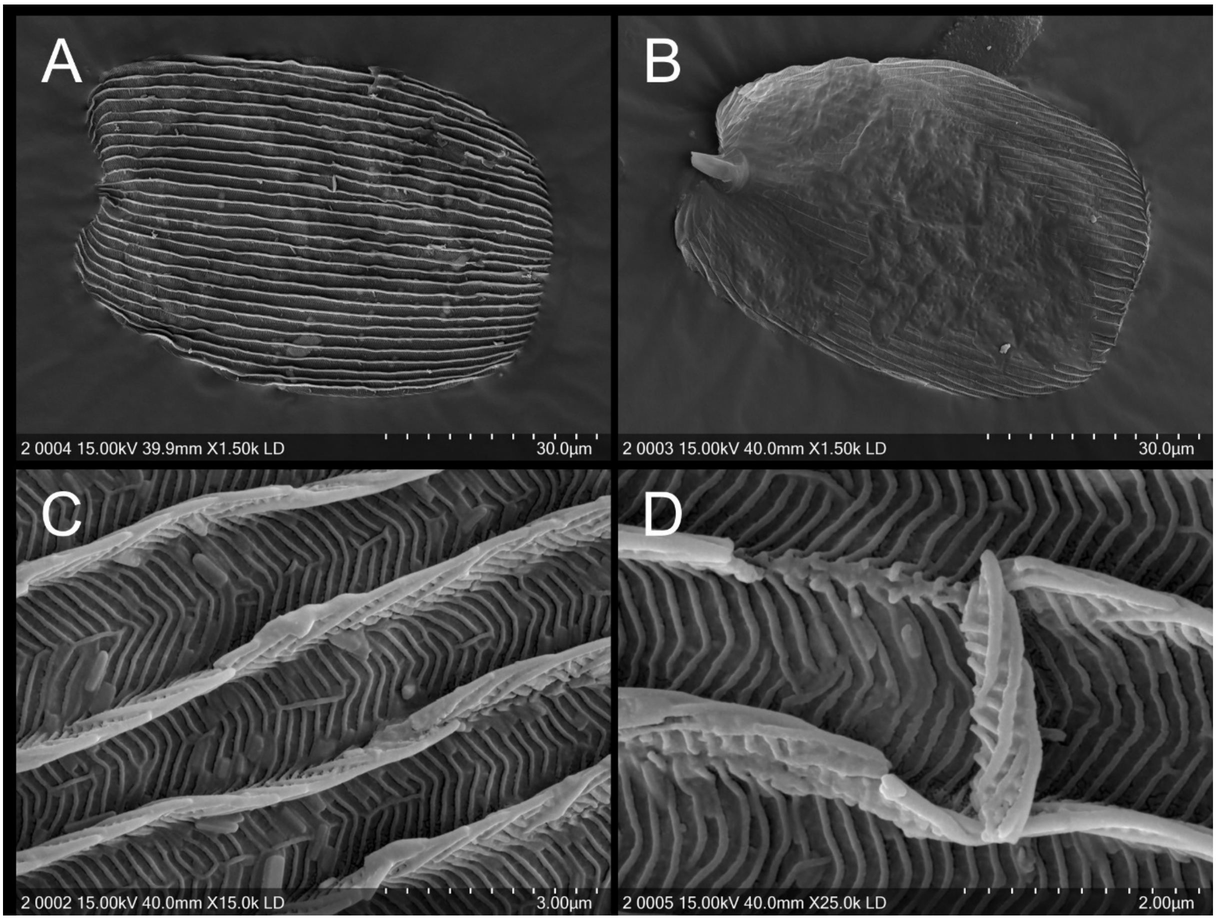


Figure 25. SEM pictures of the male forewing underside transformed scales of *Mauricenaclia peyrierasi* **comb. nov.**: A – the outer side of scale; B – the back (wing) side of scale; C-D – magnification of the outer side structure.

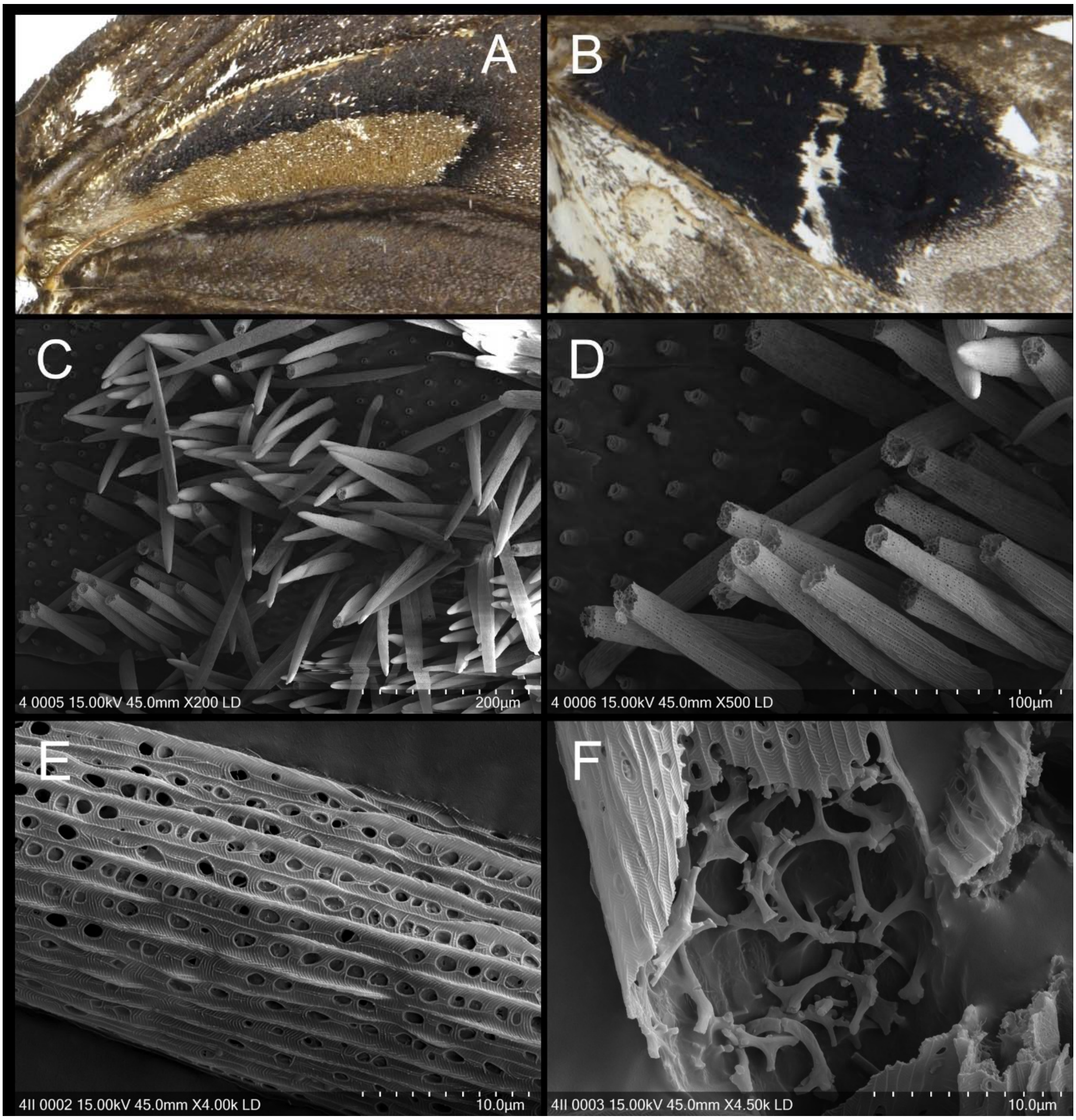


Figure 26. Transformed wing scales of *Melanonaclia nigra* male: A – longitudinal streak of pale scales in the basal portion of forewing underside; B – dark scales in the hind wing upperside; C-F – SEM pictures of the forewing underside scales.

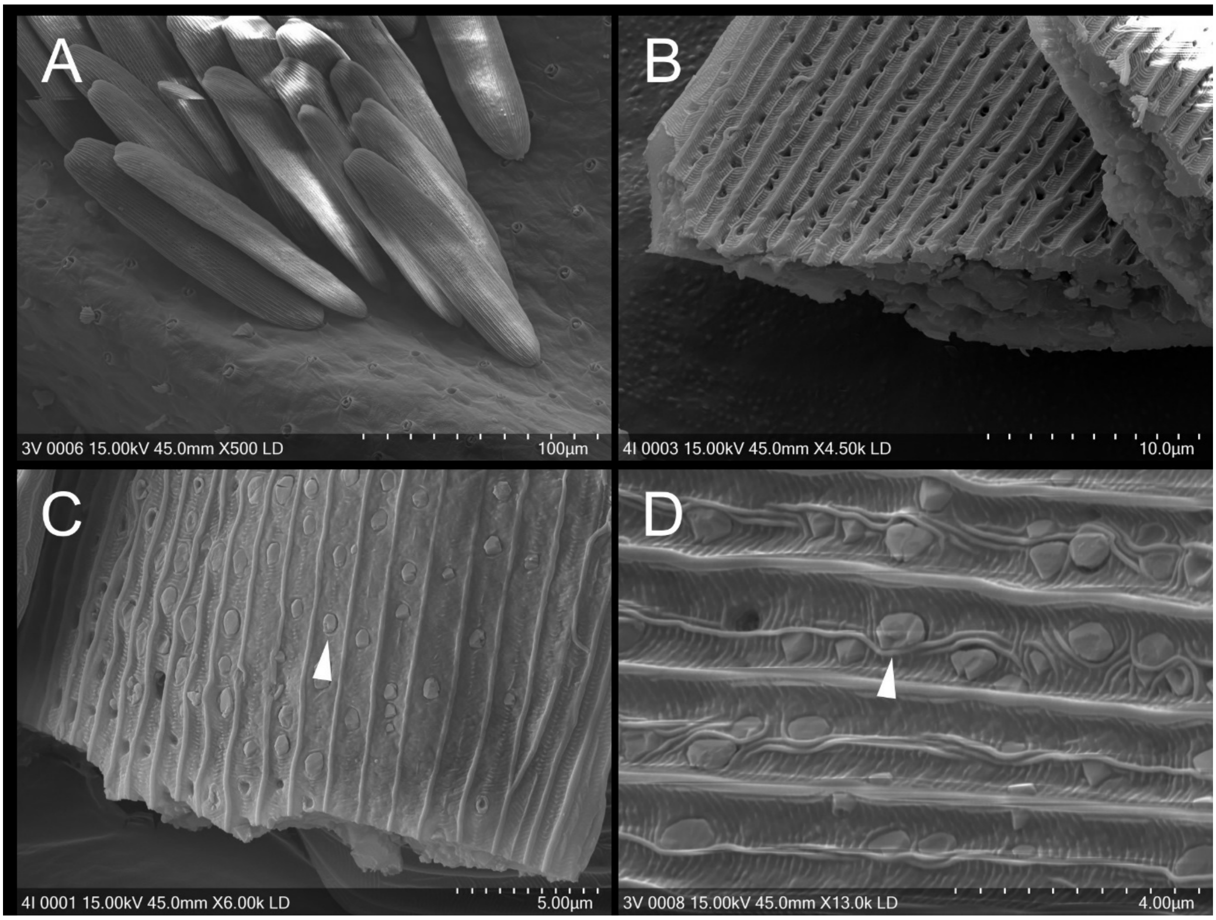


Figure 27. SEM pictures of transformed wing scales of *Melanonaclia nigra* male hindwing upperside: A – general arrangement of scales; B – scale cross section; C-D – magnification of scale surface, with crystal-like structures (arrowhead), potentially pheromone-transfer-particles (PTPs, see text).

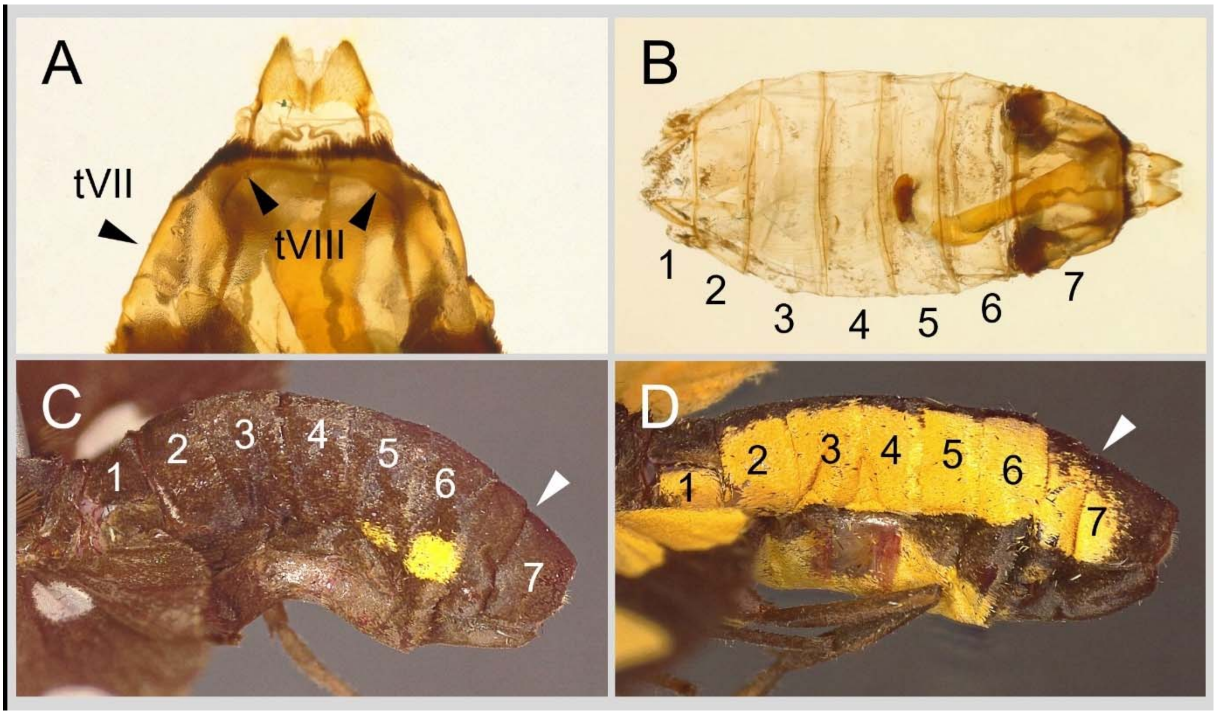


Figure 28. Arrangement of segments in the female abdomen: A – *Melanonaclia luctuosa*, 8th tergite (tVIII) reduced to a plaque located ventrally in the abdomen, along terminal portion of the 7th tergite (tVII); B – *Melanonaclia luctuosa*, dorsal view of the abdomen, numbers 1-7 indicate relevant tergites; C – *Melanonaclia luctuosa*, lateral view of the abdomen, numbers 1-7 indicate relevant tergites, arrowhead indicates the groove-like cavity across the 7th tergite, resembling the hypothetical margin between the tergites 7th and 8th (see text);

D – *Melanonaclia ranomafana* **sp. nov.**, lateral view of the abdomen, numbers 1-7 indicate relevant tergites, arrowhead indicates the groove-like cavity across the 7th tergite, analogical as in the figure C.

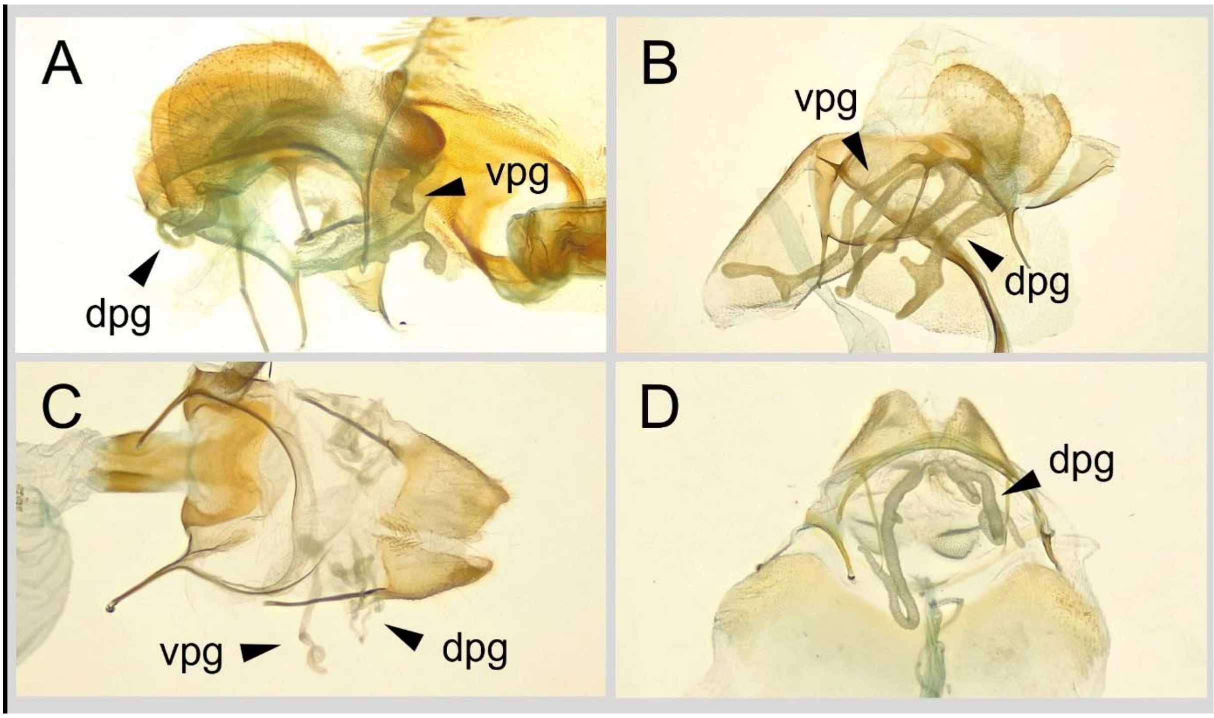


Figure 29. Female pheromone glands, vpg - ventral pheromone glands, dpg - dorsal pheromone glands: A – *Thyrosticta sylvicolens*; B – *Riconaclia bimacula* **comb. nov.**; C – *Kowalskinaclia cowani* **comb. nov.**; D – *Mauricenaclia octopunctata* **comb. nov.**, note the characteristic to the genus lack of ventral pheromone glands (see text).

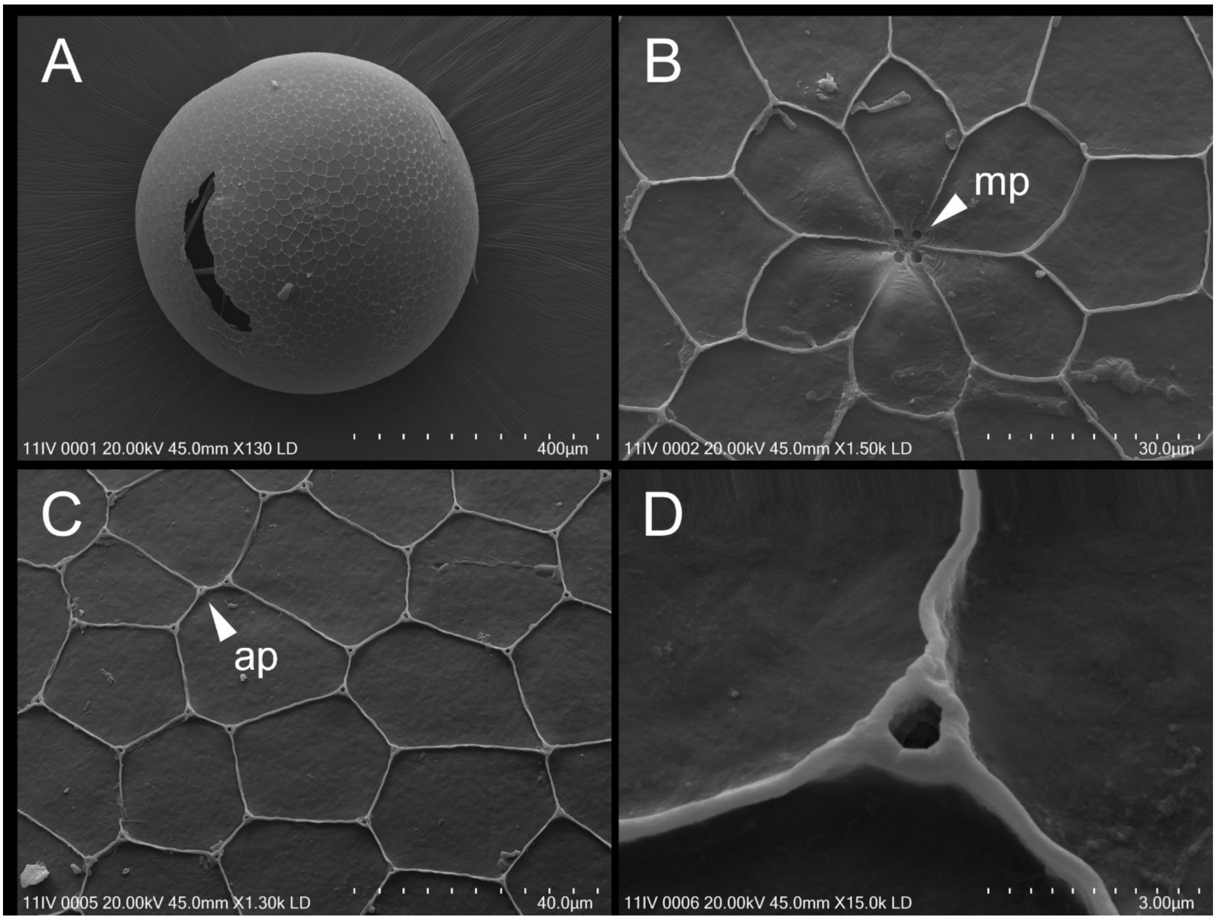


Figure 30. SEM pictures of egg of *Kowalskinaclia vieui* **comb. nov.**: A – general morphology, B – micropylar rosette, mp - micropyle; C – surface sculpture, ap - aeropyle; D – magnification of aeropyle.

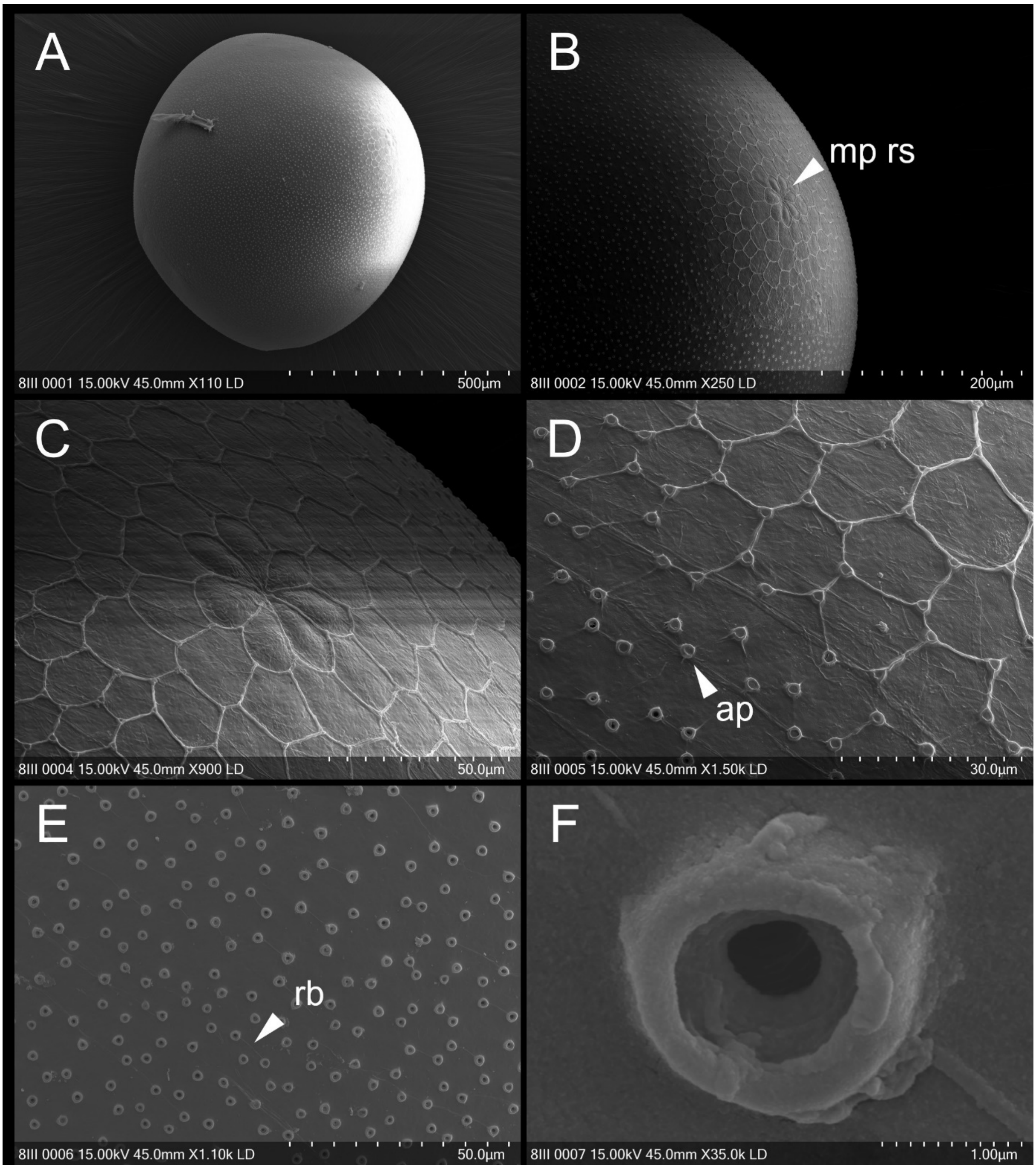


Figure 31. SEM pictures of egg of *Privatenaclia seguyi* **comb. nov.**: A-B – general morphology, mp rs - micropylar rosette; C – magnification of micropylar rosette; D-E – surface sculpture, ap - aeropyle, rb - single rib connecting aeropyles (see text); F – magnification of aeropyle.

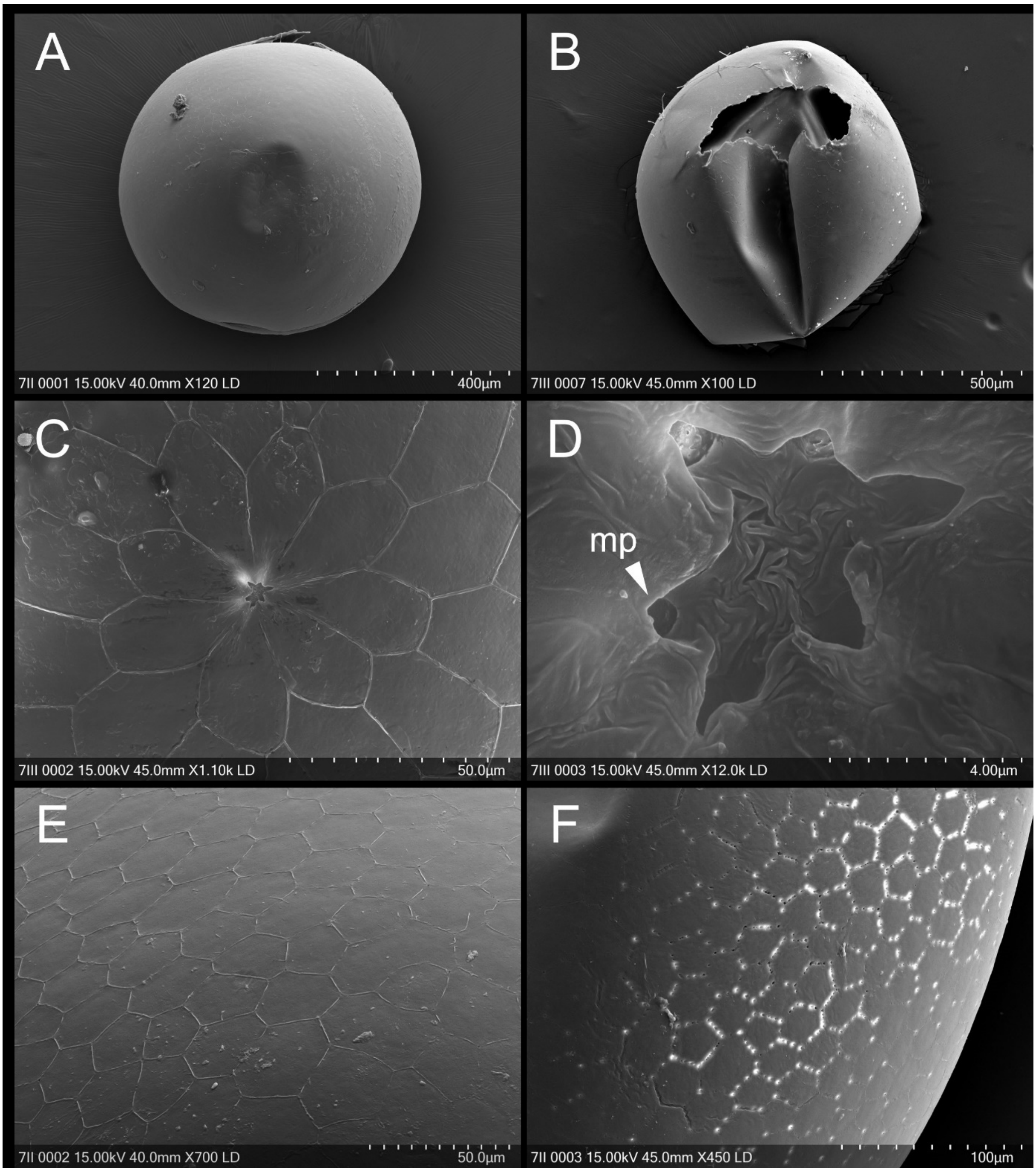


Figure 32. SEM pictures of egg of *Mauricenaclia minuta* **comb. nov.**: A-B – general morphology; C – micropylar rosette; D – micropylar plate, mp - micropyle; E-F – surface sculpture (see text).

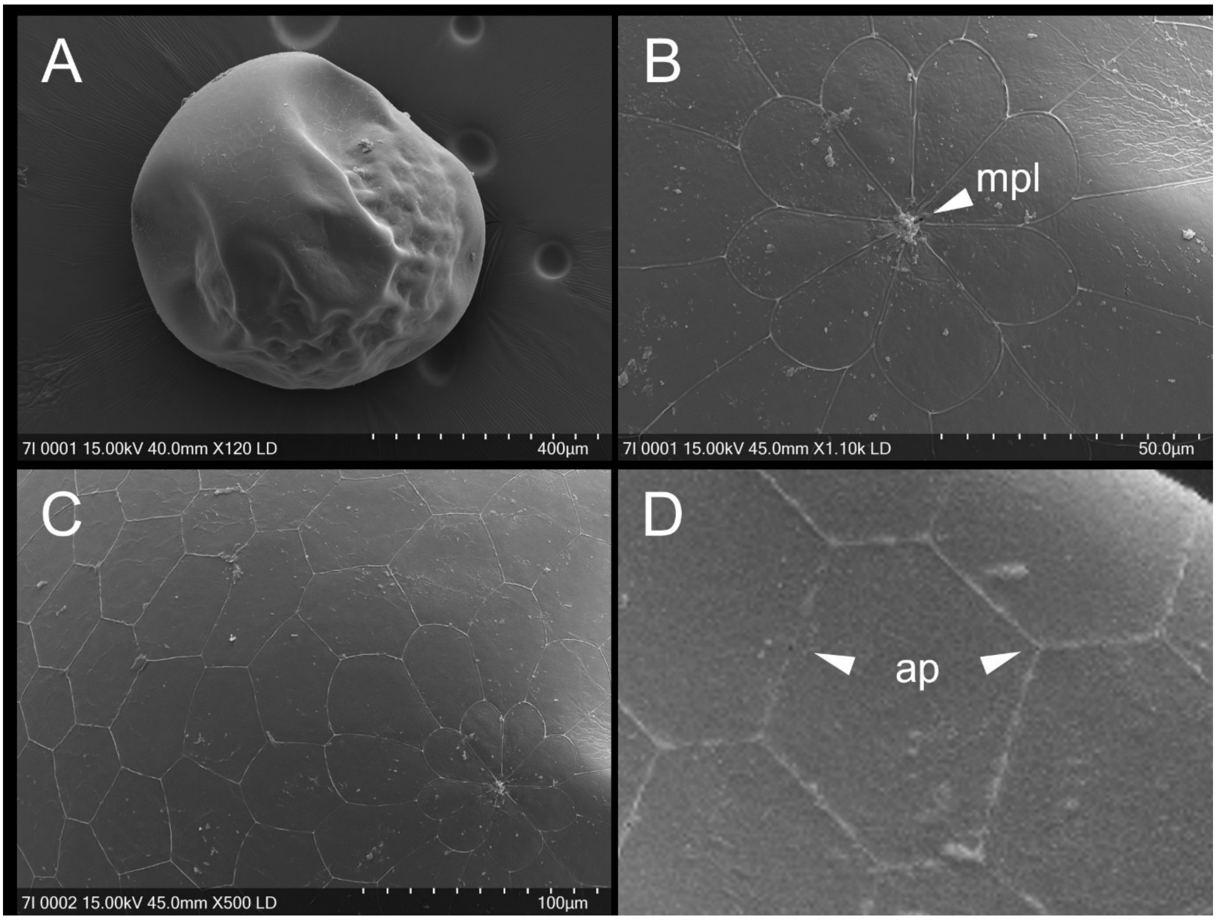


Figure 33. SEM pictures of egg of *Mauricenaclia minuta* **comb. nov.**: A – general morphology; B – micropylar rosette, mpl - micropylar plate; C-D – surface sculpture, ap - aeropyles.

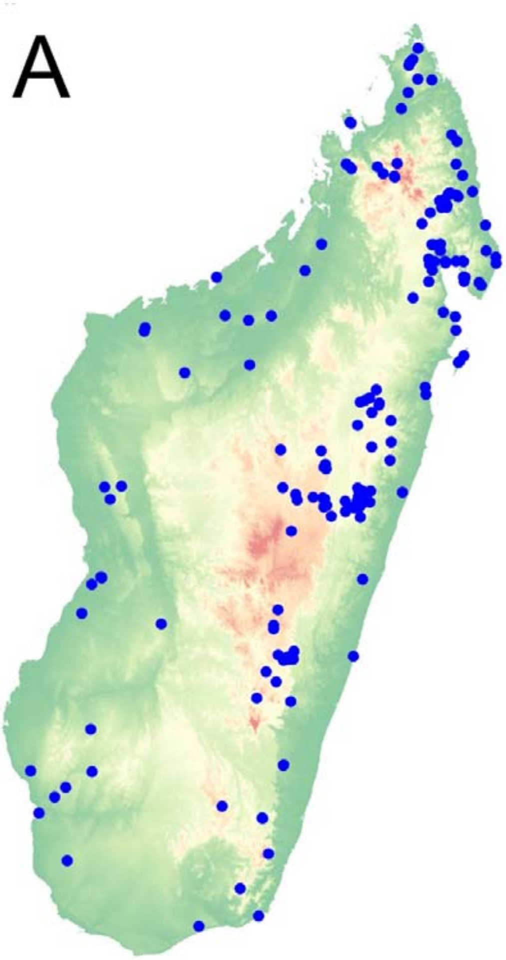


Figure 34. Map of all 191 localities, where the taxa covered in the study were collected or observed.

Figure 35. *Thyrosticta sylvicolens*, adults: A – holotype of *Pseudonaclia sylvicolens* Butler, 1878; B – holotype of *Naclia quadrimacula* Mabille, [1879]; C – holotype of *Naclia perpetua* Oberthür, 1893; D – holotype of *Naclia quadrimacula* var. *confluens* Oberthür, 1893; E – male (ISEA PAS, MAD_213); F – female (MNHN, EL82754); not to the same scale.

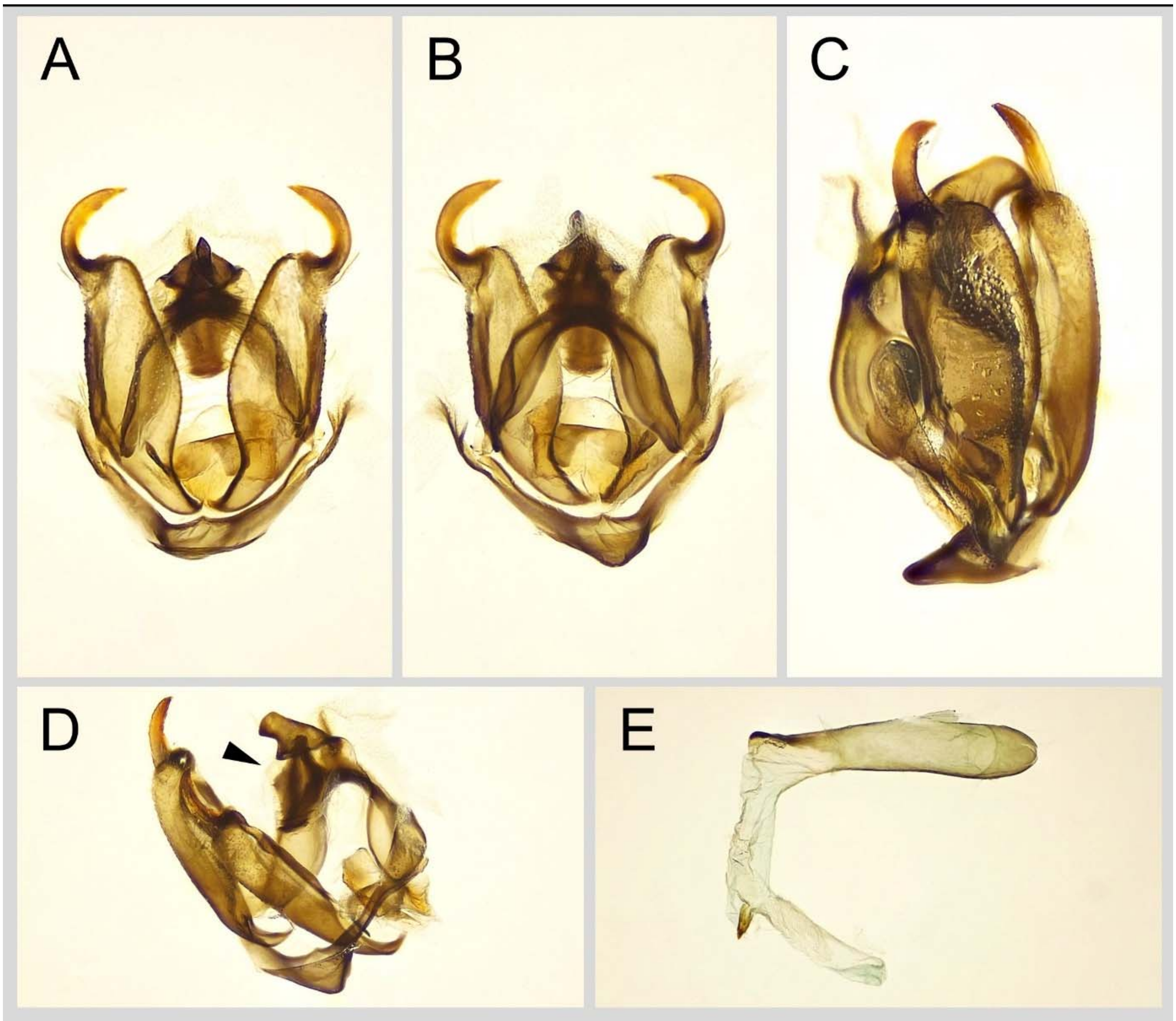


Figure 36. Male genitalia of *Thyrosticta sylvicolens*.

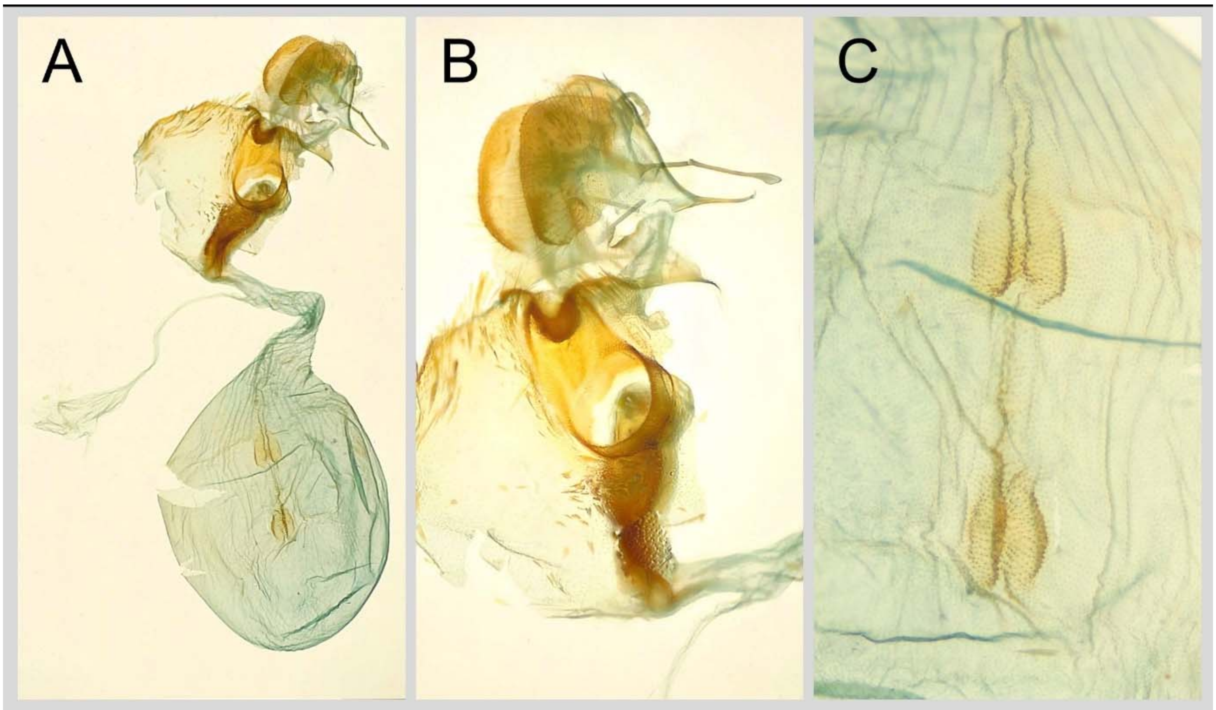
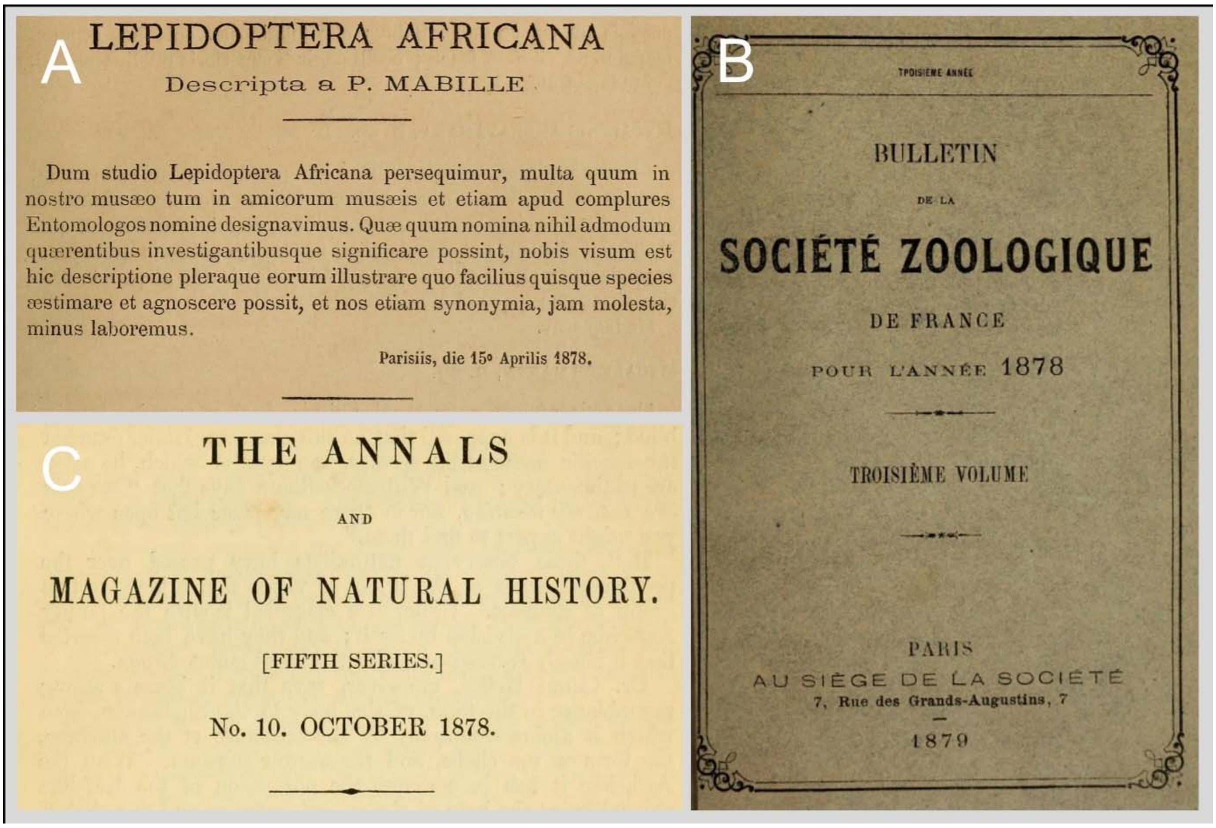


Figure 37. Female genitalia of *Thyrosticta sylvicolens*.



LEPIDOPTERA AFRICANA
Descripta a P. MABILLE

Dum studio Lepidoptera Africana persequimur, multa quum in nostro musæo tum in amicorum musæis et etiam apud complures Entomologos nomine designavimus. Quæ quum nomina nihil admodum quærentibus investigantibusque significare possint, nobis visum est hic descriptione pleraque eorum illustrare quo facilius quisque species æstimare et agnoscere possit, et nos etiam synonymia, jam molesta, minus laboremus.

Parisiis, die 15° Aprilis 1878.

TROISIÈME ANNÉE

BULLETIN
DE LA
SOCIÉTÉ ZOOLOGIQUE
DE FRANCE
POUR L'ANNÉE 1878

TROISIÈME VOLUME

PARIS
AU SIÈGE DE LA SOCIÉTÉ
7, Rue des Grands-Augustins, 7
—
1879

THE ANNALS
AND
MAGAZINE OF NATURAL HISTORY.
[FIFTH SERIES.]
No. 10. OCTOBER 1878.

Figure 38. Cover pages of the original descriptions of *Pseudonaclia sylvicolens* Butler, 1878 and *Naclia quadrimacula* Mabille, [1879]: A – the foreword to the paper by Mabille, with the date 15.iv.1878; B – wrapper of the *Bulletin*… fascicle for 1878, with the actual 1879 date of publication of Mabille's work in the bottom; C – title page of *The Annals*… containing the description by Butler, issued on 10.x.1878.

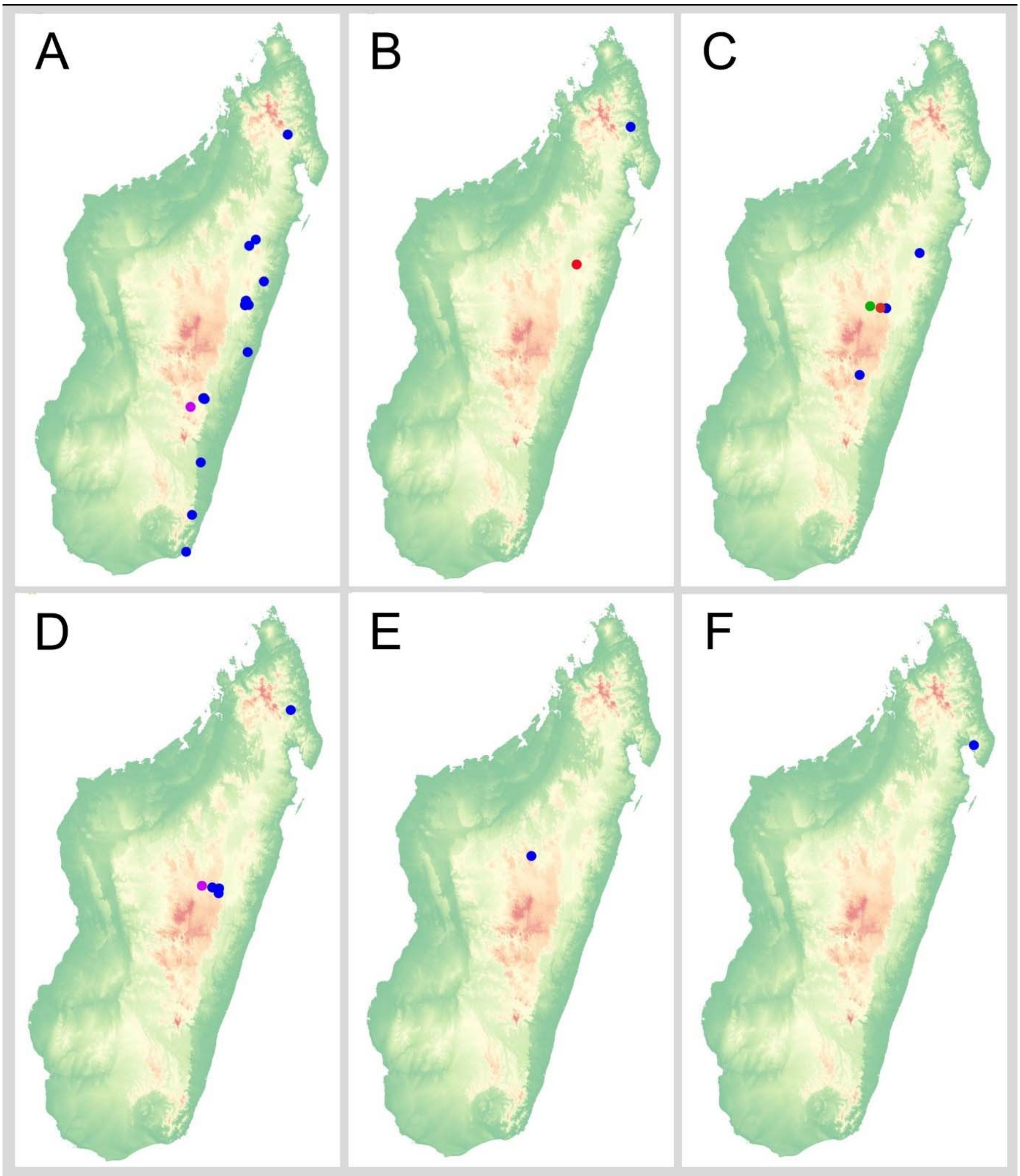


Figure 39. Distributional maps of: A – *Thyrosticta sylvicolens*; B – *Skippernaclia lacrimata* **comb. nov.** (see text); C – *Skippernaclia ankaratra* **comb. nov.**; D – unidentified specimens of *S. lacrimata* **comb. nov.** / *S. ankaratra* **comb. nov.** (see text); E – *Skippernaclia vestigii* **comb. nov.**; F – *Skippernaclia leesi* **sp. nov.**

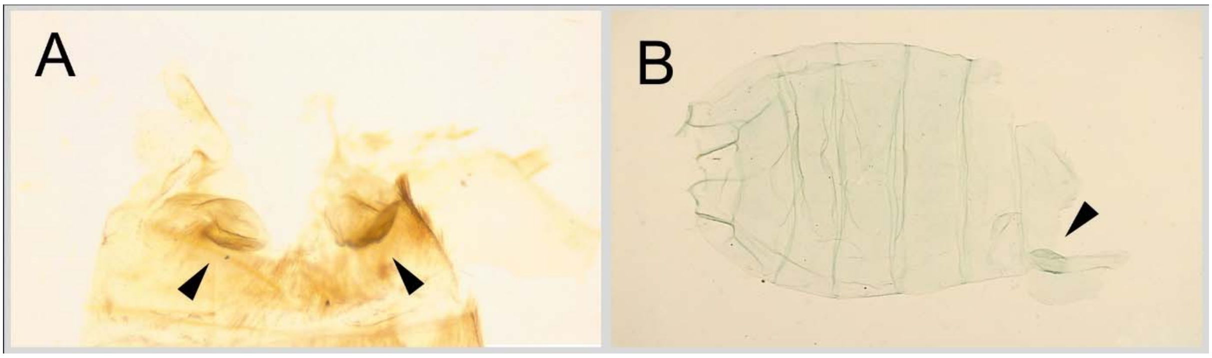


Figure 40. Pouch-like cavities between the 6th and 7th sternites in the female abdomen of *Skippernaclia* **gen. nov.**: A – *Skippernaclia lacrimata* **comb. nov.**; B – *Skippernaclia leesi* **sp. nov.** (holotype, NHMUK015109746, genitalia slide NHMUK [to be provided later]).

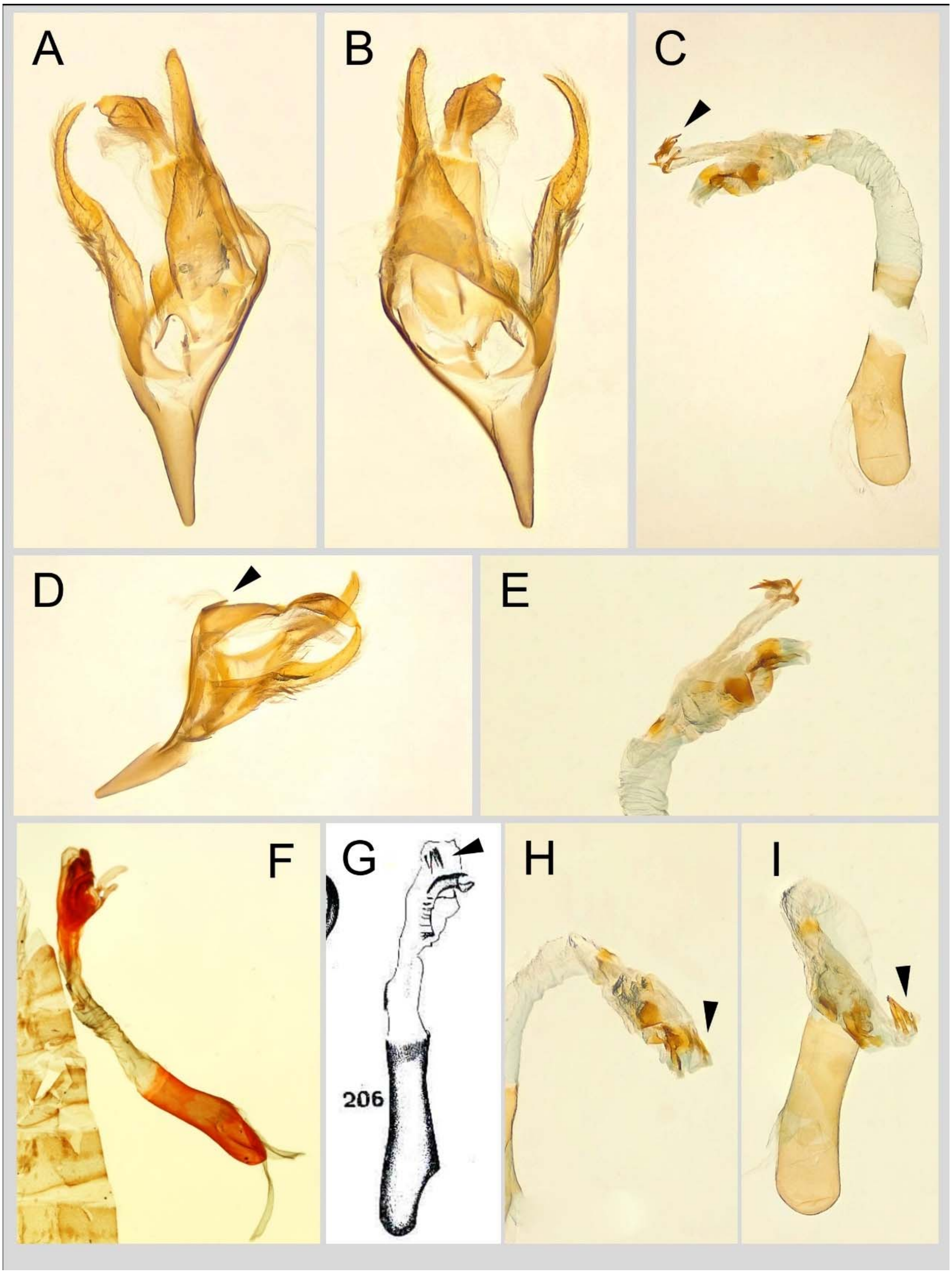


Figure 41. Male genitalia of *Skippernaclia lacrimata* **comb. nov.**, note the terminal cornuti of vesica, which are hardly visible in certain arrangements: A-E – specimen MNHN, CLV_3 - EL83636; F – the original slide P. Griveaud slide No. 264; G – the original illustration from Griveaud (1964: 88), cornuti marked with arrowhead; H-I – specimen NHMUK015109728, in I artificially bent to visualize the cornuti (arrowhead).

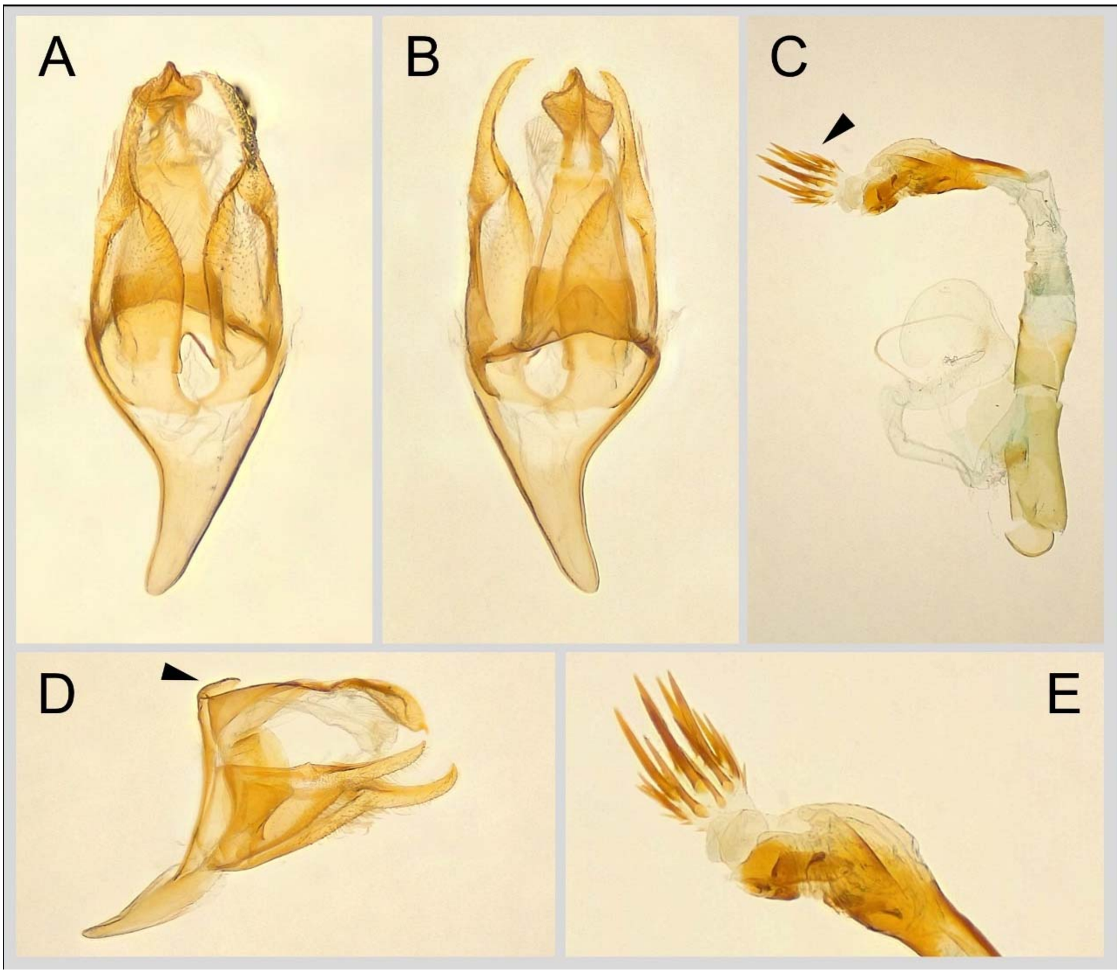


Figure 42. Male genitalia of *Skippernaclia ankaratra* **comb. nov.**

Figure 43. Male genitalia of *Skippernaclia vestigii* **comb. nov.**, original P. Griveaud slide No. 431.

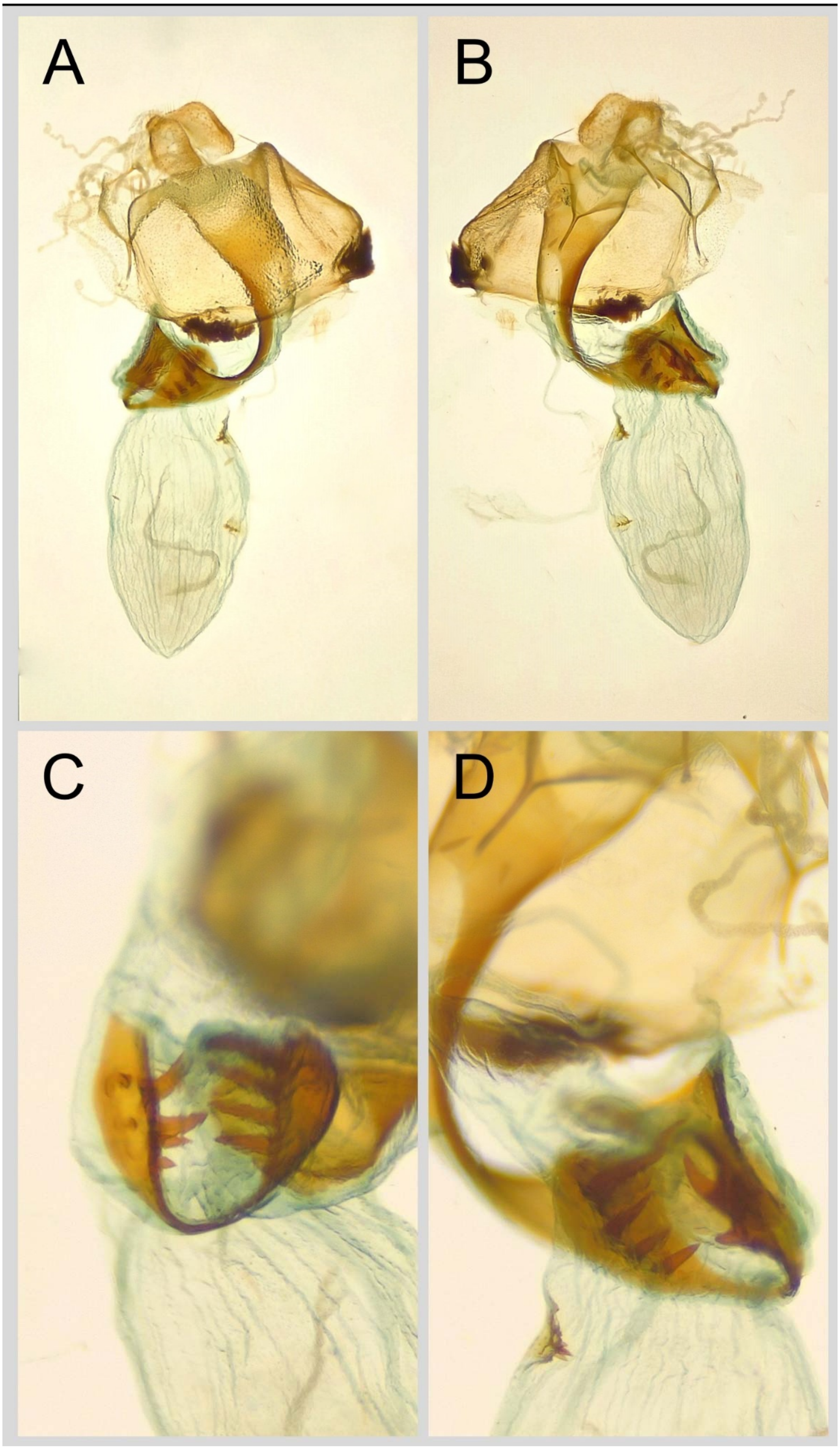


Figure 44. Female genitalia of *Skippernaclia lacrimata* **comb. nov.**

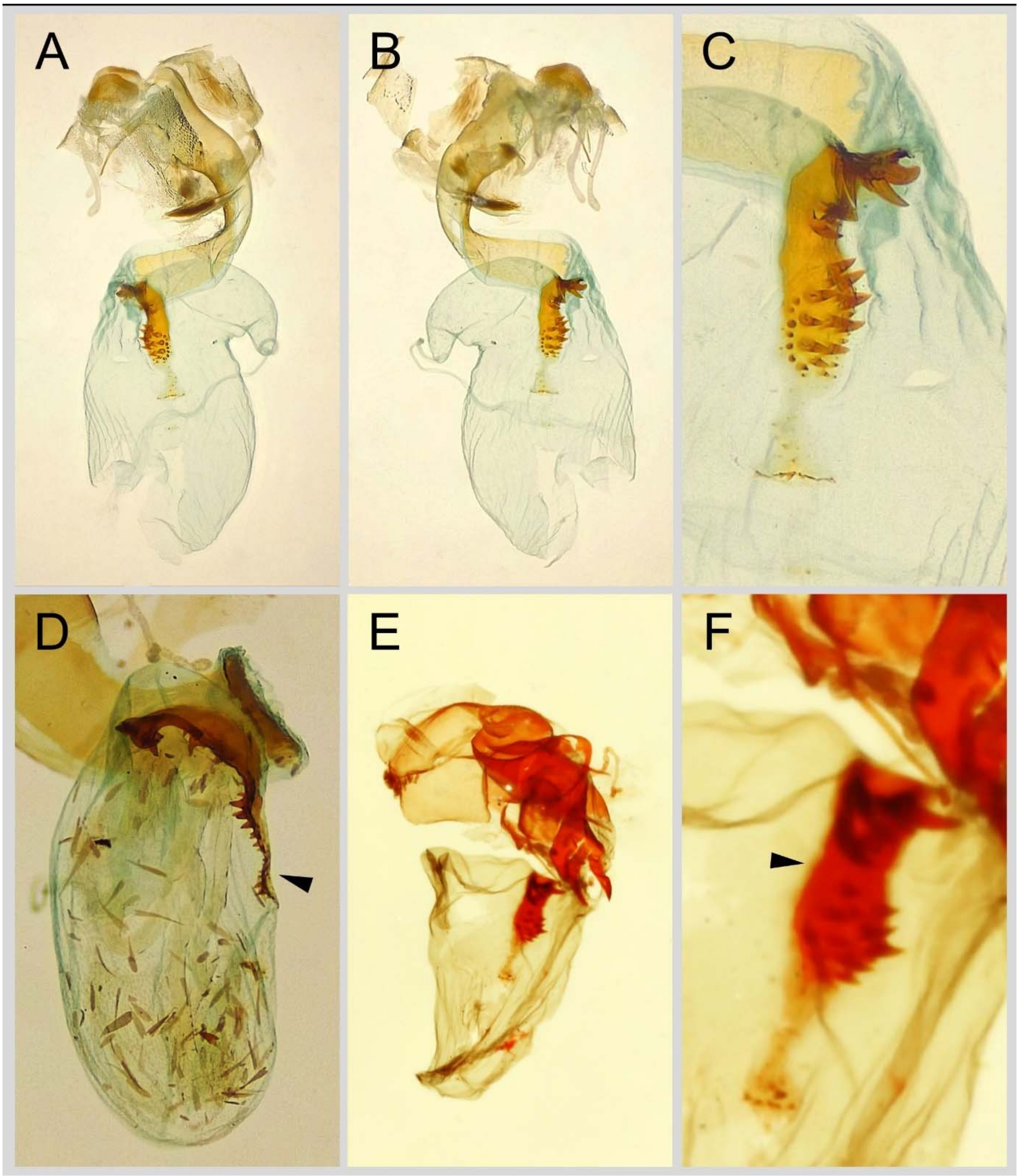


Figure 45. Female genitalia of *Skippernaclia ankaratra* **comb. nov.**: A-C – specimen ISEA PAS, DL_06-051, D – specimen ISEA PAS, MAD_110, note the elongate basal signum extended laterally (arrowhead), and colla in corpus bursae; E-F – the original P. Griveaud slide No. 265, designated as „allotype" of *Thyrosticta lacrimata* (see text), note the signum shape specific to *S. ankaratra* **comb. nov.** (arrowhead).

Figure 46. Female genitalia of *Skippernaclia vestigii* **comb. nov.**

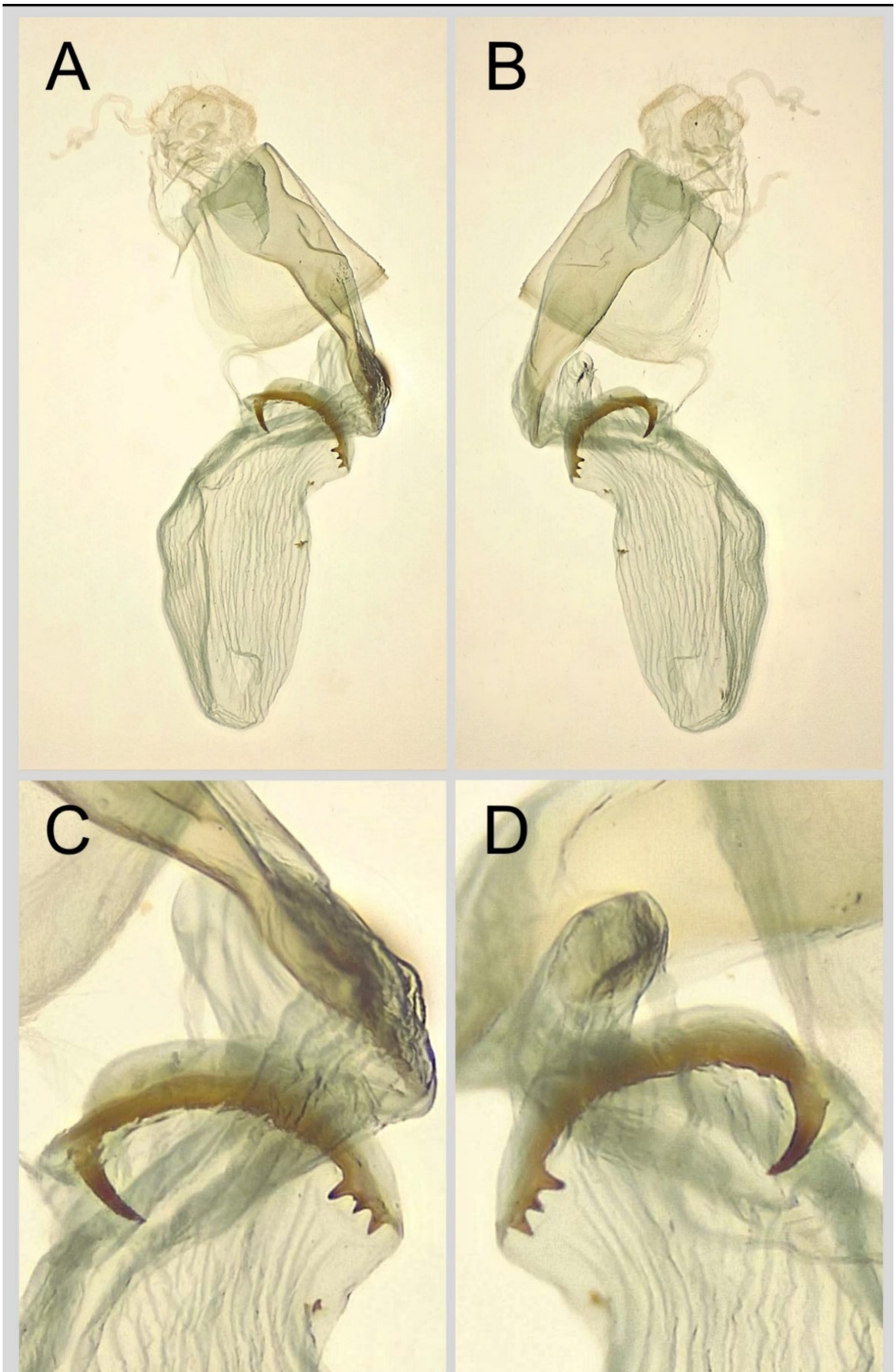


Figure 47. Female genitalia of *Skippernaclia leesi* **sp. nov.**

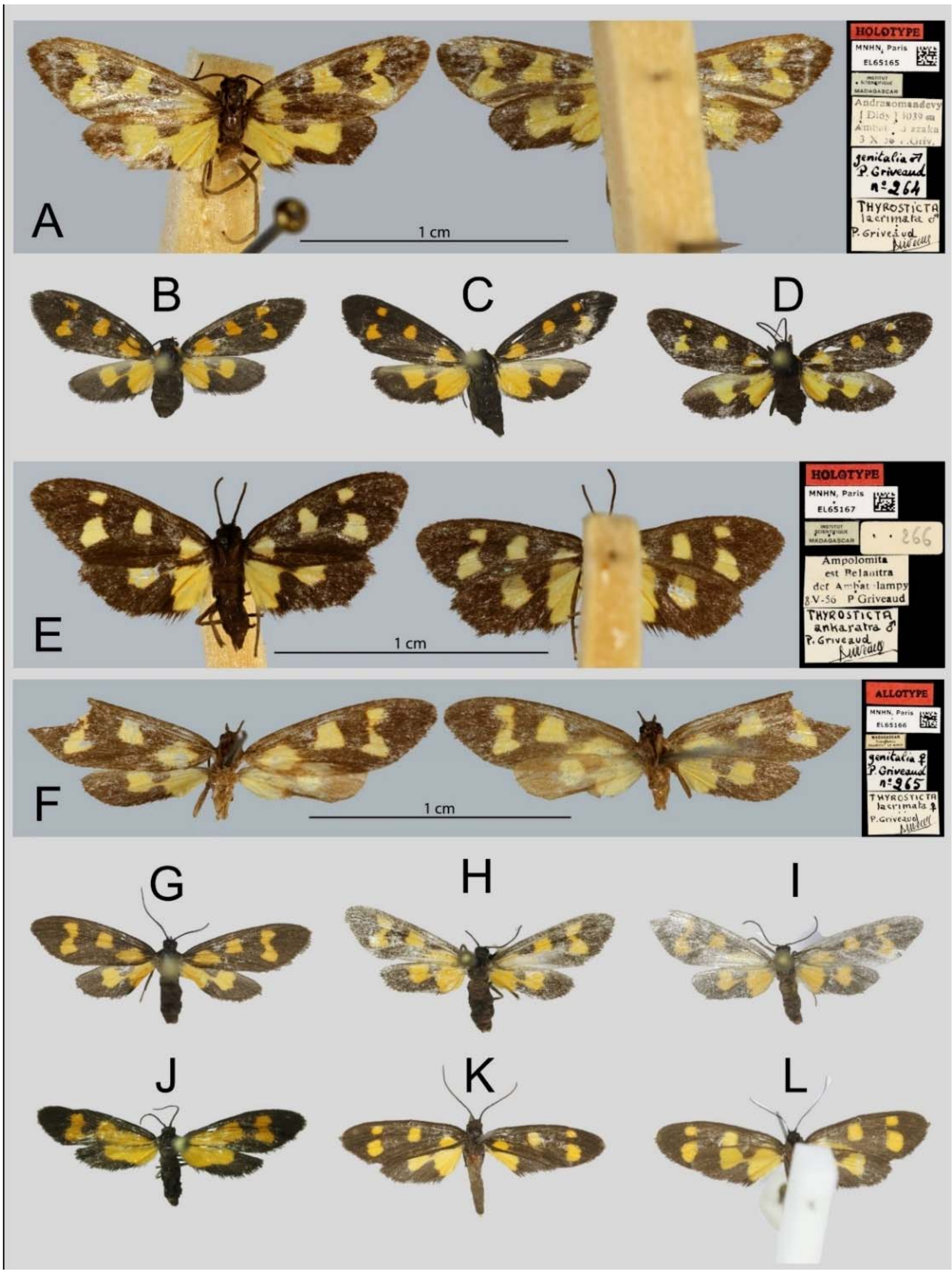


Figure 48. Genus *Skippernaclia* **gen. nov.**, adults: A – *S. lacrimata* **comb. nov.** male holotype, MNHN, EL65165; B – *S. lacrimata* **comb. nov.** female, MNHN, CLV_7; C – *S. lacrimata* **comb. nov.** male, MNHN, CLV_3; D – *S. lacrimata* **comb. nov.** male, NHMUK015109728; E – *S. ankaratra* **comb. nov.** male holotype, MNHN, EL65167; F – *S. ankaratra* **comb. nov.** female, designed by Griveaud (1964) as the allotype of *Thyrosticta lacrimata* (see text), MNHN, EL65166; G – *S. ankaratra* **comb. nov.** female, MAD_108; H – *S. ankaratra* **comb. nov.** female, MAD_110; I – *S. ankaratra* **comb. nov.** female, MAD_111; J – *S. vestigii* **comb. nov.** female, MAD_169; K – *S. leesi* **sp. nov.**, holotype, NHMUK015109746, upperside; L – *S. leesi* **sp. nov.** holotype, underside; not to the same scale.

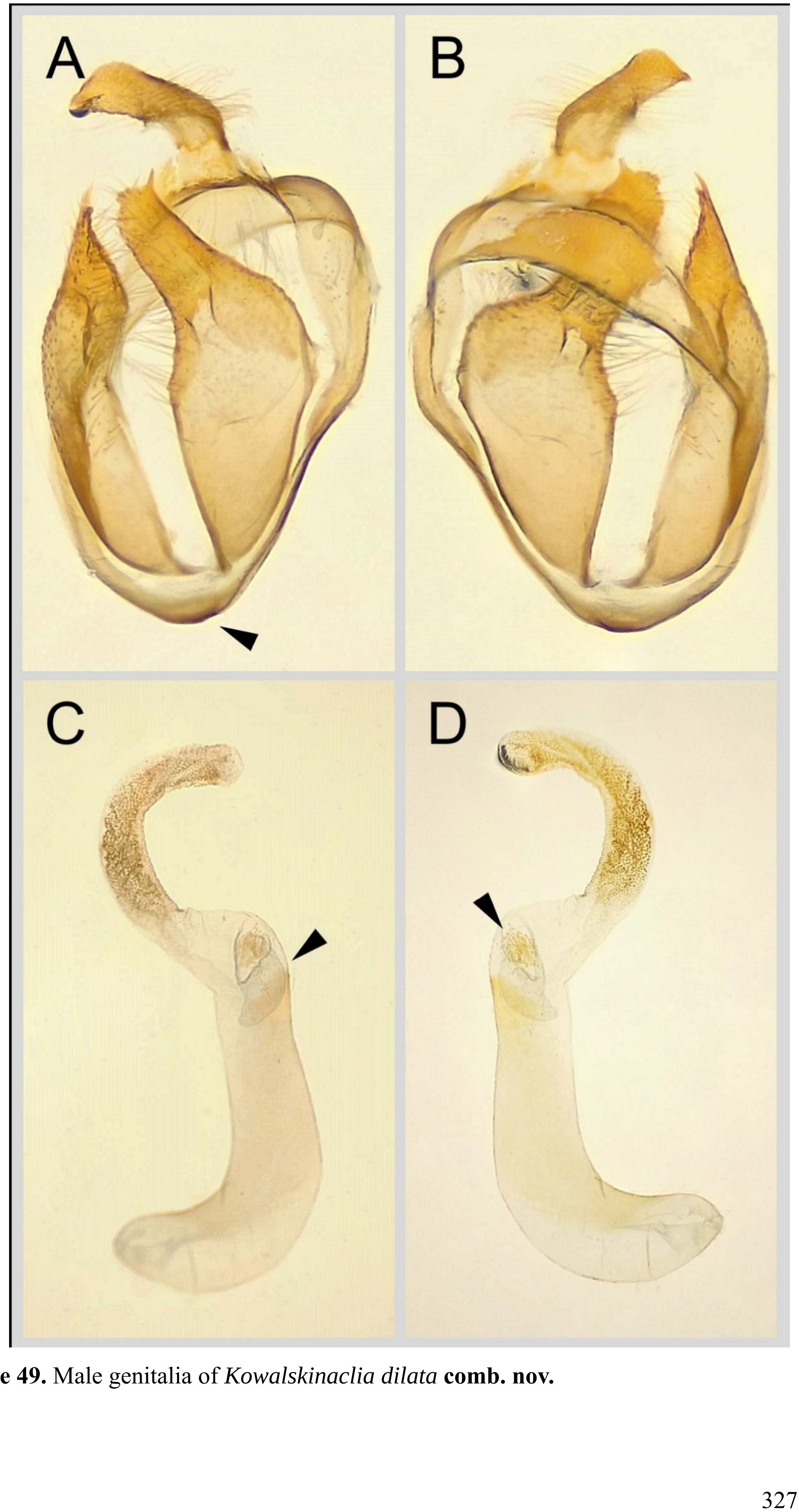


Figure 49. Male genitalia of *Kowalskinaclia dilata* **comb. nov.**

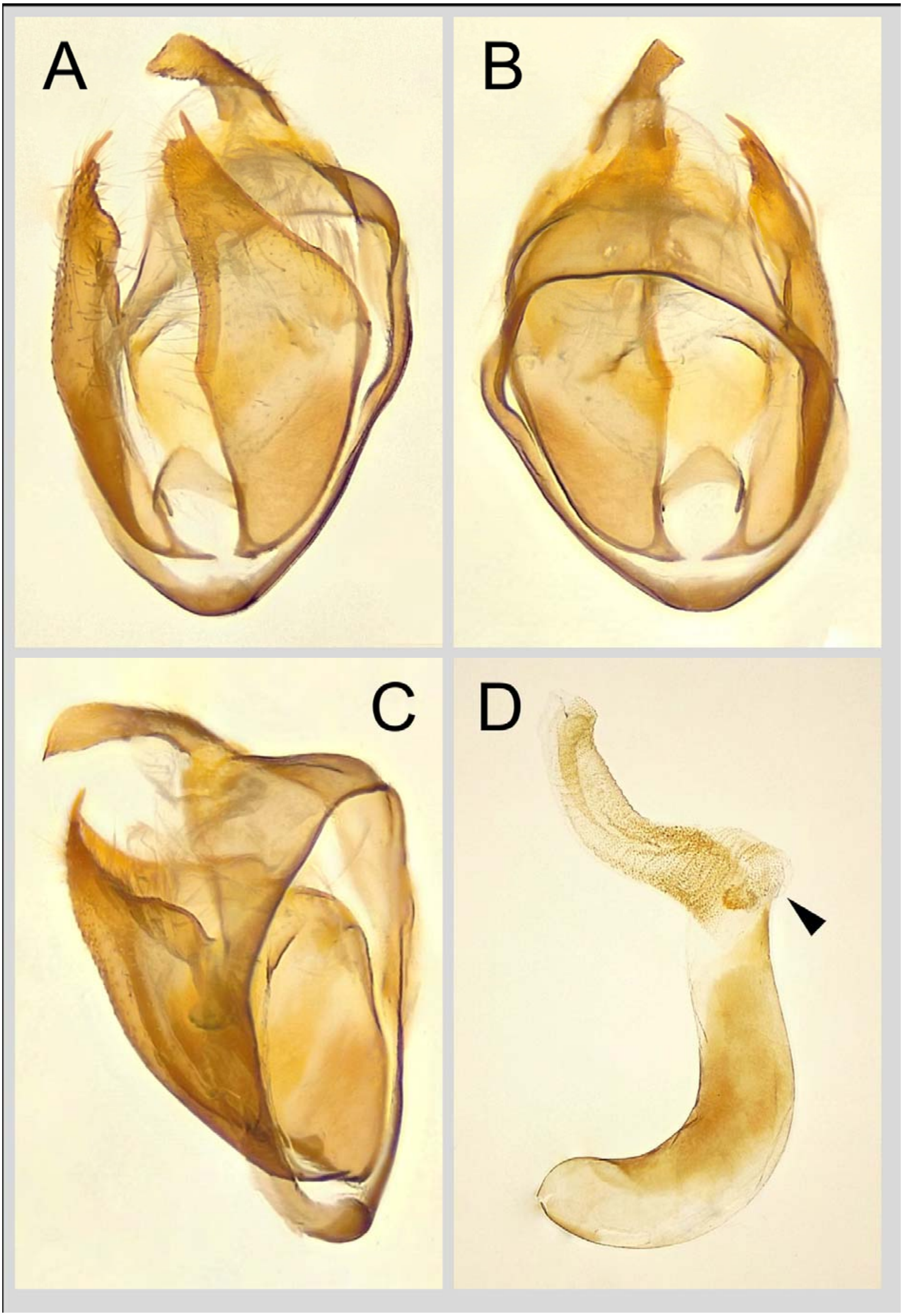


Figure 50. Male genitalia of *Kowalskinaclia vieui* **comb. nov.**

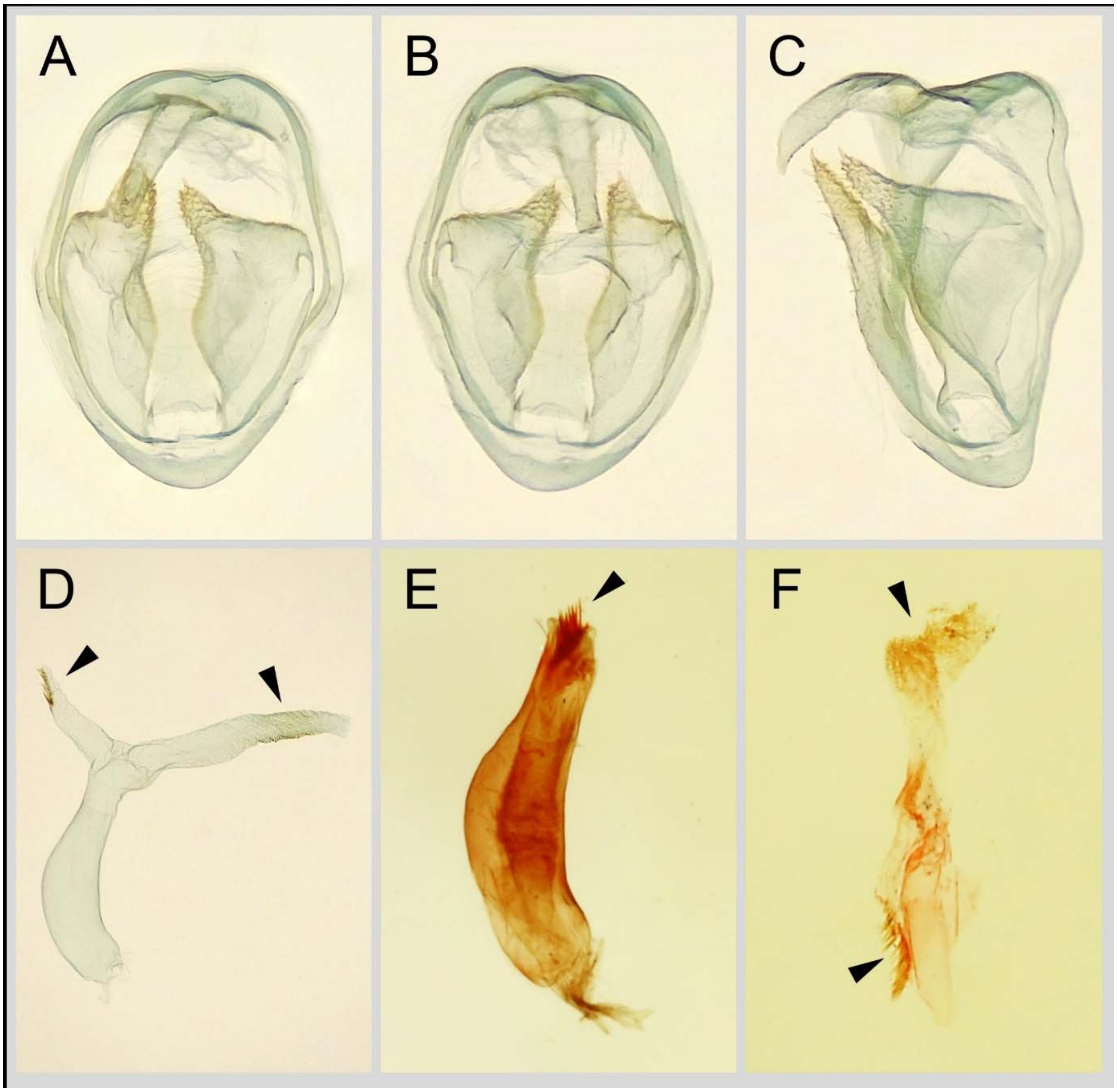


Figure 51. Male genitalia of *Kowalskinaclia cowani* **comb. nov.**: A-D – specimen ISEA PAS, MAD_025, note the cornuti of the lateral diverticulum and scobinations (arrowheads); E – phallus of the holotype of *K. cowani* **comb. nov.** (MNHN, EL65155) from the original P. Griveaud slide No. 240, note the cornuti in uneverted vesica (arrowhead); F – phallus of the holotype of *Thyrosticta incerta* **syn. nov.** (MNHN, EL65154) from the original P. Griveaud slide No. 238, note the torn vesica (arrowheads, see text).

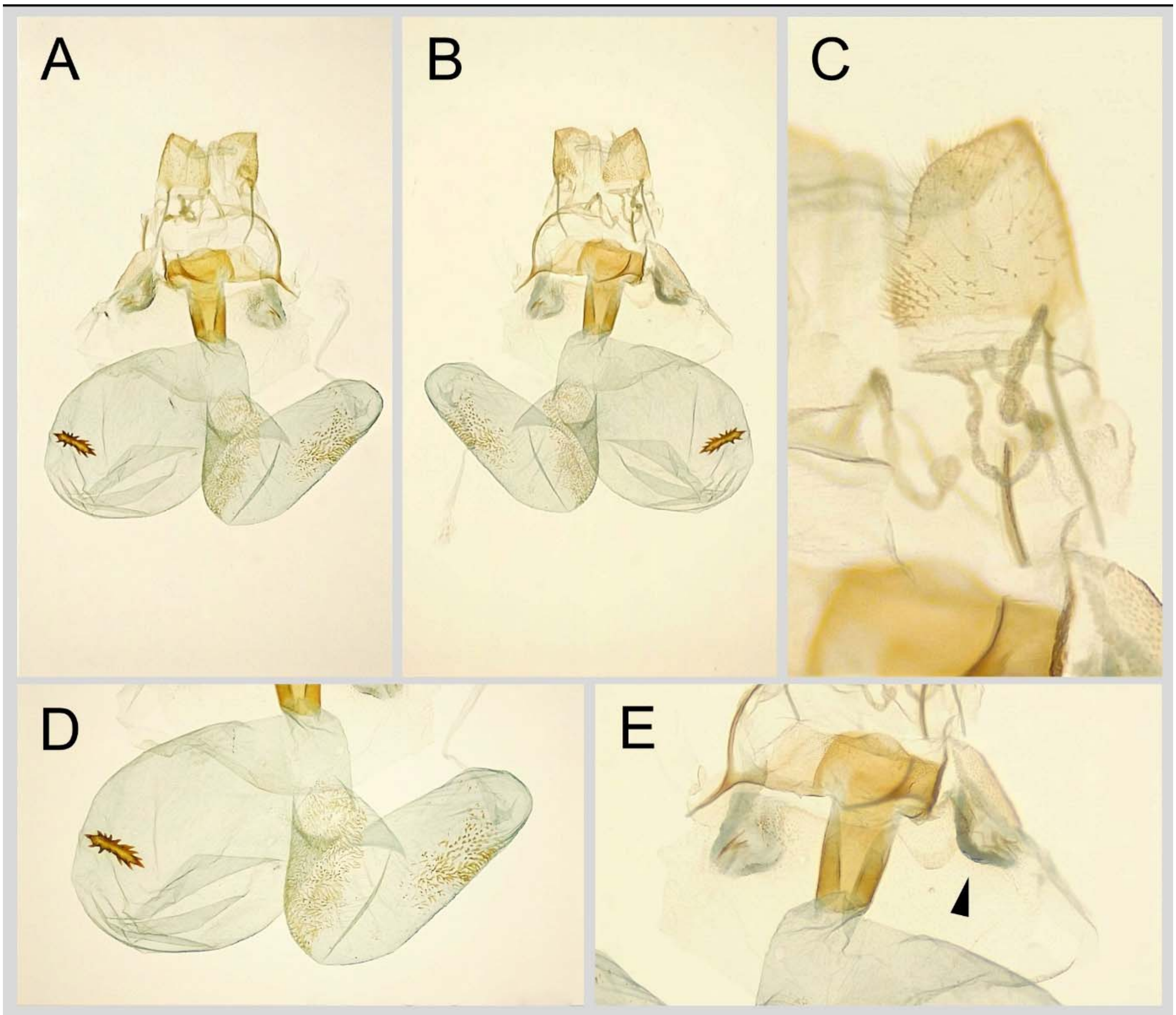


Figure 52. Female genitalia of *Kowalskinaclia vieui* **comb. nov.**, note the genus-specific cavities of the 7th sternite (arrowhead).

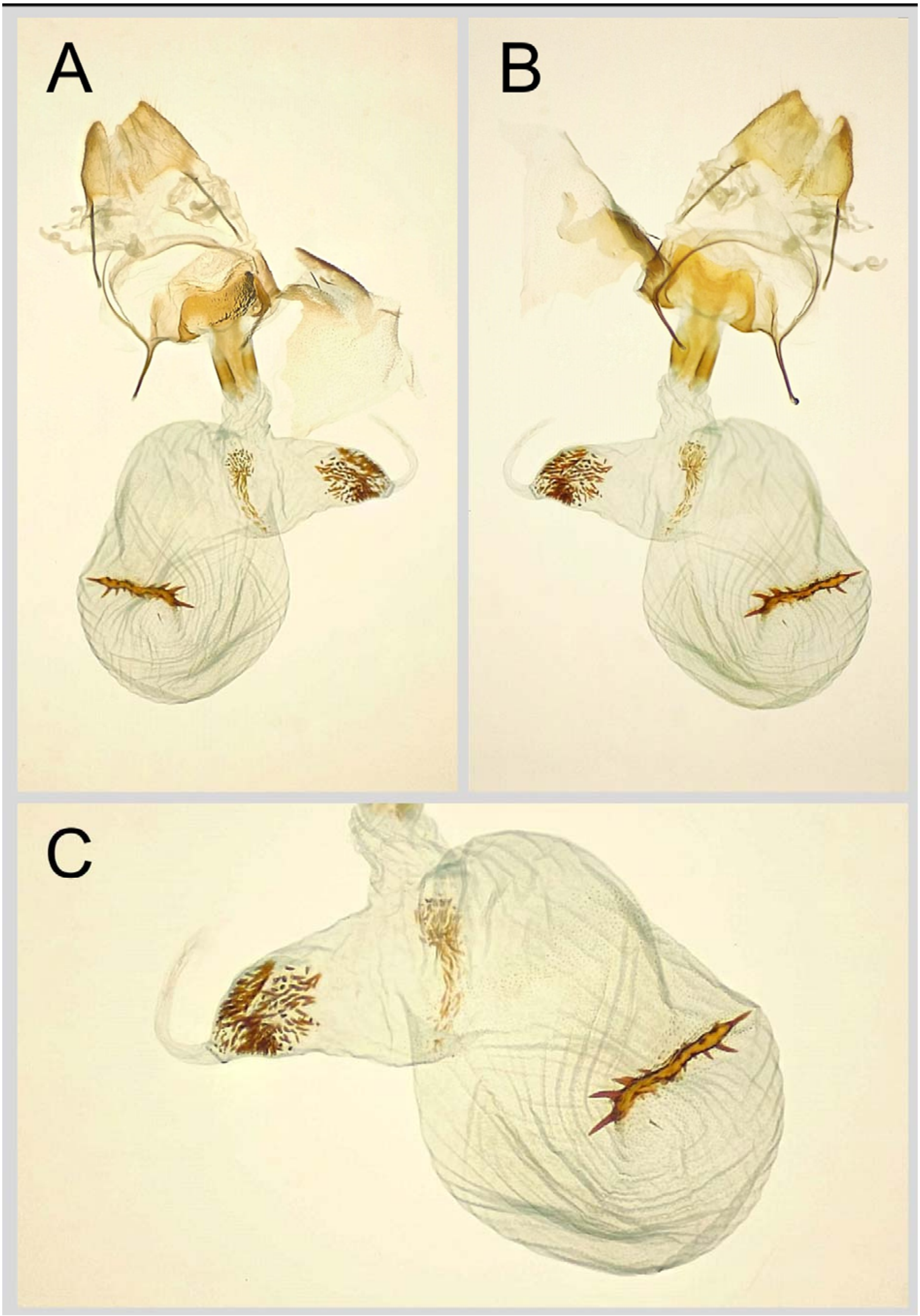


Figure 53. Female genitalia of *Kowalskinaclia cowani* **comb. nov.**

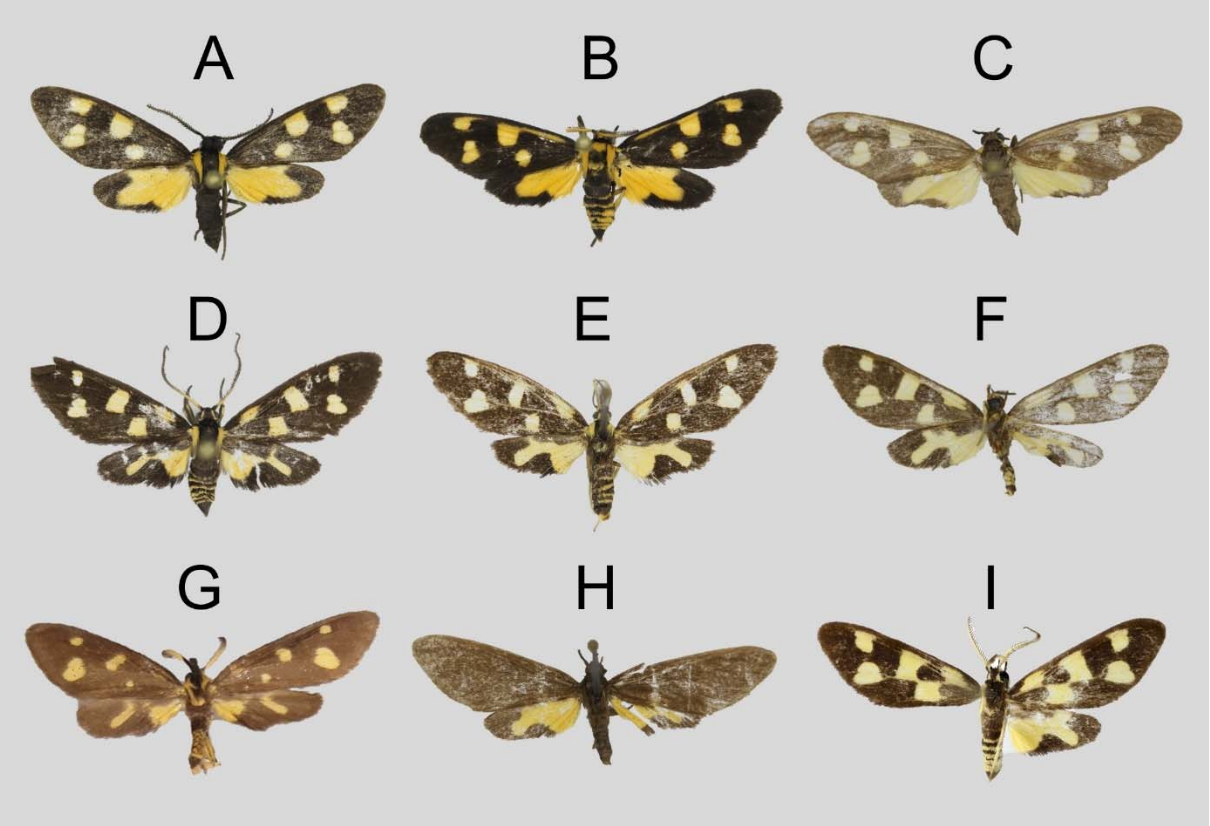


Figure 54. Genus *Kowalskinaclia* **gen. nov.**, adults: A – *K. dilata* **comb. nov.**, “black” morphotype, ISEA PAS, MAD_162, Ambohitantely S.R.; B – *K. dilata* **comb. nov.**, “yellow” morphotype, ISEA PAS, MAD_171, RS Ambohitantely.; C – *K. dilata* **comb. nov.**, “black” morphotype, Andasibe PN, ANHRTUK00215260; D – *K. vieui* **comb. nov.**, male, ISEA PAS, MAD_131; E – *K. vieui* **comb. nov.**, female, MNHN, EL74955; F – *K. vieui* **comb. nov.**, male, ISEA PAS, DL_14R-218; G – *K. vieui* **comb. nov.**, male, MNHN, EL82906; H – *K. vieui* **comb. nov.**, male, MNHN, EL74951; I – *K. vieui* **comb. nov.**, “quadrata” NHMUK010621702 (see text); not to the same scale.

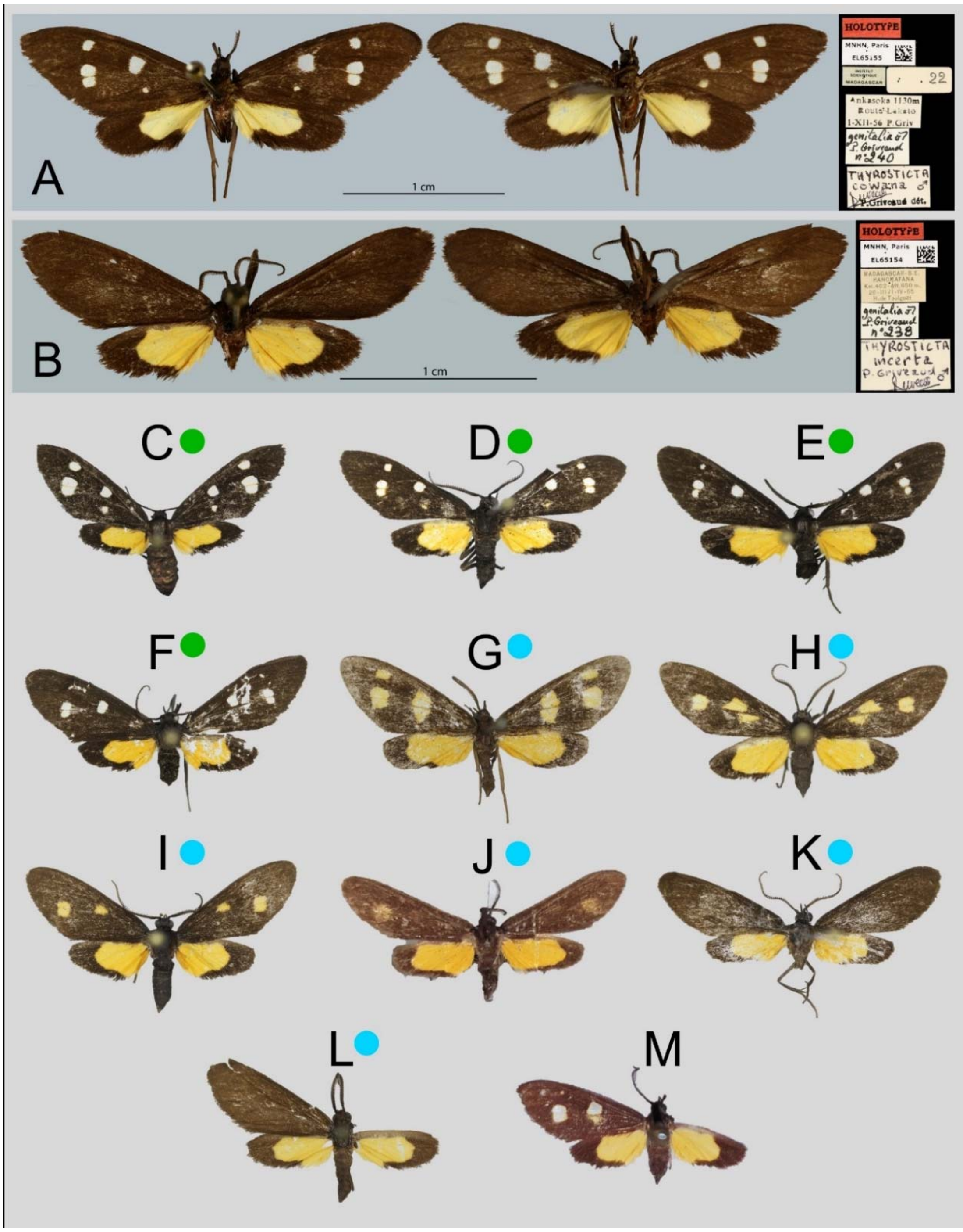


Figure 55. *Kowalskinaclia cowani* **comb. nov.** adults: A – male holotype, MNHN, EL65155; B – male holotype of *Thyrosticta incerta* **syn. nov.**, MNHN, EL65154; C – female, ISEA PAS, MAD_075; D – male, ISEA PAS, MAD_037; E – male, ISEA PAS, MAD_100; F – male, ISEA PAS, MAD_036; G – male, MNHN, EL74886; H – male, ISEA PAS, ISEZ-DNA_522; I – male, ISEA PAS, ISEZ-DNA_521; J – male, MNHN, EL82616; K – male, ISEA PAS, MAD_273; L – male, MNHN, EL74950; M – ambiguous specimen (sex unknown) from Ambohimahasoa Tsarafidy, PZBT (see text); not to the same scale.

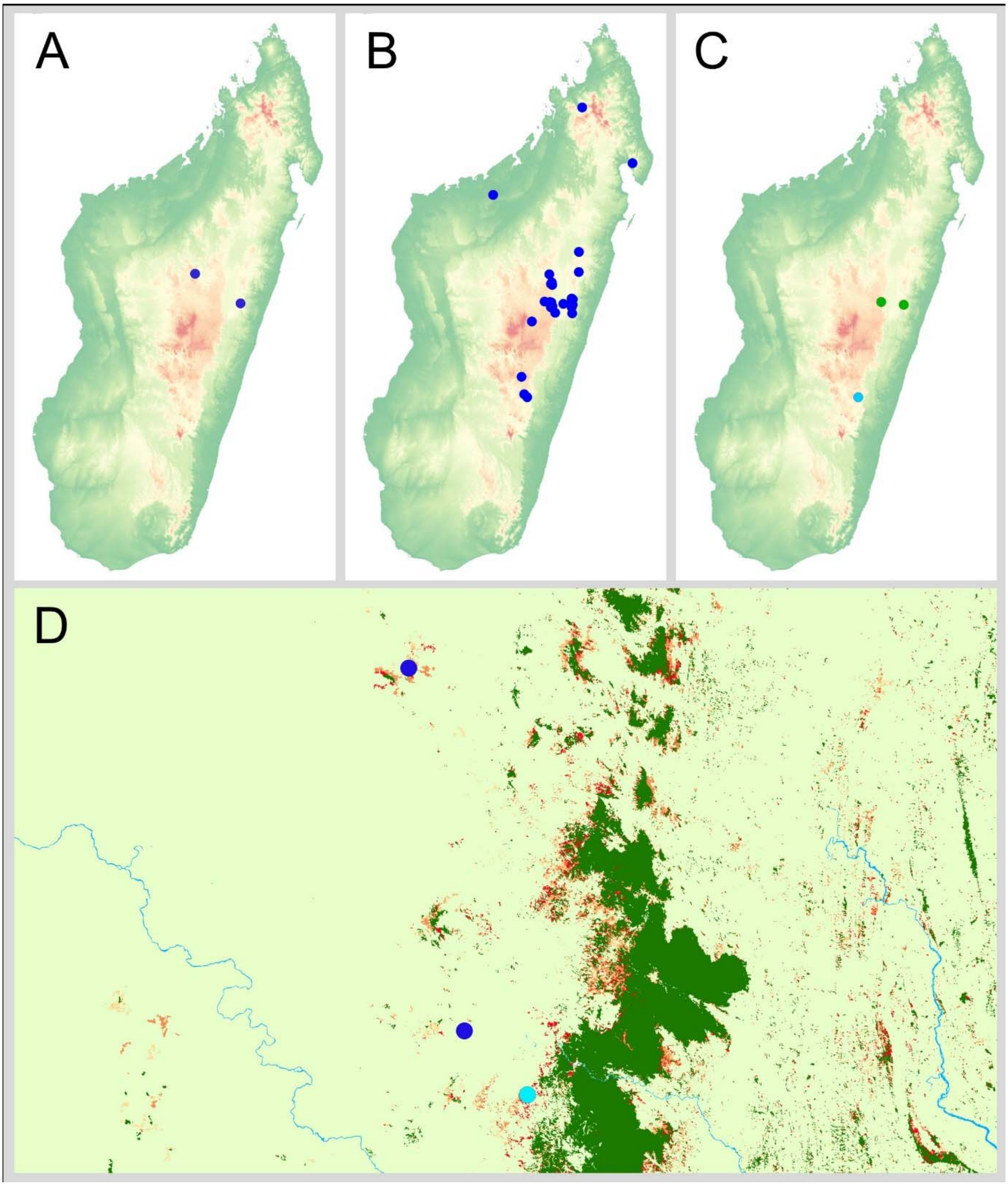


Figure 56. Distributional maps of *Kowalskinaclia* **gen. nov.**: A – *K. dilata* **comb. nov.**; B – *K. vieui* **comb. nov**.; C – specimens of *K. vieui* **comb. nov.** representing the potential cryptic species (see text), colour of the points corresponds with marks in the phylogenetic tree; D – deforestation (pale orange to red, from 2000 to 2020) in the area of occurrence of southern population of southern population of *K. vieui* **comb. nov.**

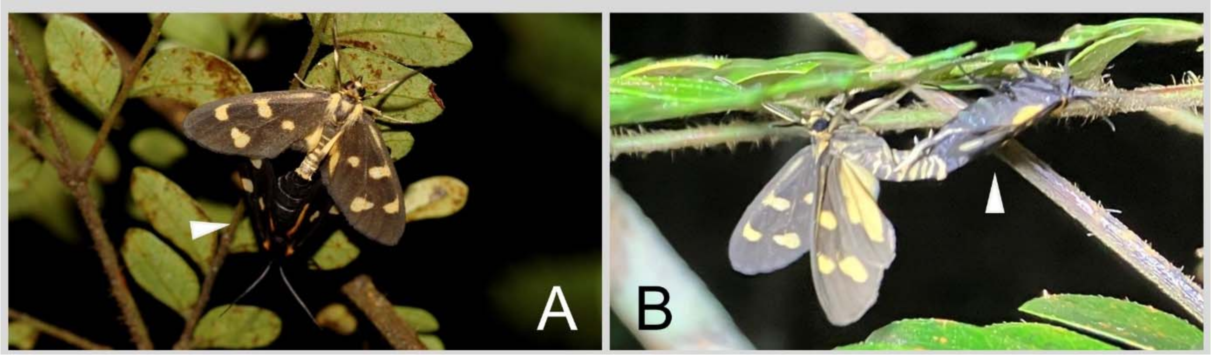


Figure 57. *Kowalskinaclia dilata* **comb. nov.** *in copula*, the first observation of the female of the species (arrowheads, see text) (photo: Len de Beer).

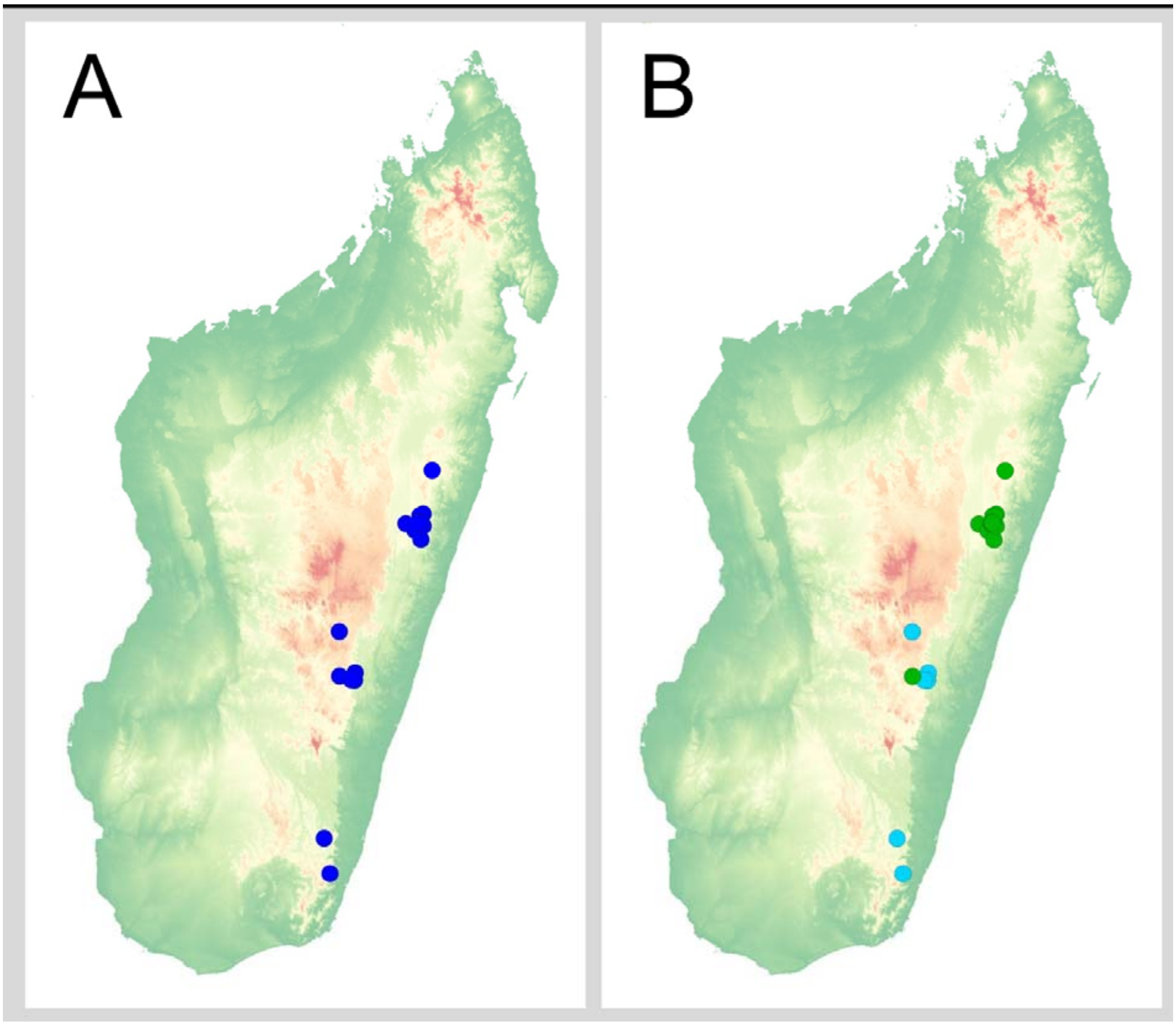


Figure 58. Distributional maps of *Kowalskinaclia cowani* **comb. nov.**: A – general distribution; B – distribution of the specimens representing the potential cryptic species (see text); colours of the dots correspond with the relevant marks in the phylogenetic tree (see text).

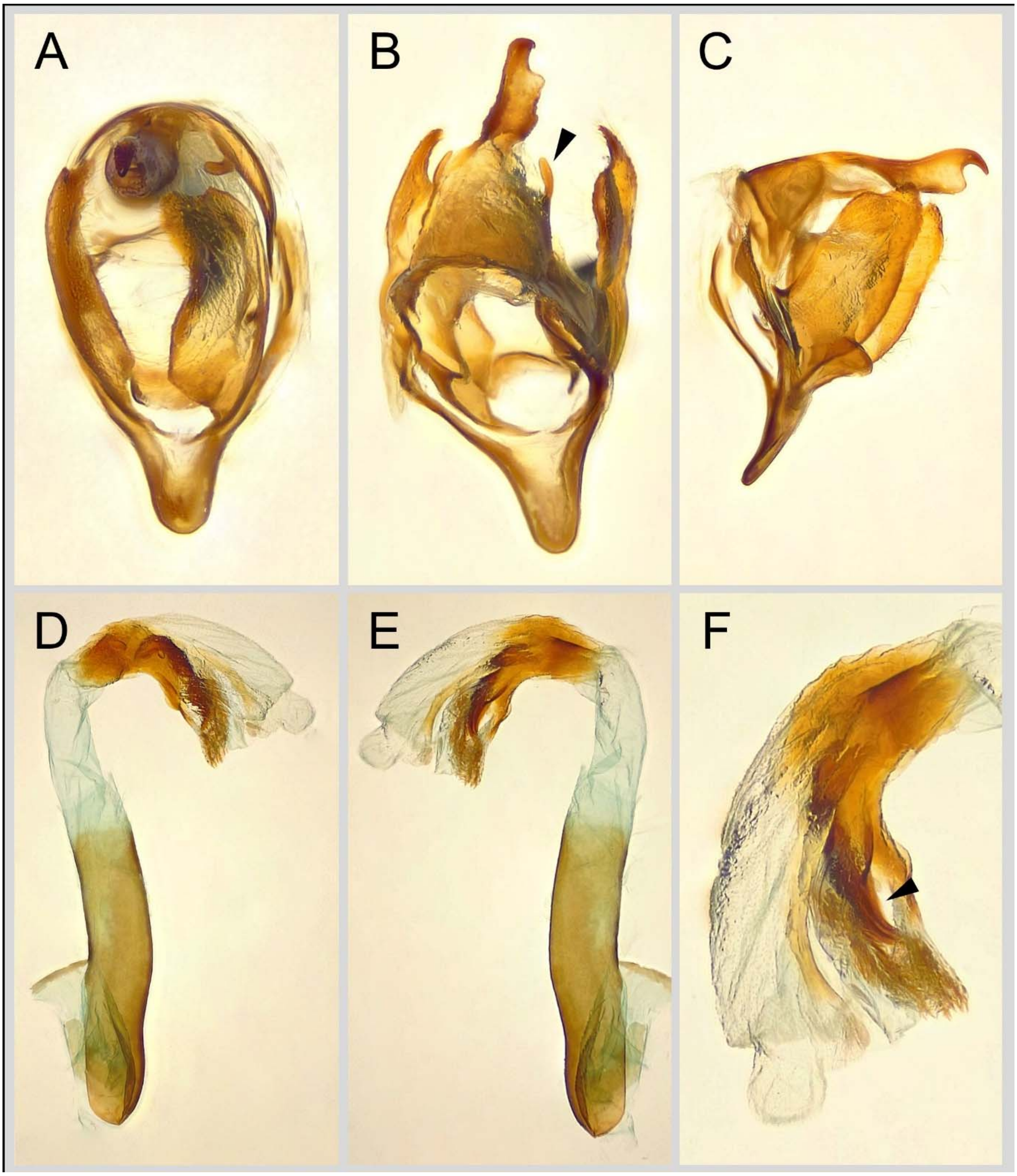


Figure 59. Male genitalia of *Privatenaclia seguyi* **comb. nov.**, note the genus-specific sublateral arms of tegumen, and the shape of the plaque on vesica (arrowheads, see text).

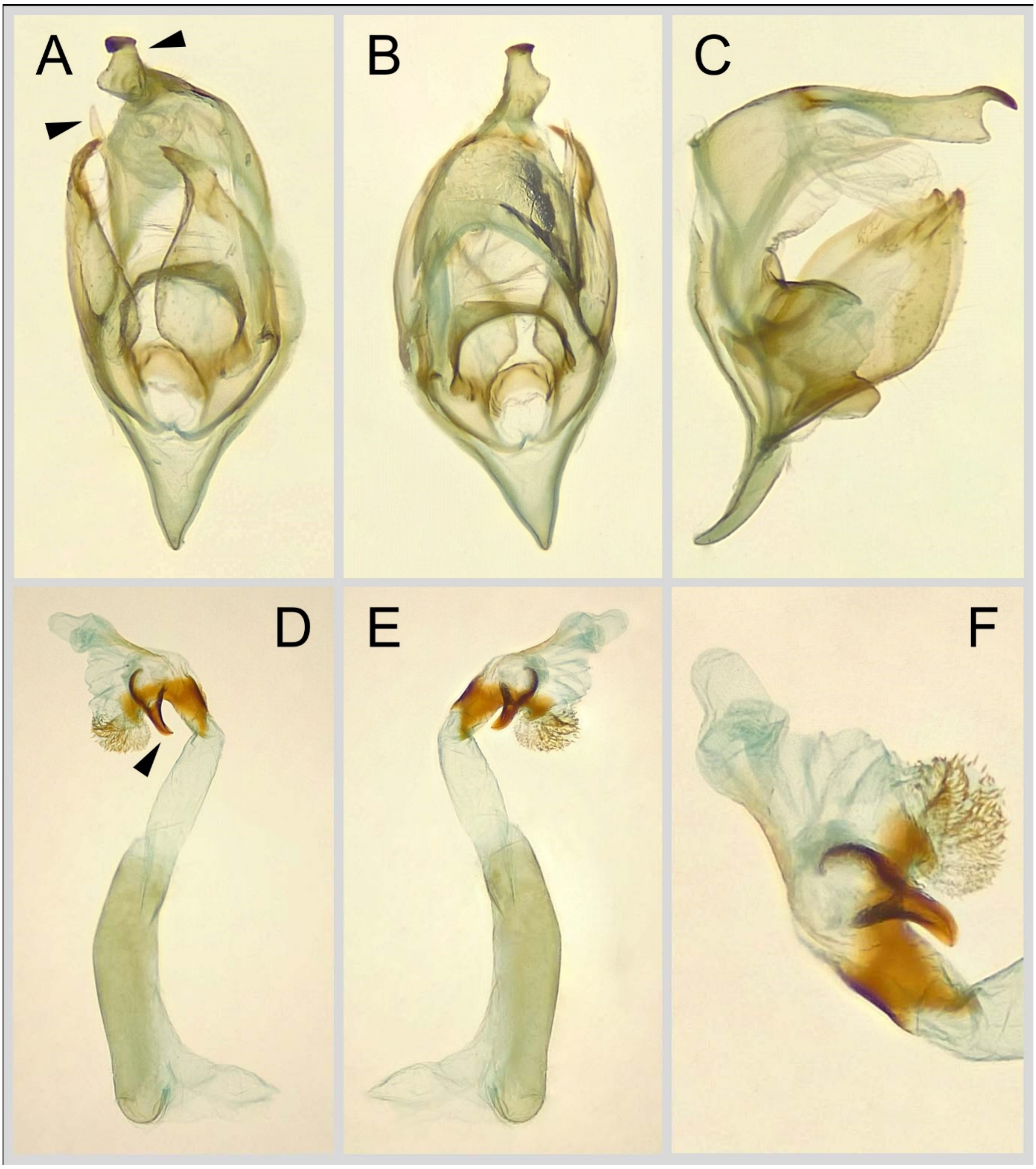


Figure 60. Male genitalia of *Privatenaclia ratovosoni* **comb. nov.**, note the genus-specific shape of the uncus, sublateral arms of the tegumen, and beak-shaped plaque on the vesica (arrowheads, see text).

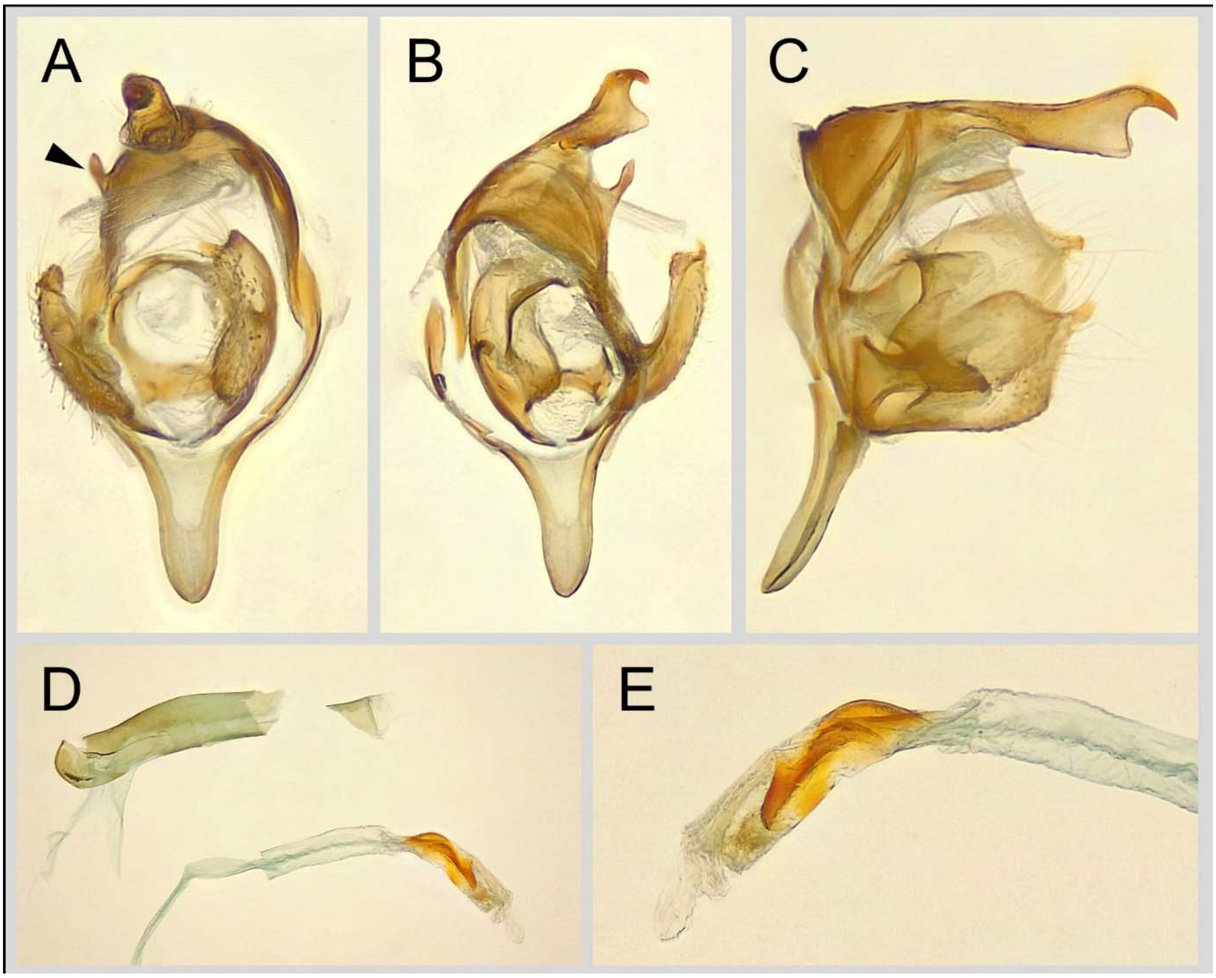


Figure 61. Male genitalia of *Privatenaclia triangulifera* **comb. nov.**

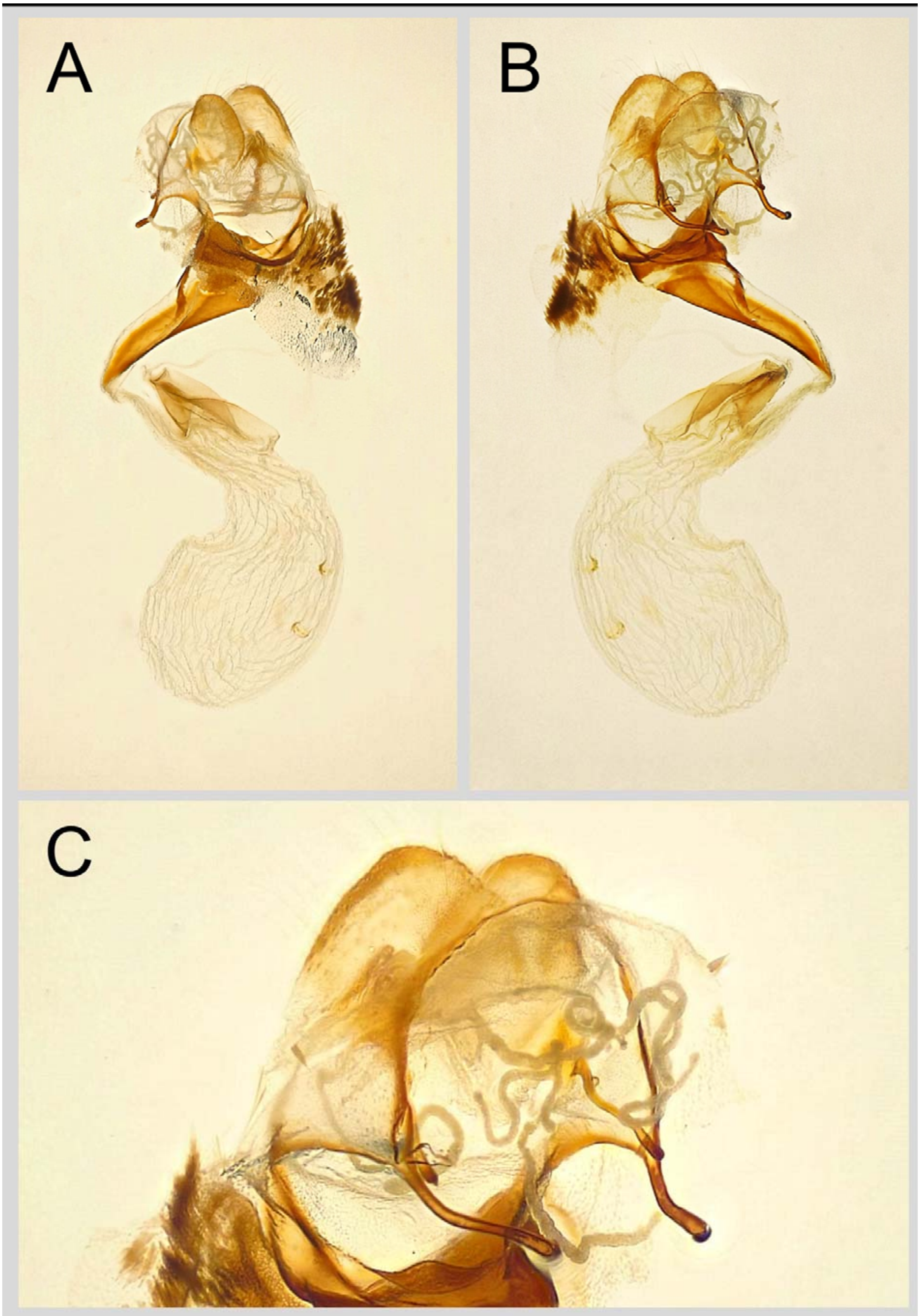


Figure 62. Female genitalia of *Privatenaclia seguyi* **comb. nov.**

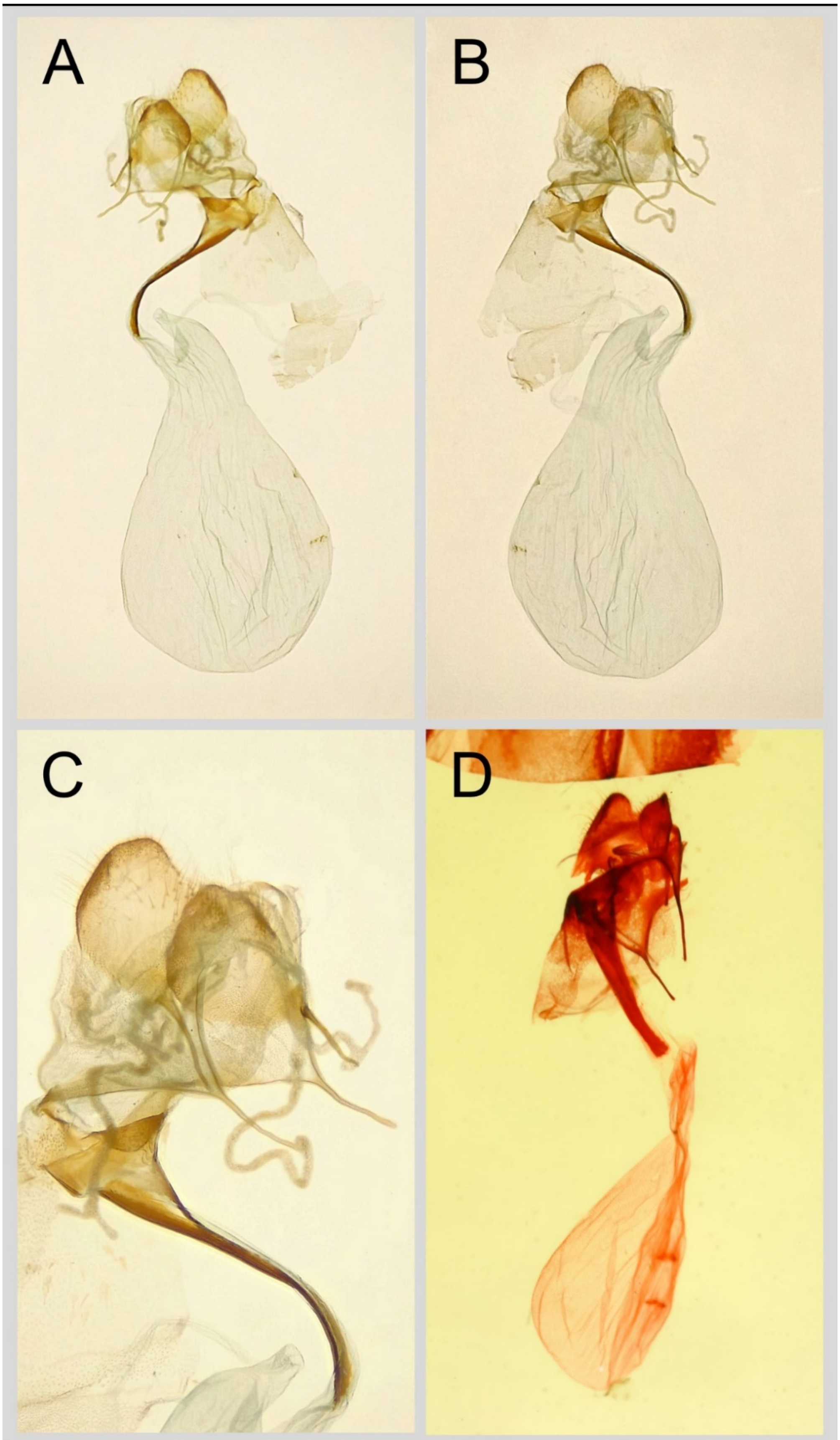


Figure 63. Female genitalia of *Privatenaclia* **gen. nov.**: A-C – *P. ratovosoni* **comb. nov.**; D – *P. triangulifera* **comb. nov.**, the original P. Griveaud slide No. 414.

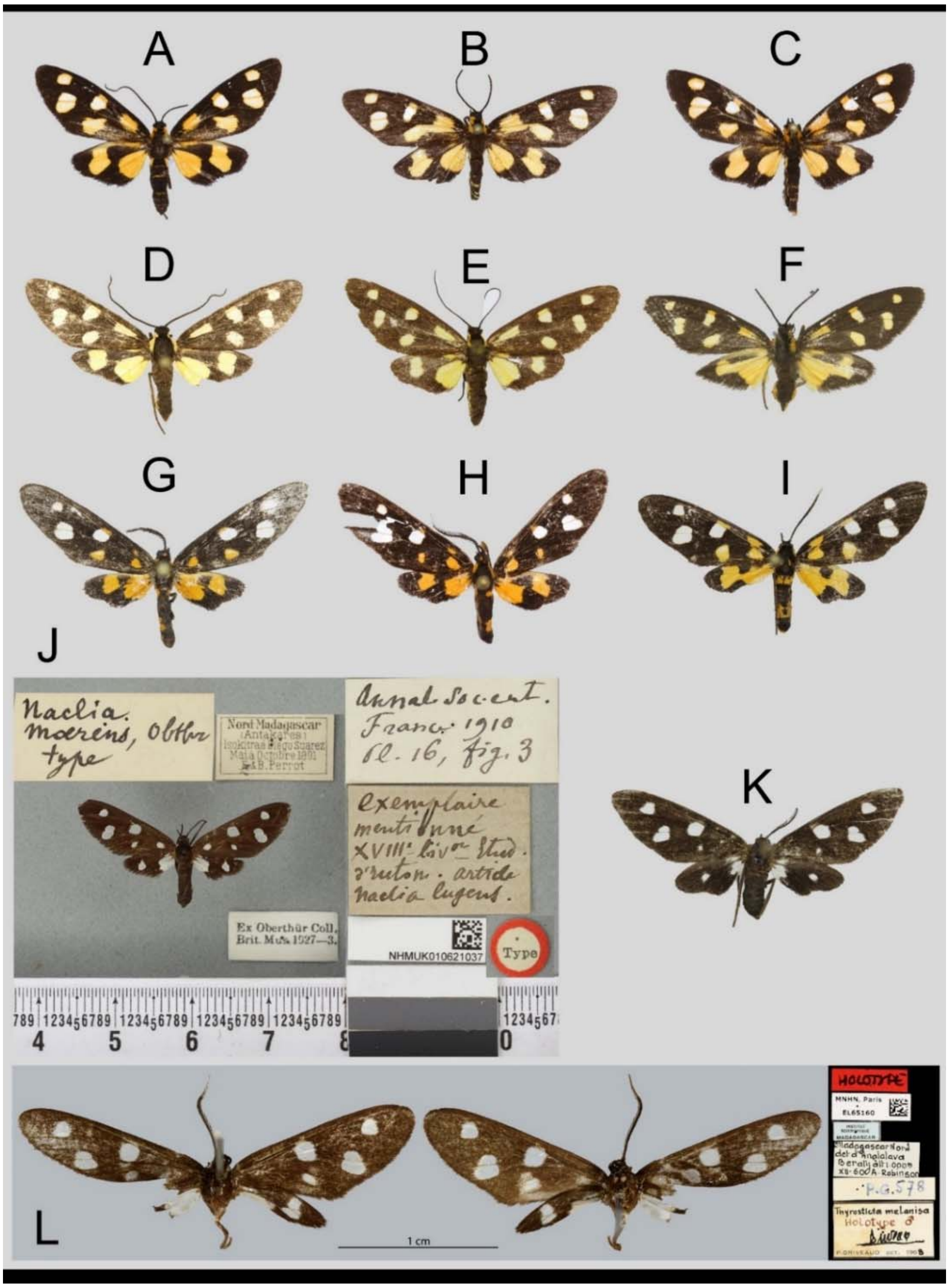


Figure 64. *Privatenaclia* **gen. nov.** and *Julienaclia* **gen. nov.**, adults: A – *P. seguyi* **comb. nov.** male, ISEA PAS, DL_2968; B – *P. seguyi* **comb. nov.** male, ISEA PAS, DL_06-347; C – *P. seguyi* **comb. nov.** female, ISEA PAS DL_2973; D – *P. ratovosoni* **comb. nov.** male, ISEA PAS, MAD_008; E – *P. ratovosoni* **comb. nov.** female, MNHN, EL82638; F – *P. triangulifera* **comb. nov.** male, ISEA PAS, MAD_274; G – *J. pauliani* **comb. nov.** male, MNHN, MA_16-6; H – *J. pauliani* **comb. nov.** male, ISEA PAS, DL_02-92; I – *J. pauliani* **comb. nov.** female, ISEA PAS, DL_02-109; J – *J. moerens* **comb. nov.** female holotype, NHMUK010621037; K – *J. moerens* **comb. nov.** male, MNHN, DL83058; L – *Thyrosticta melanisa* **syn. nov.**, male holotype, MNHN, EL65160; not to the same scale.

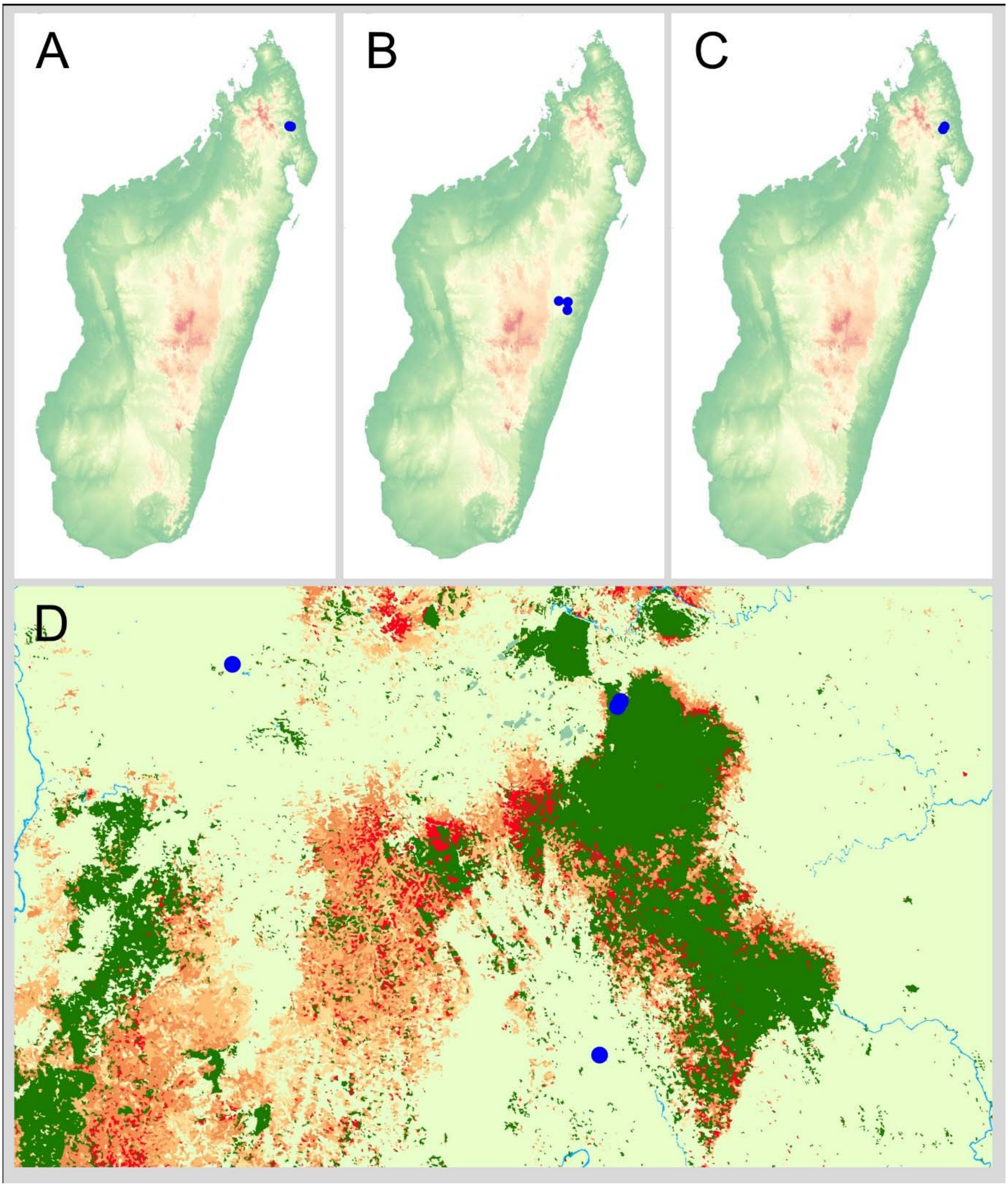


Figure 65. Distributional maps of *Privatenaclia* **gen. nov.**: A - *P. seguyi* **comb. nov.**; B – *P. ratovosoni* **comb. nov.**; C – *P. triangulifera* **comb. nov.**; D – deforestation (pale orange to red, from 2000 to 2020) in the area of occurrence of *P. ratovosoni* **comb. nov.** (see text).

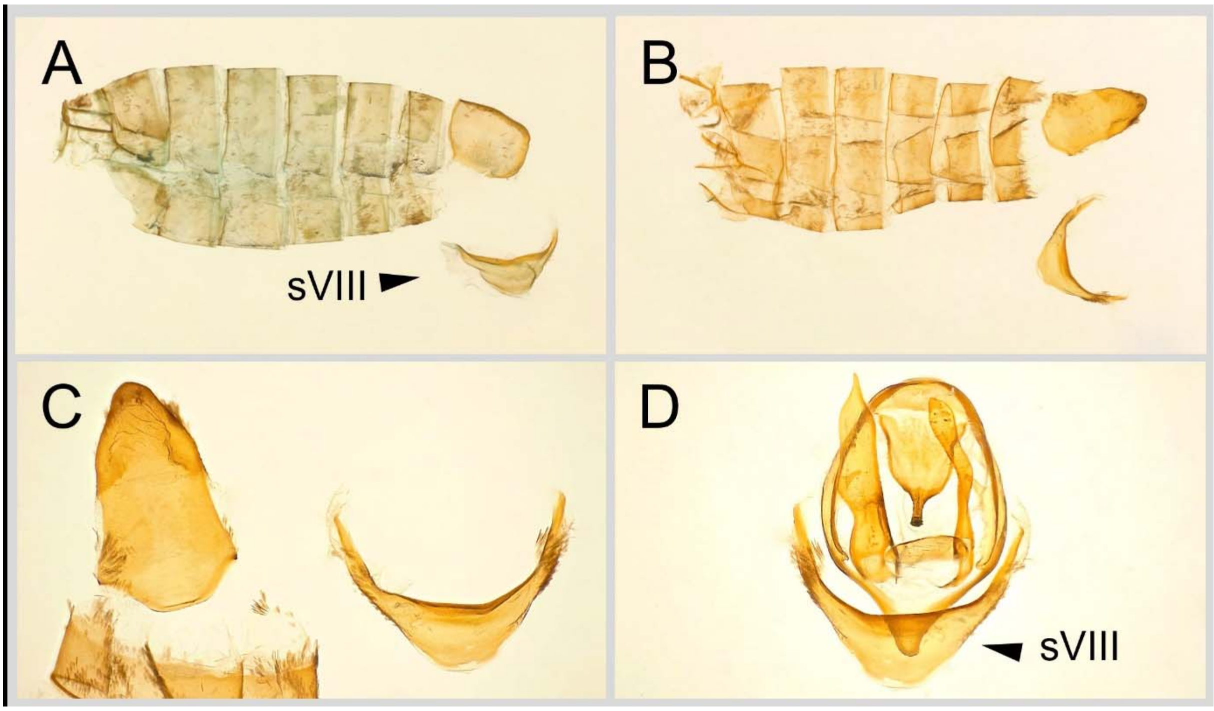


Figure 66. Male abdomen in *Julienaclia* **gen. nov.**, with transformed 8th sternite: A – *J. pauliani* **comb. nov.**; B-D – *J. moerens* **comb. nov.**; sVIII - 8th sternite.

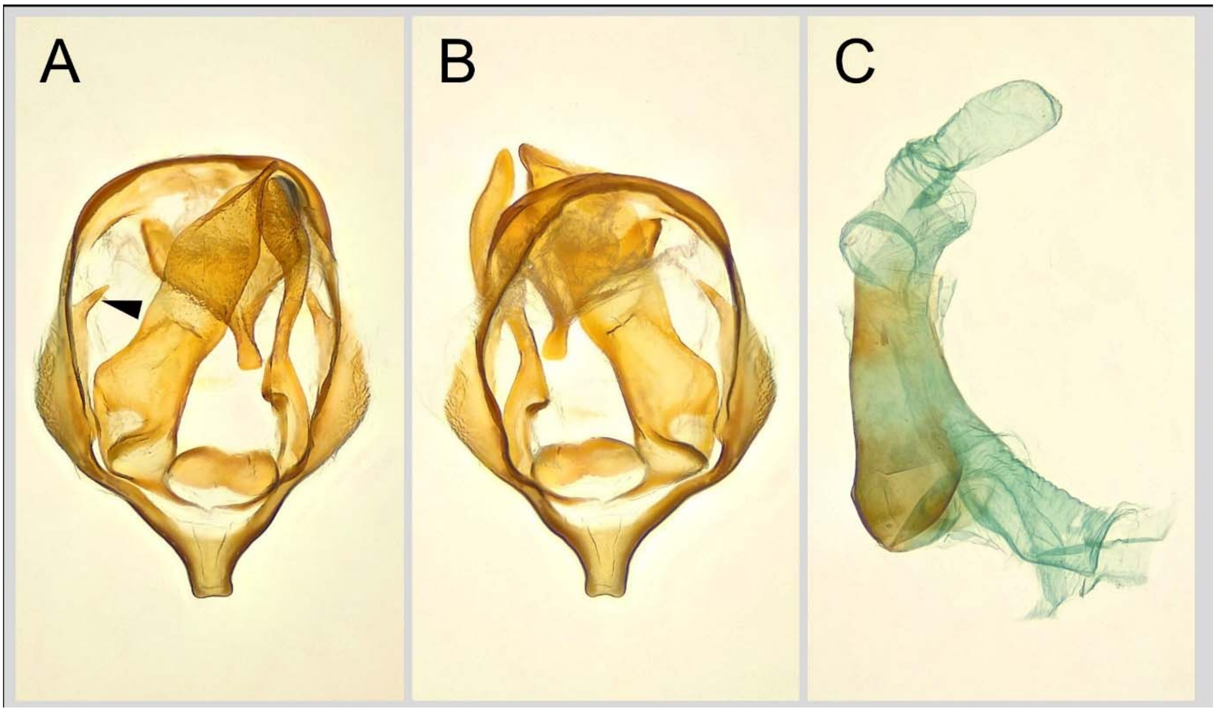


Figure 67. Male genitalia of *Julienaclia pauliani* **comb. nov.**, note the sublateral arms of tegumen (arrowhead).

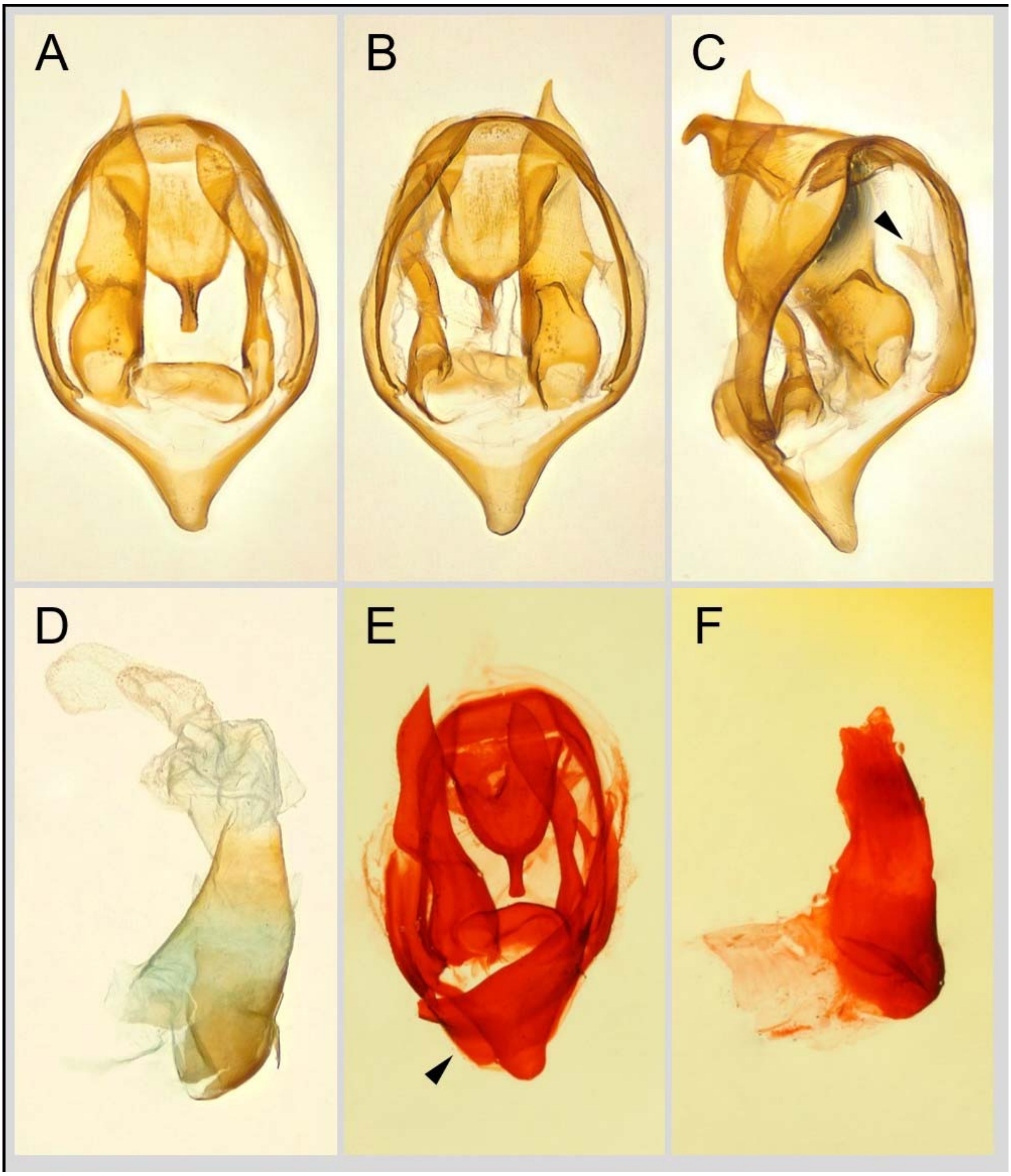


Figure 68. Male genitalia of *Julienaclia moerens* **comb. nov.**: A-D – specimen MNHN, EL83058, note the sublateral arms of tegumen (arrowhead); E-F – holotype (MNHN, EL65160), P. Griveaud original slide No. 578, note the 8th sternite still attached to the genitalia (arrowhead, see text).

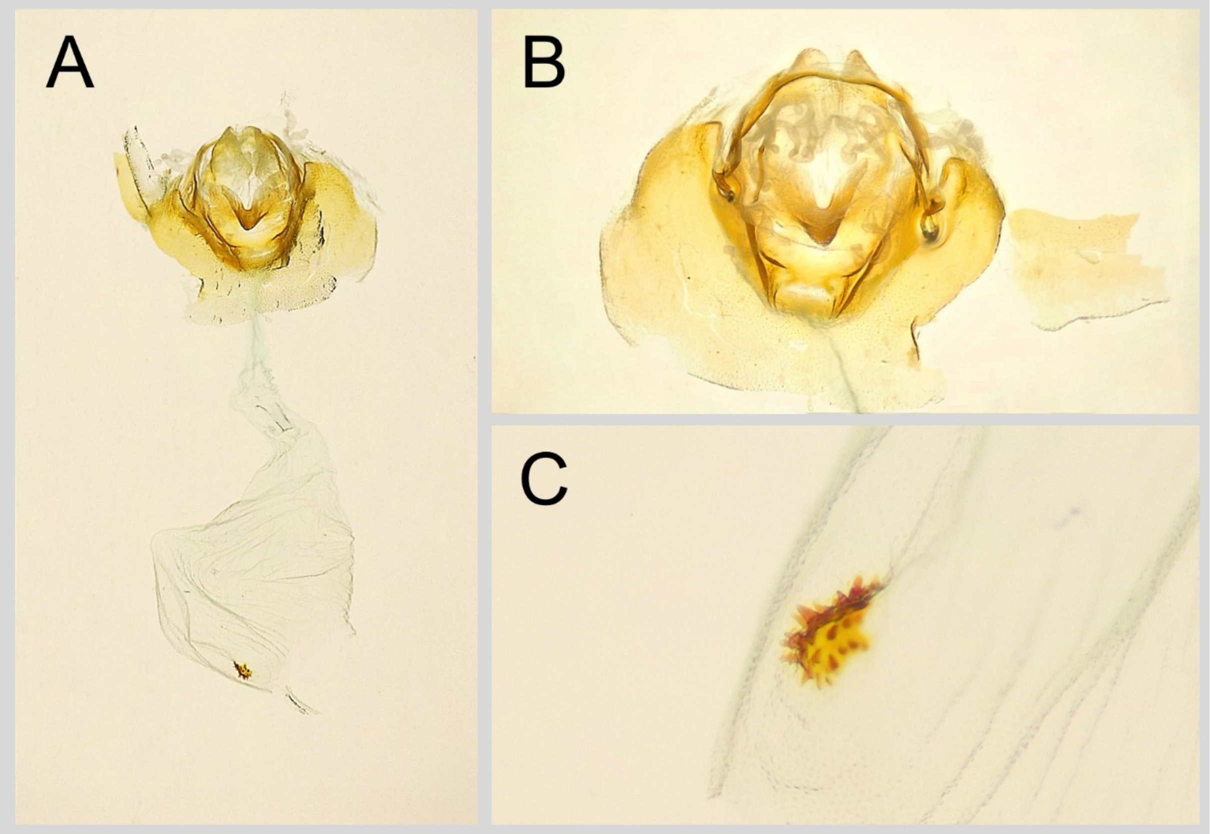


Figure 69. Female genitalia of *Julienaclia pauliani* **comb. nov.**

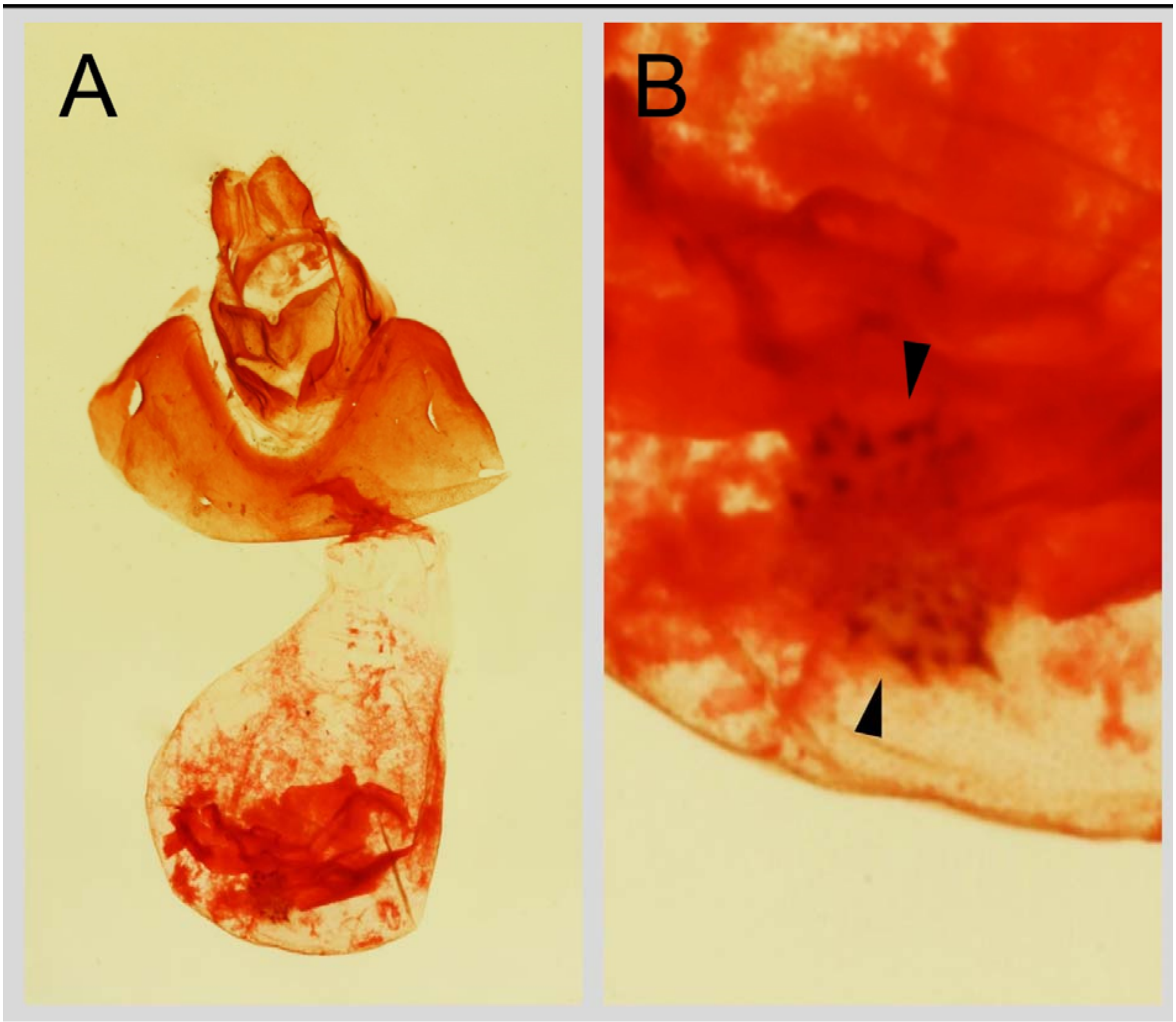


Figure 70. Female genitalia of *Julienaclia moerens* **comb. nov.**, P. Griveaud original slide No. 284, note the round signum (arrowheads, see text).

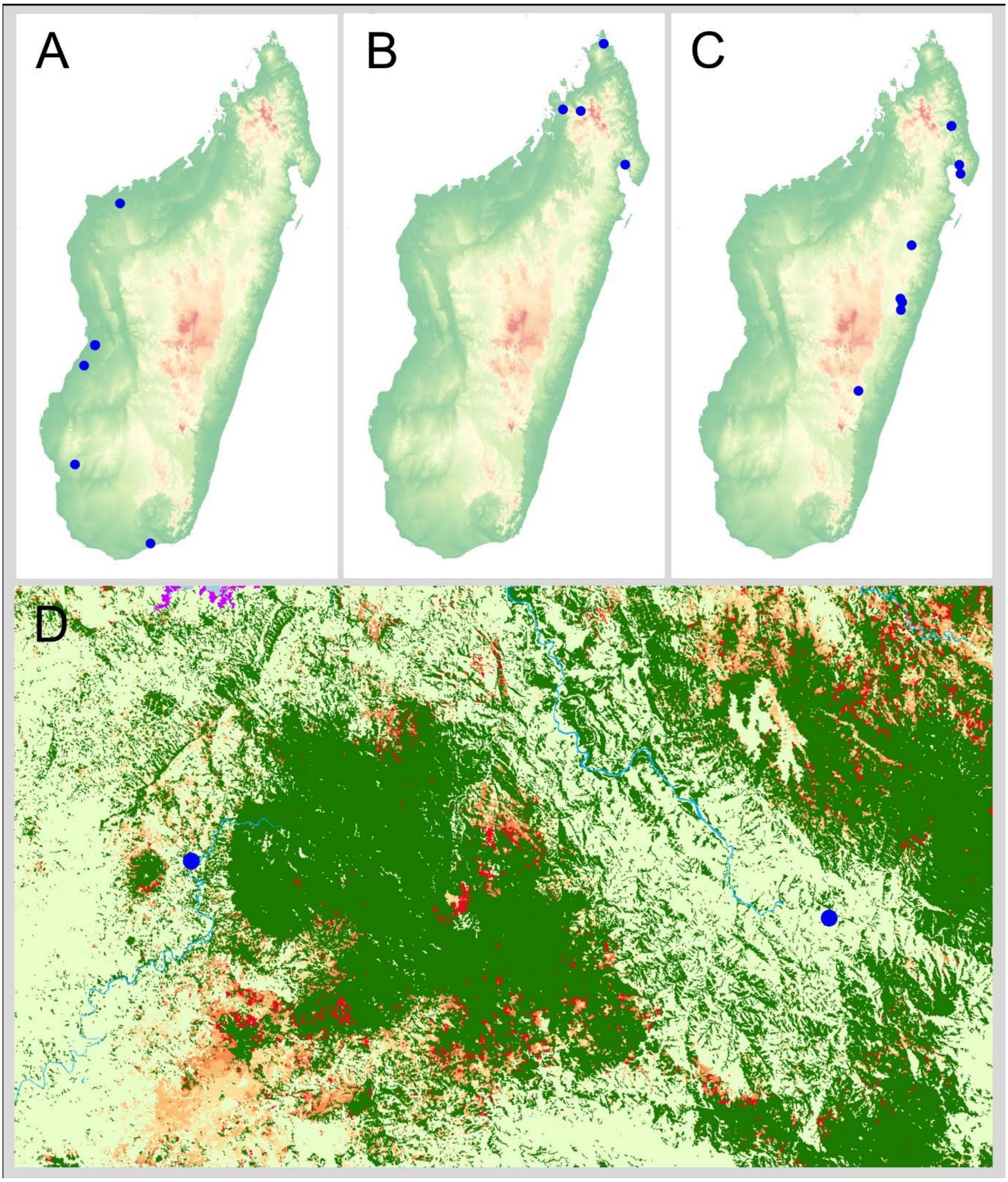


Figure 71. Distributional maps of *Julienaclia* **gen. nov.** and *Riconaclia* **gen. nov.**: A – *J. pauliani* **comb. nov.**; B – *J. moerens* **comb. nov.**; C – *R. bimacula* comb. nov.; D – deforestation (pale orange to red, from 2000 to 2020) in the western part of the range of *J. moerens* **comb. nov.**

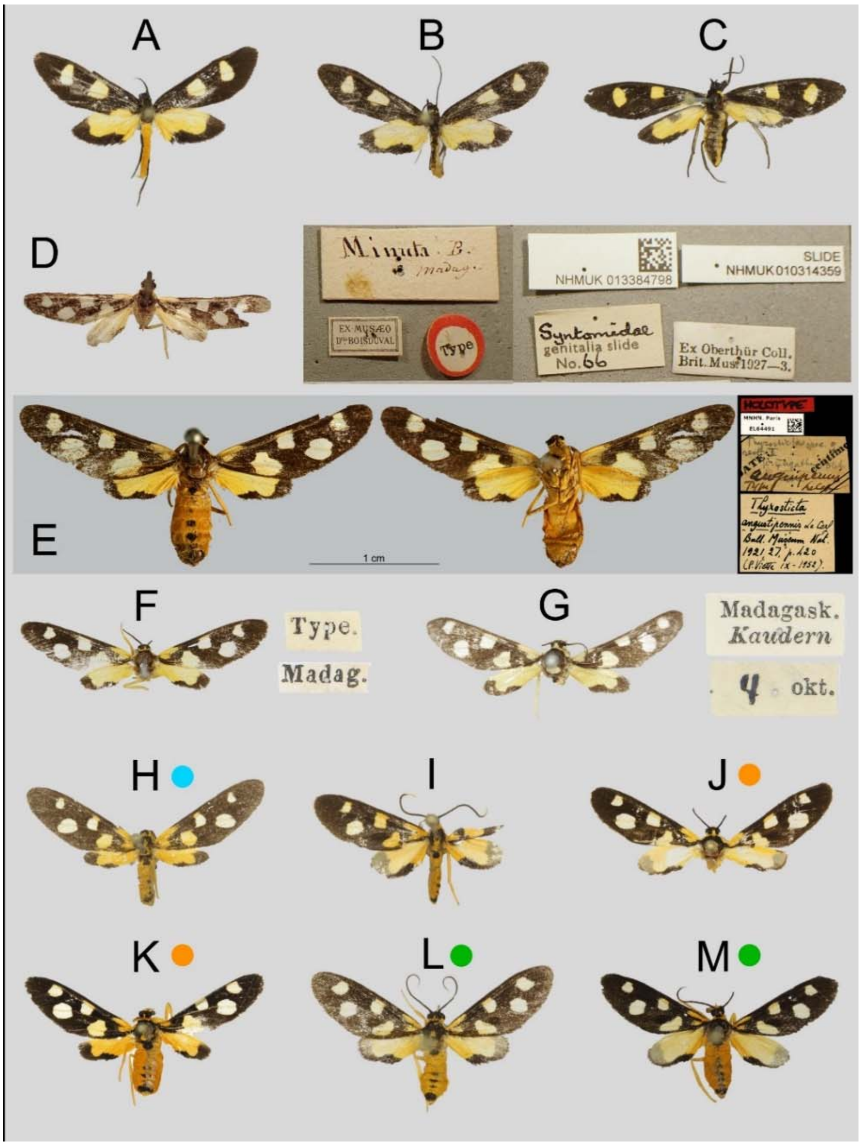


Figure 72. *Riconaclia* **gen. nov.** and *Mauricenaclia* **gen. nov.**, adults: A – *R. bimacula* **comb. nov.** male, ISEA PAS, DL_06-040; B – *R. bimacula* **comb. nov.** male, ISEA PAS, DL_06-291; C – *R. bimacula* **comb. nov.** female, NHMUK_015109726; D – *M. minuta* **comb. nov.** male holotype, NHMUK013384798 (photo: M. Wiorek); E – female holotype of *Thyrosticta angustipennis* **syn. nov.**, MNHN, EL64491; F – female lectotype of *Dysauxes subfenestrata* **syn. nov.**, NRM; G – the second female specimen of *Dysauxes subfenestrata* **syn. nov.**, NRM (see text); H – *M. minuta* **comb. nov.** female, ISEA PAS, DL_02-325; I – *M. minuta* **comb. nov.** male, ISEA PAS, DL_02-325; J – *M. minuta* **comb. nov.** male, ISEA PAS, MAD_020; K – *M. minuta* **comb. nov.** female, ISEA PAS, MAD_282; L – *M. minuta* **comb. nov.** male, ISEA PAS, MAD_260; M – *M. minuta* **comb. nov.** male, ISEA PAS, MAD_287; colours of the dots correspond with the relevant marks in the phylogenetic tree and distributional map (see text); not to the same scale.

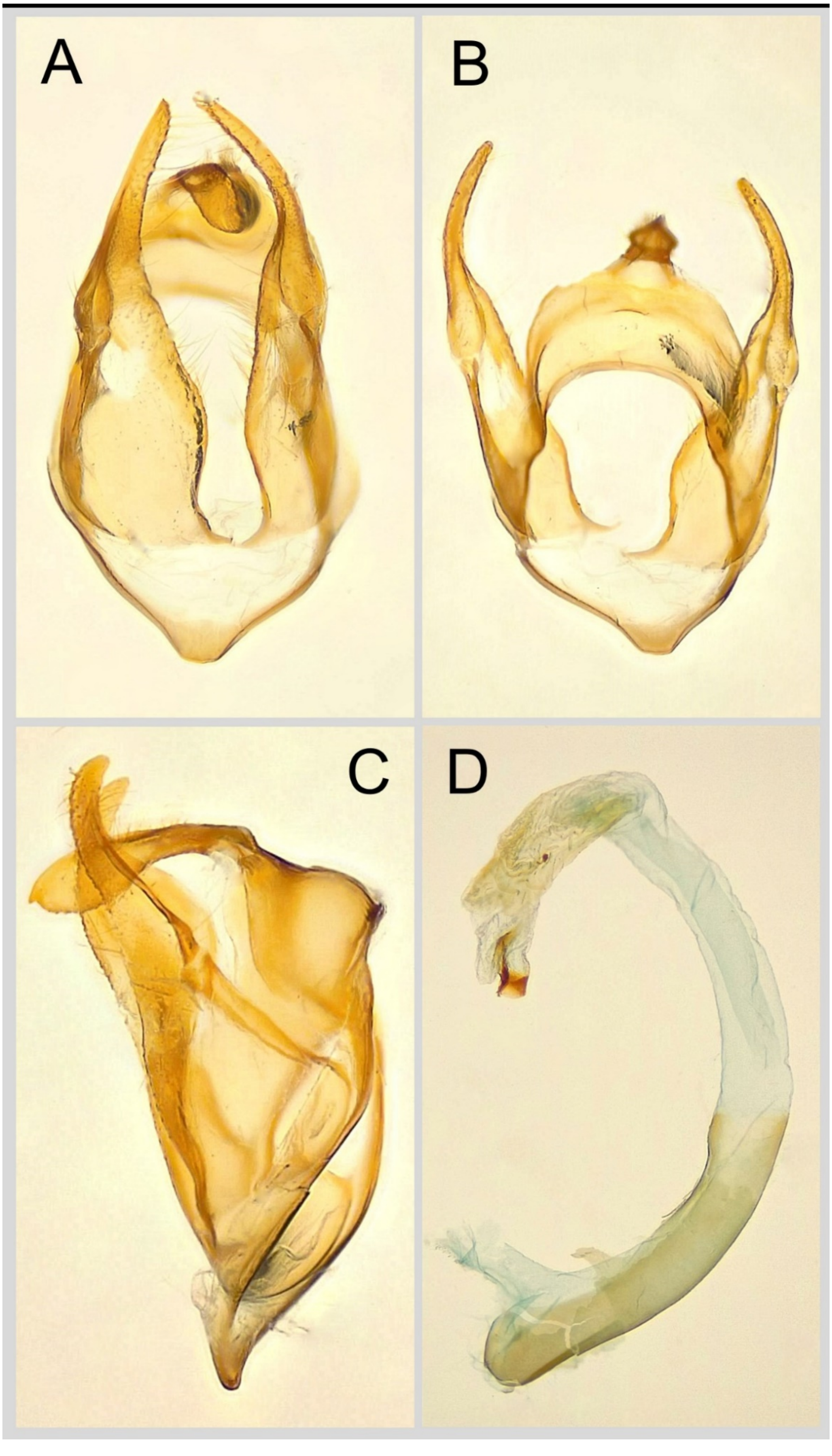


Figure 73. Male genitalia of *Riconaclia bimacula* **comb. nov.**

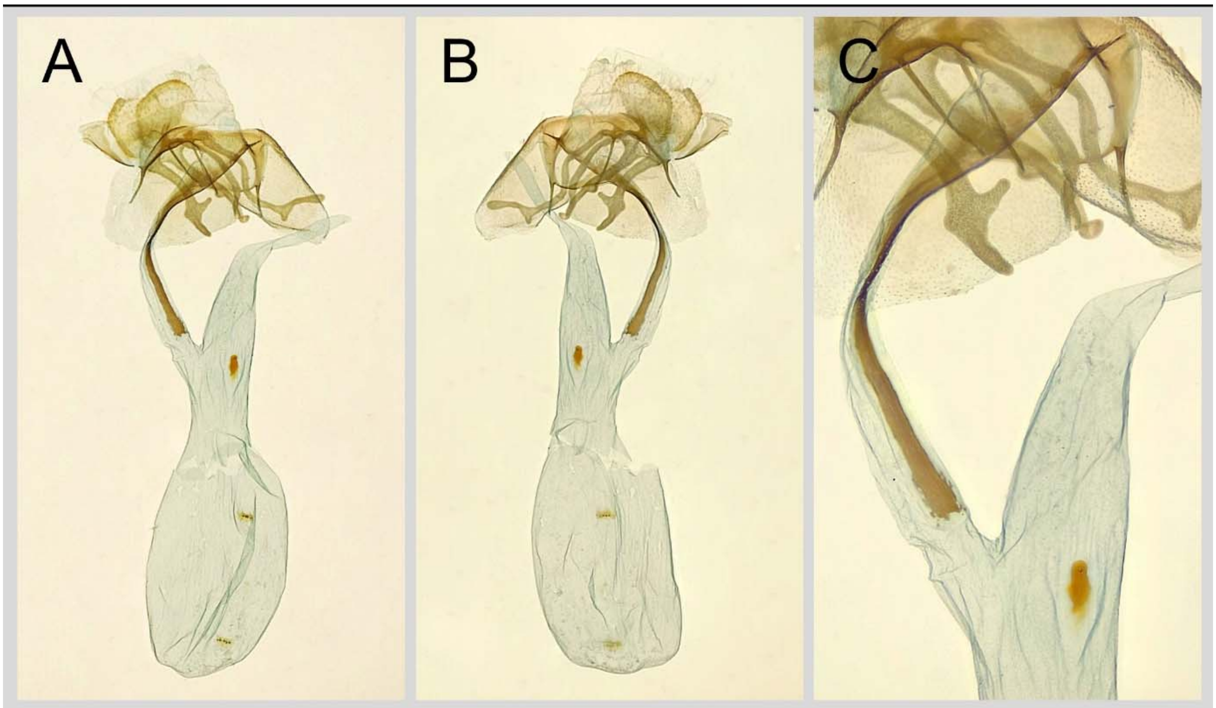


Figure 74. Female genitalia *Riconaclia bimacula* **comb. nov.**

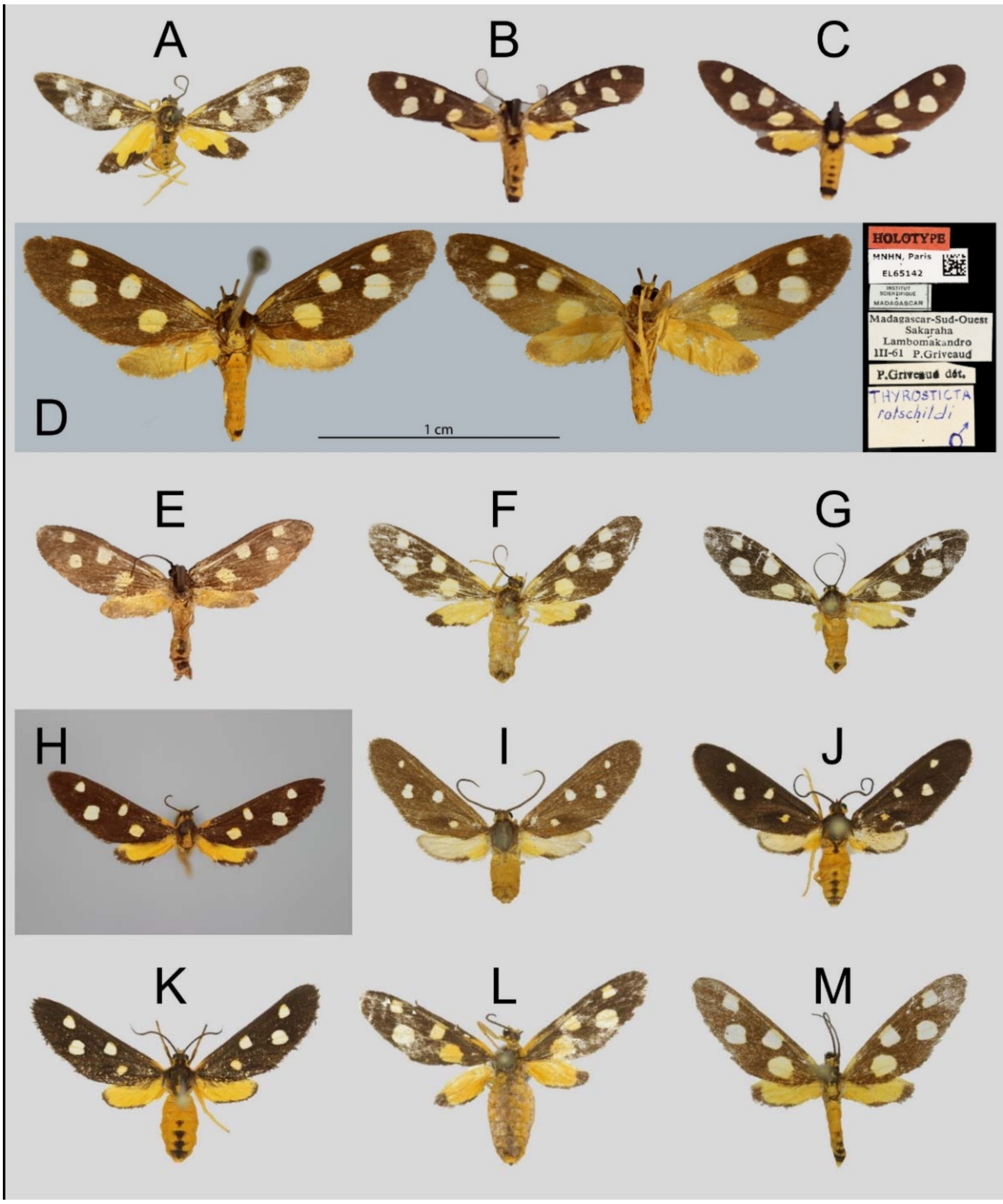


Figure 75. *Mauricenaclia* **gen. nov.**, adults: A – *M. raharizonina* **comb. nov.** male, MfN, 79fa12; B – *M. raharizonina* **comb. nov.** female, MNHN, EL82622; C – *M. raharizonina* **comb. nov.** female, MNHN, EL82621 from N Madagascar (see text); D – male holotype of *M. rothschildi* **comb. nov.**, MNHN, EL65142; E – *M. rothschildi* **comb. nov.** male, MNHN, EL74733; F – *M. rothschildi* **comb. nov.** female, ISEA PAS, DL_05-857; G – *M. rothschildi* **comb. nov.** female, ISEA PAS, MAD_212; H – female holotype of *M. octopunctata* **comb. nov.**, NHMUK013384803; I – *M. octopunctata* **comb. nov.** male, ISEA PAS, MAD_266; J – *M. octopunctata* **comb. nov.** male, ISEA PAS, MAD_263; K – *M. octopunctata* **comb. nov.** female, ISEA PAS, MAD_272; L – *M. octopunctata* **comb. nov.** female, ISEA PAS, DL_02-26; M – *M. octopunctata* **comb. nov.** female, ISEA PAS, DL_2966; not to the same scale.

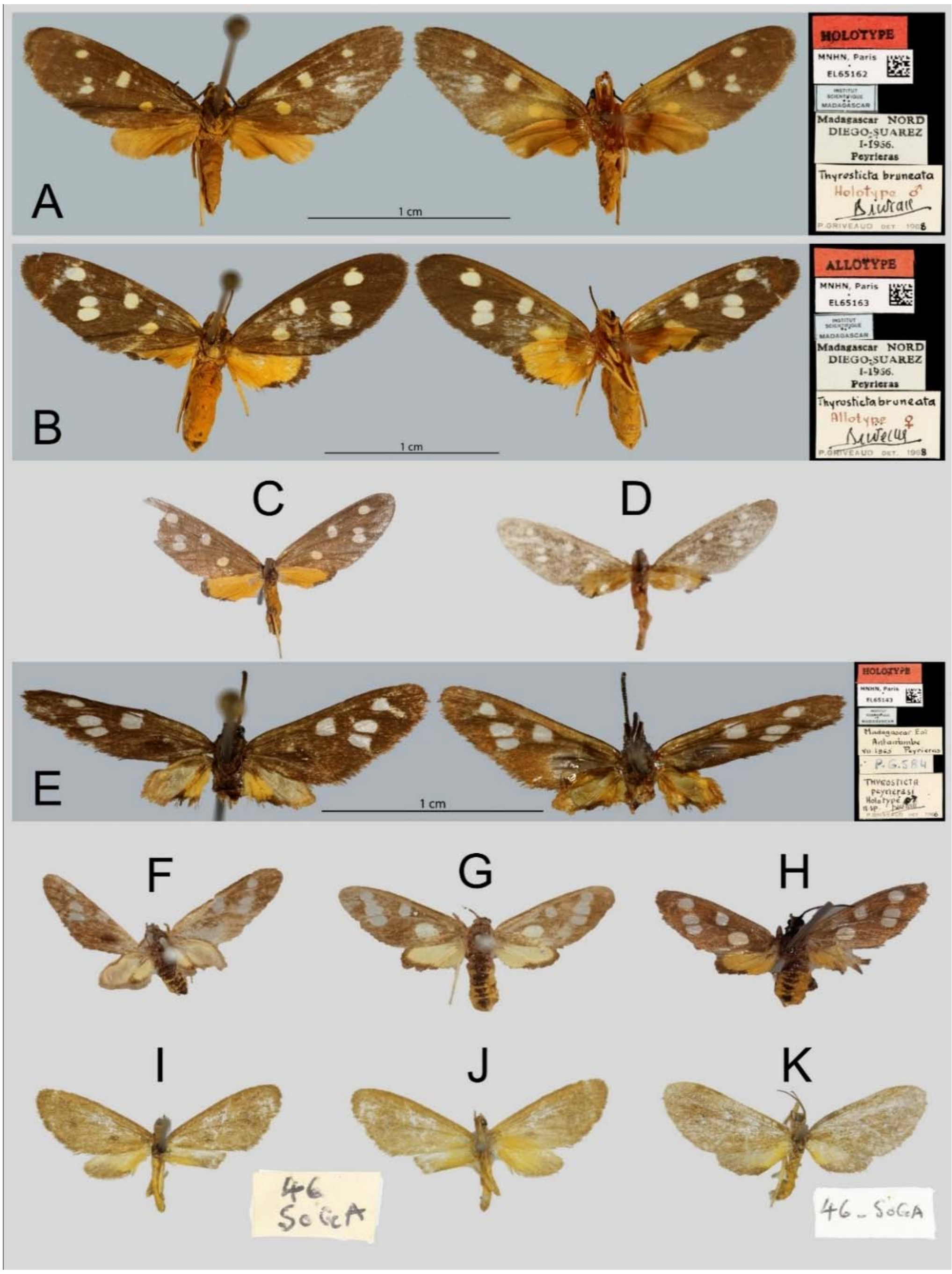


Figure 76. *Mauricenaclia* **gen. nov.**, adults: A – male holotype of *M. bruneata* **comb. nov.**, MNHN, EL65162; B – female allotype of *M. bruneata* **comb. nov.**, MNHN, EL65163; C – *M. bruneata* **comb. nov.** female, NHMUK, DL1811; D – *M. bruneata* **comb. nov.** female, MNHN, EL74968; E – male holotype of *M. peyrierasi* **comb. nov.**, MNHM, EL65143; F – *M. peyrierasi* **comb. nov.** male, SGN; G – *M. peyrierasi* **comb. nov.** female, SGN; H – *M. peyrierasi* **comb. nov.** female, NHMUK, DL1792; I-J – first male paratype of *M. apatris* **sp. nov.**, MNHN, EL81680, upperside and underside, with the only original label (see text); K – second male paratype of *M. apatris* **sp. nov.**, MNHN, EL81694, with the only original label (see text); not to the same scale.

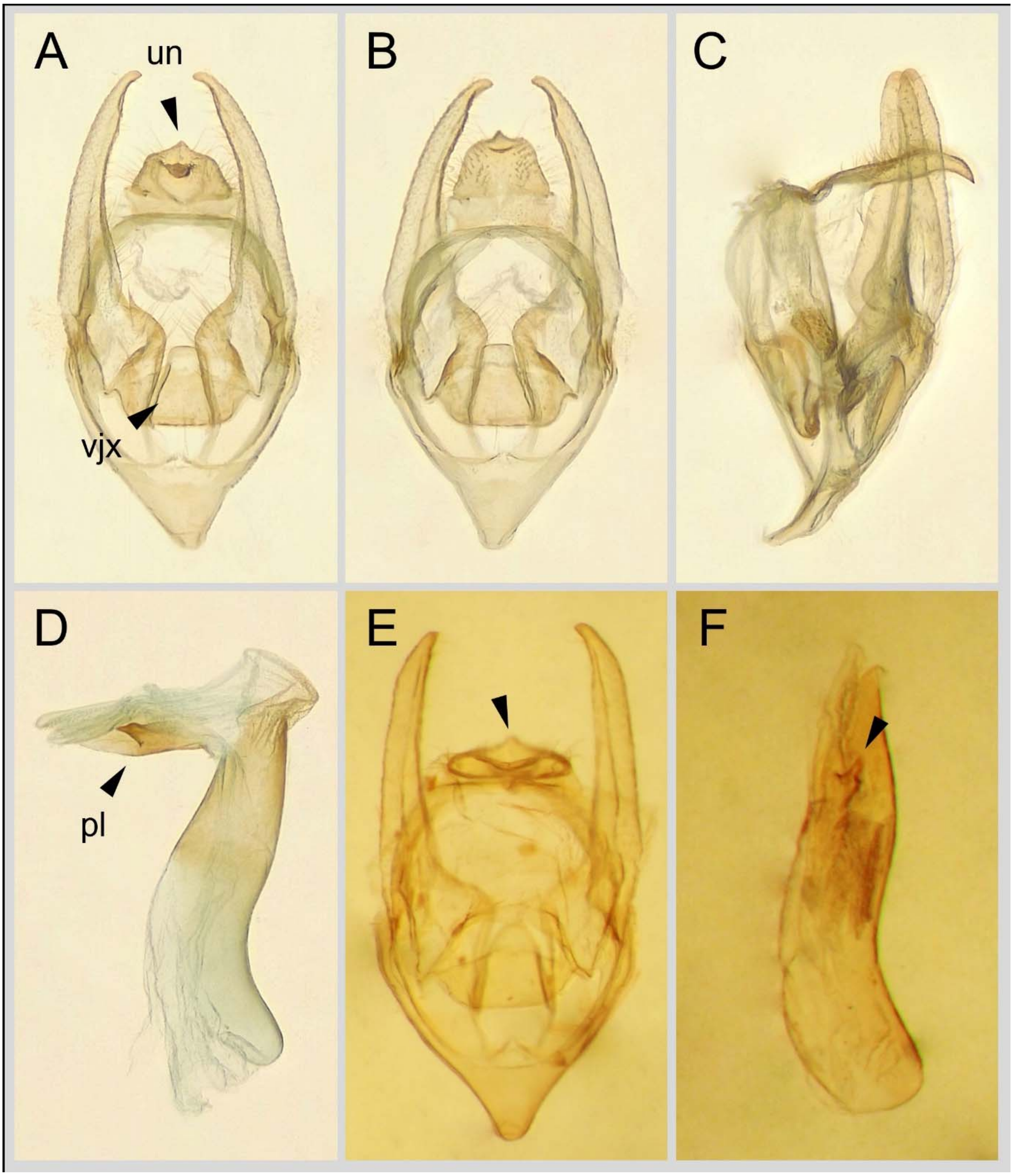


Figure 77. Male genitalia of *Mauricenaclia minuta* **comb. nov.**: A-D – specimen ISEA PAS, MAD_020, E-F – holotype, slide NHMUK010314359; un - uncus with terminal dorsal protrusion, vjx - ventral arms of juxta (apomorphy of the genus, see text), pl - plaque in vesica;

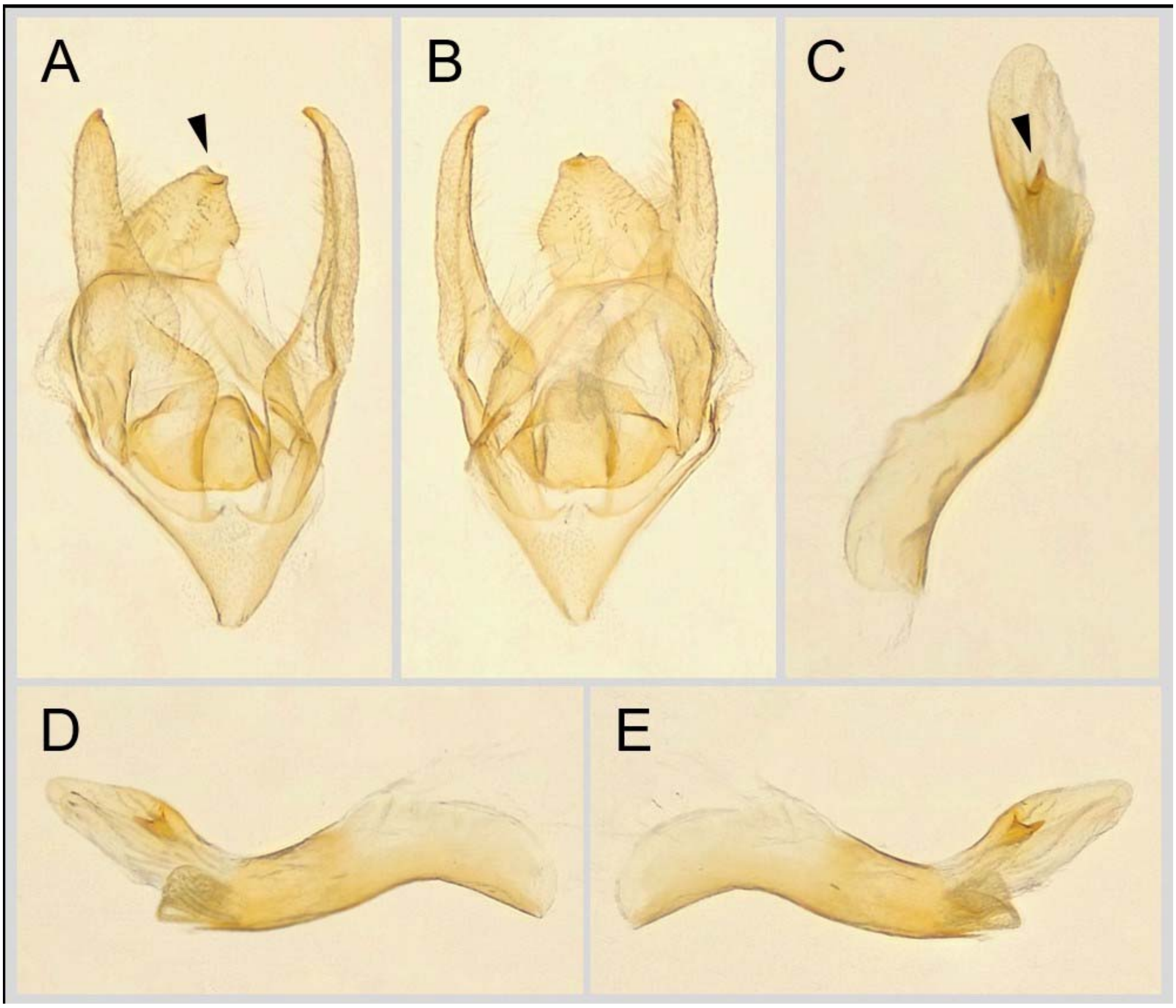


Figure 78. Male genitalia of *Mauricenaclia minuta* **comb. nov.**, specimen MNHN, EL82679, note the dorsoterminal protrusion of the uncus, and the shape of the plaque in vesica (arrowheads).

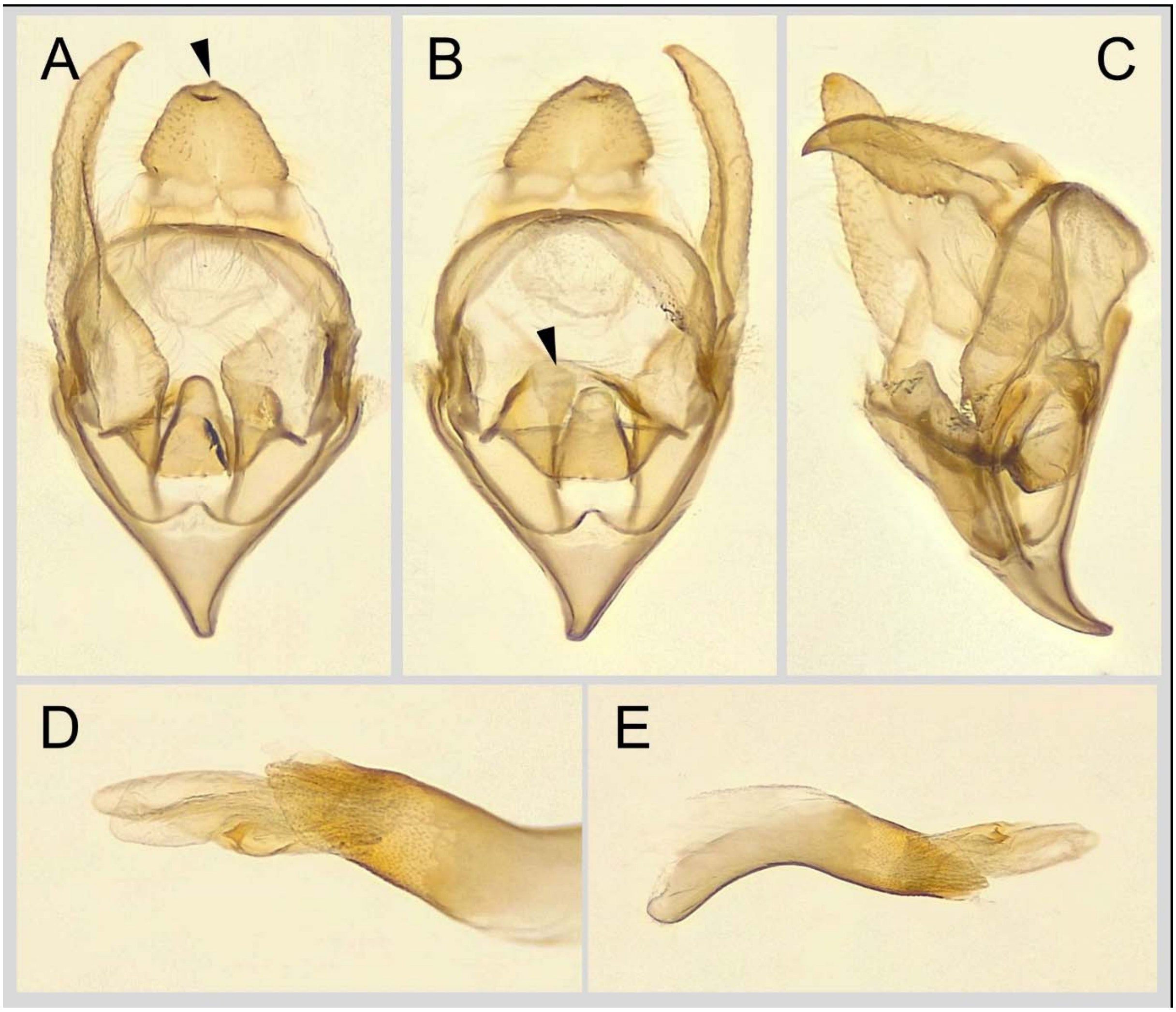


Figure 79. Male genitalia of *Mauricenaclia minuta* **comb. nov.**, specimens MNHN, EL82680, note the dorsoterminal protrusion of the uncus, and the asymmetry of juxta (arrowheads).

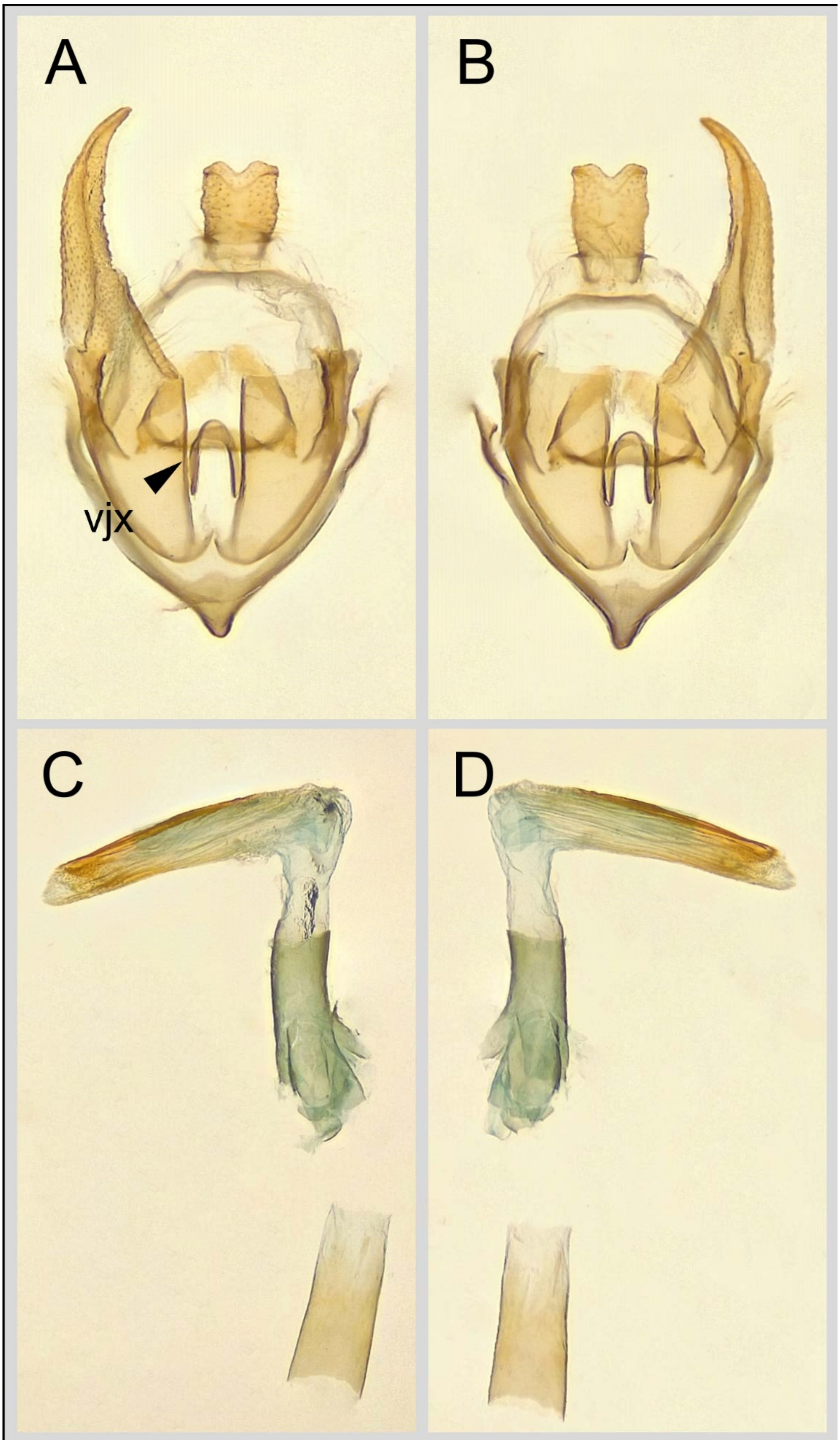


Figure 80. Male genitalia of *Mauricenaclia raharizonina* **comb. nov.**, vjx - ventral arms of juxta of the genus-specific shape (see text).

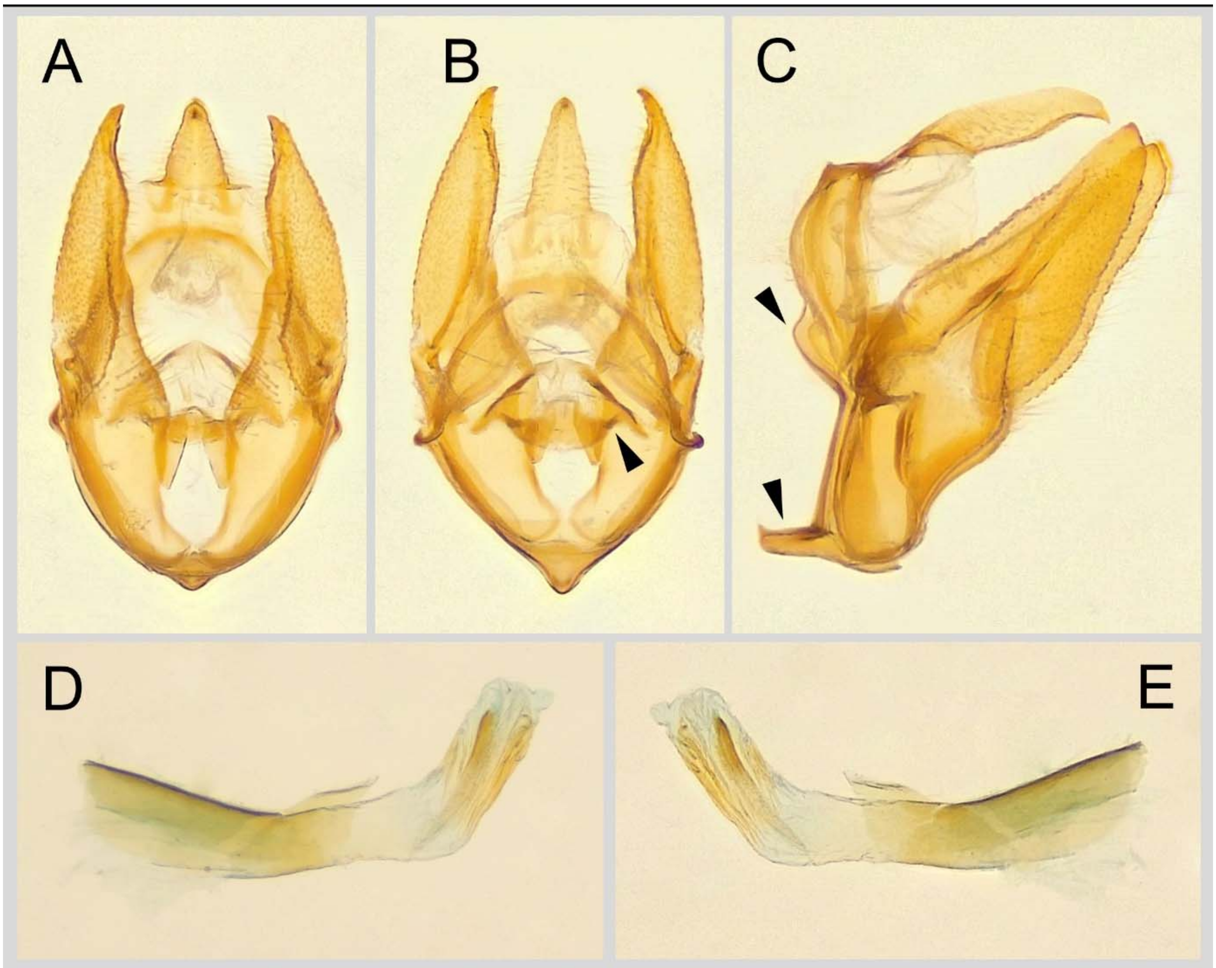


Figure 81. Male genitalia of *Mauricenaclia rothschildi* **comb. nov.**, note the shape of the lateral lobes of juxta, lateroterminal lobes of vinculum and terminal portion of saccus (arrowheads, see text).

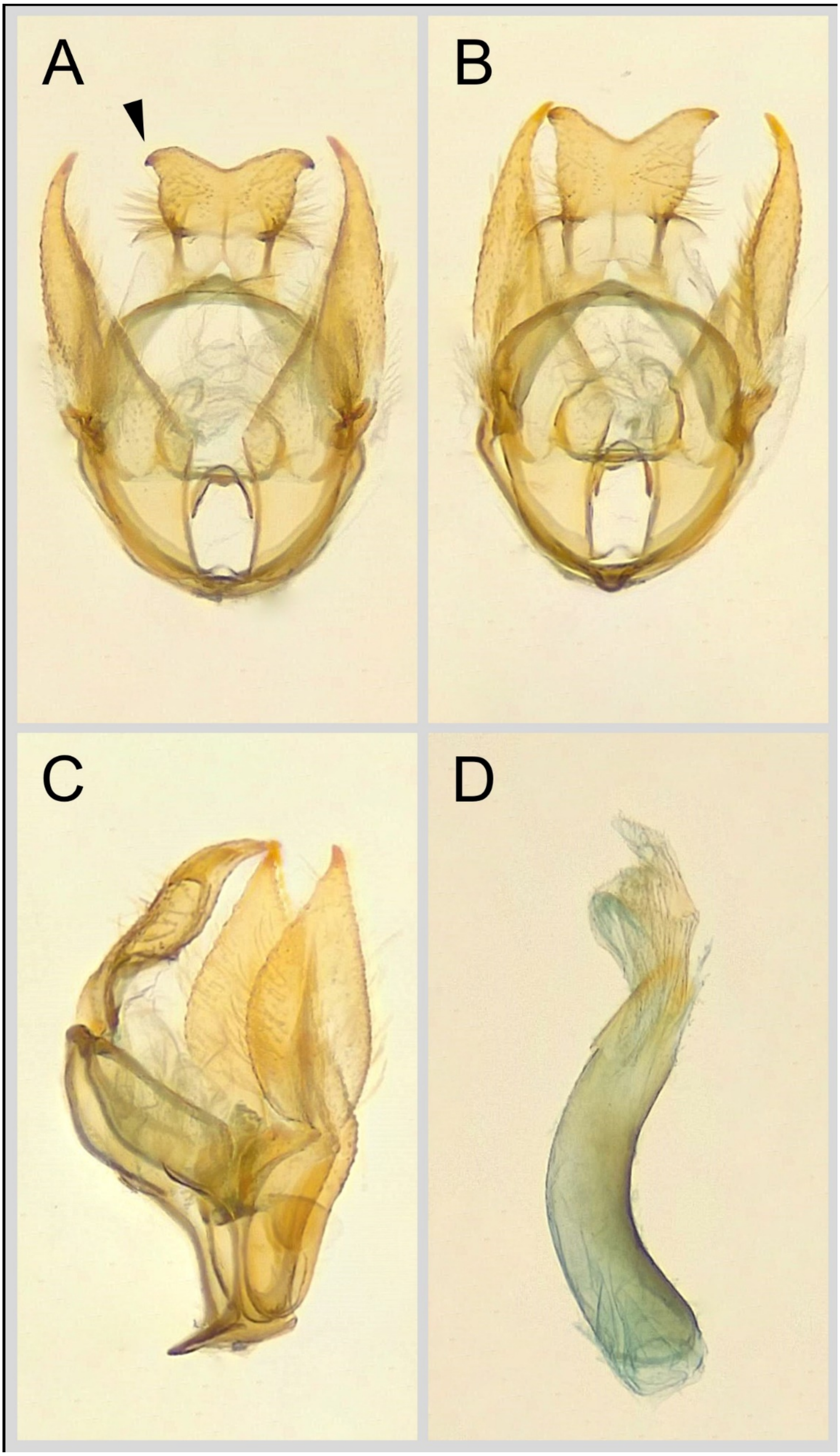


Figure 82. Male genitalia of *Mauricenaclia octopunctata* **comb. nov.**, note the lateral protrusions of uncus extending beyond its outline (arrowhead, see text).

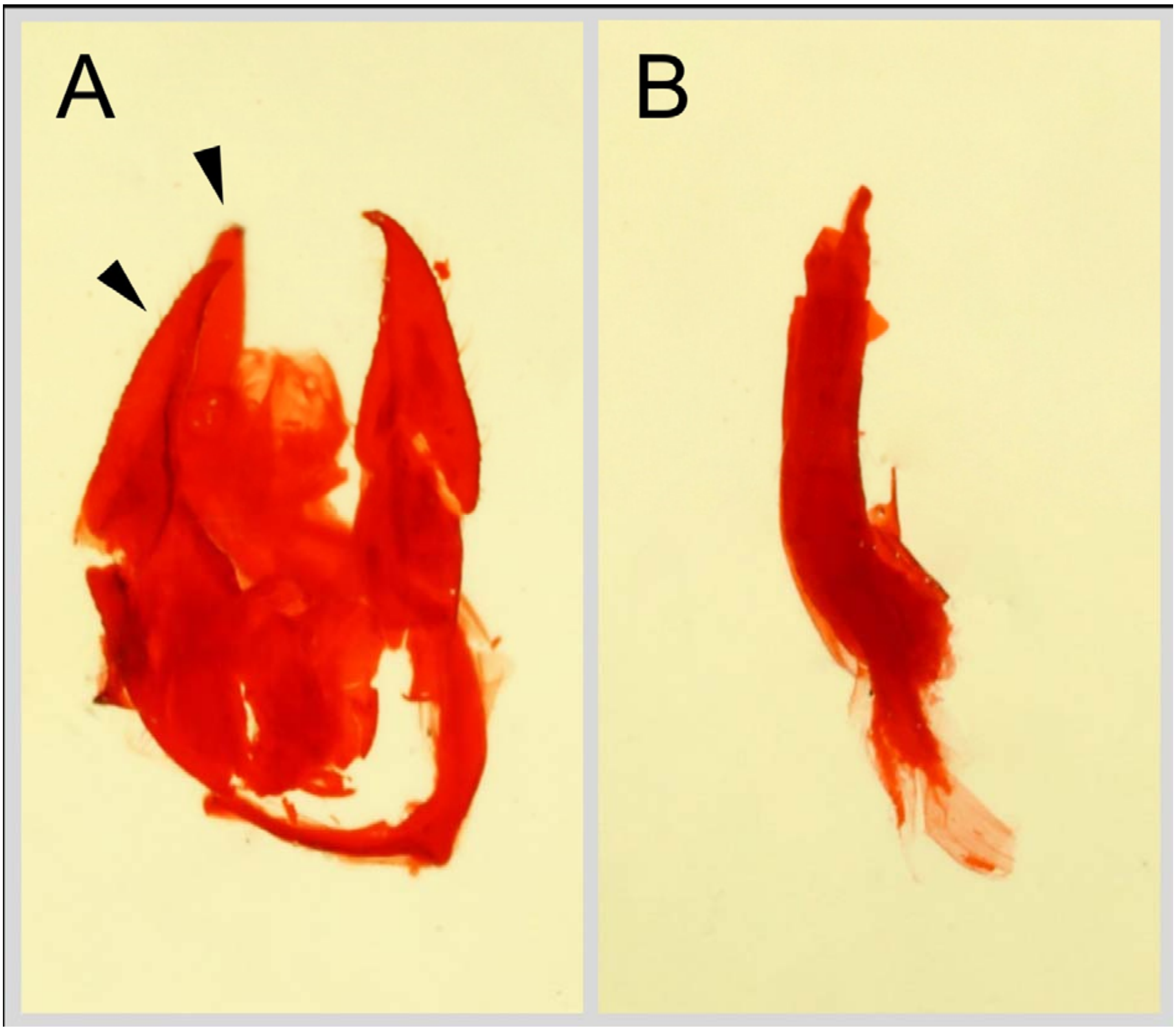


Figure 83. Male genitalia of *Mauricenaclia bruneata* **comb. nov.**, P. Griveaud original slide No. 575, note the shape of uncus and valva, similar to *Mauricenaclia rothschildi* **comb. nov.** and *Mauricenaclia apatris* **sp. nov.** (arrowheads, see text).

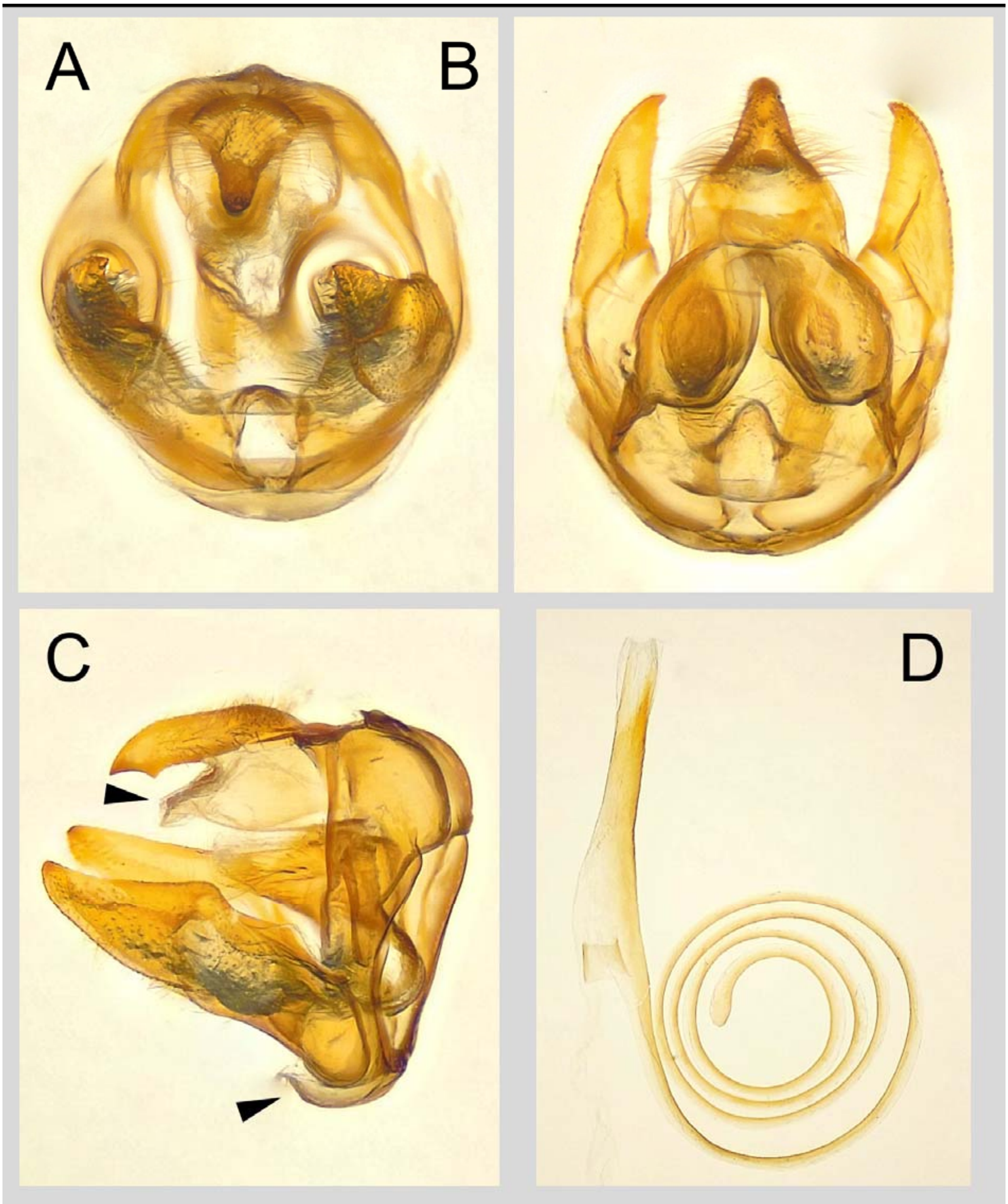


Figure 84. Male genitalia of *Mauricenaclia peyrierasi* **comb. nov.**, note the scaphium and saccus bent forwards (see text).

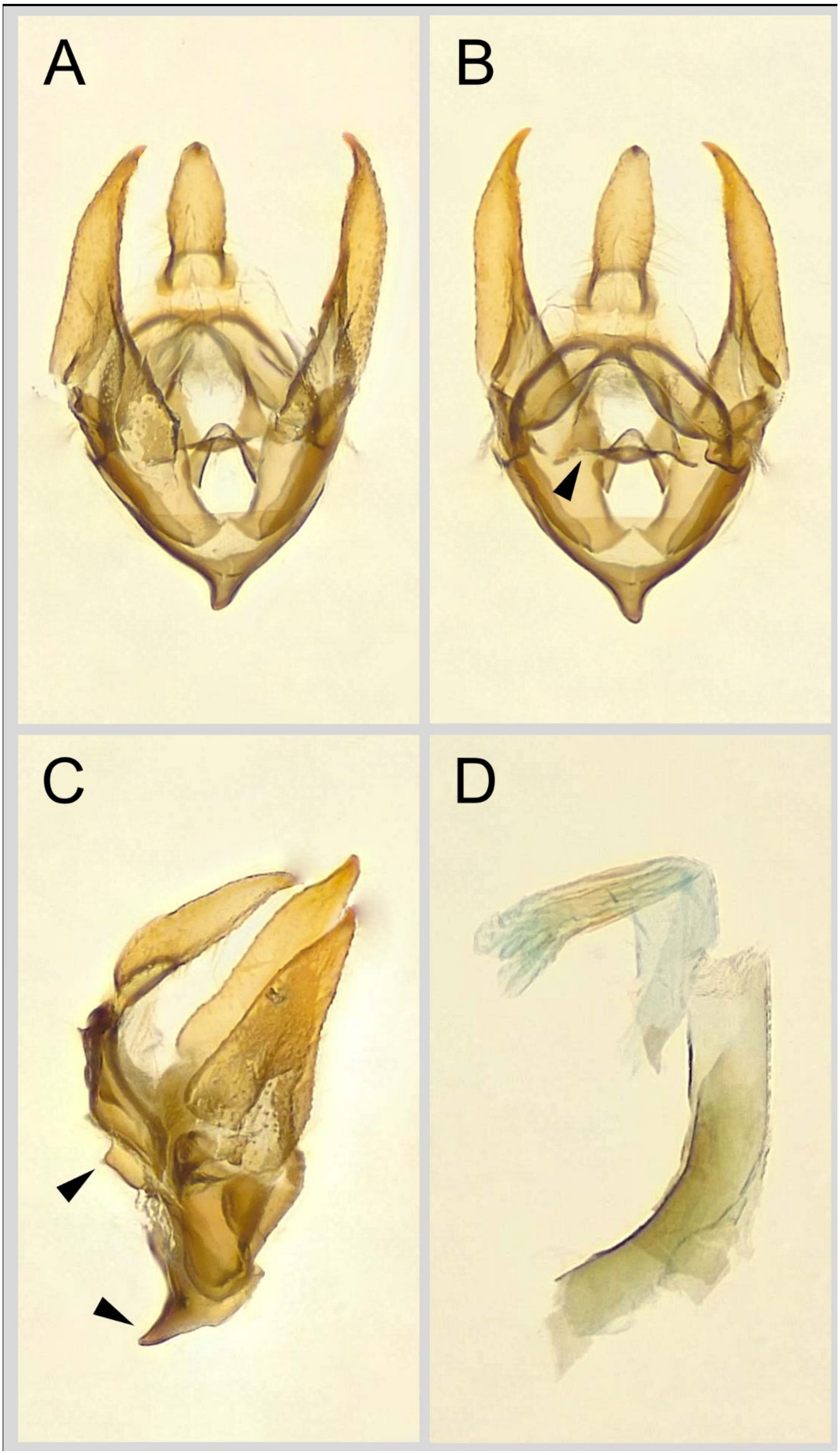


Figure 85. Male genitalia of *Mauricenaclia apatris* **sp. nov.**, note the shape of the lateral lobes of juxta, lateroterminal lobes of vinculum and terminal portion of saccus (arrowheads, see text).

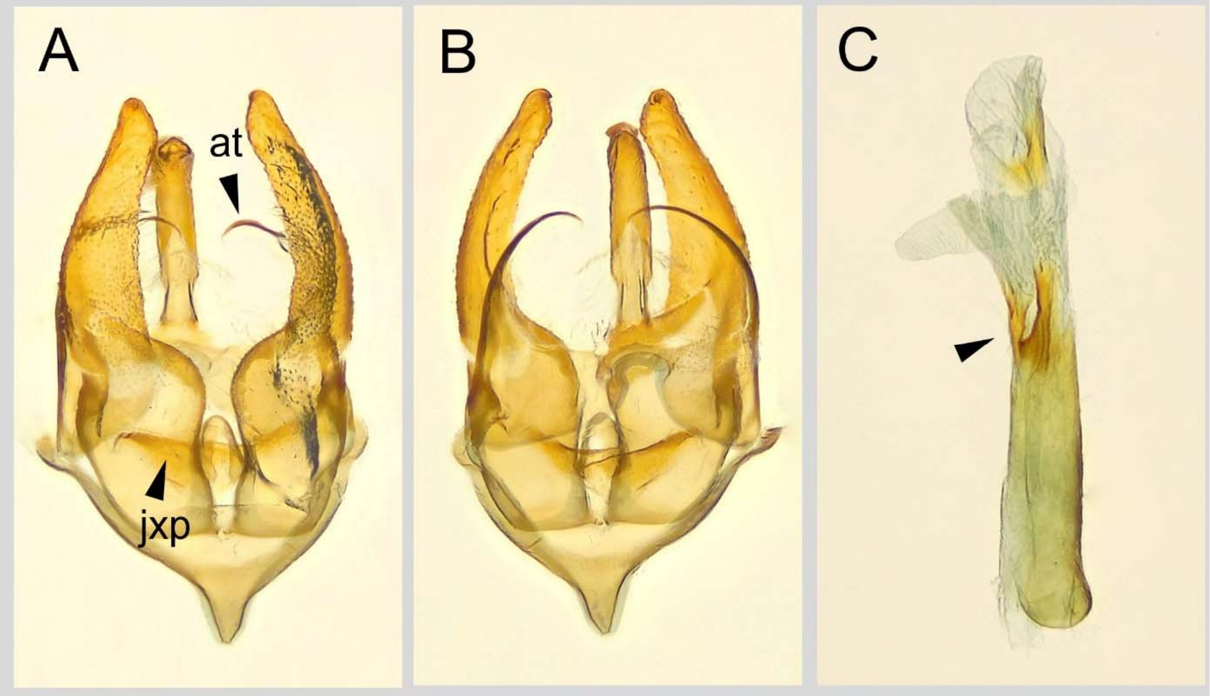


Figure 86. Male genitalia of *Pseudonaclia puella*, jxp - ventral plaque of juxta, at - sublateral arms of tegumen (see text), note the basal bifurcation in vesica (arrowhead in C).

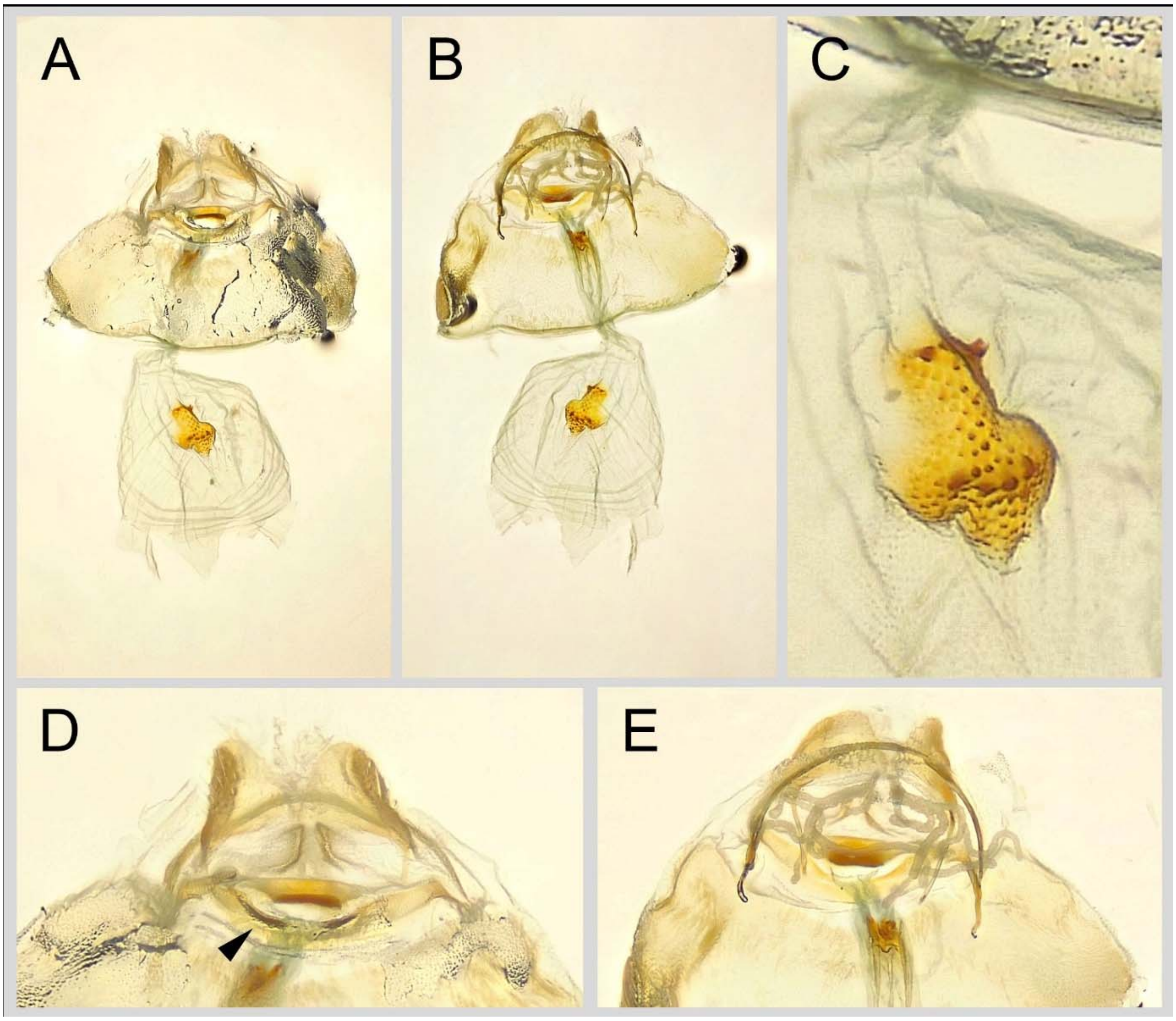


Figure 87. Female genitalia of *Mauricenaclia minuta* **comb. nov.**, specimen ISEA PAS, DL_02-325 - the specimen representing the western population of the species (see text).

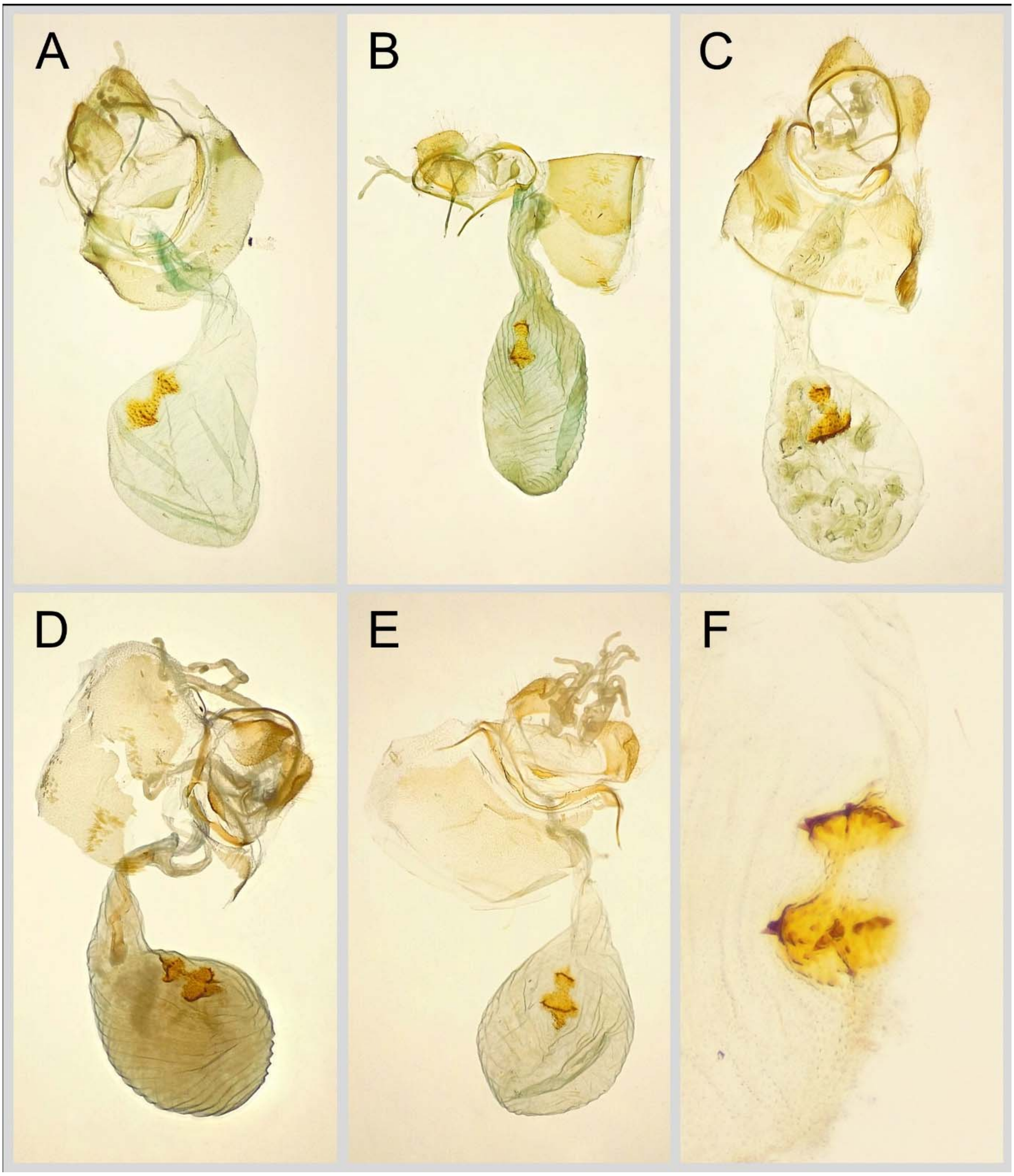


Figure 88. Variation in the female genitalia of *Mauricenaclia minuta* **comb. nov.**

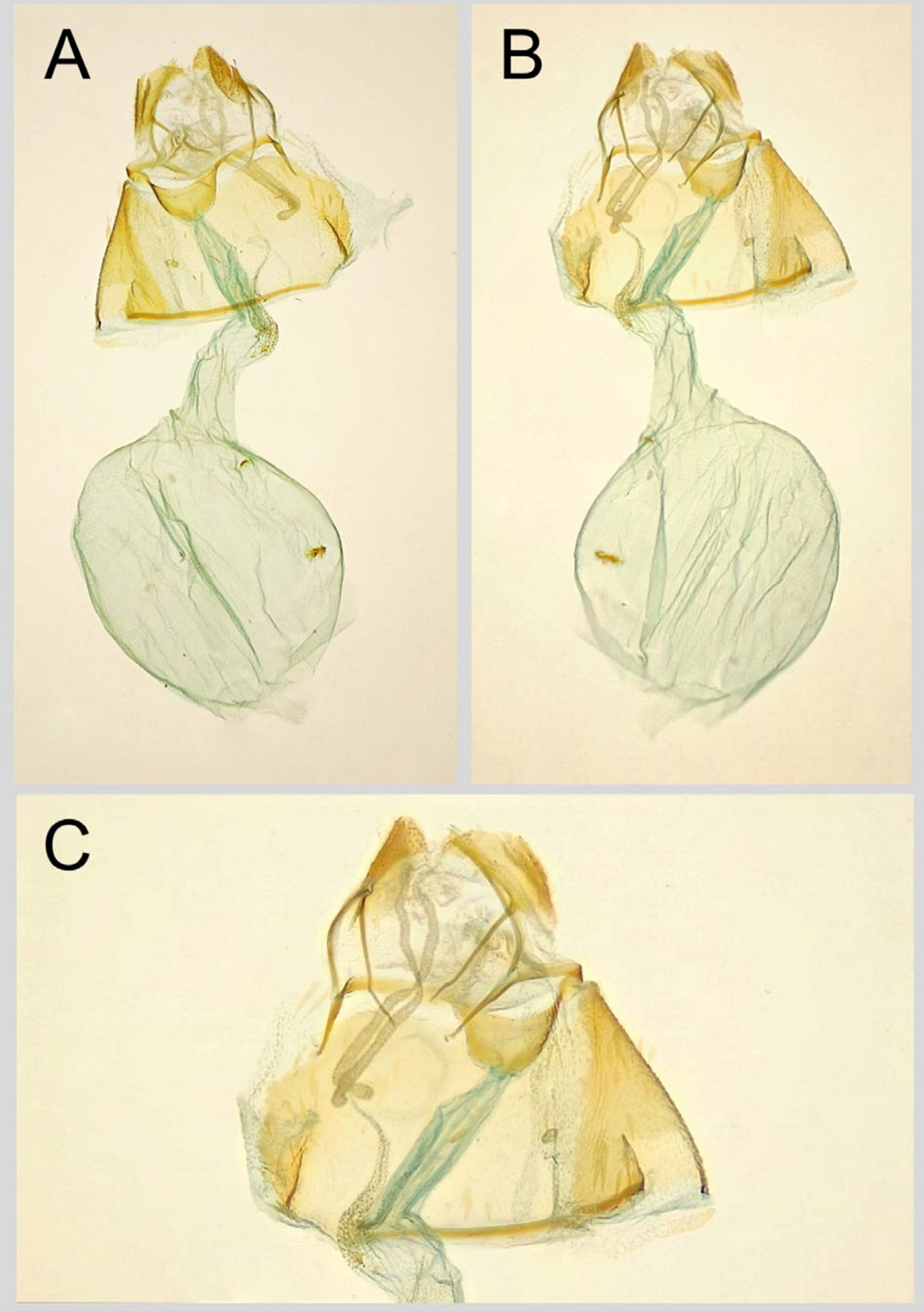


Figure 89. Female genitalia of *Mauricenaclia raharizonina* **comb. nov.**

Figure 90. Female genitalia of *Mauricenaclia rothschildi* **comb. nov.**

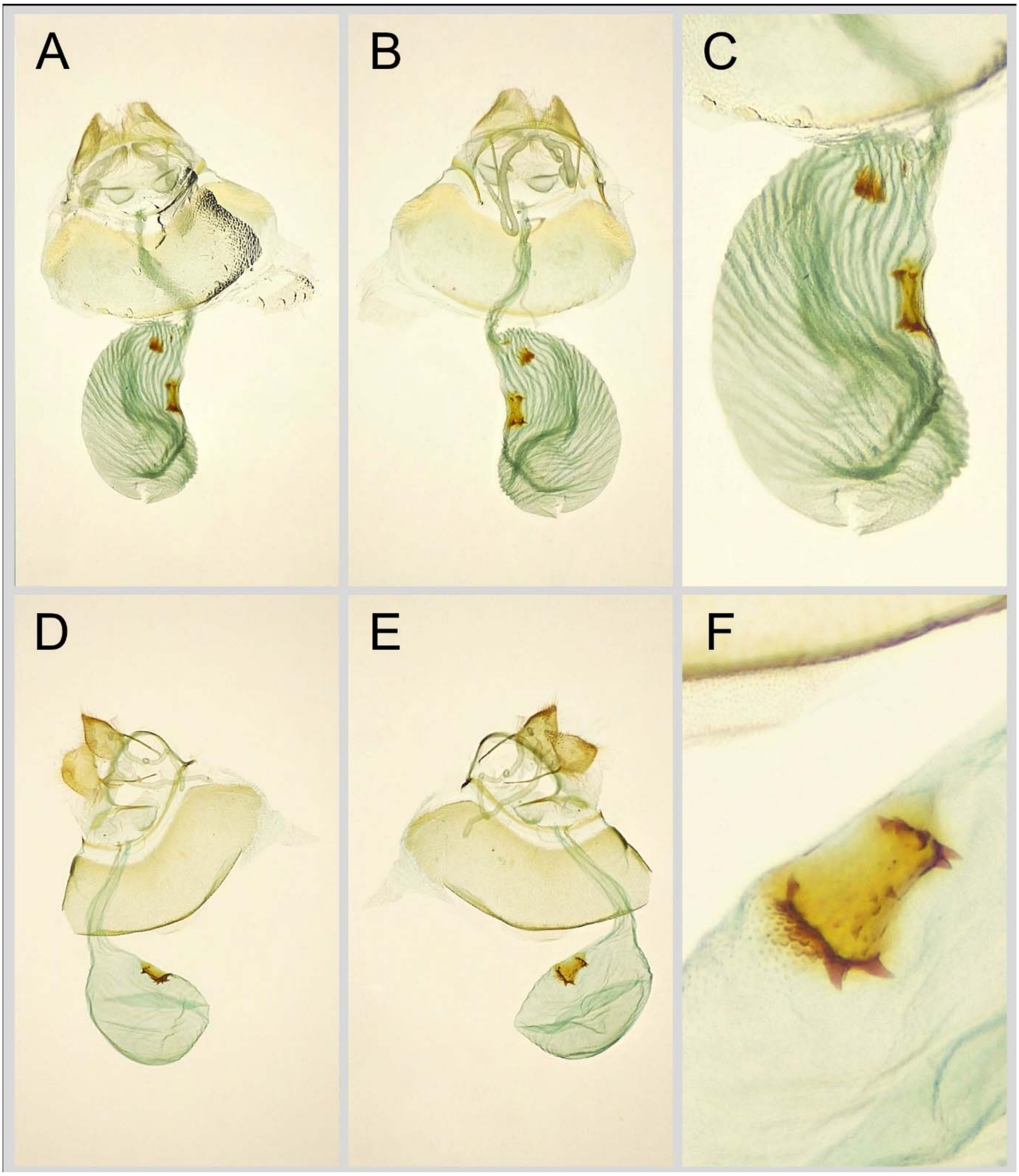


Figure 91. Female genitalia of *Mauricenaclia octopunctata* **comb. nov.**

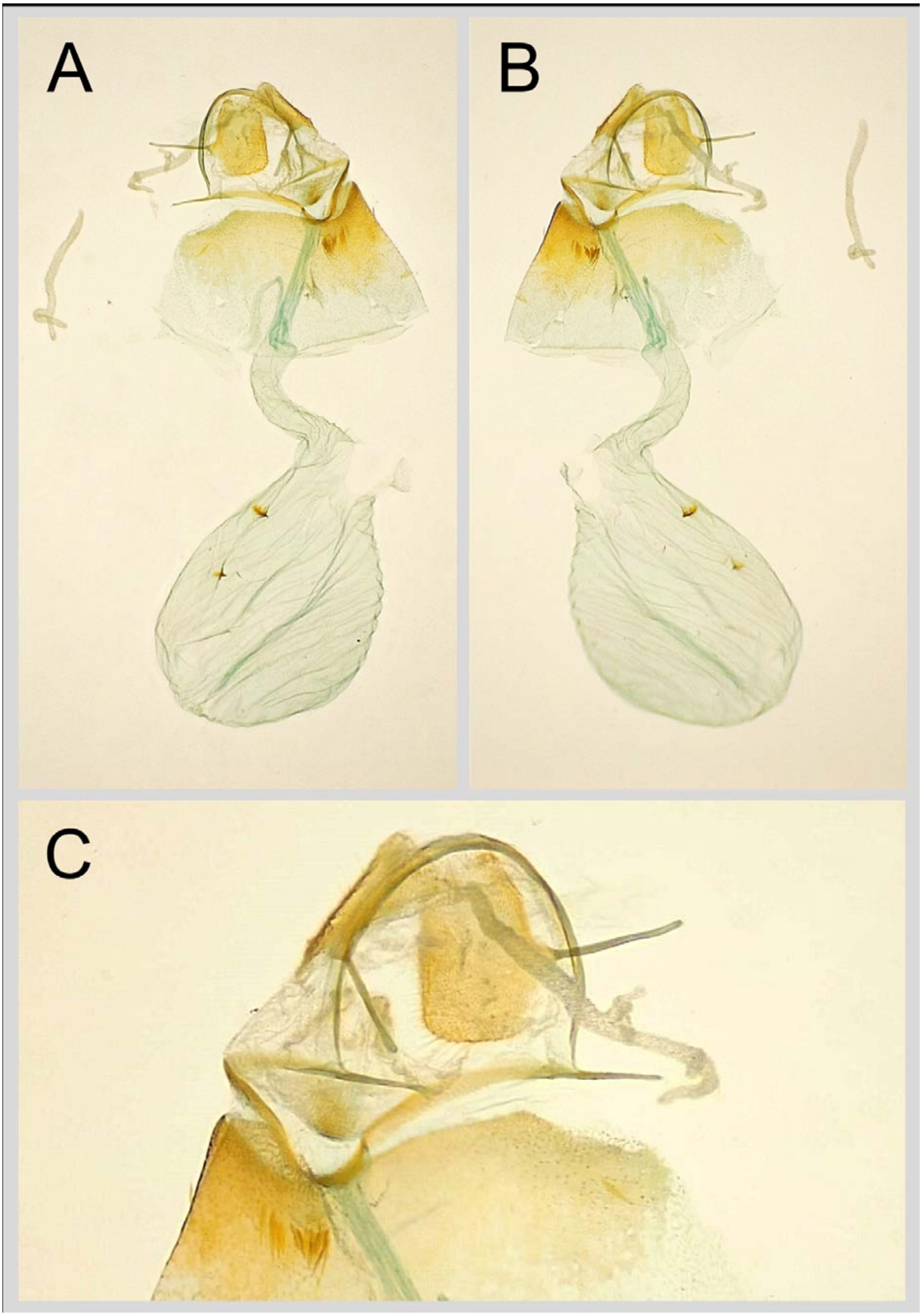


Figure 92. Female genitalia of *Mauricenaclia bruneata* **comb. nov.**

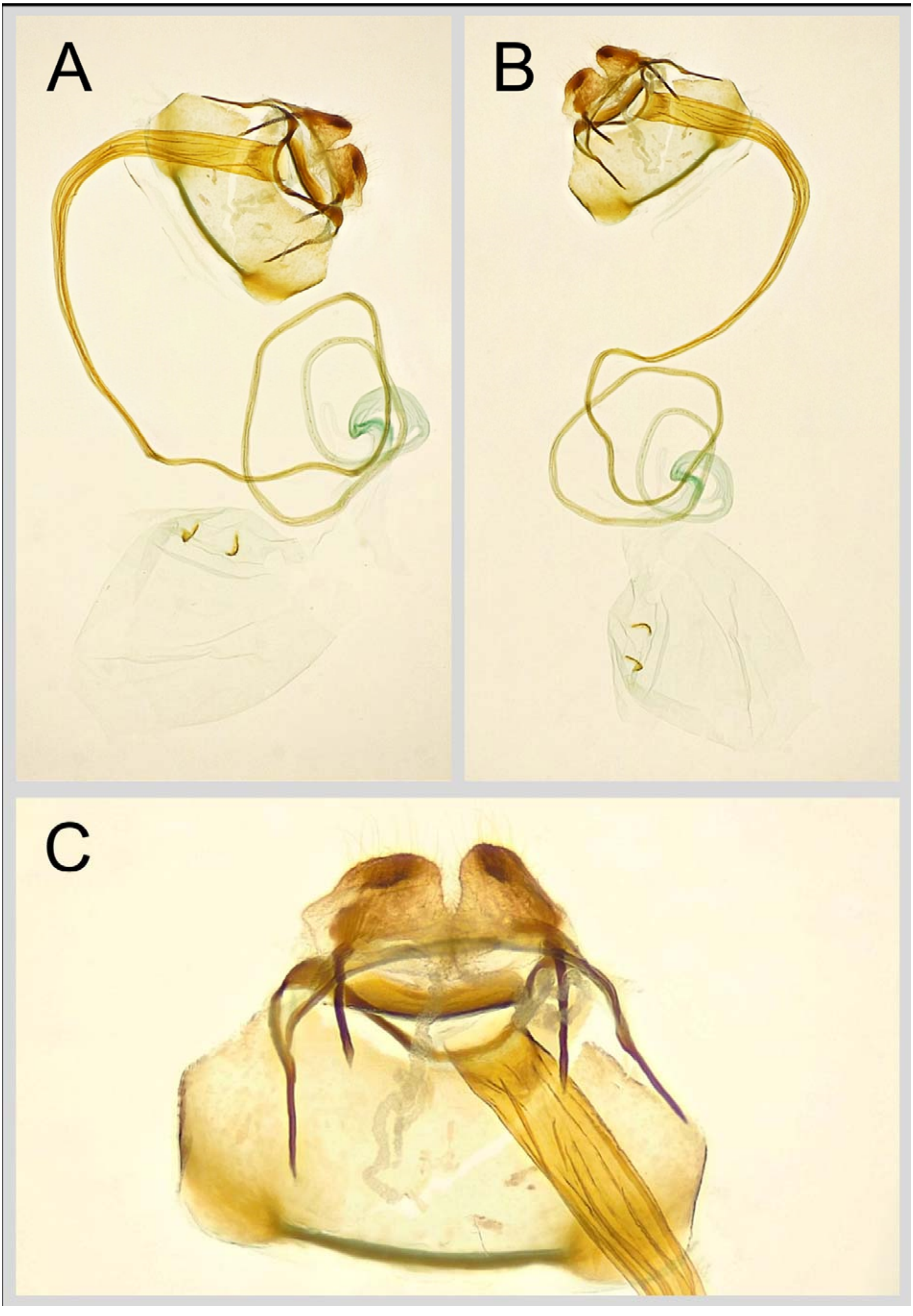


Figure 93. Female genitalia of *Mauricenaclia peyrierasi* **comb. nov.**

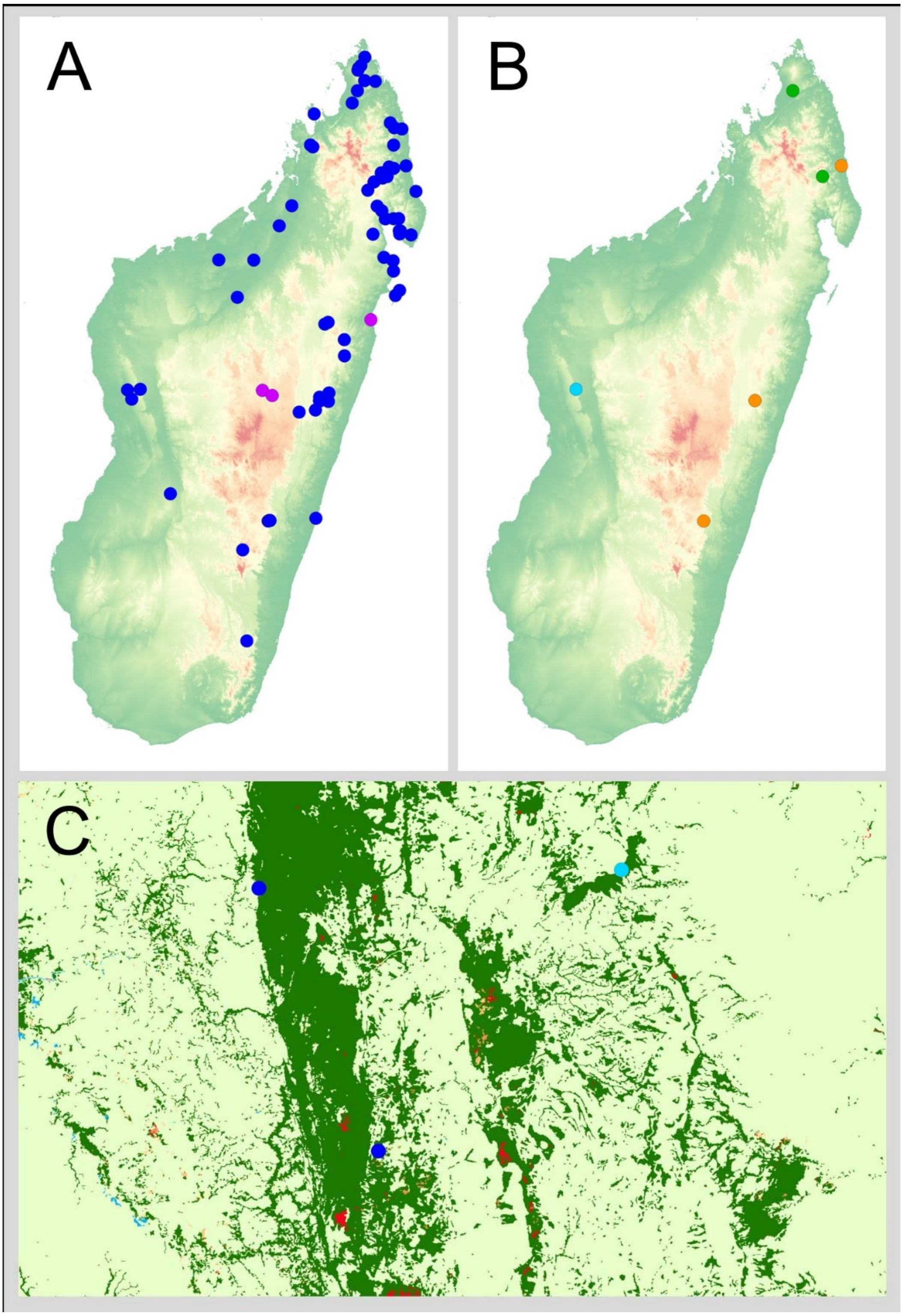


Figure 94. Distributional map of *Mauricenaclia minuta* **comb. nov.**: A – general distribution, doubtful localities marked in violet (see text); B – distribution of the specimens representing the potential cryptic species (see text); colours of the dots correspond with the relevant marks in the phylogenetic tree (see text); C – distribution of the "western" population, potentially constituting a separate, cryptic species (see text), deforestation marked with pale orange to red, from 2000 to 2020.

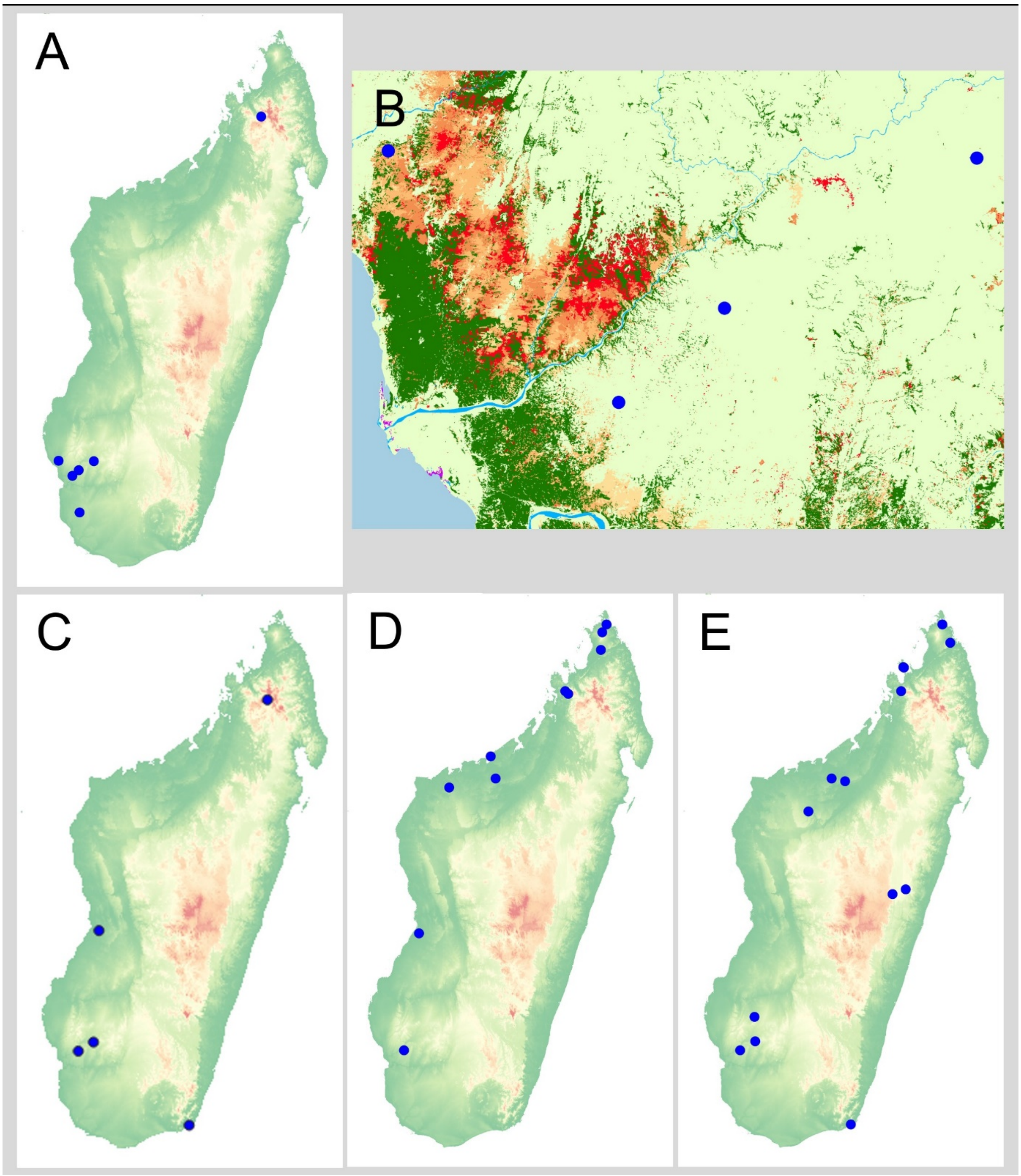


Figure 95. Distributional maps of *Mauricenaclia* **gen. nov.**: A – *M. raharizonina* **comb. nov.**; B – deforestation in the southern part of the range of *M. raharizonina* **comb. nov.** (pale orange to red, from 2000 to 2020); C – *M. rothschildi* **comb. nov.**; D – *M. octopunctata* **comb. nov.**; E – unidentified specimens of *M. rothschildi* **comb. nov.** / *M. octopunctata* **comb. nov.** (see text).

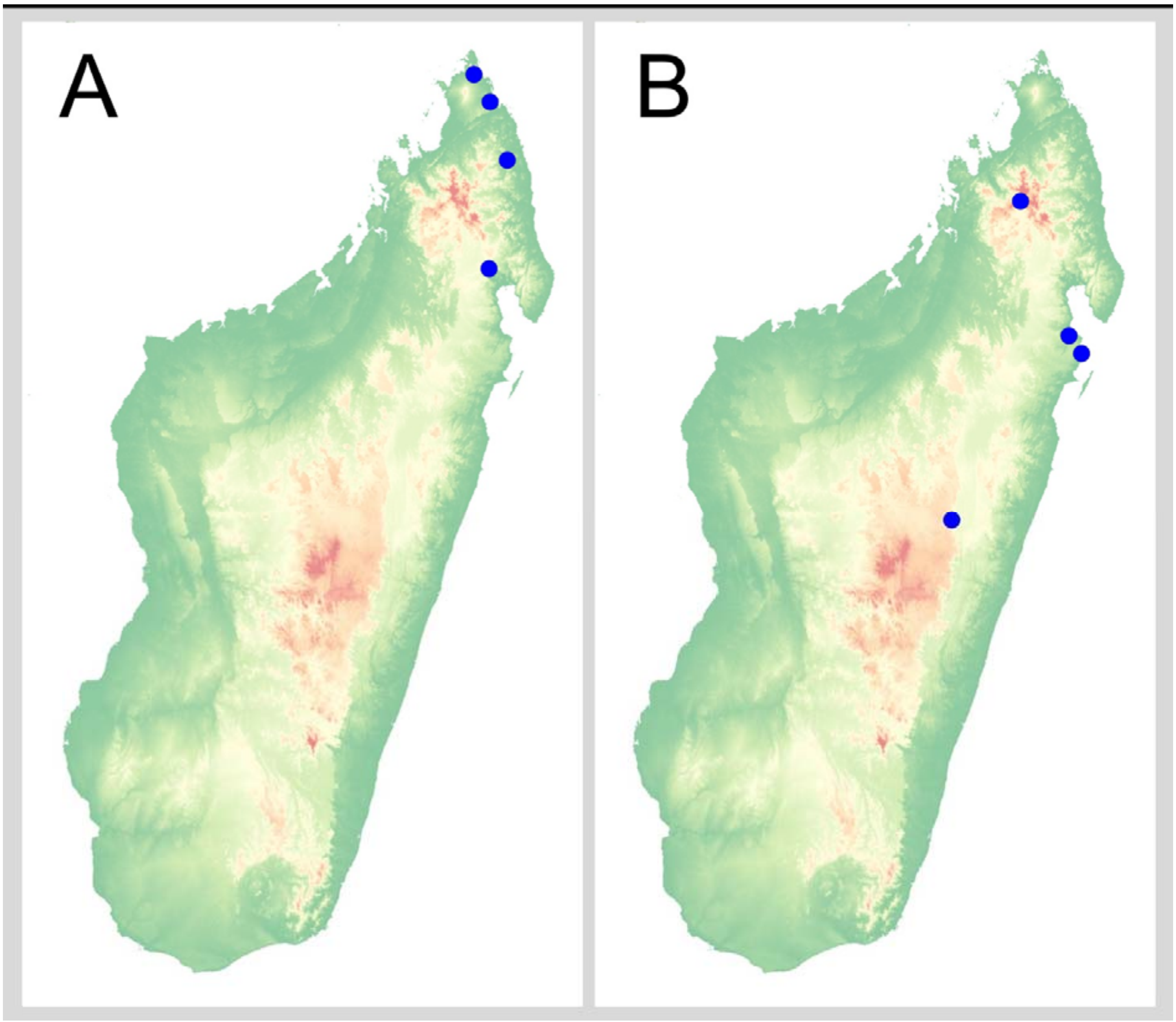


Figure 96. Distributional maps of *Mauricenaclia* **gen. nov.**: A – *M. bruneata* **comb. nov.**; B – *M. peyrierasi* **comb. nov.**

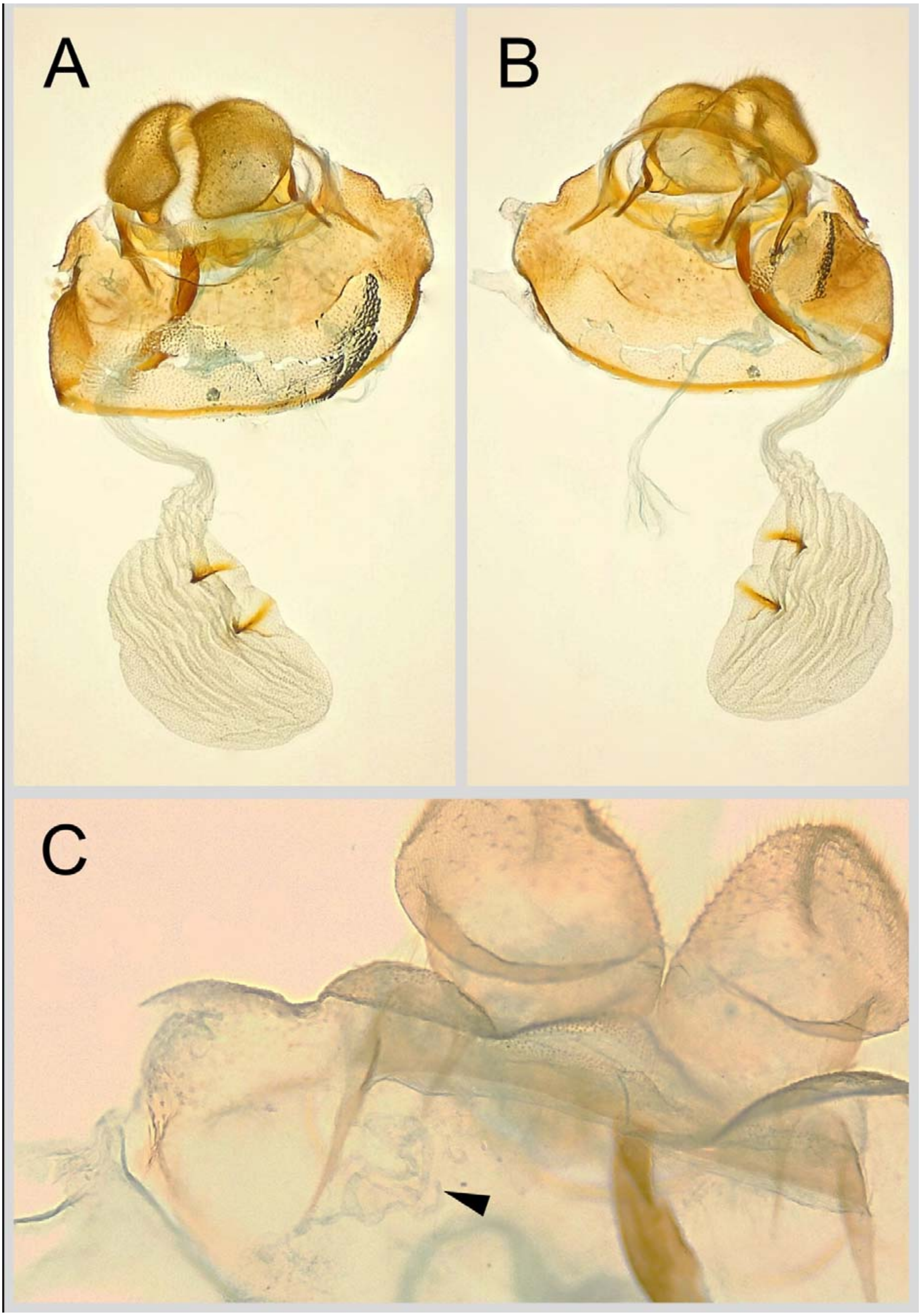


Figure 97. Female genitalia of *Pseudonaclia puella*, note the very indistinct dorsal pheromonal glands (arrowhead);

Figure 98. *Melanonaclia*, adults: A – male holotype of *M. luctuosa*, NHMUK010621695; B – *M. luctuosa* female, ISEA PAS, DL_SF11; C – *M. luctuosa* female, ISEA PAS, DL_SC3; D – female holotype of *Tritonaclia inauramacula* **syn. nov.**, MNHN, EL65140 (see text); E – female holotype of *M. lugens*, NHMUK010620990; F-G – *M. luctuosa* female, MNHN, EL74604, upperside and underside (note the ventral blotch on the abdomen); H – female "neallotype" of *M. lugens*, MNHN, EL65135; not to the same scale.

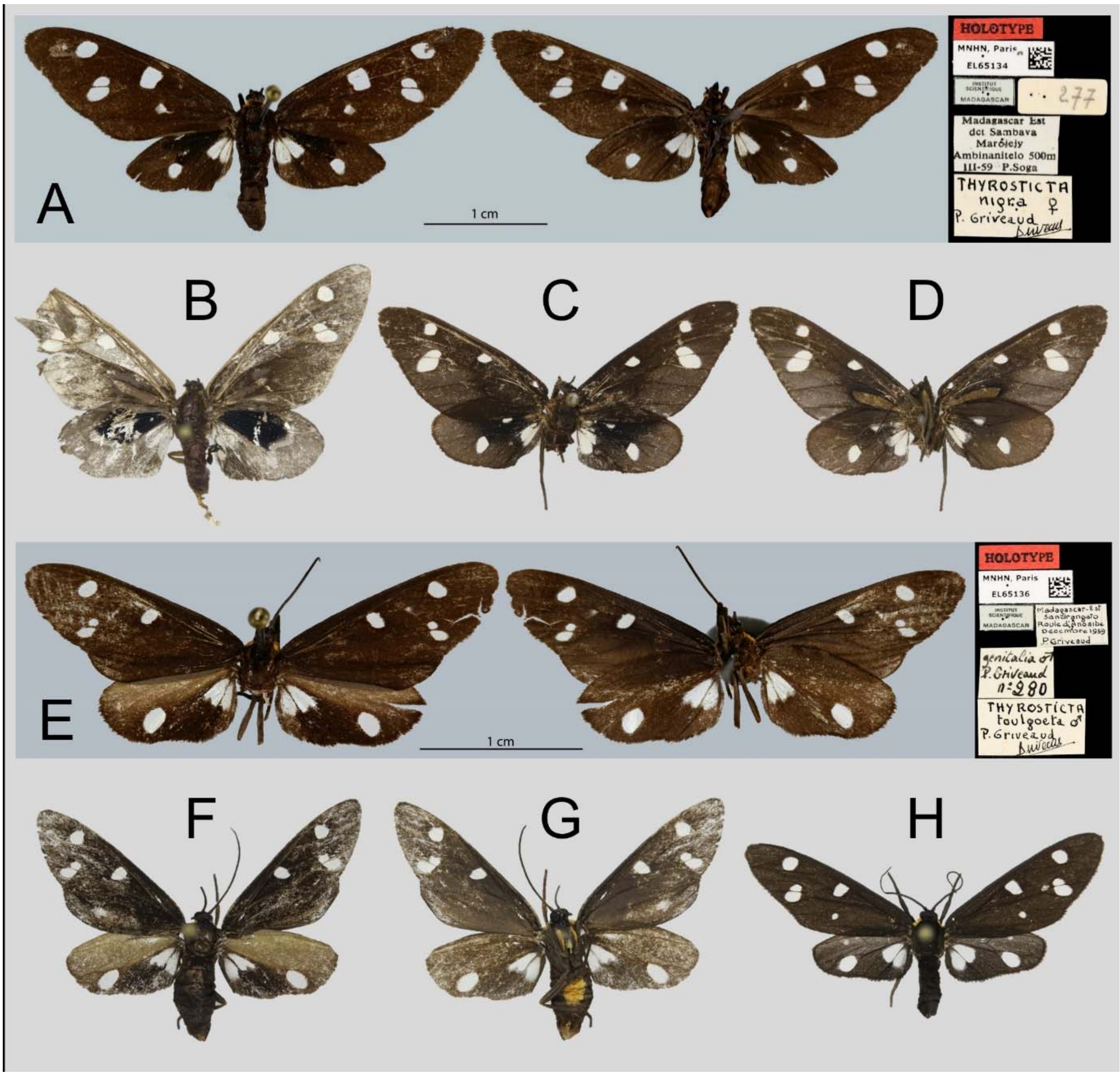


Figure 99. *Melanonaclia*, adults: A – female holotype of *M. nigra*, MNHN, EL65134; B – *M. nigra* male, ISEA PAS, DL_01-154; C-D – *M. nigra* male, NMP, upperside and underside (note the modified scales of hindwing upperside and forewing underside, see text); E – male holotype of *M. toulgoeti*, MNHN, EL65136; F-G – *M. toulgoeti* male, ISEA PAS, MAD_084, upperside and underside (note the ventral blotch on the abdomen); H – *M. toulgoeti* female, ISEA PAS, MAD_009; not to the same scale.

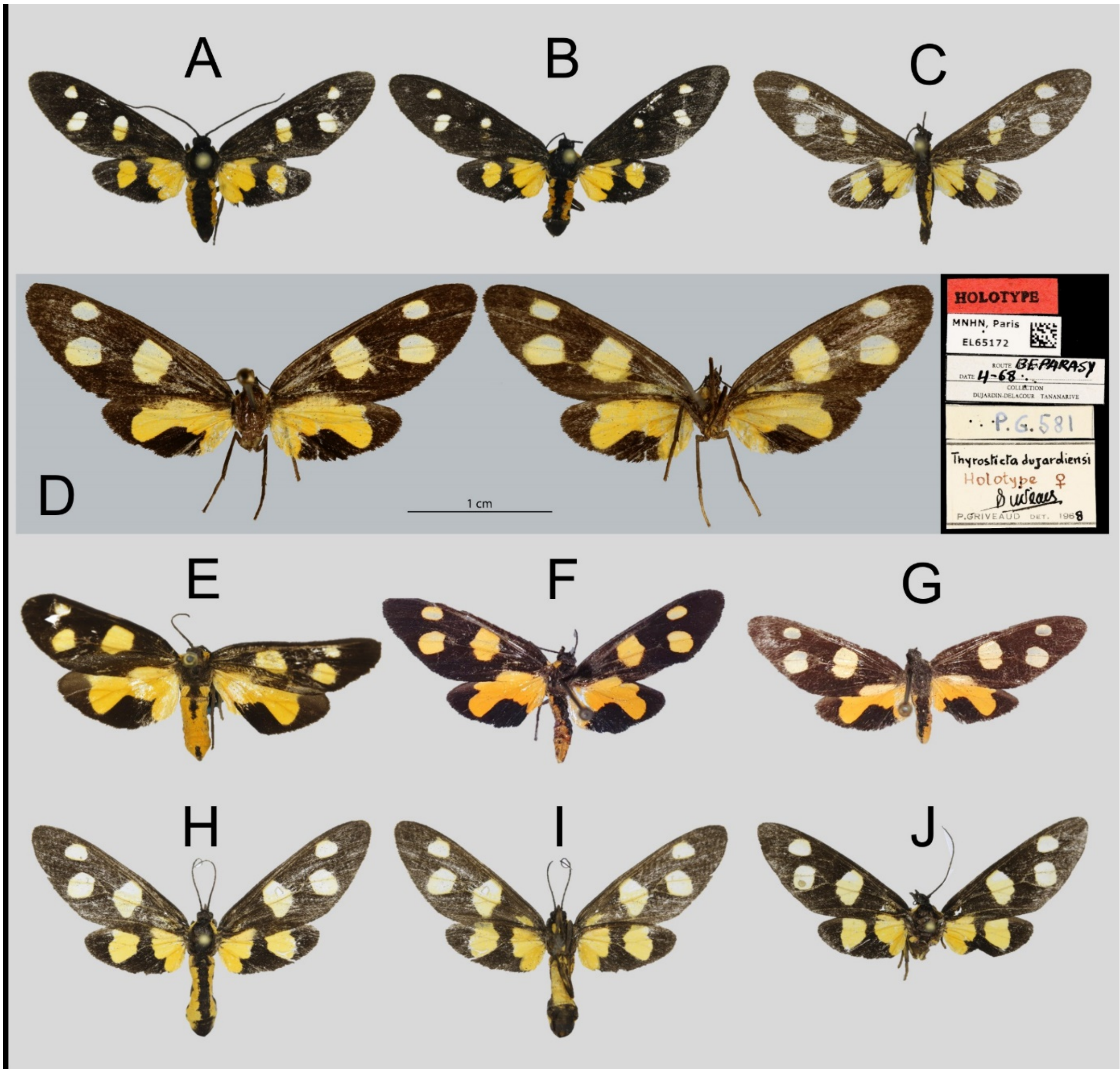


Figure 100. *Melanonaclia*, adults: A – *M. trimacula* **comb. nov.** male, ISEA PAS, ISEZ-DNA_539; B – *M. trimacula* **comb. nov.** female, ISEA PAS, ISEZ-DNA_544; C – *M. trimacula* **comb. nov.** female, ISEA PAS, DL_05-424; D – female holotype of *M. dujardini* **comb. nov.**, MNHN, EL65172; E – *M. dujardini* **comb. nov.** male, MNHN, EL82777; F-G – *M. dujardini* **comb. nov.** females, PZBT; H-I – female holotype of *M. ranomafana* **sp. nov.**, ISEA PAS, MAD_018; J – female paratype of *M. ranomafana* **sp. nov.**, ISEA PAS, MAD_019; not to the same scale.

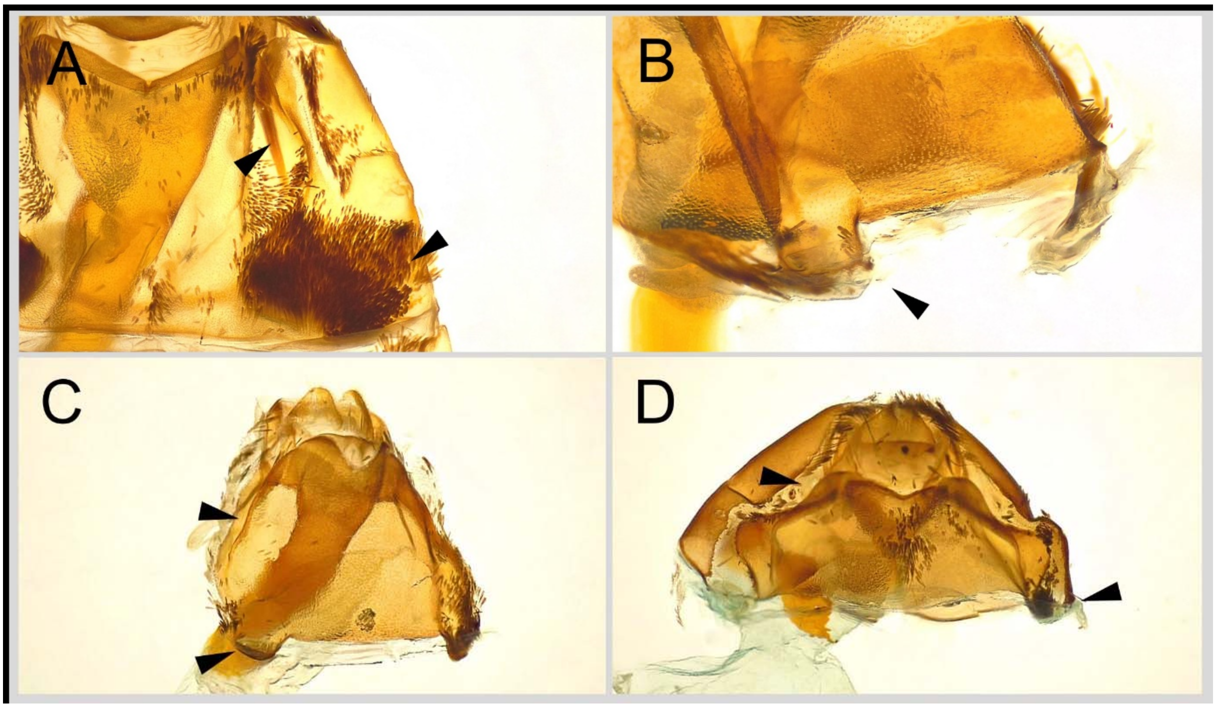


Figure 101. The terminal segments of *Melanonaclia* female abdomen, note the pouch-like protrusion on basal margin of the 7th sternite, and the lateral longitudinal cavity (arrowheads).

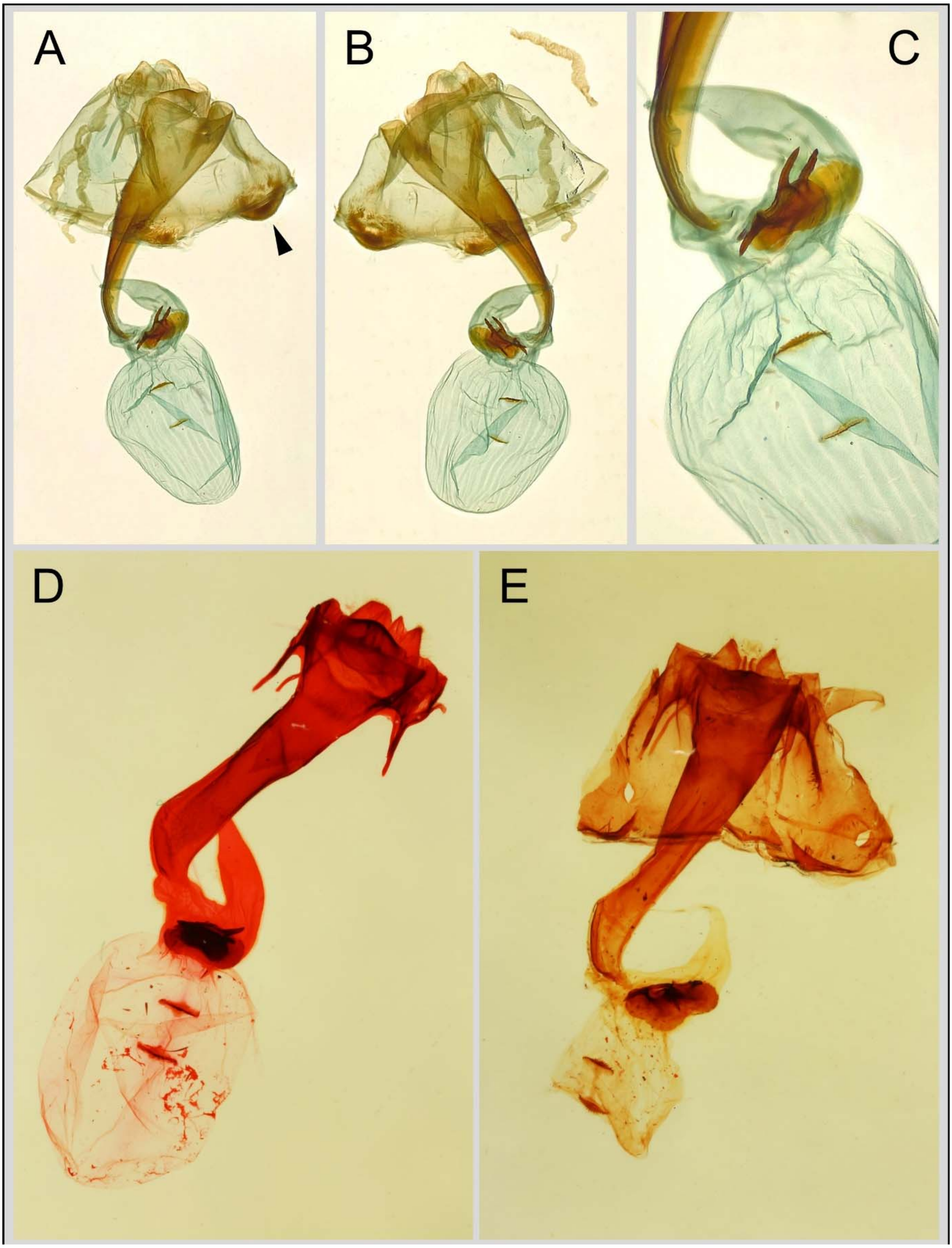


Figure 102. Female genitalia of *Melanonaclia luctuosa*, note the genus-specific pouch-like protrusion on the basal margin of the 7th sternite (arrowhead, see text).

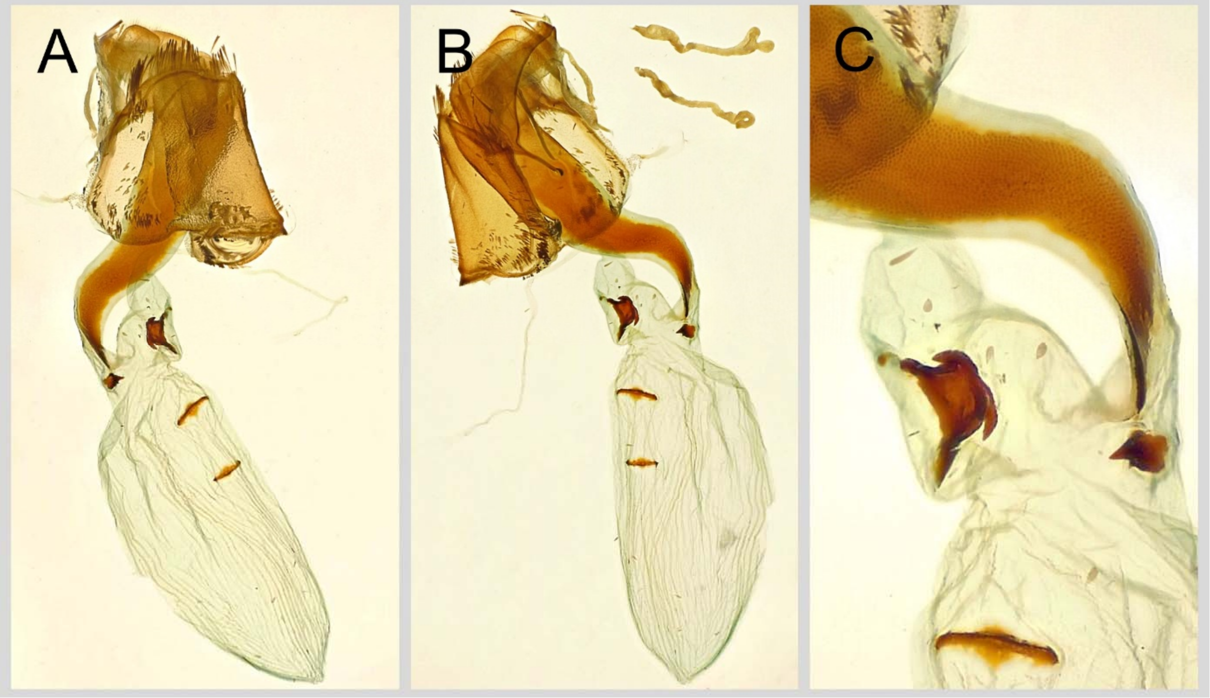


Figure 103. Female genitalia of *Melanonaclia lugens.*

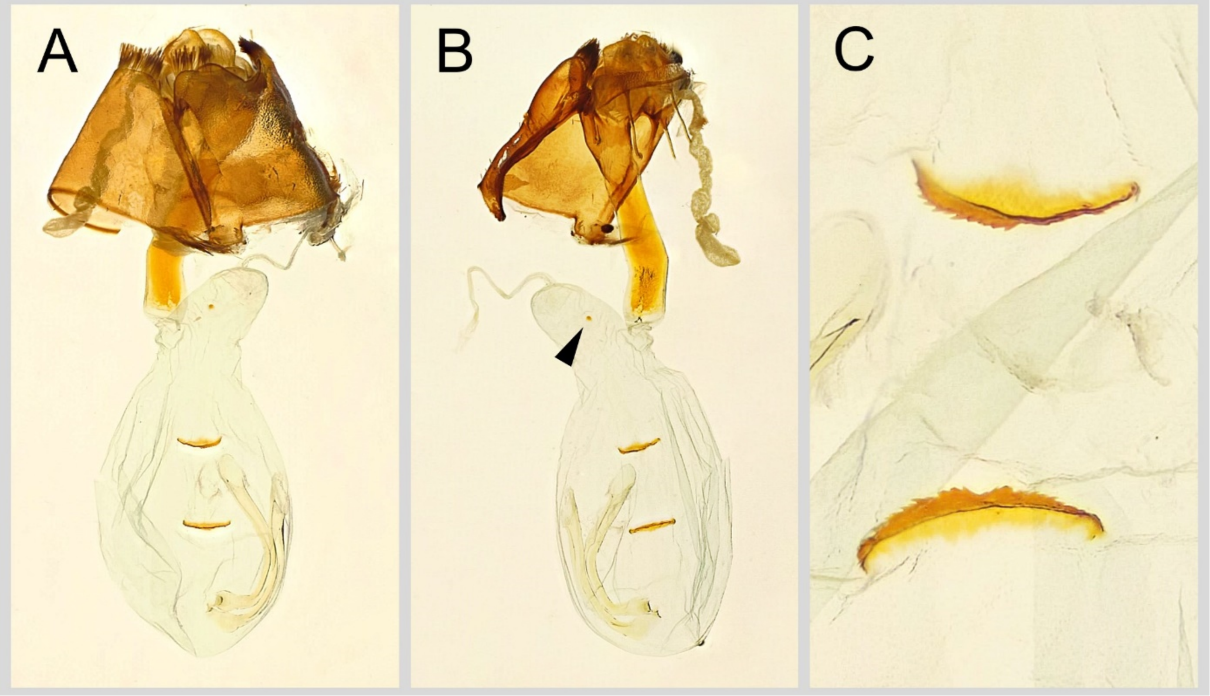


Figure 104. Female genitalia of *Melanonaclia nigra*, note the size of basal diverticulum of corpus bursae (arrowhead, see text).

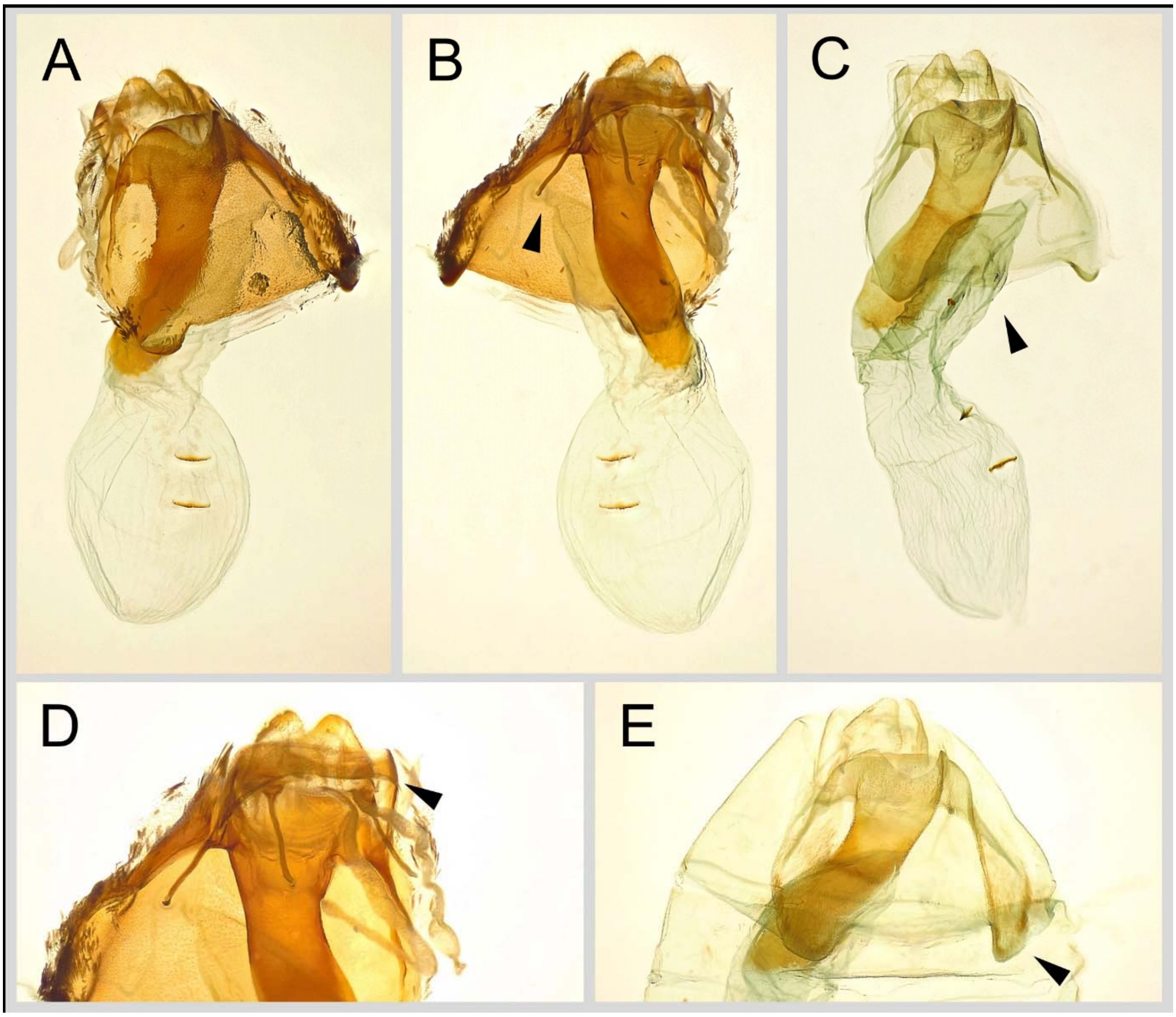


Figure 105. Female genitalia of *Melanonaclia toulgoeti*, note the size of basal diverticulum of corpus bursae, and the genus-specific pouch-like protrusion on the basal margin of the 7th sternite (arrowheads, see text).

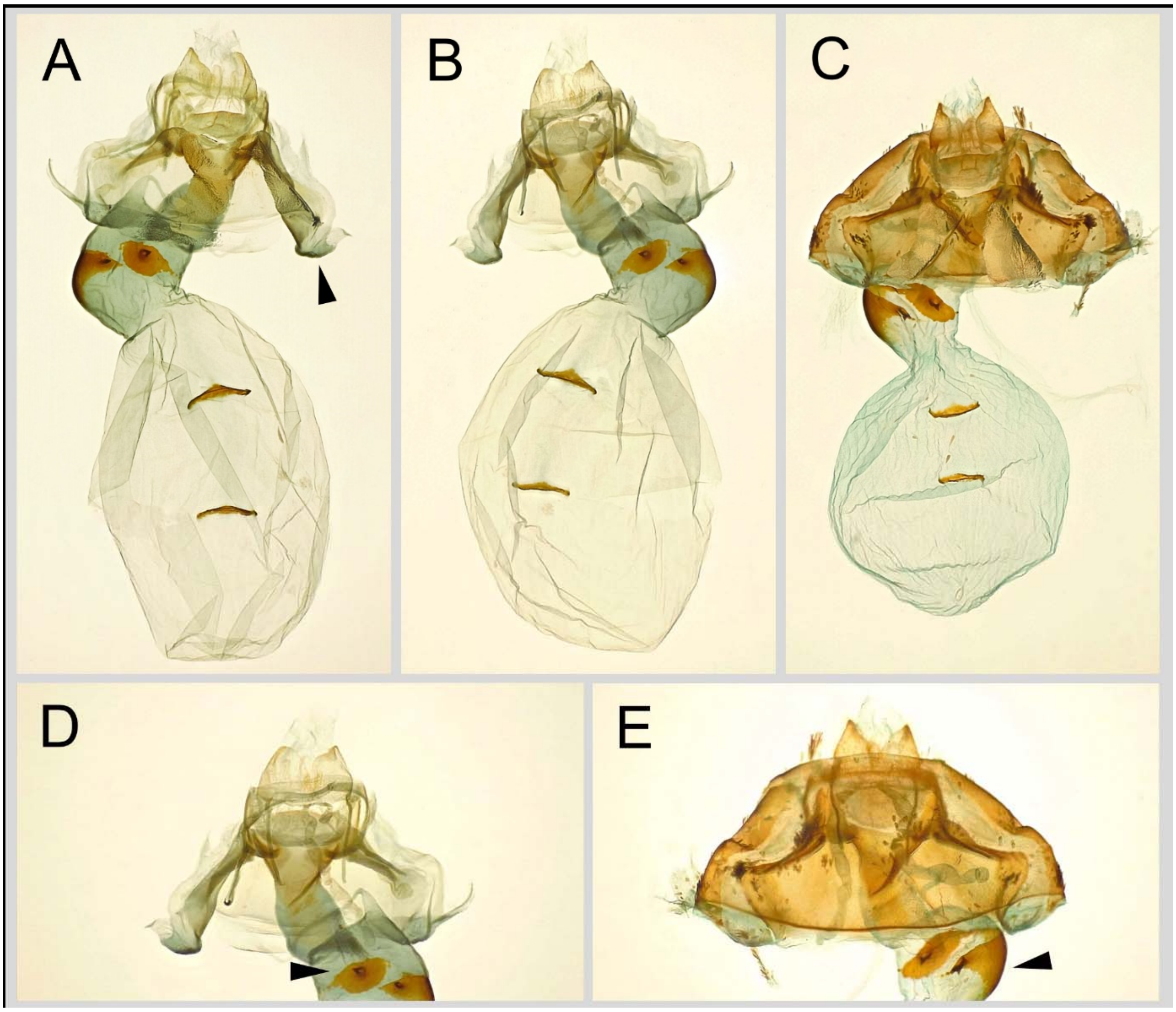


Figure 106. Female genitalia of *Melanonaclia trimacula*, note the pouch-like protrusion on the basal margin of the 7th sternite, and the shape of basal signa (arrowheads, see text).

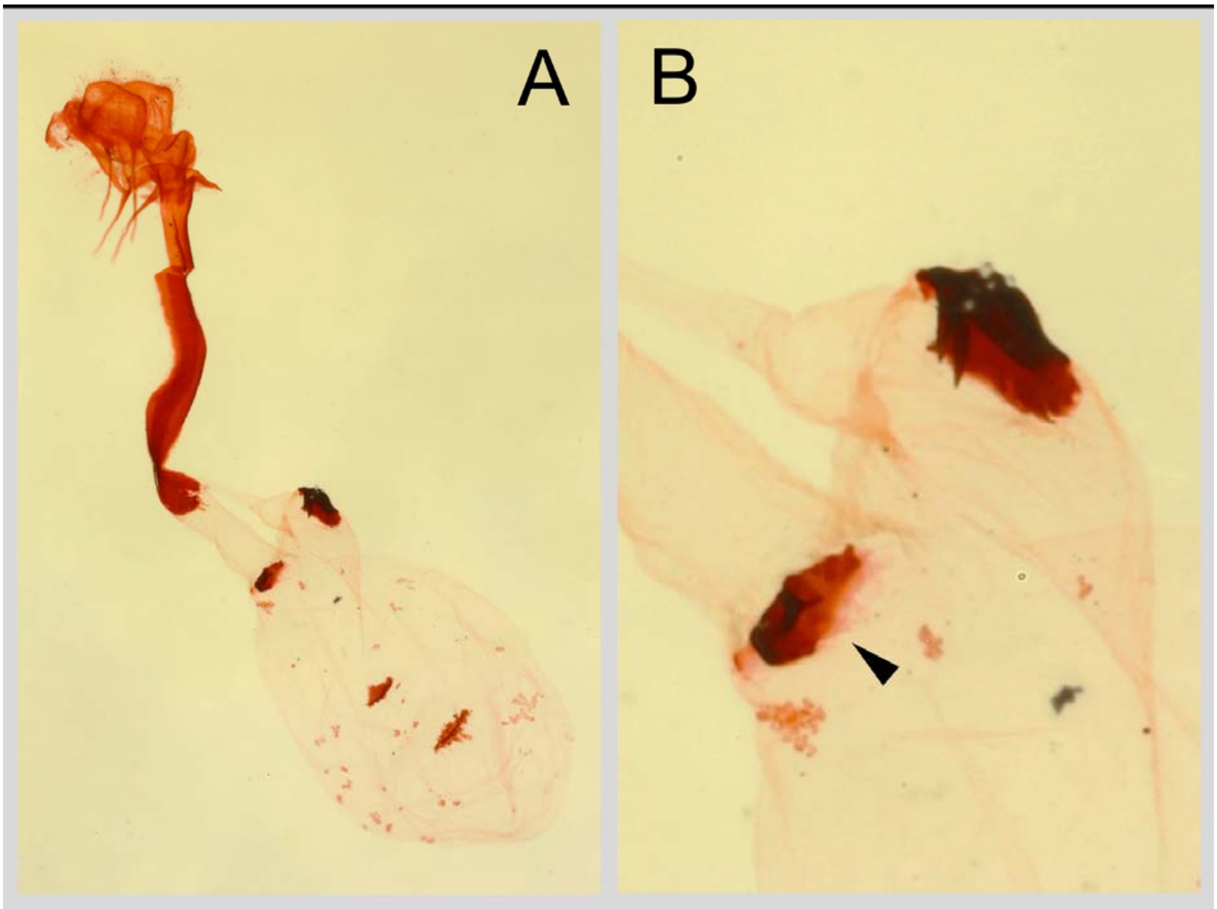


Figure 107. Female genitalia of *Melanonaclia dujardini*, P. Griveaud original slide No. 581.

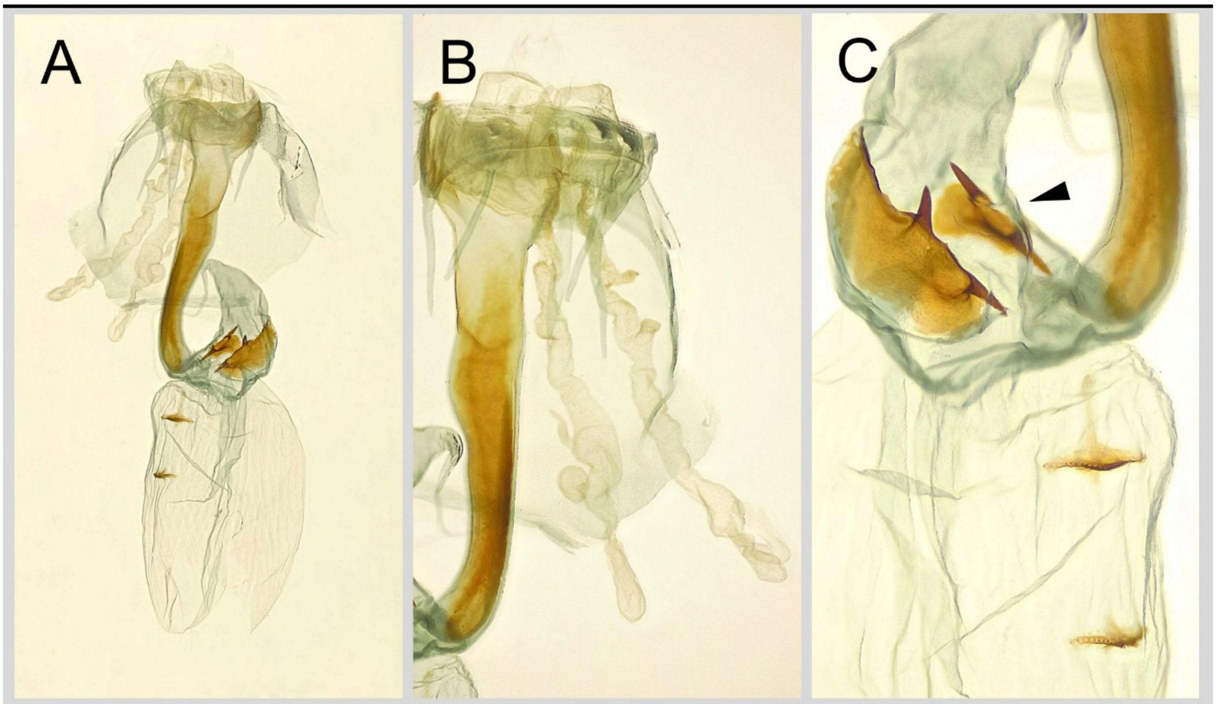


Figure 108. Female genitalia of *Melanonaclia ranomafana* **sp. nov.**, note the shape of the basal signa (see text).

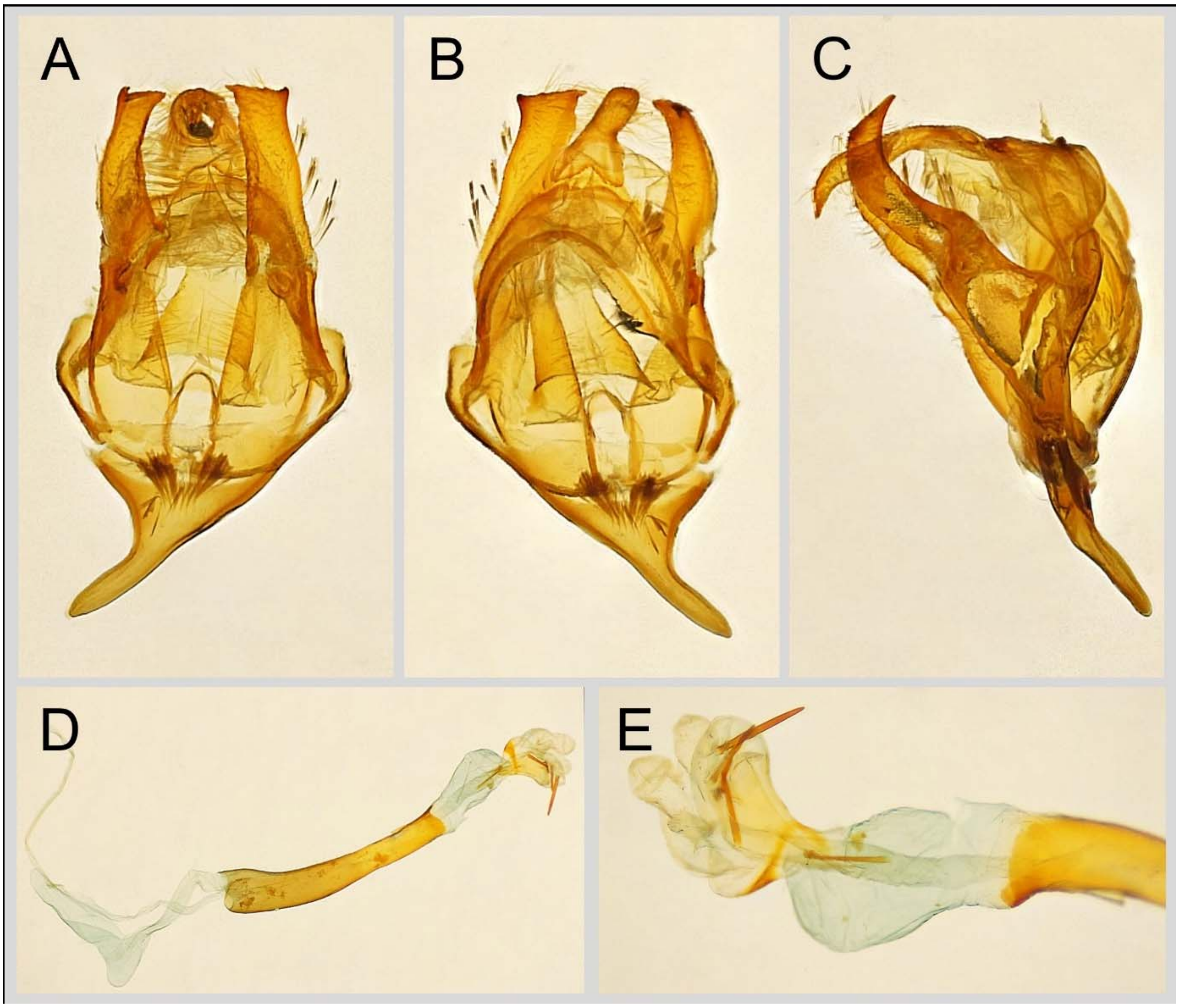


Figure 109. Male genitalia of *Melanonaclia luctuosa*.

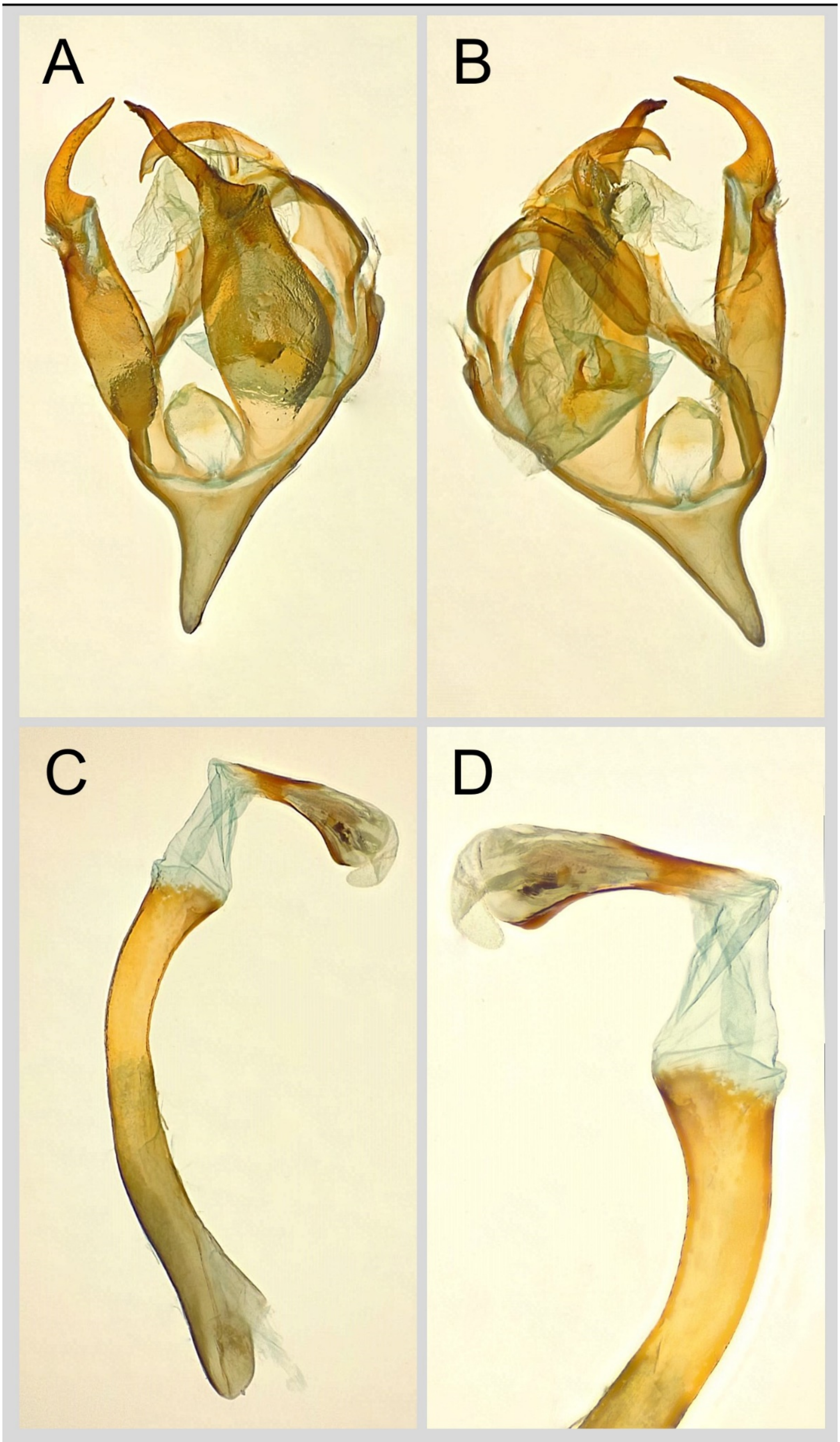


Figure 110. Male genitalia of *Melanonaclia lugens*.

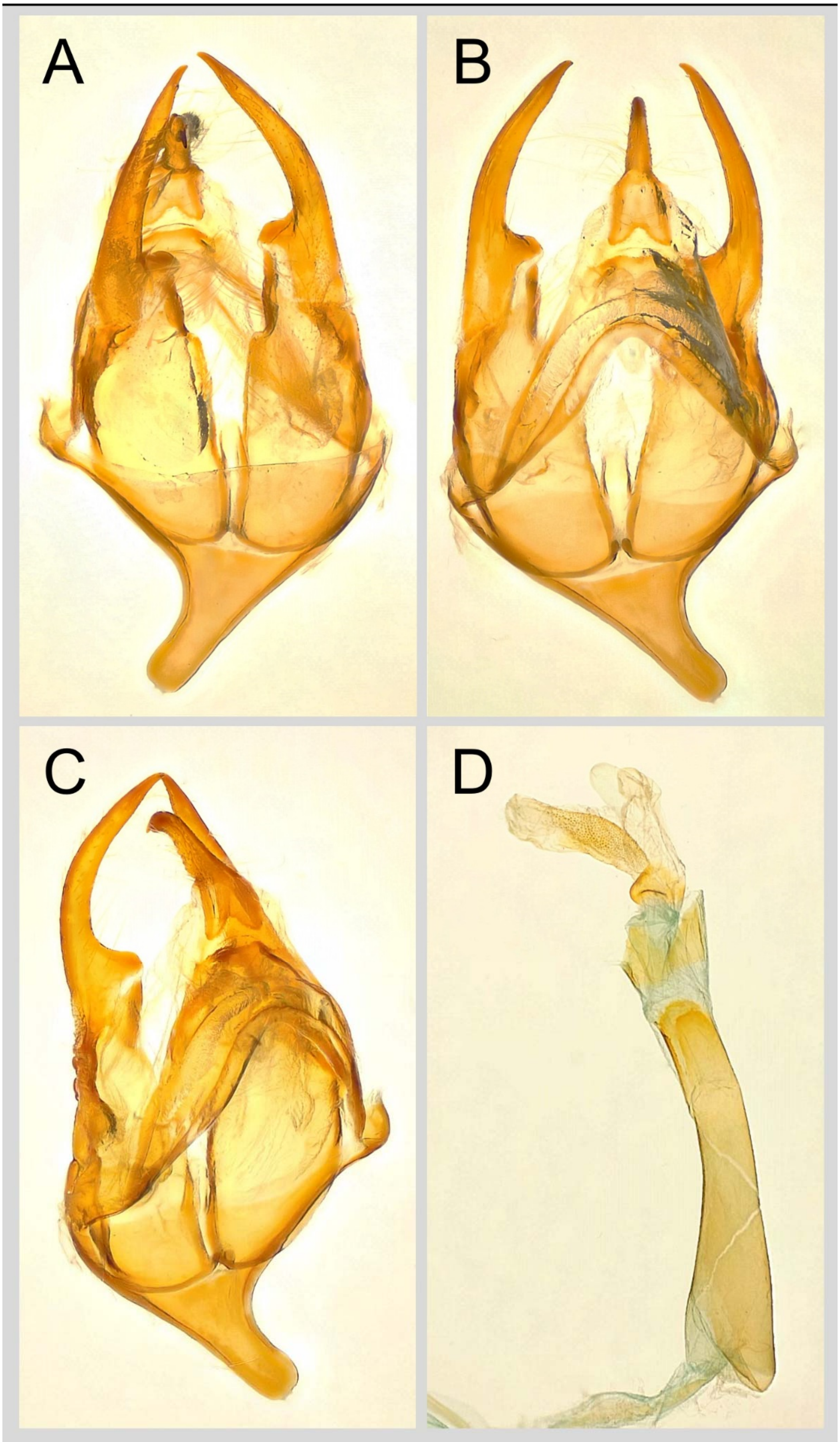


Figure 111. Male genitalia of *Melanonaclia nigra*.

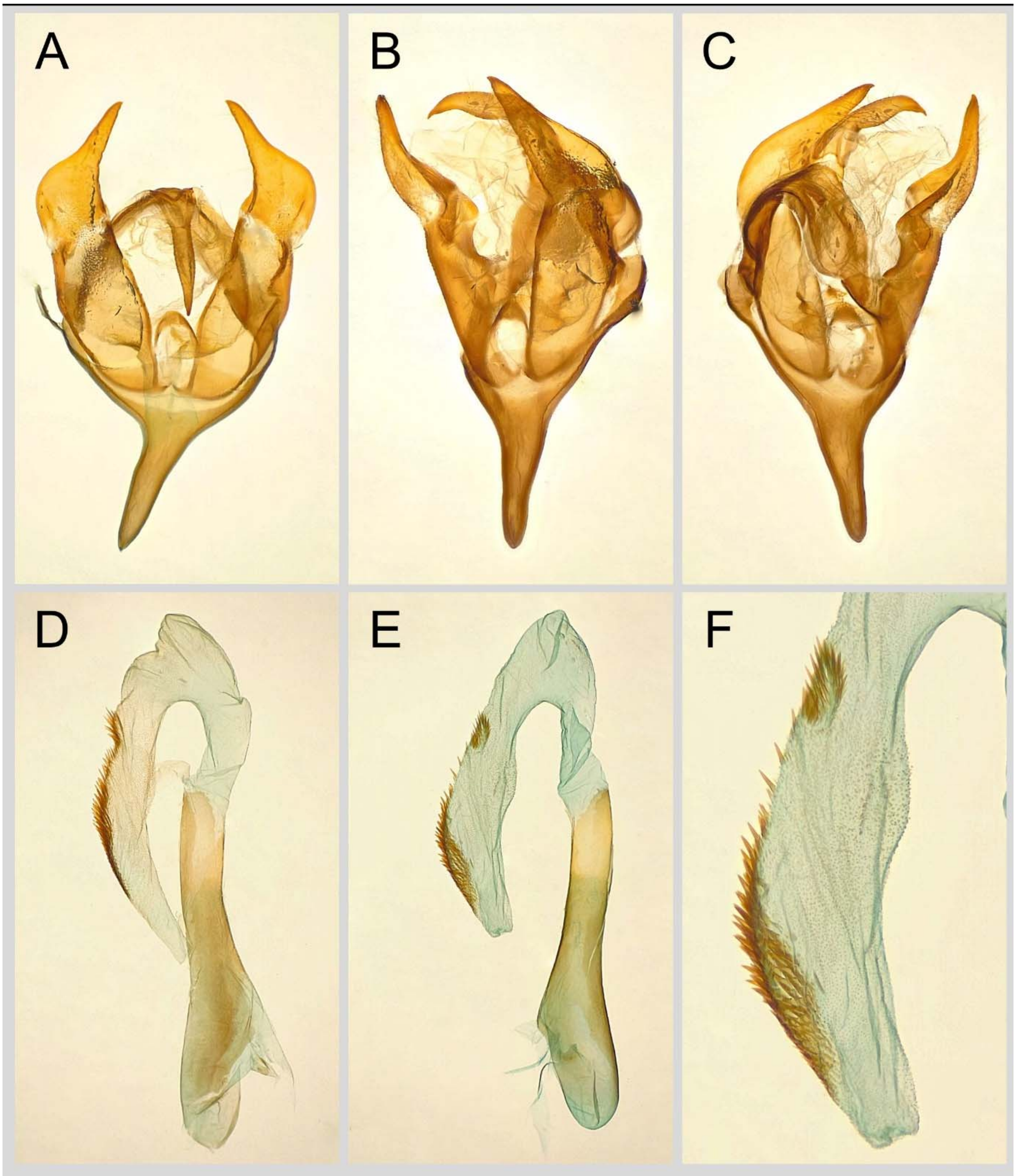


Figure 112. Male genitalia of *Melanonaclia toulgoeti*, note the variation in cornuti arrangement on vesica.

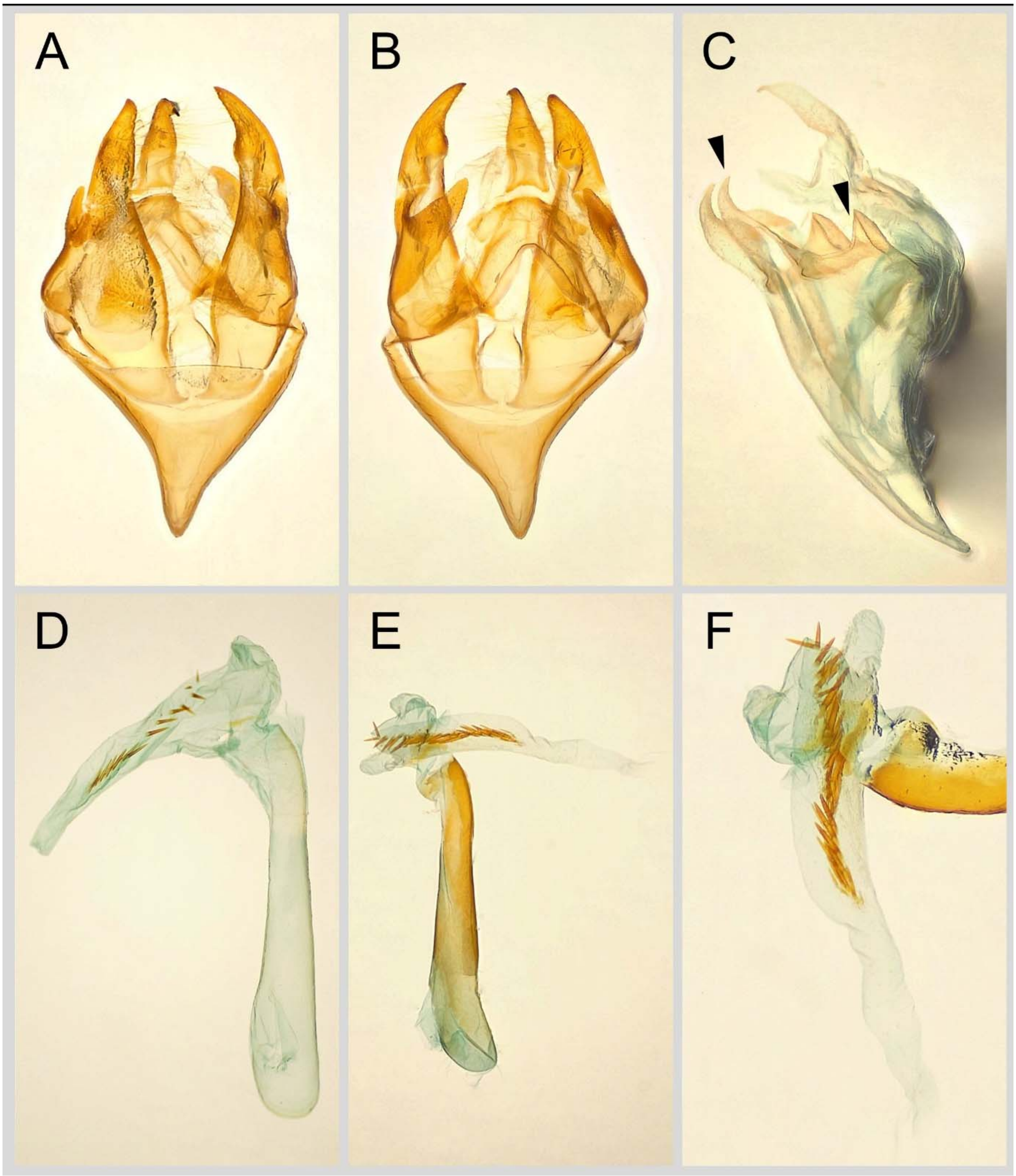


Figure 113. Male genitalia of *Melanonaclia trimacula*, note the subtriangular protrusion on costal margin of valva (arrowheads, see text).

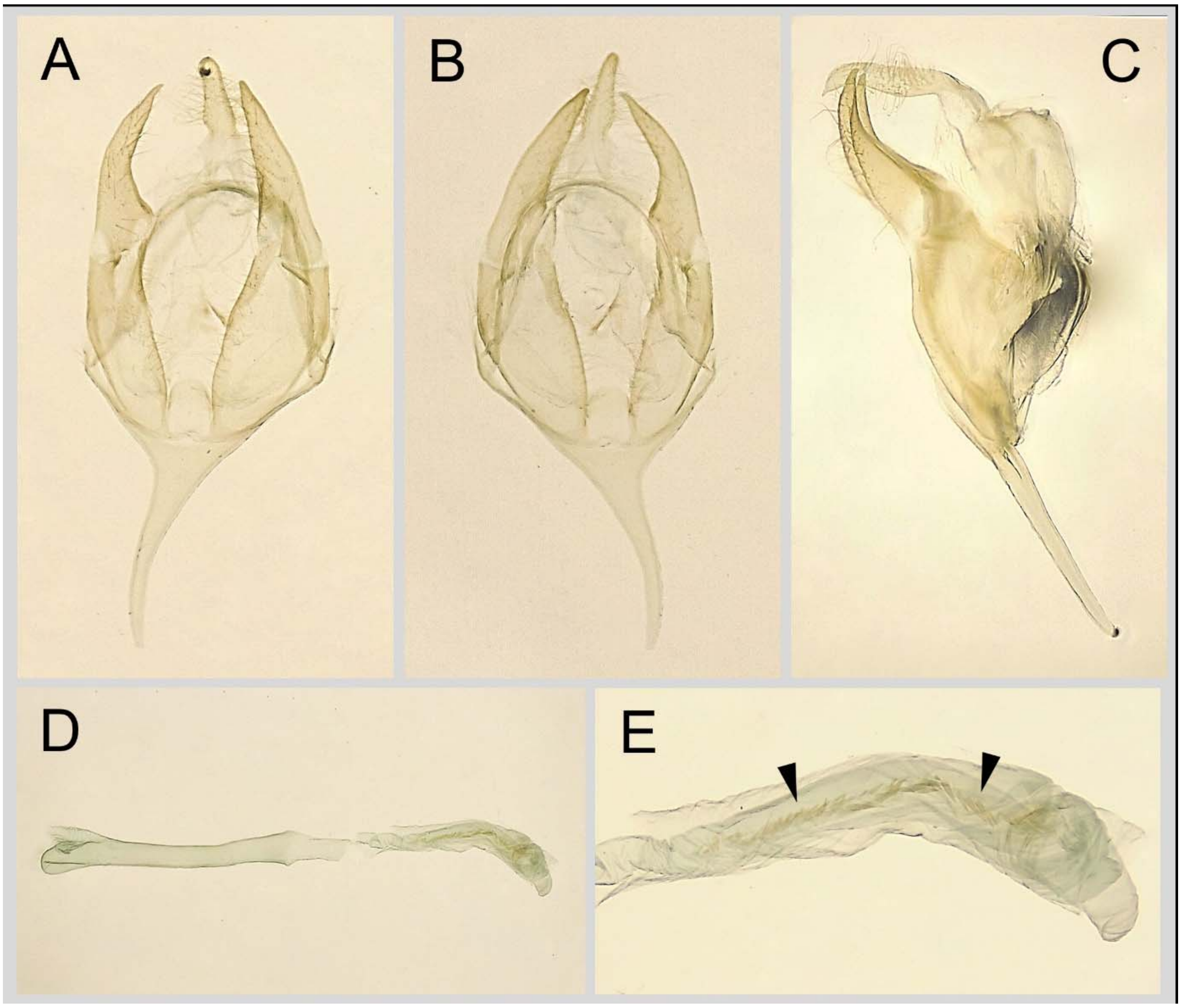


Figure 114. Male genitalia of *Melanonaclia dujardini*, note the arrangement of cornuti in vesica (arrowheads, see text).

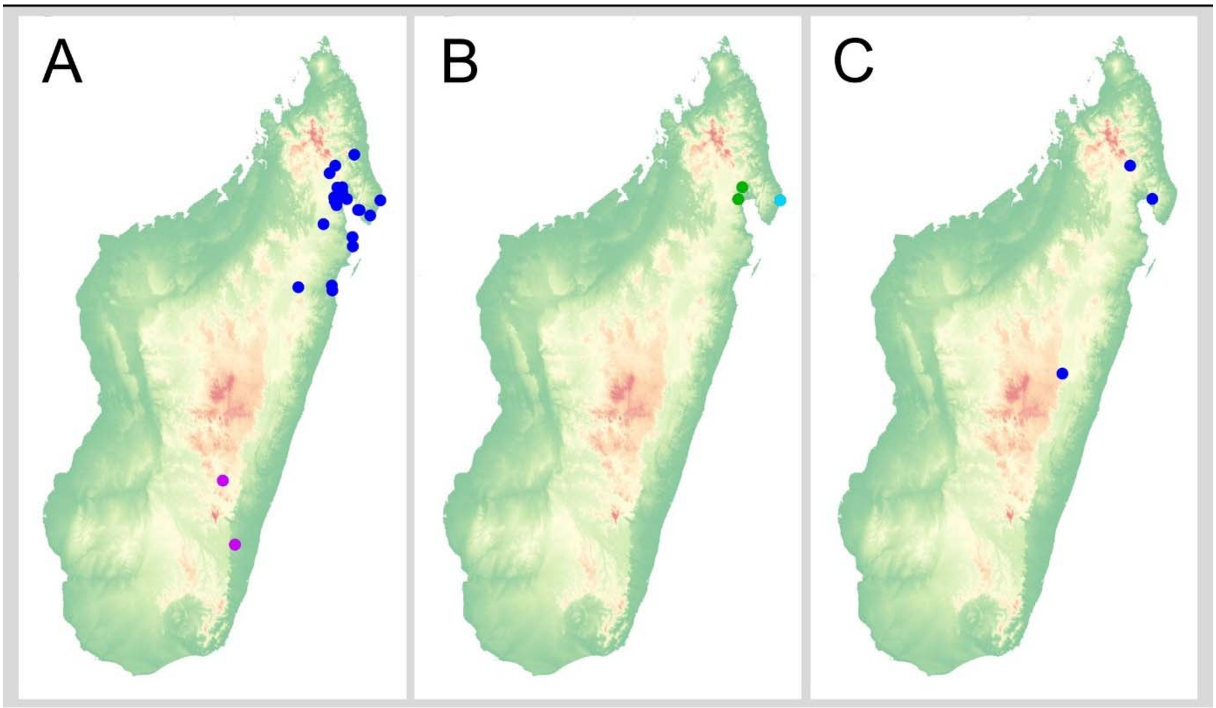


Figure 115. Distributional maps of *Melanonaclia*: A – *M. luctuosa* general distribution; B – distribution of *M. luctuosa* specimens representing the potential cryptic species (see text); colours of the dots correspond with the relevant marks in the phylogenetic tree; C – *M. lugens*.

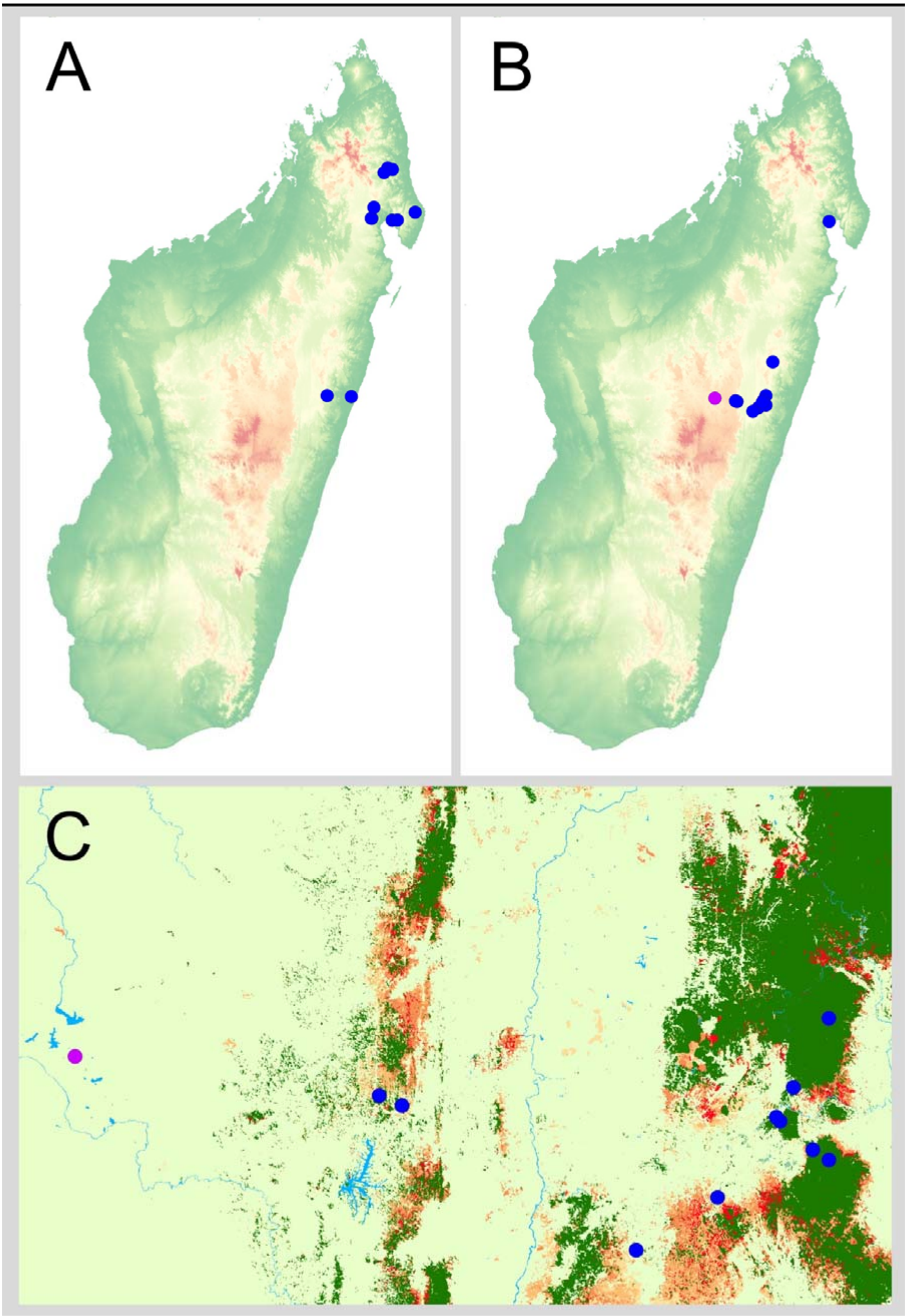


Figure 116. Distributional maps of *Melanonaclia*: A – *M. nigra*; B – *M. toulgoeti*, violet - doubtful records; C – deforestation (pale orange to red, from 2000 to 2020) in the main part of *M. toulgoeti* range.

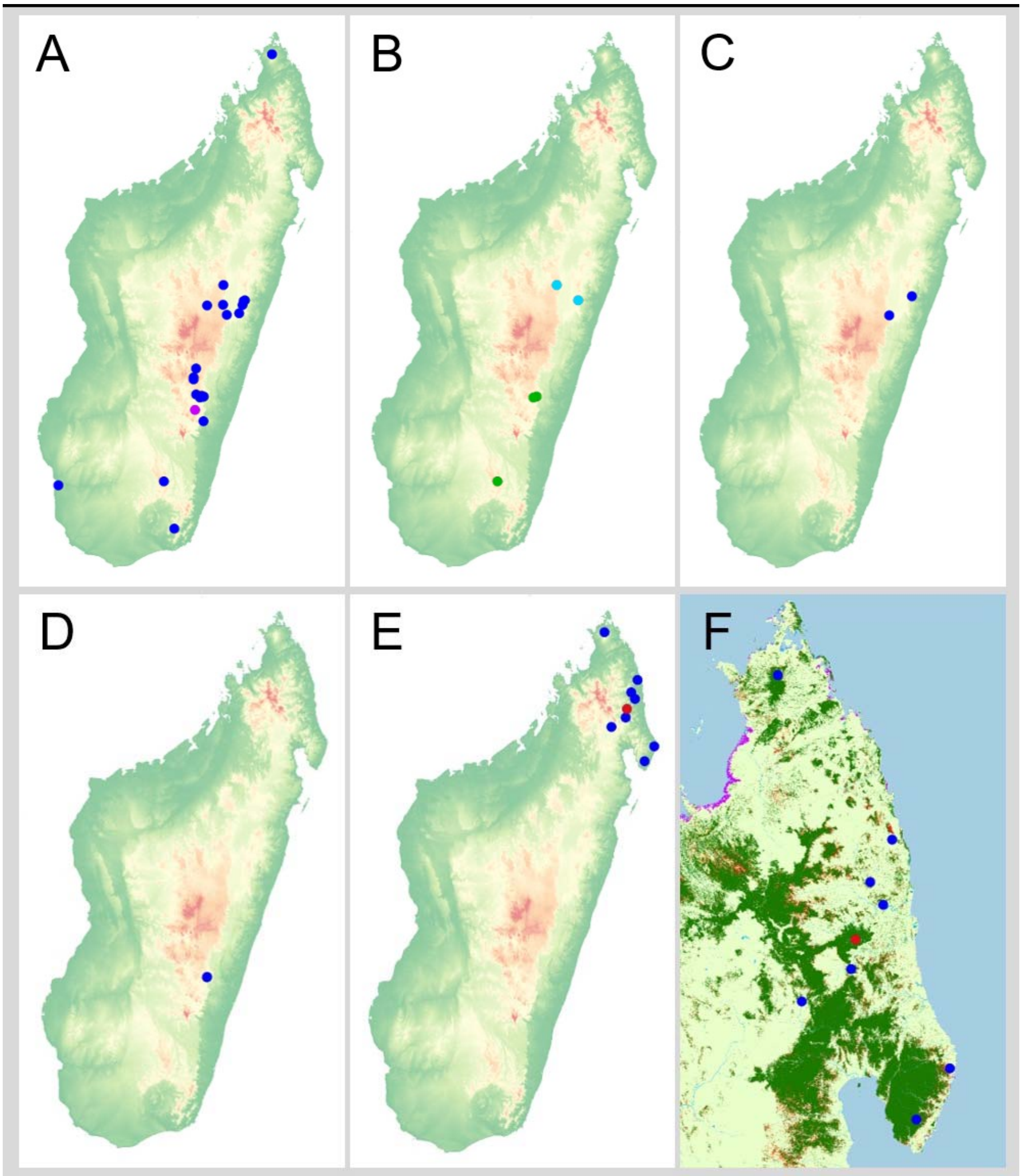


Figure 117. Distributional map of *Melanonaclia* and *Mortinaclia* **gen. nov.**: A – *Melanonaclia trimacula* **comb. nov.**, violet - doubtful records (see text); B – distribution of *M. trimacula* **comb. nov.** specimens representing the potential cryptic species (see text); colours of the dots correspond with the relevant marks in the phylogenetic tree; C – *Melanonaclia dujardini* **comb. nov.**, D – *Melanonaclia ranomafana* **sp. nov.**, E-F – *Mortinaclia perplexa* **comb. nov.**, red - holotype collecting locality.

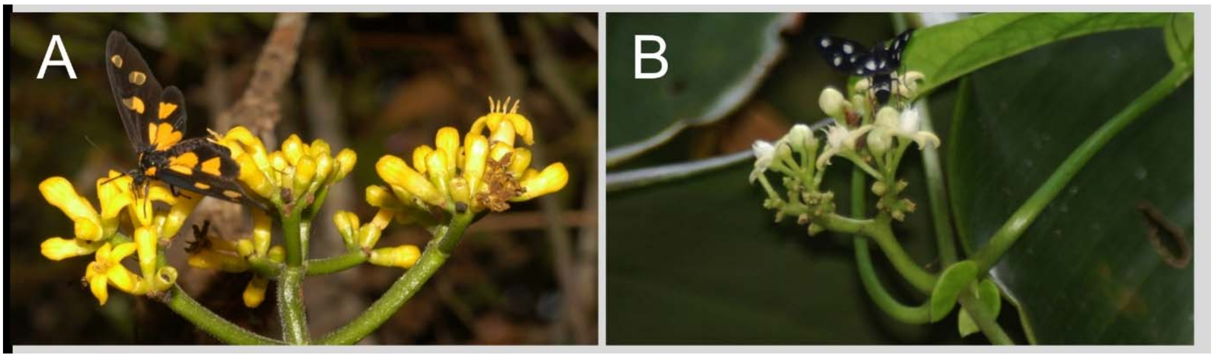


Figure 118. Observations of nectaring: A – *Melanonaclia trimacula* **comb. nov.** nectaring on flowers of *Psychotria* (*Mapourea*) sp. (Rubiaceae) in PN Ranomafana (Photo: D.C. Lees); B – *Mortinaclia perplexa* **comb. nov.** nectaring on flowers of *Cynanchum analamazaotrense* (Apocynacae: Asclepiadoideae) in Makirovana (Photo: iNaturalist observation 38824345, by the user sigrid_bt).

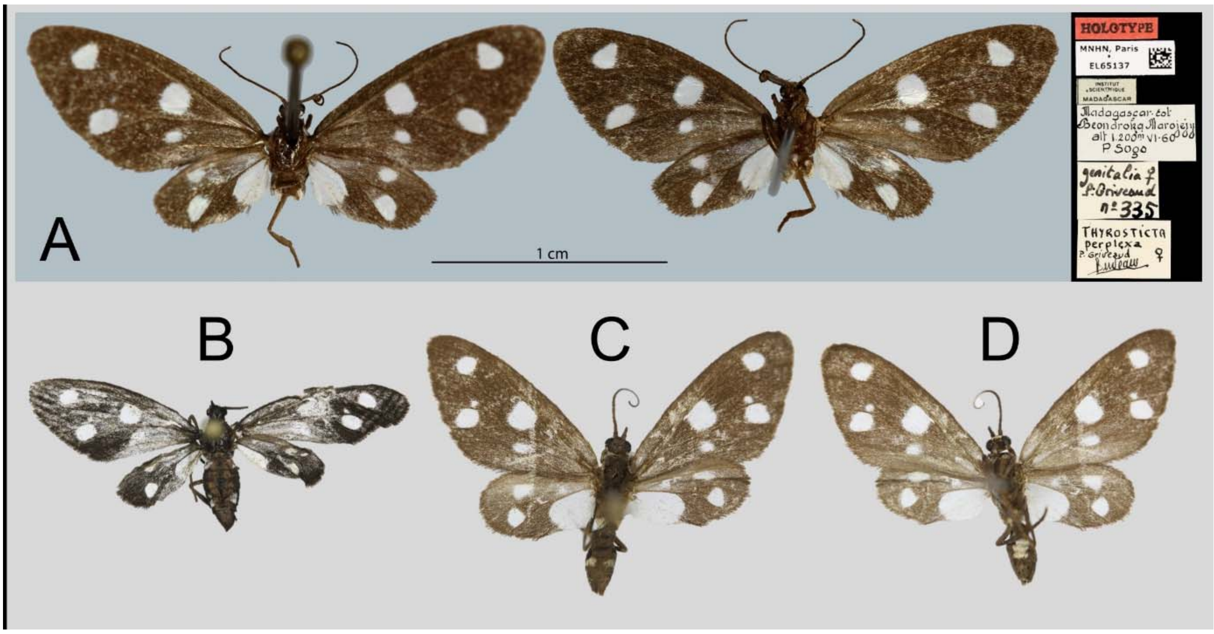


Figure 119. *Mortinaclia* **gen. nov.** - *M. perplexa* **comb. nov.** species complex (see text), adults: A – female holotype, MNHN, EL65137; B – male, ISEA PAS, MAD_286; C-D – male, MNHN, EL74947, upperside and underside; not to the same scale.

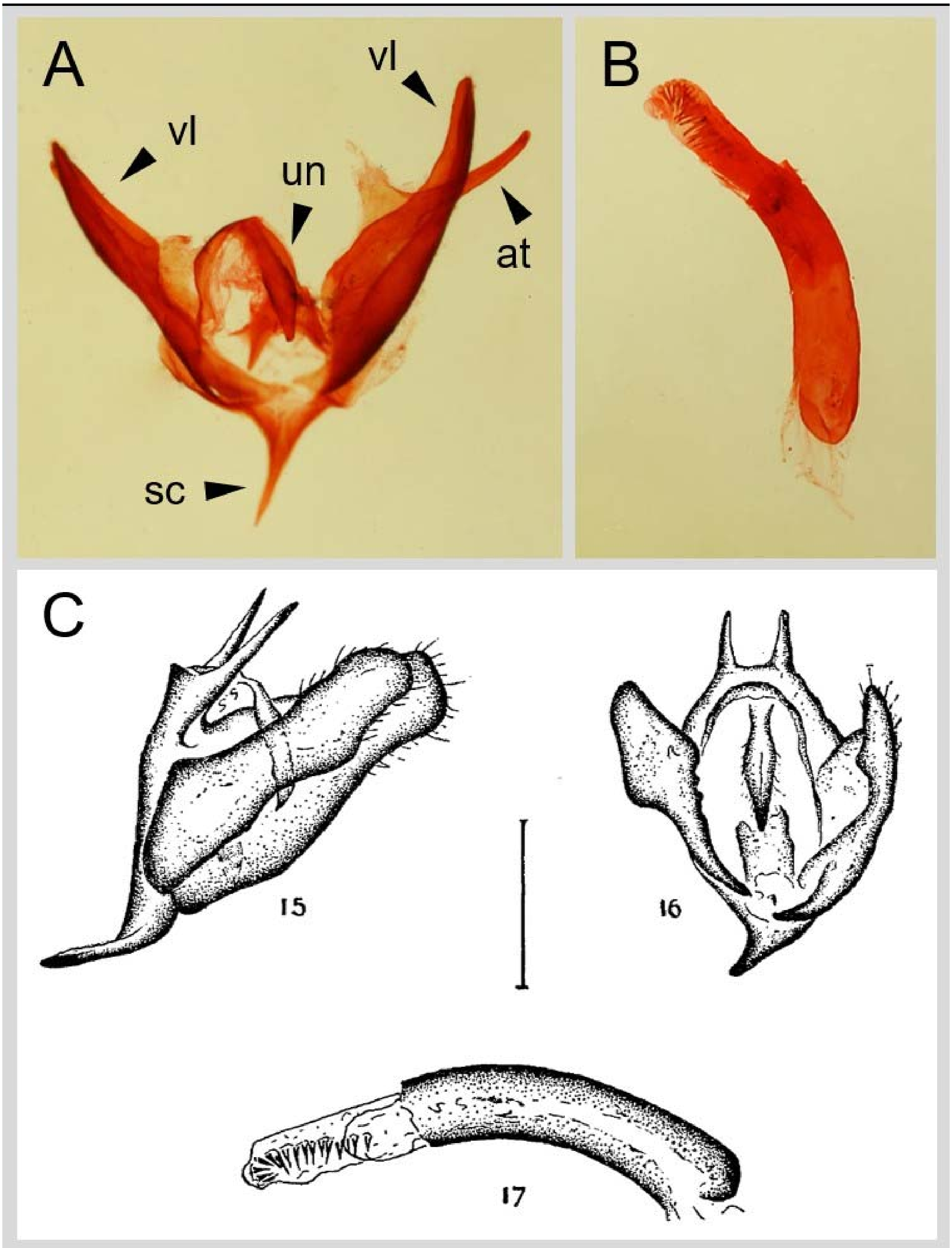


Figure 120. Male genitalia of *Mortinaclia "perplexa"* **comb. nov.**, from the *M. perplexa* **comb. nov.** species complex (see text): A-B – P. Griveaud original slide No. 580, vl - valva (note the asymmetry), un - uncus, at - sublateral arms of the tegumen, sc - saccus; C – the original illustration from Griveaud (1969: 11).

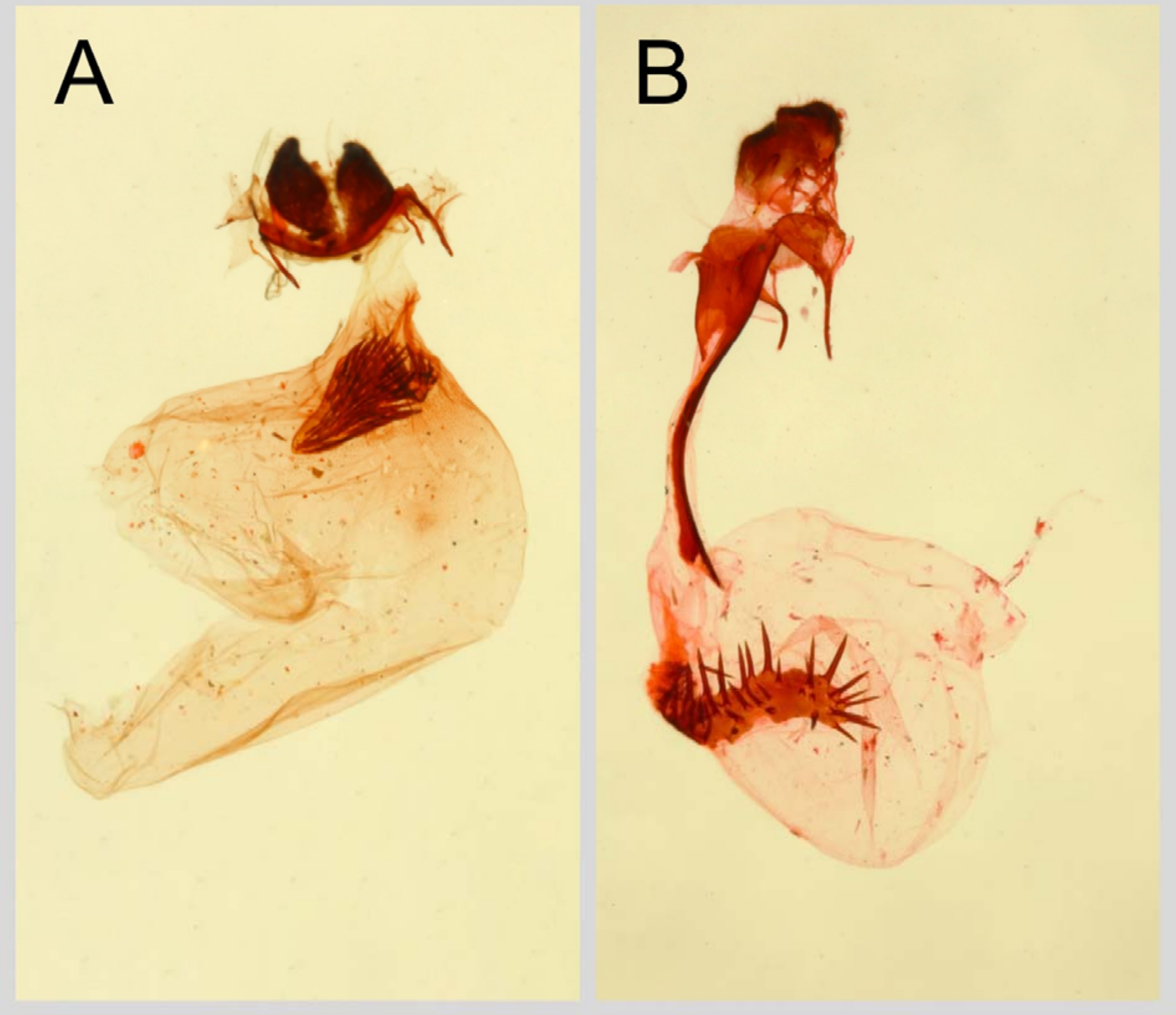


Figure 121. Female genitalia of *Mortinaclia perplexa* **comb. nov.** - *M. perplexa* **comb. nov.** species complex: A – holotype, P. Griveaud original slide No. 577; B – the slide made “for verification of the female genitalia” of the specimen collected together with the male described in Griveaud (1969) – note the dissimilarity of both slides (see text).

SUPPLEMENTARY DATA

Table S1. List of all specimens included in the study. Coll. – collection, N – number of specimens, S – sex, M – male, F – female; Collections acronyms: ISEA PAS – Institute of Systematics and Evolution of Animals Polish Academy of Sciences, Kraków, Poland; ANHRT – African Natural History Research Trust, Leominster, UK; CEP-MZUJ – Zoological Museum of the Jagiellonian University, Kraków, Poland; MfN – Museum für Naturkunde, Berlin, Germany; MNHN – Muséum national d'Histoire naturelle, Paris, France; NHMUK – Natural History Museum, London, UK; NMP – Národní Muzeum, Prague, Czech Republic; NRM – Naturhistoriska riksmuseet, Stockholm, Sweden; PZBT – Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar; SGN – Senckenberg Naturmuseum, Frankfurt am Main, Germany; SMNS – Staatliches Museum für Naturkunde, Stuttgart, Germany; coll. P. Basquin – private collection of Patrick Basquin, France.

Table S2. List of sequences used in molecular analyses, with GenBank accession numbers. The sequences which have been submitted to GenBank, but not assigned with accession numbers yet are marked with “X”, N of bases – sum of base pairs obtained for each sample.

Table S3. List of all localities, where the species covered in the paper were recorded.

Figure S1. Phylogenetic tree of the taxa included in the study, based on Maximum Likelihood analysis in RAxML.

Figure S2. Phylogenetic tree of the taxa included in the study, based on Bayesian Inference analysis in MrBayes.

Figure S3. Results of Automatic Barcode Gap Discovery (ABGD) analysis based on COI-begin (barcode region), with 34 initial partitions.

Figure S4. Results of Automatic Barcode Gap Discovery (ABGD) analysis based on COI-begin (barcode region), with 36 recursive partitions.

Figure S5. Results of Automatic Barcode Gap Discovery (ABGD) analysis based on COI-begin (barcode region), with 39 recursive partitions.

Figure S6. Results of Automatic Barcode Gap Discovery (ABGD) analysis based on EF1a-begin gene region.

Figure S7. Results of Automatic Barcode Gap Discovery (ABGD) analysis based on GAPDH gene.

File S1. Input parameters for Automatic Barcode Gap Discovery (ABGD) analyses, and results of Poisson Tree Processes (PTP) analyses with Maximum Likelihood support for partitions.

SUPPLEMENTARY TABLES

Table S1. List of all specimens included in the study. Coll. – collection, N – number of specimens, S – sex, M – male, F – female; collections acronyms: ISEA PAS – Institute of Systematics and Evolution of Animals Polish Academy of Sciences, Kraków, Poland; ANHRT – African Natural History Research Trust, Leominster, UK; CEP-MZUJ – Zoological Museum of the Jagiellonian University, Kraków, Poland; MfN – Museum für Naturkunde, Berlin, Germany; MNHN – Muséum national d'Histoire naturelle, Paris, France; NHMUK – Natural History Museum, London, UK; NMP – Národní Muzeum, Prague, Czech Republic; NRM – Naturhistoriska riksmuseet, Stockholm, Sweden; PZBT – Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar; SGN – Senckenberg Naturmuseum, Frankfurt am Main, Germany; SMNS – Staatliches Museum für Naturkunde, Stuttgart, Germany; coll. P. Basquin – private collection of Patrick Basquin, France.

Coll.	**Specimen code**	**N**	**S**	**Genus**	**Species**	**Locality**	**Collecting date (d/m/yyyy)**	**Collector**	**Altitude m a.s.l.**	**Remarks**
NHMUK	NHMUK010620992, holotype of "sylvicolens"	1	M	*Thyrosticta*	*sylvicolens*					
NHMUK	NHMUK010620991, holotype of "quadrimacula"	1	M	*Thyrosticta*	*sylvicolens*					
NHMUK	NHMUK010621036, holotype of "confluens"	1	F	*Thyrosticta*	*sylvicolens*	Madagascar, Antsianaka	1890	Perrot Freres		
NHMUK	NHMUK010620987, holotype of "perpetua"	1	F	*Thyrosticta*	*sylvicolens*	Madagascar, Tamatave et forets d'Alahakato	1888	Edouard Perrot		
ISEA PAS	MAD_213	1	M	*Thyrosticta*	*sylvicolens*	Ranomafana National Park, ValBio Centre	4.3.2020			
NHMUK	DL1795	1	F	*Thyrosticta*	*sylvicolens*	Vohiparara			1150	
MNHN	EL82766	1	M	*Thyrosticta*	*sylvicolens*	Anivorano-Kely, riv. d' Ivoay(?), Brickaville, Piste d' Ambodimanga	9.1954	A. R. (Andria Robinson?)		
MNHN	EL82765, EL82772, EL82763	3	M	*Thyrosticta*	*sylvicolens*	Madagascar Est, Lac Alaotra, Befody	22-23.8.1968	P. Griveaud		

Coll.	**Specimen code**	**N**	**S**	**Genus**	**Species**	**Locality**	**Collecting date (d/m/yyyy)**	**Collector**	**Altitude m a.s.l.**	**Remarks**
MNHN	EL82759	1	M	*Thyrosticta*	*sylvicolens*	Madagascar Est, N.O. de Manantenina, chaines anosyennes massif nord	22-29.11.1971	P. Griveaud	1050 (/1850?)	
MNHN	EL82769	1	M	*Thyrosticta*	*sylvicolens*	Madagascar Est, N.O. de Manantenina, chaines anosyennes massif nord	22-29.11.1971	P. Soga	1050 (/1850?)	
MNHN	EL82751	1	F	*Thyrosticta*	*sylvicolens*	Madagascar-Est, dct. Andapa, Anjanaharibe	4.1960	P. Soga	1600	
MNHN	EL82755, EL82752	2	F	*Thyrosticta*	*sylvicolens*	Madagascar-Est, dct. Andapa, Anjanaharibe (50 km Ouest Andapa)	3.1961	P. Soga	1600	
MNHN	EL82764, EL82770, EL82767, EL82758	4	M	*Thyrosticta*	*sylvicolens*	Madagascar-Est, dct. Andapa, Anjanaharibe (50 km Ouest Andapa)	3.1961	P. Soga	1600	
MNHN	EL82754, EL82756, EL82753	3	F	*Thyrosticta*	*sylvicolens*	Madagascar-Est, dct. Moramanga, Perinet	2.1961	P. Griveaud		
MNHN	EL82768, EL82771, EL82762, EL82760	4	M	*Thyrosticta*	*sylvicolens*	Madagascar-Est, dct. Moramanga, Perinet	2.1961	P. Griveaud		
MNHN	EL82750	1	F	*Thyrosticta*	*sylvicolens*	Madagascar-Est, N.O. de Manantenina, chaines anosyennes massif nord	22-29.11.1971	P. Soga	1050	
MNHN	EL82761, EL82757	2	M	*Thyrosticta*	*sylvicolens*	M'car Est, Sahajinga, N. Ouest Behanana	9.1967	A. Peyrieras	500	
NHMUK		1	M	*Thyrosticta*	*sylvicolens*	Ambinanindrano, west of Mahonoro	31.8.1914	G. K. Kestell-Cornish		
NHMUK		1	F	*Thyrosticta*	*sylvicolens*	E Madagascar, Imerimandrosa, Lake Aloatra				
NHMUK		1	M	*Thyrosticta*	*sylvicolens*	Foret d'Isaka, nr. Fort Dauphin	10-11.1934	R. Catala		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
NHMUK		1	F	*Thyrosticta*	*sylvicolens*	Madagascar				
NHMUK		1	M	*Thyrosticta*	*sylvicolens*	Madagascar				
NHMUK		1	F	*Thyrosticta*	*sylvicolens*	Madagascar, Ambinanindrano, 50 km W of Mahanoro	1912	G. K. Kestell-Cornish		
NHMUK		2	F	*Thyrosticta*	*sylvicolens*	Madagascar, Antsianaka	1er Semestre 1892	Perrot Freres		
NHMUK		1	F	*Thyrosticta*	*sylvicolens*	Madagascar, Antsianaka	2e Semestre 1893	Perrot Freres		
NHMUK		1	F	*Thyrosticta*	*sylvicolens*	Madagascar, Fanovana	16.3.1933	M.E. Fountaine		
NHMUK		1	M	*Thyrosticta*	*sylvicolens*	Madagascar, Fianarantsoa	2e Semestre 1892	Perrot Freres		
NHMUK		2	F	*Thyrosticta*	*sylvicolens*	Madagascar-Est, dct. Andapa, Anjanaharibe (50 km Ouest Andapa)	3.1961	P. Soga	1600	
NHMUK		1	M	*Thyrosticta*	*sylvicolens*	Madagascar-Est, dct. Andapa, Anjanaharibe (50 km Ouest Andapa)	3.1961	P. Soga	1600	
NHMUK		1	F	*Thyrosticta*	*sylvicolens*	Madagascar-Est, dct. Moramanga, Perinet	2.1961	P. Griveaud		
PZBT		1	M	*Thyrosticta*	*sylvicolens*	Madagascar Centre, Ambinanirano(a?), Kieca	10.9.1961			
PZBT		4	M	*Thyrosticta*	*sylvicolens*	Madagascar Est, dct. Andapa, Anjanaharibe	4.1960	P. Soga	1600	
PZBT		1	F	*Thyrosticta*	*sylvicolens*	Madagascar Est, dct. Andapa, Anjanaharibe (50 km Ouest Andapa)	3.1961	P. Soga	1600	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
PZBT		4	M	*Thyrosticta*	*sylvicolens*	Madagascar Est, dct. Andapa, Anjanaharibe (50 km Ouest Andapa)	3.1961	P. Soga	1600	
PZBT		3	M	*Thyrosticta*	*sylvicolens*	Madagascar Est, dct. Moramanga, Perinet	2.1961	P. Griveaud		
PZBT		9	F	*Thyrosticta*	*sylvicolens*	Madagascar Est, Foret de Vondrozo, Madiorano	4.1969	Peyrieras	500	
PZBT		5	M	*Thyrosticta*	*sylvicolens*	Madagascar Est, Foret de Vondrozo, Madiorano	4.1969	Peyrieras	500	
PZBT		4	M	*Thyrosticta*	*sylvicolens*	Madagascar Est, Lac Alaotra, Befody	22-23.8.1968	P. Griveaud		
MNHN	EL65165, holotype	1	M	*Skippernaclia*	*lacrimata*	Andranomandevy (Didy), Ambatondrazaka	3.10.1956	P. Griveaud	1039	
MNHN	CLV_3 EL83636	1	M	*Skippernaclia*	*lacrimata*	Marojejy National Park, camp 3 trap 8	10.2.2018		1320	
MNHN	CLV_7 EL83635	1	F	*Skippernaclia*	*lacrimata*	Marojejy National Park, camp 3 trap 9	10.2.2018		1320	
NHMUK	NHMUK015109728 - DL18M_1430	1	M	*Skippernaclia*	*lacrimata*	P.N. Marojejy, Antsiranana	10.2.2020		1320	
MNHN	EL65167, holotype	1	M	*Skippernaclia*	*ankaratra*	Ampolomita, est Belanitra, dct. Ambatolampy	8.5.1956	P. Griveaud		
MNHN	EL65166, allotype of "lacrimata"	1	F	*Skippernaclia*	*ankaratra*	Madagascar, Tananarive		Collecttion Le Moult		
ISEA PAS	DL_06-051	1	F	*Skippernaclia*	*ankaratra*	Zahamena, near cascade	8.11.2006		1234	
ISEA PAS	MAD_108, MAD_110, MAD_111	3	F	*Skippernaclia*	*ankaratra*	Path along river, N ad Mandraka Park	7.12.2019		1270-1310	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL82774	1	M	*Skippernaclia*	*ankaratra*	Madagascar Centre, route d' Ambositra a Ambohimanga du Sud, km 39	6-11.11.1963	P. Viette	1350	
MNHN	EL74891	1	M	*Thyrosticta*	*lacrimata / ankaratra*					
MNHN	EL82775	1	M	*Thyrosticta*	*lacrimata / ankaratra*	Ampolomita, est Belanitra, dct. Ambatolampy	5.5.1956	P. Griveaud		
MNHN	EL82748, EL82749	2	F	*Thyrosticta*	*lacrimata / ankaratra*	Madagascar Est, dct. Sambava, R.N. XII Marojejy, Ambatosoratra	11.1960	P. Soga	1700	
MNHN	EL82776	1	M	*Thyrosticta*	*lacrimata / ankaratra*	Madagascar Est, dct. Sambava, R.N. XII Marojejy, Ambatosoratra	11.1960	P. Soga	1700	
MNHN	EL82773	1	F	*Thyrosticta*	*lacrimata / ankaratra*	Madagascar, La Mandraka	11.1953	A. R. (Andria Robinson?)		
NHMUK		1	F	*Thyrosticta*	*lacrimata / ankaratra*	Madagascar, Tananarive		Le Moult		
PZBT		2	M	*Thyrosticta*	*lacrimata / ankaratra*	dct. Ambatolampy, Ampolomita, est Belanitra	9.5.1956	P. Griveaud		
PZBT		1	F	*Thyrosticta*	*lacrimata / ankaratra*	Manjakandriana, La Mandraka	31.10.1956	P. Griveaud	1250	
PZBT		1	F	*Thyrosticta*	*lacrimata / ankaratra*	Madagascar Centre, Barrage d'Andrangoloaka, Lac Mantasoa	3.1970	P. Griveaud	1389	
PZBT		2	F	*Thyrosticta*	*lacrimata / ankaratra*	Madagascar Centre, dct. Manjakandriana, La Mandraka	2.1961	P. Griveaud		

Coll.	**Specimen code**	**N**	**S**	**Genus**	**Species**	**Locality**	**Collecting date (d/m/yyyy)**	**Collector**	**Altitude m a.s.l.**	**Remarks**
PZBT		1	M	*Thyrosticta*	*lacrimata / ankaratra*	Madagascar Centre, La Mandraka	2.3.1968	Turlin		
PZBT		1	F	*Thyrosticta*	*lacrimata / ankaratra*	Madagascar Est, dct. Sambava, R.N. XII - Marojejy, Ambatosoratra	11.1960	P. Soga	1700	
PZBT		2	M	*Thyrosticta*	*lacrimata / ankaratra*	Madagascar Est, dct. Sambava, R.N. XII - Marojejy, Ambatosoratra	11.1960	P. Soga	1700	
MNHN	EL65168, holotype	1	M	*Skippernaclia*	*vestigii*	Madagascar-Centre, dct. Ankazobe, Tampoketsy, foret d' Ambohitantely	5.1961	Andria R.	1550	
ISEA PAS	MAD_169	1	F	*Skippernaclia*	*vestigii*	Ankazobe District, Ambohitantely Reserve	12.12.2019		1600	
MNHN	EL82778	1	M	*Skippernaclia*	*vestigii*	Madagascar-Centre, dct. Ankazobe, Tampoketsy, foret d' Ambohitantely	5.1961	Andria R.	1550	
PZBT		1	M	*Skippernaclia*	*vestigii*	Madagascar Centre, dct. Ankazobe, Tampoketsy, foret d'Ambohitantely	5.1961	Andria R.		
PZBT		1	M	*Skippernaclia*	*vestigii*	Madagascar Centre, Ankazobe, Tampoketsa	10.1974	A. Peyrieras		
NHMUK	NHMUK015109746	1	F	*Skippernaclia*	*leesi* sp. nov.	Madagascar NE, Ambohitsitondroin' Mahalavona, ridge, primary forest	28.12.1993	D.C. Lees	1209	11-12 AM
MNHN	EL65153, holotype	1	M	*Kowalskinaclia*	*dilata*	Ankazobe, Tampoketsy, Ambohitantely	27.12.1956	P. Griveaud		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
ISEA PAS	MAD_135, MAD_136, MAD_137, MAD_138, MAD_139, MAD_140, MAD_141, MAD_142, MAD_144, MAD_145, MAD_146, MAD_147, MAD_148, MAD_150, MAD_151, MAD_152, MAD_153, MAD_154, MAD_155, MAD_156, MAD_157, MAD_158, MAD_159, MAD_160, MAD_161, MAD_162, MAD_163, MAD_164, MAD_165, MAD_170, MAD_171	31	M	*Kowalskinaclia*	*dilata*	Ankazobe District, Ambohitantely Reserve	11.12.2019		1600	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
ISEA PAS	MAD_190, MAD_191, MAD_192, MAD_193, MAD_194, MAD_196, MAD_197, MAD_198, MAD_199, MAD_200, MAD_201	11	M	*Kowalskinaclia*	*dilata*	Ankazobe District, Ambohitantely Reserve	13.3.2020		1600	
ISEA PAS	MAD_202, MAD_203, MAD_195	3	M	*Kowalskinaclia*	*dilata*	Ankazobe District, Ambohitantely Reserve	14.3.2020		1600	
ANHRTUK	ANHRTUK00215262, ANHRTUL00215260	2	M	*Kowalskinaclia*	*dilata*	Andasibe PN	12.4.2011			
ANHRTUK	ANHRTUK00215261	1	M	*Kowalskinaclia*	*dilata*	Ankazobe District, Ambohitantely Reserve	24-29.11.2011		1530	
MNHN	EL82590	1	M	*Kowalskinaclia*	*dilata*	Madagascar-Centre, dct. Ankazobe, Tampoketsy, foret d'Ambohitantely	5.1961	Andria R.	1550	
MNHN	EL74892	1	M	*Kowalskinaclia*	*dilata*	Madagascar Centre, N. d'Ankazobe , tampoketsa d'Ambohitantely	26-28.3.1968	P. Griveaud	1600	
PZBT		2	M	*Kowalskinaclia*	*dilata*	Madagascar Centre, dct. Ankazobe, Tampoketsy, foret d'Ambohitantely	5.1961	Andria.R	1550	
PZBT		2	M	*Kowalskinaclia*	*dilata*	Madagascar Centre, Ankazobe, Ambohitantely	4.1967	P. Griveaud		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
PZBT		1	M	*Kowalskinaclia*	*dilata*	Madagascar Centre, dct. Ankazobe, Tampoketsy, foret d'Ambohitantely	5.1961	Andria.R	1550	
PZBT		1	M	*Kowalskinaclia*	*dilata*	Madagascar Centre, Ankazobe, Tampoketsa	4.1972	Rakotoarisolo		
PZBT		1	M	*Kowalskinaclia*	*dilata*	Madagascar Centre, Ankazobe, Tampoketsa	10.1974	A. Peyrieras		
MNHN	EL65171 holotype	1	M	*Kowalskinaclia*	*vieui*	Moramanga, Ankasoka	2(/11?).1956	R. Vieu		
ISEA PAS	MAD_060	1	M	*Kowalskinaclia*	*vieui*	Andasibe-Mantadia National Park, Belakato Trail	28.11.2019		1020	
ISEA PAS	MAD_005	1	F	*Kowalskinaclia*	*vieui*	Moramanga, Andasibe, vic. Anevoka, Foret Pluviale de Maromitza Nature Reserve	21.11.2004		1150	
ISEA PAS	MAD_004	1	M	*Kowalskinaclia*	*vieui*	Moramanga, Andasibe, vic. Anevoka, Foret Pluviale de Maromitza Nature Reserve	21.11.2004		1150	
ISEA PAS	MAD_131, MAD_132	2	M	*Kowalskinaclia*	*vieui*	Path along river, N ad Mandraka Park	7.12.2019		1270-1310	
ISEA PAS	DL_14R-218	1	M	*Kowalskinaclia*	*vieui*	Ranomafana	8.11.2014		1336	
MNHN	EL82823, EL82827	2	M	*Kowalskinaclia*	*vieui*	Andranotobaka, Ambatolampy	3.1957	P. Griveaud	1400	
MNHN	EL82834	1	M	*Kowalskinaclia*	*vieui*	Ankasoka	2.3.1957	R. Vieu	1130	
MNHN	EL82829, EL82847	1	M	*Kowalskinaclia*	*vieui*	Ankasoka, Route Lakato	2.12.1956	P. Griveaud	1130	
MNHN	EL82840, EL82841, EL82839, EL82830, EL82828	5	M	*Kowalskinaclia*	*vieui*	Ankasoka, Route Lakato	29.11.1956	P. Griveaud	1130	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL82846	1	M	*Kowalskinaclia*	*vieui*	Ankasoka, Route Lakato	30.11.1956	P. Griveaud	1130	
MNHN	EL82852, EL74904, EL74908, EL74907, EL74906, EL74905	6	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, 8 km S.E. d'Anjozorobe, foret de Vanjamanitra	20-23.10.1966	P. Griveaud, J. Vadon, P. Viette	1380	
MNHN	EL74893, EL74894, EL74899, EL74900, EL82914, EL82913, EL82912, EL82907, EL82910	9	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, env. Ambohimahasoa, canton de Tsarafidy foret d'Ankafina	12-18.11.1963	P. Viette	1450	
MNHN	EL82825, EL82862, EL82872, EL82864, EL82890	5	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, env. d'Ambohimahasoa, canton de Tsarafidy, foret d' Ankafina	3.1967	P. Griveaud	1400	
MNHN	EL82888, EL82900, EL82901, EL74914, EL74916, EL74918, EL74919, EL74920, EL74917, EL74915, EL74921	11	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, Est du lac Mantasoa, frt Ambohiboatavo	3.1973	P. Griveaud, A. Peyrieras	1340	
MNHN	EL82873, EL74903	2	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, foret a l'Est du lac de Mantasoa, Andrangoloaka	27.2-6.3.1970	P. Griveaud	1389	
MNHN	EL82855	1	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, La Mandraka	5.2.1970	B. Turlin		
MNHN	EL82904	1	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, Mandraka	12.1967	Turlin		
MNHN	EL82919	1	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, Mandraka	28.1.1963	Turlin		

Coll.	**Specimen code**	**N**	**S**	**Genus**	**Species**	**Locality**	**Collecting date (d/m/yyyy)**	**Collector**	**Altitude m a.s.l.**	**Remarks**
MNHN	EL74951, EL74952, EL74953	3	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, Pays Betsileo, route du Sud, km 292	14-15.2(/11?).1974	P. Viette et A. Peyrieras	1700	
MNHN	EL74909, EL74913, EL74912, EL74911, EL74910	5	M	*Kowalskinaclia*	*vieui*	Madagascar Est , route de Lakato, 15 km Ankasoka	22-24.3.1971	P. Griveaud	1100	
MNHN	EL74902, EL74901	2	M	*Kowalskinaclia*	*vieui*	Madagascar Est, Ankasoka, det Moramanga	21.10.1957	P. Griveaud	1130	
MNHN	EL82905	1	M	*Kowalskinaclia*	*vieui*	Madagascar Est, Ankasoka, Route de Lakato	10.1965	Monsarrat		
MNHN	EL82908	1	M	*Kowalskinaclia*	*vieui*	Madagascar Est, Ankasoka, Route de Lakato	4.1967	P. Griveaud		

MNHN	EL82844, EL82835, EL82837, EL82838, EL82843, EL82824, EL82842, EL82826, EL82845, EL82899, EL82887, EL82898, EL82892, EL82891, EL82886, EL82884, EL82874, EL82896, EL82876, EL82889, EL82883, EL82882, EL82881, EL82868, EL82869, EL82897, EL82878, EL82865, EL82895, EL82851, EL82870, EL82867, EL82885, EL82861, EL82859, EL82863, EL82879, EL82853, EL82856, EL82871, EL82894, EL82857, EL82858, EL82866, EL82875, EL82854, EL82880, EL82877, EL82893, EL82850, EL82860, EL74942, EL74940, EL74943, EL74930, EL74941, EL74934, EL74944, EL74932, EL74946, EL74933, EL74929, EL74945, EL74939, EL74928, EL74931, EL74935, EL74937, EL74936, EL74938	70	M	*Kowalskinaclia*	*vieui*	Madagascar Est, Ankasoka, Route de Lakato, km 15	11.1962	R. Vieu	1130

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL82903, EL82902, EL82906, EL82917, EL82916, EL82918, EL74922, EL74923, EL74926, EL74925, EL74924, EL74927	12	M	*Kowalskinaclia*	*vieui*	Madagascar Est, Ankasoka, Route de Lakato, km 15	17-21.10.1963	P. Viette	1100	
MNHN	EL82832, EL82833, EL82849, EL74896	4	M	*Kowalskinaclia*	*vieui*	Madagascar Est, Ankasoka, Route de Lakato, km 15	2-10.1.1959	P. Viette	1100	
MNHN	EL74955	1	F	*Kowalskinaclia*	*vieui*	Madagascar Est, route de Lakato, 15 km Ankasoka	17-21.10.1963	P. Viette	1100	
MNHN	EL82909	1	M	*Kowalskinaclia*	*vieui*	Madagascar Nord, district d' Ambanja, Beangona Ambevy	12.12.1963	P. Viette	135	
MNHN	EL74897	1	M	*Kowalskinaclia*	*vieui*	Madagascar, Andranotobaka, Ambatolampy	3.1957	P. Griveaud	1400	
MNHN	EL74895	1	M	*Kowalskinaclia*	*vieui*	Madagascar, Perinet, Mange	8.1965			
MNHN	EL82836, EL82848, EL82831	3	M	*Kowalskinaclia*	*vieui*	Madagascar-Est, dct. Moramanga, Ankasoka	21.10.1957	P. Griveaud	1130	
MNHN	EL82915	1	M	*Kowalskinaclia*	*vieui*	Reserve nat. III, Ambatovositra, Andranomalaza	1.1957	P. Soga		
MNHN	EL82911	1	M	*Kowalskinaclia*	*vieui*	Reserve nat. III, Andranomalaza, vallée d' Ivelona	10.1957	P. Soga		
MNHN	EL74898	1	M	*Kowalskinaclia*	*vieui*					
NHMUK	NHMUK010621702, "quadrata"	1	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, dct. Ambohimahasoa, foret Tsarafidy	12.1959 - 1.1960	P. Griveaud	1450	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
NHMUK	NHMUK010620996	1	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, dct. Ambohimahasoa, foret Tsarafidy	12.1959 - 1.1960	P. Griveaud	1450	
NHMUK	NHMUK015109747	1	M	*Kowalskinaclia*	*vieui*	Madagascar E, Mantadia, Mahanara River, 8.6 km N from Tanambotsiry, camp 1, riparian forest below old logging track	16.3.1993		1050-1150	actinic light, 02:00-05:00
NHMUK		4	M	*Kowalskinaclia*	*vieui*	Madagascar Est, route de Lakato km 15, Ankasoka	11.1962	R.Vieu	1130	
NHMUK	NHMUK015109748	1	M	*Kowalskinaclia*	*vieui*	Madagascar NE, Ambohitsitondroin' Mahalavona, ridge, primary forest	28.2.1993		1175-1225	11:00-12:00
PZBT		10	M	*Kowalskinaclia*	*vieui*	Ambatolampy, Andranotobaka	3.1957	P. Griveaud	1400	
PZBT		1	M	*Kowalskinaclia*	*vieui*	Ampijoroa, Ankarafantsika	1.1957	P.Griveaud	170	
PZBT		2	M	*Kowalskinaclia*	*vieui*	Ankasoka, Route Lakato	29.11.1956	P. Griveaud	1130	
PZBT		1	F	*Kowalskinaclia*	*vieui*	Beparasy	4.1968	Dujardin, Delacour C.		
PZBT		3	M	*Kowalskinaclia*	*vieui*	Lakato	1.1969	Collection Dujardin-Delacour		
PZBT		1	M	*Kowalskinaclia*	*vieui*	Lakato	11 (/1?).1965	Collection Dujardin-Delacour		
PZBT		1	M	*Kowalskinaclia*	*vieui*	Lakato	11.1965	Collection Dujardin-Delacour		
PZBT		1	M	*Kowalskinaclia*	*vieui*	Lakato	7.1965	Collection Dujardin-Delacour		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
PZBT		6	M	*Kowalskinaclia*	*vieui*	Lakato	7.11.1964	Collection Dujardin-Delacour		
PZBT		1	M	*Kowalskinaclia*	*vieui*	Ranomafana	1.12.1964	Dujardin, Delacour C.		
PZBT		1	M	*Kowalskinaclia*	*vieui*	Andranomandevy, (Didy), Ambatondrazaka	28.9.1956	P. Griveaud	1039	
PZBT		1	M	*Kowalskinaclia*	*vieui*	dct. Ambatolampy, Ampolomita, est Belanitra	8.5.1956	P. Griveaud		
PZBT		1	F	*Kowalskinaclia*	*vieui*	Madagascar Centre, 8 km S.E. d' Anjozorobe, foret de Vanjamanitra	20-23.10.1966	P. Griveaud, J. Vadon, P. Viette	1380	
PZBT		4	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, Andrangoloaka, Est lac Mantasoa	3.1972	Griveaud et Peyrieras		
PZBT		1	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, Anjozorobe, Vanjamanitra	5.1967	P.Griveaud		
PZBT		2	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, Barrage d'Andrangoloaka, Lac Mantasoa	3.1970	P. Griveaud	1389	
PZBT		4	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, dct. Ambohimahasoa, foret Tsarafidy	1.1961	P.Griveaud	1450	
PZBT		1	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, dct. Ambohimahasoa, foret Tsarafidy	2.1959 -1.1960	P.Griveaud	1450	
PZBT		1	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, dct. Manjakandriana, La Mandraka	9.1960	P. Griveaud		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
PZBT		1	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, La Mandraka	24.2.1971	Turlin		
PZBT		1	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, La Mandraka (P.K. 69)	13.11.1969	Turlin	1200	
PZBT		1	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, La Mandraka (P.K. 69)	8.11.1969	Turlin	1200	
PZBT		1	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, Mandraka	4.2.1968	Turlin		
PZBT		1	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, s-Pr. Anjozorobe, Analavory	2.1966	P.Griveaud	1420	
PZBT		1	F	*Kowalskinaclia*	*vieui*	Madagascar Centre, Tsarafidy	1.1966	P. Griveaud	1450	
PZBT		6	M	*Kowalskinaclia*	*vieui*	Madagascar Centre, Tsarafidy	1.1966	P. Griveaud	1450	
PZBT		2	M	*Kowalskinaclia*	*vieui*	Madagascar Est, Analamazoatra, Perinet	7.1967	P. Griveaud		
PZBT		1	M	*Kowalskinaclia*	*vieui*	Madagascar Est, Ankasoka, Rte de Lakato	10.1965	Monsarrat		
PZBT		1	M	*Kowalskinaclia*	*vieui*	Madagascar Est, dct. Moramanga, Ankasoka	1.10.1957	P.Griveaud		
PZBT		2	M	*Kowalskinaclia*	*vieui*	Madagascar Est, dct. Moramanga, Ankasoka	21.10.1957	P. Griveaud	1130	
PZBT		1	M	*Kowalskinaclia*	*vieui*	Madagascar Est, dct. Moramanga, Ankasoka	22.10.1967	P. Griveaud	1130	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
SMNS		1	?	*Kowalskinaclia*	*vieui*	Madagascar Est, Moramanga, Andasibe, vic. Anevoka, Foret pluviale de Maromiza PN	17.11.2004	J. Berg, D. Bartsch	1110	clearing on mountain-ridge in disturbed primary montagne forest
MNHN	EL65155, holotype	1	M	*Kowalskinaclia*	*cowani*	Route Lakato, Ankasoka	1.12.1956 -	P. Griveaud	1130	
MNHN	EL65154, holotype of "incerta"	1	M	*Kowalskinaclia*	*cowani*	Madagascar S.-E., Ranomafana, km 402	26.3.1955 - 1.4.1955	H. de Toulgoët	650	
ISEA PAS	MAD_100, MAD_101	2	M	*Kowalskinaclia*	*cowani*	Andasibe-Mantadia National Park, Eulopia Trail	1.12.2019		970	
ISEA PAS	MAD_025	1	M	*Kowalskinaclia*	*cowani*	Andasibe-Mantadia National Park, Feon'ny Ala Hotel	26.11.2019		950	
ISEA PAS	MAD_029	1	F	*Kowalskinaclia*	*cowani*	Andasibe-Mantadia National Park, Parc Mitsinjo	27.11.2019		945-980	
ISEA PAS	MAD_035	1	F	*Kowalskinaclia*	*cowani*	Andasibe-Mantadia National Park, Rianasu Circuit	29.11.2019		980	
ISEA PAS	MAD_036, MAD_037	2	M	*Kowalskinaclia*	*cowani*	Andasibe-Mantadia National Park, Rianasu Circuit	29.11.2019		980	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
ISEA PAS	MAD_075	1	F	*Kowalskinaclia*	*cowani*	Maromizaha Protected Area	29.11.2019		1170	
ISEA PAS	MAD_273	1	M	*Kowalskinaclia*	*cowani*	Ranomafana National Park, Radar Station	11.4.2018		1600	
ISEA PAS	ISEZ-DNA_522	1	M	*Kowalskinaclia*	*cowani*	Ranomafana National Park, ValBio Centre	10.4.2018		920	
ISEA PAS	ISEZ-DNA_556	1	F	*Kowalskinaclia*	*cowani*	Ranomafana National Park, ValBio Centre	11.4.2018		900-970	
ISEA PAS	ISEZ-DNA_521	1	M	*Kowalskinaclia*	*cowani*	Ranomafana National Park, ValBio Centre	12.4.2018		920	
ISEA PAS	ISEZ-DNA_558	1	M	*Kowalskinaclia*	*cowani*	Ranomafana National Park, ValBio Centre	12.4.2018		900-970	
MNHN	EL74967	1	M	*Kowalskinaclia*	*cowani*					
MNHN	EL82613, EL82611, EL82612	3	M	*Kowalskinaclia*	*cowani*	Madagascar Centre, dct. Ambohimahasoa, foret Tsarafidy	12.1959 - 1.1960	P. Grivaud	1450	
MNHN	EL82605, EL82606, EL82607, EL82608, EL82616	5	M	*Kowalskinaclia*	*cowani*	Madagascar Centre, env. Ambohimahasoa, canton de Tsarafidy, foret d' Ankafina	3.1967	P. Griveaud	1400	
MNHN	EL82601, EL82599, EL82598	3	M	*Kowalskinaclia*	*cowani*	Madagascar Centre, env. Ambohimahasoa, canton de Tsarafidy, foret d' Ankafina	12-18.11.1963	P. Viette	1450	
MNHN	EL82592, EL74950	2	M	*Kowalskinaclia*	*cowani*	Madagascar Centre, route d' Ambositra à Ambohimanga du Sud, km 39	6.-11.11.1963	P. Viette	1350	
MNHN	EL82594	1	F	*Kowalskinaclia*	*cowani*	Madagascar Centre, Tsarafidy	1.1966	P. Grivaud	1450	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL82604, EL82596, EL82603, EL82597	4	M	*Kowalskinaclia*	*cowani*	Madagascar Centre, Tsarafidy	1.1966	P. Griveaud	1450	
MNHN	EL82600	1	M	*Kowalskinaclia*	*cowani*	Madagascar Est, env. De Perinet, foret d' Analamazoatra	24.11.1954	P. Viette	910	
MNHN	EL82602, EL74556, EL74884	3	M	*Kowalskinaclia*	*cowani*	Madagascar Est, N.O. de Manantenina, chaines anosyennes massif nord	22-29.11.1971	P. Griveaud	1050	
MNHN	EL82614, EL82615	2	M	*Kowalskinaclia*	*cowani*	Madagascar S.-E., Ranomafana, km 402	26.3-1.4.1955	H. de Toulgoët	650	
MNHN	EL74885, EL74886, EL82591	3	M	*Kowalskinaclia*	*cowani*	Madagascar Sud Est, foret de Befotaka, Midongy du Sud	3-7.3.1959	P. Viette et P. Griveaud	950	
MNHN	EL82593	1	F	*Kowalskinaclia*	*cowani*	Madagascar-Centre, dct. Ambohimahasoa, foret Tsarafidy	1.1961	P. Griveaud	1450	
MNHN	EL82610, EL82609	2	M	*Kowalskinaclia*	*cowani*	Madagascar-Est, dct Moramanga, Ankasoka	21.10.1957	P. Griveaud	1130	
MNHN	EL82595	1	F	*Kowalskinaclia*	*cowani*	Sahamalato, Perinet	1(?).1949(?)	P.C. (P. Cachan)		
NHMUK	NHMUK010620993	1	M	*Kowalskinaclia*	*cowani*	Madagascar-Centre, dct. Ambohimahasoa, foret Tsarafidy	12.1959 - 1.1960	P. Griveaud	1450	
PZBT		2	M	*Kowalskinaclia*	*cowani*	Lakato	1.1969	Collection Dujardin-Delacour		
PZBT		1	M	*Kowalskinaclia*	*cowani*	Lakato	11.1965	Collection Dujardin-Delacour		
PZBT		1	M	*Kowalskinaclia*	*cowani*	Lakato	2.1969	Collection Dujardin-Delacour		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
PZBT		2	M	*Kowalskinaclia*	*cowani*	Lakato	7.11.1964	Dujardin, Delacour C.		
PZBT		1	M	*Kowalskinaclia*	*cowani*	Lakato	8.9.1966	Collection Dujardin-Delacour		
PZBT		1	M	*Kowalskinaclia*	*cowani*	Andranomandevy, (Didy), Ambatondrazaka	27.9.1966	P. Griveaud	1039	
PZBT		1	?	*Kowalskinaclia*	*cowani*	Madagascar Centre, dct. Ambohimahasoa, foret Tsarafidy	1.1961	P. Griveaud	1450	
PZBT		16	M	*Kowalskinaclia*	*cowani*	Madagascar Centre, dct. Ambohimahasoa, foret Tsarafidy	1.1961	P. Griveaud	1450	
PZBT		1	?	*Kowalskinaclia*	*cowani*	Madagascar Centre, dct. Ambohimahasoa, foret Tsarafidy	12.1959 - 1.1960	P. Griveaud	1450	
PZBT		1	F	*Kowalskinaclia*	*cowani*	Madagascar Centre, dct. Ambohimahasoa, foret Tsarafidy	12.1959 - 1.1960	P. Griveaud		
PZBT		3	M	*Kowalskinaclia*	*cowani*	Madagascar Centre, dct. Ambohimahasoa, foret Tsarafidy	12.1959 - 1.1960	P. Griveaud	1450	
PZBT		1	M	*Kowalskinaclia*	*cowani*	Madagascar Centre, Foret de Tsarafidy	8-12.3.1968	Griveaud	1350	
PZBT		1	M	*Kowalskinaclia*	*cowani*	Madagascar Centre, Tsarafidy	1.1961	P. Griveaud	1450	
PZBT		3	M	*Kowalskinaclia*	*cowani*	Madagascar Est, Ankasina, Route Lakato	3.1970			
PZBT		1	M	*Kowalskinaclia*	*cowani*	Madagascar Est, dct. Moramanga, Ankasoka	21.10.1957	P. Griveaud	1130	
PZBT		1	F	*Kowalskinaclia*	*cowani*	Madagascar Est, dct. Moramanga, Perinet	2.1961	P. Griveaud		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
PZBT		1	M	*Kowalskinaclia*	*cowani*	Madagascar Est, dct. Moramanga, Perinet	2.1961	P. Griveaud		
PZBT		1	M	*Kowalskinaclia*	*cowani*	Madagascar Est, Route de Lakato	6-10.8.1971	Peyrieras		
PZBT		1	?	*Kowalskinaclia*	*cowani*	Madagascar S.E., Ranomafana, km 402	26.3.-1.4.1955	H. de Toulgoet	650	
PZBT		1	M	*Kowalskinaclia*	*cowani*	Madagascar S.E., Ranomafana, km 402	26.3.-1.4.1955	H. de Toulgoet	650	
PZBT		1	M	*Kowalskinaclia*	*cowani*	Madagascar Sud - Est, Midongy du Sud, foret de Befotaka	3-7.3.1959	P. Viette et P. Griveaud	950	
SGN		1	M	*Kowalskinaclia*	*cowani*	Madagascar occ.,		Hildebrandt		
MNHN	EL65158, holotype	1	M	*Privatenaclia*	*seguyi*	Madagascar-Est, dct. Sambava R.N. XII-Marojejy, Beondroka	12.1960	P. Soga	1200	
ISEA PAS	DL_06-320, DL_06-321, DL_06-324, DL_06-327	4	M	*Privatenaclia*	*seguyi*	Marojejy	13.11.2006	D.C. Lees	1240	
ISEA PAS	DL_06-347	1	M	*Privatenaclia*	*seguyi*	Marojejy	14.11.2006	D.C. Lees	1240	
ISEA PAS	DL_06-406	1	M	*Privatenaclia*	*seguyi*	Marojejy	18.11.2006	D.C. Lees	1250	
ISEA PAS	DL_2968	1	M	*Privatenaclia*	*seguyi*	Marojejy	23.11.2014	D.C. Lees	1240	
ISEA PAS	DL_2973	1	F	*Privatenaclia*	*seguyi*	Marojejy	26.1.2014	D.C. Lees	1240	
ISEA PAS	DL_2974	1	M	*Privatenaclia*	*seguyi*	Marojejy	31.1.2014	D.C. Lees	1240	
MNHN	EL82673	1	M	*Privatenaclia*	*seguyi*	Madagascar-Est, dct. Sambava R.N. XII-Marojejy, Beondroka	12.1960	P. Soga	1200	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
PZBT		2	M	*Privatenaclia*	*seguyi*	Madagascar-Est, dct. Sambava R.N. XII-Marojejy, Beondroka	12.1960	P. Soga	1200	
MNHN	EL65157, holotype	1	M	*Privatenaclia*	*ratovosoni*	Madagascar Est, dct. Moramanga, Ankasoka - Rte Lakato	3.1962	Ratovoson	1130	
ISEA PAS	MAD_008	1	M	*Privatenaclia*	*ratovosoni*	Moramanga, Andasibe, vic. Anevoka, Foret Pluviale de Maromitza Nature Reserve	21.11.2004	D.C. Lees	1150	
MNHN	EL83630, EL83631, EL83632, EL83633, EL83634	5	M	*Privatenaclia*	*ratovosoni*	Lakato	11.1965			
MNHN	EL74880	1	M	*Privatenaclia*	*ratovosoni*	Madagascar Est, route de Lakato, Ankasoka	17-21.10.1963	P. Viette	1100	
MNHN	EL82638	1	F	*Privatenaclia*	*ratovosoni*	Madagascar Est, route de Lakato, km 15 Ankasoka	11.1962	R. Vieu	1130	
MNHN	EL82635, EL82633, EL82636, EL82630, EL82629	5	M	*Privatenaclia*	*ratovosoni*	Madagascar Est, route de Lakato, km 15 Ankasoka	11.1962	R. Vieu	1130	
MNHN	EL82625, EL82628, EL82627, EL82637, EL82624, EL82634, EL82632, EL82626, EL82631, EL82623	10	M	*Privatenaclia*	*ratovosoni*	Madagascar Est, route de Lakato, km 15 Ankasoka	17-21.10.1963	P. Viette	1100	
NHMUK		1	M	*Privatenaclia*	*ratovosoni*	Madagascar Est, route de Lakato km 15, Ankasoka	17.10.1963 - 21.10.1963	P. Viette	1100	
coll. P. Basquin		1	?	*Privatenaclia*	*ratovosoni*	Madagascar, Lakato Forest	5.10.2002	P. Basquin	1100	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
PZBT		2	M	*Privatenaclia*	*ratovosoni*	Lakato	11.1965	Collection Dujardin-Delacour		
PZBT		1	M	*Privatenaclia*	*ratovosoni*	Lakato	30.8.1965	Dujardin, Delacour C.		
PZBT		1	F	*Privatenaclia*	*ratovosoni*	Lakato	07.11.1964	Dujardin, Delacour C.		
PZBT		3	M	*Privatenaclia*	*ratovosoni*	Lakato	07.11.1964	Dujardin, Delacour C.		
PZBT		1	M	*Privatenaclia*	*ratovosoni*	Madagascar Est, dct. Moramanga, Ankasoka Rte Lakato	1.1962	Ratovoson	1130	
SMNS		13	?	*Privatenaclia*	*ratovosoni*	Madagascar Est, Moramanga, Andasibe, vic. Anevoka, Foret pluviale de Maromiza PN	16.12.2006	J. Berg, D. Bartsch	1100-1150	at day, mountain ridge in primary forest
SMNS		1	?	*Privatenaclia*	*ratovosoni*	Madagascar Est, Moramanga, Andasibe, vic. Anevoka, Foret pluviale de Maromiza PN	08.12.2006	J. Berg, D. Bartsch	1100-1150	at day, mountain ridge in primary forest
MNHN	EL65156, holotype	1	M	*Privatenaclia*	*triangulifera*	Madagascar-Est, dct. Sambava R.N. XII-Marojejy, Ambatosoratra	11.1960	P. Soga	1700	
ISEA PAS	MAD_274	1	M	*Privatenaclia*	*triangulifera*	, Antsirarana, R.N.I. de Marojejy, 11.0 km NW	13.11.1996 - 19.11.1996	E. L. Quinter	1875	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
						Manantenina, source Andranomifototra R.				
MNHN	EL82618, EL82617	2	M	*Privatenaclia*	*triangulifera*	Madagascar-Est, dct. Sambava R.N. XII-Marojejy, Ambatosoratra	11.1960	P. Soga	1700	
MNHN	EL82619	1	F	*Privatenaclia*	*triangulifera*	Madagascar-Est, dct. Sambava R.N. XII-Marojejy, Ambatosoratra	11.1960	P. Soga	1700	
PZBT		1	M	*Privatenaclia*	*triangulifera*	Madagascar-Est, dct. Sambava R.N. XII-Marojejy, Ambatosoratra	11.1960	P. Soga		
MNHN	EL65159, holotype	1	M	*Julienaclia*	*pauliani*	Morondava, foret sud de Befasy	01.01.1956	R. Paulian		
ISEA PAS	DL_02-92	1	M	*Julienaclia*	*pauliani*	Kirindy Nord	18.1.2002	D.C. Lees	86	
ISEA PAS	DL_02-109	1	F	*Julienaclia*	*pauliani*	Kirindy Nord	19.1.2002	D.C. Lees	86	
ISEA PAS	MAD_209	1	F	*Julienaclia*	*pauliani*	Morondava Region, 70 m N ad Kirindy Ecolodge	27.2.2020	Ł. Przybyłowicz	70	
MNHN	MA_16-6 - EL83628	1	M	*Julienaclia*	*pauliani*	Tsingy massif, Parc national des Tsingy de Namoroka	26.10.2016	R. Rougerie	116	
MNHN	EL74854	1	F	*Julienaclia*	*pauliani*	Madagascar Ouest, route nationale 7, 64 km E. de Tulear foret d'Andranovory	8.12.1966	P. Viette et P. Griveaud	500	
MNHN	EL82674	1	M	*Julienaclia*	*pauliani*	Madagascar, Tulear Pr., Andranovory	24.3.1968	K.M.G. & P.D.	200	
NHMUK	DL1788	1	M	*Julienaclia*	*pauliani*	Kirindy Nord	30.12.2004	D.C. Lees	100	
PZBT		1	M	*Julienaclia*	*pauliani*	Madagascar Sud, Ambovombe		R. Paulian		

Coll.	**Specimen code**	**N**	**S**	**Genus**	**Species**	**Locality**	**Collecting date (d/m/yyyy)**	**Collector**	**Altitude m a.s.l.**	**Remarks**
NHMUK	NHMUK010621037, holotype	1	F	*Julienaclia*	*moerens*	Nord Madagascar, Antakares, Isokitra a Diego Suarez	10.1891	F & B Perrot		
MNHN	EL65160, holotype of "melanisa"	1	M	*Julienaclia*	*moerens*	Madagascar Nord, dct. d' Analalava, Beraty	12.1960	A. Robinson	1000	
MNHN	EL83058	1	M	*Julienaclia*	*moerens*	Madagascar Sambir, distr. D'Ambanja, N. de Beangona-Ambevy Andronomafana	1.1965	P. Soga	250	
PZBT		1	F	*Julienaclia*	*moerens*	Madagascar Est, Baie d'Antongil, Hiaraka	24-27.1.1968	P. Griveaud et A. Peyrieras	570	
PZBT		1	F	*Julienaclia*	*moerens*	Madagascar				
MNHN	EL65170, holotype	1	M	*Riconaclia*	*bimacula*	Madagascar Est, dct. Sambava, R.N. XII - Marojejy, Col Central	01.1960	P. Soga	1700	
ISEA PAS	ISEZ-DNA_518	1	F	*Riconaclia*	*bimacula*	Andasibe-Mantadia National Park, Vakona Lodge	5.4.2018	Ł. Przybyłowicz	1000	
ISEA PAS	DL_06-291	1	M	*Riconaclia*	*bimacula*	Marojejy, Camp 2	12.11.2006	D.C. Lees	850	
ISEA PAS	MAD_073	1	M	*Riconaclia*	*bimacula*	Maromizaha Protected Area	29.11.2019	Ł. Przybyłowicz	1170	
ISEA PAS	NHMUK015109726	1	F	*Riconaclia*	*bimacula*	Masoala, Be Dinta, survey site W9L1, ridge	8.11.1993	D.C. Lees	700	
ISEA PAS	MAD_218	1	M	*Riconaclia*	*bimacula*	Ranomafana Region, 3,5 km SW Vorondolo	8.3.2020	Ł. Przybyłowicz	1180	
ISEA PAS	DL_06-040	1	M	*Riconaclia*	*bimacula*	Zahamena	5.11.2006	D.C. Lees	1064	
NHMUK	NHMUK015109729	1	M	*Riconaclia*	*bimacula*	Madagascar NE, Ambohitsitondroin' Mahalavona, ridge, primary forest	28.2.1993	D.C. Lees	1159-1259	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
PZBT		2	M	*Riconaclia*	*bimacula*	Lakato	10.1968	Dujardin, Delacour C.		
NHMUK	NHMUK010314359, holotype	1	M	*Mauricenaclia*	*minuta*	Madagascar				
MNHN	EL64491, holotype of "angustipennis	1	F	*Mauricenaclia*	*minuta*					
NRM	MAD_015, lectotype of "subfenestrata"	1	F	*Mauricenaclia*	*minuta*	Madagascar				
ISEA PAS	DL_02-238	1	M	*Mauricenaclia*	*minuta*	Ambahibe	29.1.2002	D.C. Lees	119	
ISEA PAS	MAD_289	1	F	*Mauricenaclia*	*minuta*	Andasibe-Mantadia PN, Feon'ny Ala Hotel		Ł. Przybyłowicz	950	
ISEA PAS	MAD_261	1	F	*Mauricenaclia*	*minuta*	Ankarana National Park, Ankarana Lodge	9.11.2018	Ł. Przybyłowicz	500	
ISEA PAS	MAD_260, MAD_262	2	M	*Mauricenaclia*	*minuta*	Ankarana National Park, Ankarana Lodge	9.11.2018	Ł. Przybyłowicz	500	
ISEA PAS	DL1802	1	F	*Mauricenaclia*	*minuta*	Feony-ala, near Analamazaotra	28.2.2002	D.C. Lees	969	
ISEA PAS	DL_02-325	1	F	*Mauricenaclia*	*minuta*	P.N. Bemaraha, Analamanitsy, eastern cliff	4.2.2002	D.C. Lees	752	
ISEA PAS	MAD_020	1	M	*Mauricenaclia*	*minuta*	Ranomafana National Park	2.5.2014	P. Sharland	1050	
ISEA PAS	MAD_282	1	F	*Mauricenaclia*	*minuta*	Sava region, Ambodiala, direction Antalaha	30.10.2017	A. Wurz	40	woody fallows

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
ISEA PAS	MAD_288, MAD_287	2	M	*Mauricenaclia*	*minuta*	Sava region, Ambodiala, direction Antalaha	23.10.2017	A. Wurz	303	V24-VM-S1, vanilla agroforest, alternative locality Ambavala 4
ISEA PAS	BC MDG 1434	1	M	*Mauricenaclia*	*minuta*	Madagascar N, Ankarana PN, Ankarana Lodge	9-11.11.2018		500	
Joel Minet MNHN		1	M	*Mauricenaclia*	*minuta*	Madagascar Est, Ifanadiana, Ranomafana	"probablement 1965"	P. et J. Minet		
MNHN	EL82658	1	F	*Mauricenaclia*	*minuta*	Ifasy, Ambilobé				
MNHN	EL82647	1	F	*Mauricenaclia*	*minuta*	Ile Ste Marie, Foret de Kalalo	4.1960	P. Griveaud	70	
MNHN	EL82665, EL82666, EL82664, EL82681, EL82680	5	M	*Mauricenaclia*	*minuta*	Ile Ste Marie, Foret de Kalalo	4.1960	P. Griveaud	70	
MNHN	EL74766	1	F	*Mauricenaclia*	*minuta*	Madagascar E., Midongy du S.	8.1926	R. Decary		
MNHN	EL82646	1	F	*Mauricenaclia*	*minuta*	Madagascar Est, Antanambe	7.1965	A. Peyrieras		
MNHN	EL82725	1	F	*Mauricenaclia*	*minuta*	Madagascar Est, dct. Andapa R.N. XII-Marojejy, Ankobahina	4.1961	P. Soga	650	
MNHN	EL82677	1	M	*Mauricenaclia*	*minuta*	Madagascar Est, dct. Maroantsetra, Marogavo	29.10.1960	A. Peyrieras		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL74868	1	F	*Mauricenaclia*	*minuta*	Madagascar Est, district d'Andapa, Ambatoarano	10.1961	P. Soga	830	
MNHN	EL82690, EL82682	2	M	*Mauricenaclia*	*minuta*	Madagascar Est, district Sambava, Marojejy, Ambinanitelo	12.1958	P. Griveaud	500	
MNHN	EL82679	1	M	*Mauricenaclia*	*minuta*	Madagascar Est, Manombo	7.1965	A. Peyrieras		
MNHN	EL74869	1	F	*Mauricenaclia*	*minuta*	Madagascar Est, Route Sambava-Andapa, Belalono	21-23.11.1968	P. Griveaud, A. Peyrieras et P. Viette	100	
MNHN	EL82649	1	F	*Mauricenaclia*	*minuta*	Madagascar N.W., stat. de Bevazaha, Ankarafantsika	18.11.1951	P. Viette		
MNHN	EL82642, EL82640, EL82676, EL82675, EL82718, EL82717, EL82716, EL82714, EL82712, EL82719, EL82713, EL82715, EL82711, EL82710, EL82705, EL74862, EL74864, EL74860, EL74863, EL74861, EL74867, EL74866, EL74865	23	F	*Mauricenaclia*	*minuta*	Madagascar Nord, , Foret d' Analamerana (Cote Nord-Ouest)	14-19.8.1973	A. Peyrieras		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL82660, EL82678, EL82699, EL82696, EL82692, EL82689, EL82687, EL74872, EL74874, EL74876, EL74873, EL74875	13	M	*Mauricenaclia*	*minuta*	Madagascar Nord, , Foret d' Analamerana (Cote Nord-Ouest)	14-19.8.1973	A. Peyrieras		
MNHN	EL82722, EL74870	2	F	*Mauricenaclia*	*minuta*	Madagascar Nord, 37 km S. de Vohémar, foret d' Analalava	10-14.11.1968	P. Griveaud, A. Peyrieras, P. Viette	25	
MNHN	EL82652	1	F	*Mauricenaclia*	*minuta*	Madagascar Nord, dct. d' Analalava, Beraty	12.1960	A. Robinson	1000	
MNHN	EL74871	1	M	*Mauricenaclia*	*minuta*	Madagascar Nord, Montagne d'Ambre	20-22.8.1973	A. Peyrieras		
MNHN	EL82669, EL82670	2	M	*Mauricenaclia*	*minuta*	Madagascar Nord, Montagne d'Ambre, Les Roussettes	4.12.1958	P. Viette	1000	
MNHN	EL82685	1	M	*Mauricenaclia*	*minuta*	Madagascar Nord, Region de Sadjoavato, Foret de Sahafary	23-25.8.1973	A. Peyrieras		
MNHN	, EL82644, EL82639, EL82645, EL82648, EL82709, EL82707, EL82704, EL82703, EL82706, EL82702, EL82701, EL82708	12	F	*Mauricenaclia*	*minuta*	Madagascar Ouest, Route nat. 6, 40 km N de Port-Bergé	8.1973	A. Peyrieras		
MNHN	EL82694	1	M	*Mauricenaclia*	*minuta*	Madagascar Ouest, Route nat. 6, 40 km N de Port-Bergé	8.1973	A. Peyrieras		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL82691	1	M	*Mauricenaclia*	*minuta*	Madagascar Sambirano, Nosy-Be, Foret de Lokobe	1.1960	A. Robinson		
MNHN	EL82643	1	F	*Mauricenaclia*	*minuta*	Madagascar W, Ankarafantsika, Ampijoroa	14.11.1951	P. Viette		
MNHN	EL82655	1	F	*Mauricenaclia*	*minuta*	Madagascar, Baie d' Antongil, Antanambe	1898	A. Mocquerys		
MNHN	EL82723	1	F	*Mauricenaclia*	*minuta*	Madagascar, foret d' Ambre	18.3.1939	R. Jeannel		
MNHN	EL74877	1	M	*Mauricenaclia*	*minuta*	Madagascar, Montagne d'Ambre	12.1948	Renaud Paulian ?		sur *Cinchona succirubra*; 3-4 ans
MNHN	EL82671	1	M	*Mauricenaclia*	*minuta*	Madagascar, Rogez, Foret Cote Est	4.1938(?)	A. Seyrig		
MNHN	EL83637	1	F	*Mauricenaclia*	*minuta*	Madagascar, Route Anosibe P.K. 27	6(?).1972			
MNHN	EL82653	1	F	*Mauricenaclia*	*minuta*	Madagascar-Est, dct Sambava, Reserve nat. XII Marojejy-Andrakata	2.1959	P. Soga		
MNHN	EL82650, EL82654, EL82641, EL82724	4	F	*Mauricenaclia*	*minuta*	Madagascar-Est, dct. Andapa R.N. XII-Marojejy, Ankobahina	4.1961	P. Soga	650	
MNHN	EL82667, EL82672, EL82668, EL82663, EL65161	5	M	*Mauricenaclia*	*minuta*	Madagascar-Est, dct. Andapa R.N. XII-Marojejy, Ankobahina	4.1961	P. Soga	650	
MNHN	EL82656	1	F	*Mauricenaclia*	*minuta*	Madagascar-Est, dct. Andapa R.N. XII-Marojejy, Ankobahina	5.1961	P. Soga	650	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL82688	1	M	*Mauricenaclia*	*minuta*	Madagascar-Est, dct. Andapa R.N. XII-Marojejy, Ankobahina	5.1961	P. Soga	650	
MNHN	EL82662, EL82661	2	M	*Mauricenaclia*	*minuta*	Madagascar-Est, dct. Maroantsetra, Marogavo	29.10.1960	A. Peyrieras		
MNHN	EL82651, EL82659, EL82721, EL82720	4	F	*Mauricenaclia*	*minuta*	Madagascar-Est, Dist. Mananara-N, Seranambe		J. Vadon, A. Peyrieras		
MNHN	EL82683, EL82684, EL82686, EL82697, EL82695, EL82700, EL82698, EL82693	8	M	*Mauricenaclia*	*minuta*	Madagascar-Est, Dist. Mananara-N, Seranambe		J. Vadon, A. Peyrieras		
MNHN	EL82657	1	F	*Mauricenaclia*	*minuta*	Madagascar-Est, district Sambava, Marojejy, Ambinanitelo	12.1958	P. Griveaud	500	
NHMUK		6	F	*Mauricenaclia*	*minuta*					
NHMUK		1	M	*Mauricenaclia*	*minuta*					
NHMUK	MAD_299, MAD_300, MAD_301	1	F	*Mauricenaclia*	*minuta*	Antsiranana, Masoala PN, Ambatoavy, near river Masioposa, tavy	21.2.1993	D.C. Lees	180	tavy area
NHMUK	MAD_294	1	F	*Mauricenaclia*	*minuta*	Antsiranana, RS Manongarivo, Mt. Betampona	22.7.1994	D.C. Lees	800	
NHMUK		1	F	*Mauricenaclia*	*minuta*	Diego Suarez	-	Dr. Martin		
NHMUK		3	F	*Mauricenaclia*	*minuta*	Fenerive	1er Trimestre 1896	Perrot Freres		
NHMUK	MAD_296, MAD_297, MAD_298	3	F	*Mauricenaclia*	*minuta*	Masoala PN, river Andranomaloto, towards Ambohitsitoindroina Mahalevona	24.2.1993	D.C. Lees	600	tavy area

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
NHMUK	MAD_295	1	F	*Mauricenaclia*	*minuta*	Sava region, Andrakata, direction Andapa	22.7.1994	D.C. Lees	800	
NHMUK		57	F	*Mauricenaclia*	*minuta*	Ste Marie de Madagascar	10-12.1896	Perrot Freres		
NHMUK		21	M	*Mauricenaclia*	*minuta*	Ste Marie de Madagascar	10-12.1896	Perrot Freres		
NHMUK		2	F	*Mauricenaclia*	*minuta*	Sud de Madagascar	4.1922(?)	M. Lamberton		
NHMUK		1	M	*Mauricenaclia*	*minuta*	Sud de Madagascar	4.1922(?)	M. Lamberton		
NHMUK		3	M	*Mauricenaclia*	*minuta*	Baie d' Antongil, Antanambe	3-4.1897	A. Mocquerys		
NHMUK	NHMUK015109744	1	M	*Mauricenaclia*	*minuta*	Madagascar NE, Masoala, Antanandava, Antafononana R. (survey site W7L2)	17.1.1994	D.C. Lees	40	
NHMUK	NHMUK015109745	1	F	*Mauricenaclia*	*minuta*	Madagascar NE, Masoala, coastal path just S of Andranobe R. camp, "tavy area"	11.2.1993		0	14:02 PM
NHMUK		1	F	*Mauricenaclia*	*minuta*	Madagascar				
NHMUK		3	F	*Mauricenaclia*	*minuta*	Madagascar		H. Perrot		
NHMUK		2	F	*Mauricenaclia*	*minuta*	Madagascar				
NHMUK		3	M	*Mauricenaclia*	*minuta*	Madagascar				
NHMUK		1	F	*Mauricenaclia*	*minuta*	Madagascar	1883	L. Humblot		
NHMUK		2	F	*Mauricenaclia*	*minuta*	Madagascar, Diego Suarez	2.1917	G. Melou		
NHMUK		2	F	*Mauricenaclia*	*minuta*	Madagascar, Diego Suarez	16.1.1917	J. Melou		
NHMUK		1	M	*Mauricenaclia*	*minuta*	Madagascar, Fenerive	1er Trimestre 1896	Perrot Freres		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
NHMUK		2	F	*Mauricenaclia*	*minuta*	Madagascar, Fenerive	1er Trimestre 1896	Perrot Freres		
NHMUK		1	F	*Mauricenaclia*	*minuta*	Madagascar, Fito	5.1897	Perrot Freres		
NHMUK		1	F	*Mauricenaclia*	*minuta*	Madagascar, Ile ste Marie, Foret de Kalalao	4.1960	P. Griveaud	70	
NHMUK		1	M	*Mauricenaclia*	*minuta*	Madagascar, Ile ste Marie, Foret de Kalalao	4.1960	P. Griveaud	70	
NHMUK		4	F	*Mauricenaclia*	*minuta*	Madagascar, Maevatanana				
NHMUK		1	M	*Mauricenaclia*	*minuta*	Madagascar, Mananjara	11.1918	M. Le Moult		
NHMUK		1	M	*Mauricenaclia*	*minuta*	Madagascar, Mananjary	1918 (1913?)	G. Melou		
NHMUK		2	F	*Mauricenaclia*	*minuta*	Madagascar, Maroantsetra				
NHMUK		1	F	*Mauricenaclia*	*minuta*	Madagascar, Nord et Centre de Madagascar				
NHMUK		2	F	*Mauricenaclia*	*minuta*	Madagascar, plantations du Sambirano	-	Collection le Moult		
NHMUK		3	F	*Mauricenaclia*	*minuta*	Madagascar, Tamatave et forets d'Alahakato	1er Semestre 1888	Edouard Perrot		
NHMUK		1	M	*Mauricenaclia*	*minuta*	Madagascar, Tamatave et forets d'Alahakato	1er Semestre 1888	Edouard Perrot		
NHMUK		1	F	*Mauricenaclia*	*minuta*	Madagascar, Tananarive	1916(?)	Lamberton(?)		
NHMUK		1	F	*Mauricenaclia*	*minuta*	Madagascar, Tananarivo Dist.	1916			

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
NHMUK		1	F	*Mauricenaclia*	*minuta*	Madagascar-Est, dct. Andapa, R.N. XII-Marojejy, Ankobahina	4.1961	P. Soga	650	
NHMUK		1	M	*Mauricenaclia*	*minuta*	Madagascar-Est, dct. Andapa, R.N. XII-Marojejy, Ankobahina	4.1961	P. Soga	650	
NHMUK		2	M	*Mauricenaclia*	*minuta*	Madagascar-Est, Dist. Mananara-N, Seranambe	-	Vadon-Peyrieras		
NRM	MAD_014	1	F	*Mauricenaclia*	*minuta*	Madagascar	4(?).10(?)			
PZBT		1	M	*Mauricenaclia*	*minuta*	Ankarafantsika, Ampijoroa	2.9.1956	P. Griveaud	120	
PZBT		1	F	*Mauricenaclia*	*minuta*	Ile ste Marie, Ambodena	10.1960	P. Griveaud		
PZBT		6	F	*Mauricenaclia*	*minuta*	Ile ste Marie, Foret de Kalalao	4.1960	P. Griveaud	70	
PZBT		6	M	*Mauricenaclia*	*minuta*	Ile ste Marie, Foret de Kalalao	4.1960	P. Griveaud	70	
PZBT		1	M	*Mauricenaclia*	*minuta*	Lac Alaotra				
PZBT		1	M	*Mauricenaclia*	*minuta*	Madagascar Centre, Ambalavao				
PZBT		1	F	*Mauricenaclia*	*minuta*	Madagascar Est, Ambodivoanio	8.1965	Peyrieras		
PZBT		2	F	*Mauricenaclia*	*minuta*	Madagascar Est, Analabe, 42 km Nord Sambava	15-20.11.1968	Griveaud et Viette		
PZBT		1	M	*Mauricenaclia*	*minuta*	Madagascar Est, Antanadavahely, Antalaha	7.1966	Jacquemin	50	
PZBT		2	M	*Mauricenaclia*	*minuta*	Madagascar Est, Behanana - Ouest Rantabe, Piste Mandritsara	9.1967	Peyrieras	500	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
PZBT		1	F	*Mauricenaclia*	*minuta*	Madagascar Est, dct. Andapa, Anjanaharibe (50 km Ouest Andapa)	2(?).1961	P. Soga	1750	
PZBT		4	M	*Mauricenaclia*	*minuta*	Madagascar Est, dct. Andapa, R.N. XII-Marojejy, Ankobahina	4.1961	P. Soga	650	
PZBT		1	M	*Mauricenaclia*	*minuta*	Madagascar Est, dct. Andapa, R.N. XII-Marojejy, Ankobahina	5.1961	P. Soga	650	
PZBT		2	M	*Mauricenaclia*	*minuta*	Madagascar Est, dct. Maroantsetra, Marogavo	29.10.1960 -	Peyrieras		
PZBT		1	M	*Mauricenaclia*	*minuta*	Madagascar Est, dct. Sambava, R.N. XII - Marojejy, Andasy II	4.1961	P. Soga	1300	
PZBT		1	M	*Mauricenaclia*	*minuta*	Madagascar Est, dct. Sambava, Reserve nat. XII, Marojejy - Andrakata	2.1959	P. Soga		
PZBT		1	F	*Mauricenaclia*	*minuta*	Madagascar Est, district Sambava, Marojejy, Ambinanitelo	12.1958	P. Griveaud	500	
PZBT		2	F	*Mauricenaclia*	*minuta*	Madagascar Est, Foret Analalava, Vohemar	10-14.11.1968	Griveaud et Viette		
PZBT		1	F	*Mauricenaclia*	*minuta*	Madagascar Est, Mahitsy Arongana, Nord Maroantsetra, Sur Riv. Itsikiory	7-8.1967	Peyrieras	600	
PZBT		1	M	*Mauricenaclia*	*minuta*	Madagascar Est, Manombo	7.1965	Peyrieras		
PZBT		2	F	*Mauricenaclia*	*minuta*	Madagascar Est, Maroantsetra, Hiaraka	3.1969	Bozilahy	500-1000	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
PZBT		1	F	*Mauricenaclia*	*minuta*	Madagascar Est, Ouest Mitanoka, Vallee Onibe	10.1966	Jacquemin		
PZBT		1	F	*Mauricenaclia*	*minuta*	Madagascar Est, Route de Beparasy	8.1970			
PZBT		2	M	*Mauricenaclia*	*minuta*	Madagascar Est, Route de Beparasy	8.1970			
PZBT		1	F	*Mauricenaclia*	*minuta*	Madagascar Est, Route Milanoa foret Bevitsika, Vohemar	9.11.1968	Griveaud et Viette		
PZBT		1	F	*Mauricenaclia*	*minuta*	Madagascar Est, Route Sambava - Andapa, Belalono, env. Alt. Maroambihy	25.11.1967	Peyrieras		
PZBT		1	F	*Mauricenaclia*	*minuta*	Madagascar Nord, dct. d'Analalava, Manongarivo	12.1960	A. Robinson	1150	
PZBT		1	M	*Mauricenaclia*	*minuta*	Madagascar Nord, dct. d'Analalava, Beraty	12.1960	A. Robinson	1000	
PZBT		1	F	*Mauricenaclia*	*minuta*	Madagascar Nord, Diego Suarez	1.1966	Peyrieras		
PZBT		1	F	*Mauricenaclia*	*minuta*	Madagascar Nord, Montagne d'Ambre, Les Roussettes	9-12.1958	Andria Robinson	1100	
PZBT		1	F	*Mauricenaclia*	*minuta*	Madagascar Sambirano, Nosy-Be, foret de Lokobe	1.1960	Andria Robinson		
SGN		2	F	*Mauricenaclia*	*minuta*	Madagascar, Lokobe		Ebenau		
SMNS		1	?	*Mauricenaclia*	*minuta*	Madagascar Est, Moramanga, vic. Andasibe, Headquater NAT near Hotel Feon n'y Ala, S/W of Foret de "Analmazaotra" NR	19.12.2006	J. Berg, D. Bartsch	1000	at day

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL65141, holotype	1	M	*Mauricenaclia*	*raharizonina*	Madagascar Sud, Sakaraha, Zombitsy	18.12.1959	P. Raharizonina	600	
MfN	79fa12	1	M	*Mauricenaclia*	*raharizonina*	SW Madagascar, Andranohinaly, "waldgebiet" (forest area)	2.(/11?).1904			
MNHN	EL82621	1	F	*Mauricenaclia*	*raharizonina*	Madagascar Nord, contreforts du Tsaratanana, Haut Sambirano, vallée de la Besanetribe	5-9.12.1963	P. Viette	1200	
MNHN	EL82622	1	F	*Mauricenaclia*	*raharizonina*	Madagascar Sud, plateau Mahafaly, 11/12 km Ouest d' Ankalirano	18-31.1.1974	P. Viette	250	
MNHN	EL74768	1	F	*Mauricenaclia*	*raharizonina*	Madagascar Sud, Sakaraha, Zombitsy	18.12.1959	P. Raharizonina	600	
NHMUK		1	F	*Mauricenaclia*	*raharizonina*	Madagascar, Tulear Pr., Andranovory	24.3.1968	K.M.G & P.D.	200	
NRM		1	?	*Mauricenaclia*	*raharizonina*	Andranohinaly	2.(/11?).1904	Voeltzkow		
PZBT		1	M	*Mauricenaclia*	*raharizonina*	Madagascar Sud Ouest, Sakaraha, Lambomakandro	3.1961	P. Griveaud		
PZBT		2	M	*Mauricenaclia*	*raharizonina*	Madagascar Sud, Sakaraha, Zombitsy	18.12.1959	P. Raharizonina	600	
MNHN	EL65142	1	M	*Mauricenaclia*	*rothschildi*	Madagascar-Sud-Ouest, Sakaraha, Lambomakandro	3.1961	P. Griveaud		
ISEA PAS	MAD_212	1	F	*Mauricenaclia*	*rothschildi*	Morondava Region, 60 m E ad Kirindy Ecolodge	29.2.2020	Ł. Przybyłowicz	60	
ISEA PAS	DL_05-857	1	F	*Mauricenaclia*	*rothschildi*	Tsaratanana	24.12.2004	D.C. Lees	1441	
MNHN	EL74567	1	M	*Mauricenaclia*	*rothschildi*	Madagascar	1867	A. Grandidier		
MNHN	EL74773	1	M	*Mauricenaclia*	*rothschildi*	Madagascar, Ankandro	26.10.1934	Catala		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL74956, EL74957	2	M	*Mauricenaclia*	*rothschildi*	Madagascar, Fort Dauphin	-			
MNHN	EL74774, EL74777, EL74776, EL74775, EL74778	5	M	*Mauricenaclia*	*rothschildi*	Madagascar-Sud-Ouest, Sakaraha, Lambomakandro	3.1961	P. Griveaud		
NHMUK		1	F	*Mauricenaclia*	*rothschildi*	Madagascar Sud Ouest, Sakaraha, Lambomakandro	3.1961	P. Griveaud		slide Syntomid 73
NHMUK		2	M	*Mauricenaclia*	*rothschildi*	Madagascar Sud Ouest, Sakaraha, Lambomakandro	3.1961	P. Griveaud		slide Syntomid 72
NHMUK		1	M	*Mauricenaclia*	*rothschildi*	Madagascar, Tulear Pr., Andranovory	24.3.1968	K.M.G. & P.D.	200	
PZBT		34	M	*Mauricenaclia*	*rothschildi*	Madagascar Sud Ouest, Sakaraha, Lambomakandro	.3.1961 -	P. Griveaud		
PZBT		1	M	*Mauricenaclia*	*rothschildi*	Madagascar, Fort Dauphin	2(/11?).1939(?)	A. Seyrig		
NHMUK	NHMUK013384803, holotype	1	M	*Mauricenaclia*	*octopunctata*	Madagascar, Diego Suarez	05.02.1917	G. Melou		
ISEA PAS	DL_2966	1	F	*Mauricenaclia*	*octopunctata*	Andringitra	4.12.2011	D.C. Lees	253	
ISEA PAS	MAD_259, MAD_272	2	F	*Mauricenaclia*	*octopunctata*	Ankarana National Park, Ankarana Lodge	9.11.2018	D. Stadie & R. Fiebig	500	
ISEA PAS	MAD_263, MAD_265	1	M	*Mauricenaclia*	*octopunctata*	Ankarana National Park, Ankarana Lodge	9.11.2018	D. Stadie & R. Fiebig	500	
ISEA PAS	MAD_266	1	M	*Mauricenaclia*	*octopunctata*	Montagne d'Ambre National Park, 3 km SE Joffreville	9.11.2018	D. Stadie & R. Fiebig	970	
ISEA PAS	DL_02-26	1	F	*Mauricenaclia*	*octopunctata*	RS Andranomena	15.1.2002	D.C. Lees	35	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	MA_16-9 - EL83629	1	M	*Mauricenaclia*	*octopunctata*	Parc national des Tsingy de Namoroka, Namoroka village - Deparapangi	29.10.2016	R. Rougerie, C. Villement	73	over flowers of Entada leptostachya
MNHN	EL82727, EL82726	2	M	*Mauricenaclia*	*octopunctata*	Madagascar Nord, dct. d'Analalava, Beraty	12.1960	A. Robinson	1000	
NHMUK		1	M	*Mauricenaclia*	*octopunctata*	Madagascar Nord, dct d'Analalava, Beraty	.12.60	A. Robinson	1000	slide Syntomid 70
NHMUK		1	M	*Mauricenaclia*	*octopunctata*	Madagascar, Diego Suarez	2-4.17(=1917?)	G. Melou		slide Syntomid 79
NHMUK	NHMUK013384804	1	F	*Mauricenaclia*	*octopunctata*	Madagascar, Diego Suarez	2.1917(?)	G. Melou		
NHMUK		1	M	*Mauricenaclia*	*octopunctata*	Madagascar, Tulear Pr., Andranovory	24.3.1968	K.M.G. & P.D.	200	
PZBT		1	M	*Mauricenaclia*	*octopunctata*	Ankarafantsika, Ampijoroa	2.9.1956	P. Griveaud	120	
PZBT		2	M	*Mauricenaclia*	*octopunctata*	Madagascar Nord, dct d' Analalava, Beraty	12.1960	A. Robinson	1000	
PZBT		1	M	*Mauricenaclia*	*octopunctata*	Madagascar Ouest, Terrain d' Aviation, Majunga	1.1960	A. Robinson		
MNHN	EL74767	1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Hera, Ankazoabo				
MNHN	EL82729	1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar Nord, dct. d' Analalava, Beraty	12.1960	A. Robinson	1000	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL74954	1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar Nord, Foret D'Analamerana, Cote Nord-Ouest	14-19.8.1973	A. Peyrieras		IMG_20220324_172840
MNHN	EL82730	1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar, Fort Dauphin	5.1937	A. Seyrig		
MNHN	EL82728, EL74796, EL74795, EL74794, EL74793, EL74792, EL74791, EL74790, EL74789, EL74788, EL74786, EL74785, EL74784, EL74783, EL74782, EL74781, EL74787, EL74780, EL74779	19	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar-Sud-Ouest, Sakaraha, Lambomakandro	3.1961	P. Griveaud		
NHMUK		1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar, Diego Suarez	24.12.1916	J. Melou		
NHMUK		1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar, Diego Suarez	8.1.1917	J. Melou		
NHMUK		1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar, Sambirano, Nosy-Be foret de Lokobe	1.1960	Andria Robinson		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
NHMUK		1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar, Tulear Pr., Andranovory	24.3.1968	K.M.G. & P.D.	200	
PZBT		1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Beparasy	1972			
PZBT		1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Beparasy	10.1970			
PZBT		1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Fort Dauphin				
PZBT		2	F	*Mauricenaclia*	*rothschildi / octopunctata*	Sakaraha	1.1966	Collection Dujardin-Delacour		
PZBT		1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar Est, Ankasina, Route Lakato	3.1970			
PZBT		6	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar Nord, dct d' Analalava, Beraty	12.1960	A. Robinson	1000	
PZBT		1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar Ouest, Ankarafantsika, Ampijoroa	12.1969	P. Raharizonina	800 or 900	
PZBT		1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar Ouest, Ankarafantsika, Lac d' Ampijoroa	3-10.12.1969	Viossat et Ratovoson		
PZBT		1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar Ouest, Causses de Kelifaly, foret de Kasijy	21-25.10.1974	Gabriel Auguste		
PZBT		2	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar Sambirano, Nosy-Be, Station Oceanographique	1.1960	A. Robinson		
PZBT		3 2	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar Sud Ouest, Sakaraha, Lambomakandro	3.1961	P. Griveaud		

Coll.	**Specimen code**	**N**	**S**	**Genus**	**Species**	**Locality**	**Collecting date (d/m/yyyy)**	**Collector**	**Altitude m a.s.l.**	**Remarks**
SGN		1	F	*Mauricenaclia*	*rothschildi / octopunctata*	Madagascar oc.,		Hildebrandt		
MNHN	EL65162, holotype	1	M	*Mauricenaclia*	*bruneata*	Madagascar Nord, Diego-Suarez	1.1966	A. Peyrieras		
MNHN	EL82735, EL82734, EL82733, EL65163	4	F	*Mauricenaclia*	*bruneata*	Madagascar Nord, Diego-Suarez	1.1966	A. Peyrieras		
MNHN	EL82731	1	M	*Mauricenaclia*	*bruneata*	Madagascar Nord, Diego-Suarez	1.1966	A. Peyrieras		
MNHN	EL82732, EL74968	2	F	*Mauricenaclia*	*bruneata*	Madagascar Nord, Foret d'Analamerana (cote nord-ouest)	14-19.8.1973	A. Peyrieras		
NHMUK	DL1811	1	F	*Mauricenaclia*	*bruneata*	Maitsoarongana, just above camp	7.12.2001	D.C. Lees	675	
PZBT		1	F	*Mauricenaclia*	*bruneata*	Madagascar Est, Route Milanoa foret Bevitsika, Vohemar	9.11.1968	Griveaud et Viette		
PZBT		3	F	*Mauricenaclia*	*bruneata*	Madagascar Nord, Diego Suarez	1.1966	Peyrieras		
MNHN	EL65143, holotype	1	M	*Mauricenaclia*	*peyrierasi*	Madagascar Est, Antanambe	7.1965	A. Peyrieras		
Joel Minet MNHN		1	F	*Mauricenaclia*	*peyrierasi*	Madagascar Centre, La Mandraka	11.7.1971	P. et J. Minet		
Joel Minet MNHN		1	F	*Mauricenaclia*	*peyrierasi*	Madagascar Centre, La Mandraka	29.5.1971	P. et J. Minet		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
Joel Minet MNHN		1	F	*Mauricenaclia*	*peyrierasi*	Madagascar Centre, La Mandraka	pupation 8.1972	P. et J. Minet		"Ab ovo ponte d'une ♀ provenant de La Mandraka (Madagascar Centre) eclosion: VIII-1972 (A Fabregues [Herault])" / Thyrosticta peyrierasi Griveaud ♂
Joel Minet MNHN		2	M	*Mauricenaclia*	*peyrierasi*	Madagascar Centre, La Mandraka	pupation 8.1972	P. et J. Minet		"Ab ovo ponte d'une ♀ provenant de La Mandraka (Madagascar Centre) eclosion: VIII-1972 (A Fabregues [Herault])" / Thyrosticta peyrierasi Griveaud ♂
MNHN	EL74769	1	F	*Mauricenaclia*	*peryrierasi*	Madagascar Est, Antanambe	7.1965	A. Peyrieras		
MNHN	EL74770	1	F	*Mauricenaclia*	*peryrierasi*	Madagascar Est, Ambodivoanio	8.1965	A. Peyrieras		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL74878	1	M	*Mauricenaclia*	*peyrierasi*		23.5.1971(?)			
NHMUK	DL1792	1	F	*Mauricenaclia*	*peyrierasi*	Tsaratanana, descent	24.12.2004	D.C. Lees	1630	
PZBT		1	F	*Mauricenaclia*	*peyrierasi*	Madagascar Est, Antanambe	7.1965	Peyrieras		
PZBT		1	F	*Mauricenaclia*	*peyrierasi*	Madagascar Centre, La Mandraka	9.10.1971	Minet		
PZBT		1	F	*Mauricenaclia*	*peyrierasi*	Madagascar Centre, La Mandraka	13.11.1969	Turlin	1200	
PZBT		5	M	*Mauricenaclia*	*peyrierasi*	Madagascar Centre, La Mandraka	9.10.1971	Minet		
PZBT		1	M	*Mauricenaclia*	*peyrierasi*	Madagascar Centre, La Mandraka	31.1.1970	Turlin		
PZBT		3	M	*Mauricenaclia*	*peyrierasi*	Madagascar Centre, La Mandraka	11.1974	A. Peyrieras		
SGN		1	F	*Mauricenaclia*	*peyrierasi*	Madagascar occ.,		Hildebrandt		
SGN		1	M	*Mauricenaclia*	*peyrierasi*	Madagascar occ.,		Hildebrandt		
MNHN	EL83055, holotype	1	M	*Thyrosticta*	*apatris* sp. nov.			P. Soga		
MNHN	EL81694, EL81680	2	M	*Thyrosticta*	*apatris* sp. nov.			P. Soga		
NHMUK	NHMUK010621695, holotype	1	M	*Melanonaclia*	*luctuosa*	Madagascar, Fenerive	1 trimestre 1896	Perrot Freres		
MNHN	EL65140 - holotype of "inauramacula"	1	F	*Melanonaclia*	*luctuosa*	Madagascar-Est, dct. Andapa, Anjanaharibe	4.1960	P. Soga	1600	
ISEA PAS	DL_2960	1	F	*Melanonaclia*	*luctuosa*	Makira	23.6.1998	D.C. Lees	500	
ISEA PAS	DL_SC3	1	F	*Melanonaclia*	*luctuosa*	Makira, Anjanaharibe Mt.	2.2.2003	D.C. Lees	652	
ISEA PAS	DL_SG4	1	F	*Melanonaclia*	*luctuosa*	Makira, Bivontro	14.12.2002	D.C. Lees	762	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
ISEA PAS	DL_SF11	1	F	*Melanonaclia*	*luctuosa*	Makira, Vohitaly	26.12.2002	D.C. Lees		
ISEA PAS	TR45	1	F	*Melanonaclia*	*luctuosa*	Masoala, Manosona	27.1.1994	D.C. Lees	25	
ISEA PAS	DL_2980	1	F	*Melanonaclia*	*luctuosa*	Masoala, Ratsiaranana	1.9.1994	D.C. Lees	10	
MNHN	EL74669	1	F	*Melanonaclia*	*luctuosa*	Madagascar, Fianarantsoa				
MNHN	EL74667	1	F	*Melanonaclia*	*luctuosa*	Madagascar Est, Antanambe	7.1965	A. Peyrieras		
MNHN	EL74670	1	M	*Melanonaclia*	*luctuosa*	Madagascar Est, Antanambe	7.1966(?)	A. Peyrieras		
MNHN	EL74589	1	F	*Melanonaclia*	*luctuosa*	Madagascar Est, Dist. Mananara-N, Seranambe		J. Vadon, A. Peyrieras		
MNHN	EL74592	1	F	*Melanonaclia*	*luctuosa*	Madagascar Est, Lac Alaotra, Befody	22-23.8.1968	P. Griveaud		
MNHN	EL74671	1	F	*Melanonaclia*	*luctuosa*	Madagascar Est, Manombo	7.1965	A. Peyrieras		
MNHN	EL74594, EL74587, EL74593, EL74591, EL74590, EL74586, EL74588	7	F	*Melanonaclia*	*luctuosa*	Madagascar Est, Rte Sambava - Andapa, env. alt. Maroambihy, Belalono	25.11.1967	A. Peyrieras		
MNHN	EL74584, EL74583, EL74582, EL74580, EL74579, EL74578, EL74581	7	M	*Melanonaclia*	*luctuosa*	Madagascar Est, Rte Sambava - Andapa, env. alt. Maroambihy, Belalono	25.11.1967	A. Peyrieras		
MNHN	EL74585	1	M	*Melanonaclia*	*luctuosa*	Madagascar N.E., env. de Maroantsetra, Ambodivoangy		J. Vadon		
MNHN	EL74672, EL74668	2	F	*Melanonaclia*	*luctuosa*	Madagascar, Baie d' Antongil, Antanambe	1898	A. Mocquerys		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL74665	1	F	*Melanonaclia*	*luctuosa*	Madagascar-Est, dct. Andapa, Anjanaharibe (50 km Ouest Andapa)	3.1961	P. Soga	1600	
MNHN	EL74666	1	M	*Melanonaclia*	*luctuosa*	Madagascar-Est, dct. Andapa, Anjanaharibe (50 km Ouest Andapa)	3.1961	P. Soga	1600	
NHMUK	DL-01-126 / DL1819	1	F	*Melanonaclia*	*luctuosa*	Madagascar, Maitsoarongana, just above camp	7.12.2001	D.C. Lees	650-700	
NHMUK	NHMUK015109826	1	F	*Melanonaclia*	*luctuosa*	Masoala, Antanandava, Antafononana River (survey site W7L2)	17.1.1994	D.C. Lees	20-60	
NHMUK	NHMUK015109823	1	F	*Melanonaclia*	*luctuosa*	Masoala, Be Dinta, R. Anaovandrano headwaters	15.2.1993	D.C. Lees	480	10:45:00 riprian forest swamp forest, light gap in forest
NHMUK	NHMUK015109825	1	M	*Melanonaclia*	*luctuosa*	Masoala, Be Dinta, R. Anaovandrano headwaters	15.2.1993	D.C. Lees	480	12:00, riprian forest swamp forest, light gap in forest
NHMUK	NHMUK015109827	1	F	*Melanonaclia*	*luctuosa*	Masoala, S of Andranobe R. camp, coastal path	30.1.1993	D.C. Lees	0-30	12:00PM, actinic light

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
NHMUK	NHMUK015109824	1	F	*Melanonaclia*	*luctuosa*	Masoala, S of Andranobe R. camp, coastal path, site T1	29.1.1993	D.C. Lees	0-30	in copula
NHMUK		1	M	*Melanonaclia*	*luctuosa*	Sud de Madagascar		Recu de M. Lamberton		
NHMUK		1	F	*Melanonaclia*	*luctuosa*	Sud de Madagascar	4.1922(?)	Recu de M. Lamberton		
NHMUK		3	M	*Melanonaclia*	*luctuosa*	Sud de Madagascar	4.1922(?)	Recu de M. Lamberton		
NHMUK		1	F	*Melanonaclia*	*luctuosa*	Sud de Madagascar, Vondrozo	4.1922(?)	Recu de M. Lamberton		
PZBT		1	F	*Melanonaclia*	*luctuosa*	Madagascar Est, Ambodiazomamy, Ouest de Voloina 500 m	9.1967	Peyrieras		
PZBT		1	F	*Melanonaclia*	*luctuosa*	Madagascar Est, Antampona	4.1966	Peyrieras		
PZBT		1	F	*Melanonaclia*	*luctuosa*	Madagascar Est, Antanambe	7.1965	Peyrieras		
PZBT		1	F	*Melanonaclia*	*luctuosa*	Madagascar Est, det. Maroantsetra, Tampanambo	11.1960	Vadon-Peyrera		
PZBT		2	M	*Melanonaclia*	*luctuosa*	Madagascar Est, Mahitsy - Arongana, Nord Maroantsetra Sur. Riv. Itsikiory 600m	7-8.1967	Peyrieras		
PZBT		9	F	*Melanonaclia*	*luctuosa*	Madagascar Est, Rte Sambava Andapa Belolona, env. Alt. Maroambihy	25.11.1967	Peyrieras		
PZBT		2	M	*Melanonaclia*	*luctuosa*	Madagascar Est, Rte Sambava Andapa	25.11.1967	Peyrieras		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
						Belolona, env. Alt. Maroambihy				
PZBT		4	F	*Melanonaclia*	*luctuosa*	Madagascar Est, Sahajinga, N. Ouest. Behanana 500m	9.1967	Peyrieras		
PZBT		1	F	*Melanonaclia*	*luctuosa*	Madagascar				
NHMUK	NHMUK010620990, lectotype	1	F	*Melanonaclia*	*lugens*	Madagascar, Antsianaka	1 semestre 1892	Perrot Freres		
MNHN	EL74602	1	F	*Melanonaclia*	*lugens*	Madagascar Est, dct. Andapa, Anjanaharibe	4.1960	P. Soga	1600	
MNHN	EL65135, EL74601, EL74600, EL74599	4	M	*Melanonaclia*	*lugens*	Madagascar Est, dct. Andapa, Anjanaharibe	4.1960	P. Soga	1600	
MNHN	EL74598, EL74597	2	M	*Melanonaclia*	*lugens*	Madagascar Est, dct. Andapa, Anjanaharibe (50 km Ouest Andapa)	3.1961	P. Soga	1600	
MNHN	EL74604, EL74603	2	F	*Melanonaclia*	*lugens*	Madagascar Est, dct. Andapa, Anjanaharibe (50 km Ouest Andapa)		P. Soga	1600	
NHMUK		1	F	*Melanonaclia*	*lugens*	Madagascar Est, det. Andapa, Anjanaharibe	4.1960	P.Soga	1600	
NHMUK	NHMUK015109818	1	M	*Melanonaclia*	*lugens*	Masoala, Andranomaloto River, Camp 2	27.2.1993	D.C. Lees	750	02:00:00, riparian primary forest, actinic light
PZBT		1	F	*Melanonaclia*	*lugens*	Madagascar Est, det. Andapa , Anjanaharibe	4.1960	P. Soga	1600	

Coll.	**Specimen code**	**N**	**S**	**Genus**	**Species**	**Locality**	**Collecting date (d/m/yyyy)**	**Collector**	**Altitude m a.s.l.**	**Remarks**
PZBT		1	F	*Melanonaclia*	*lugens*	Madagascar Est, det. Andapa , Anjanaharibe (50 km Ouest Andapa)	3.1961	P. Soga	1600	
PZBT		1	F	*Melanonaclia*	*lugens*	Madagascar, Beparasy	4.12.1965			
MNHN	EL65134, holotype	1	F	*Melanonaclia*	*nigra*	Madagascar Est, dct Sambava, Marojejy, Ambinanitelo	3.1959	P. Soga	500	
ISEA PAS		1	F	*Melanonaclia*	*nigra*	Antsirarana, R.N.I. de Marojejy, 10.0 km NW Manantenina, tributary Manantenina R.	15-22.10.1996	E. Quinter, T. Nguyen	750	
ISEA PAS	DL_SG29	1	F	*Melanonaclia*	*nigra*	Makira, Bivontro	17.12.2002		850	
ISEA PAS	DL_SG30	1	F	*Melanonaclia*	*nigra*	Makira, Bivontro	17.12.2002		820	
ISEA PAS	DL_01-154	1	M	*Melanonaclia*	*nigra*	Makira, Maitsoarongana	5.12.2001		690	
MNHN	EL74596	1	F	*Melanonaclia*	*nigra*	Madagascar Est, dct Sambava, R.N. XII Marojejy, Ambatosoratra	11.1960	P. Soga	1700	
MNHN	EL74595	1	M	*Melanonaclia*	*nigra*	Madagascar Est, dct Sambava, R.N. XII Marojejy, Ambatosoratra	11.1960	P. Soga	1700	
NHMUK	NHMUK010620986	1	F	*Melanonaclia*	*nigra*	Madagascar Est, Voarifomy Rogez	5.1960	Mr Stanly		
NHMUK		1	F	*Melanonaclia*	*nigra*	Madagascar, Brickaville				
NHMUK		1	M	*Melanonaclia*	*nigra*	Madagascar, Maitsoarongana, S. of camp	7.12.2001	D.C. Lees	650-700	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
NHMUK	NHMUK015109814	1	M	*Melanonaclia*	*nigra*	Masoala, Ambavony R., Site W2-L1, Piste 3300	28.11.1993	D.C. Lees	225-275	12:50:00, DL1840, shady stream bed, showing wing waving behaviour on melastome low down
NHMUK	NHMUK015109813	1	M	*Melanonaclia*	*nigra*	Masoala, Andranomaloto River, Camp 2	26.2.1993	D.C. Lees	750	riparian forest, in copula at dusk
NMP		3	F	*Melanonaclia*	*nigra*	Madagascar				
NMP		2	M	*Melanonaclia*	*nigra*	Madagascar				
PZBT		1	F	*Melanonaclia*	*nigra*	Madagascar Est, Baie d'Antongil, Hiaraka	24.1.1968	P. Griveaud et A. Peyrieras	570	
PZBT		2	M	*Melanonaclia*	*nigra*	Madagascar Est, Baie d'Antongil, Hiaraka	24.1.1968	P. Griveaud et A. Peyrieras	570	
PZBT		1	F	*Melanonaclia*	*nigra*	Madagascar Est, det. Sambava, R. N. XII Marojejy Ambatosoratra	11.1960	P. Soga	1700	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL65136, holotype	1	M	*Melanonaclia*	*toulgoeti*	Madagascar Est, Sandrangato, Route d' Anosibe	.12.1959 -	P. Griveaud		
ISEA PAS	MAD_083	1	F	*Melanonaclia*	*toulgoeti*	Andasibe-Mantadia National Park, Eulopia Trail	1.12.2019		970	
ISEA PAS	MAD_082, MAD_084, MAD_085	3	M	*Melanonaclia*	*toulgoeti*	Andasibe-Mantadia National Park, Eulopia Trail	1.12.2019		970	
ISEA PAS	MAD_033	1	M	*Melanonaclia*	*toulgoeti*	Andasibe-Mantadia National Park, Reserve Analamazoatra	28.11.2019		940-1020	
ISEA PAS	ISEZ-DNA_538	1	F	*Melanonaclia*	*toulgoeti*	Andasibe-Mantadia National Park, Vakona Lodge	4.4.2018		1000	
ISEA PAS	ISEZ-DNA_519	1	F	*Melanonaclia*	*toulgoeti*	Andasibe-Mantadia National Park, Vakona Lodge	5.4.2018		1000	
ISEA PAS	MAD_074	1	F	*Melanonaclia*	*toulgoeti*	Maromizaha Protected Area	29.11.2019		1170	
ISEA PAS	MAD_009	1	F	*Melanonaclia*	*toulgoeti*	Moramanga, Andasibe, vic. Anevoka, Foret Pluviale de Maromitza Nature Reserve	17.11.2004		1100	
ISEA PAS	MAD_127, MAD_128, MAD_129, MAD_134	4	F	*Melanonaclia*	*toulgoeti*	path along river, N ad Mandraka Park	7.12.2019		1270-1310	
ISEA PAS	MAD_133	1	M	*Melanonaclia*	*toulgoeti*	path along river, N ad Mandraka Park	7.12.2019		1270-1310	
MNHN	EL74607	1	F	*Melanonaclia*	*toulgoeti*	Andranomandevy (Didy), Ambatondrazaka	30.9.1956	P. Griveaud	1039 (/1099?)	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL74606	1	F	*Melanonaclia*	*toulgoeti*	Madagascar Est, Maroantsetra		J. Vadon		
MNHN	EL74611	1	F	*Melanonaclia*	*toulgoeti*	Madagascar Est, Périnet	11.3.1955 - 19.3.1955	H. de Toulgoët	950	
MNHN	EL74605	1	F	*Melanonaclia*	*toulgoeti*	Madagascar Est, route de Lakato km 10, Ambodiriana	3.1957	P. Griveaud, R. Vieu	1050	
NHMUK	DL1801	1	F	*Melanonaclia*	*toulgoeti*	Varigohitra, Maroantsetra	5.1.2003	D.C. Lees	67	
NHMUK		2	M	*Melanonaclia*	*toulgoeti*	Madagascar				
NHMUK		1	M	*Melanonaclia*	*toulgoeti*	Madagascar, Perinet, foret de l'est		Le Moult		
NHMUK		2	F	*Melanonaclia*	*toulgoeti*	Madagascar, Tananarive		Le Moult		
NHMUK		3	M	*Melanonaclia*	*toulgoeti*	Madagascar, Tananarive		Le Moult		
NHMUK		1	M	*Melanonaclia*	*toulgoeti*	Madagascar, Tananarive				
PZBT		1	M	*Melanonaclia*	*toulgoeti*	Madagascar Centre, det. Manjakandriana, La Mandraka	2.1961	P. Griveaud		
PZBT		1	M	*Melanonaclia*	*toulgoeti*	Madagascar Centre, Manjakandriana, La Mandraka	4.1972	P. Brondel		
PZBT		1	F	*Melanonaclia*	*toulgoeti*	Madagascar Est, Rte d'Anosibe	23.3.1968	Turlin		
SGN		1	F	*Melanonaclia*	*toulgoeti*	Madagascar, S. Betseleo (misspelled Betsileo)		Hildebrandt		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
Stuttgart		1	M ?	*Melanonaclia*	*toulgoeti*	Madagascar Est, Moramanga, Andasibe, vic. Anevoka, Foret pluviale de Maromiza PN	30.11.2006	J. Berg, D. Bartsch	1110	clearing on mountain-ridge in disturbed primary forest, at light
Stuttgart		1	M ?	*Melanonaclia*	*toulgoeti*	Madagascar Est, Moramanga, Andasibe, vic. Anevoka, Foret pluviale de Maromiza PN	6.12.2006	J. Berg, D. Bartsch	1110	clearing on mountain-ridge in disturbed primary forest, at light
NHMUK	NHMUK013384731, holotype	1	M	*Melanonaclia*	*trimacula*					

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
CEP-MZUJ	CEP-MZUJ 19/2018	1	M	*Melanonaclia*	*trimacula*	Ranomafana National Park, ValBio Centre	10.4.2018	Sz. Safian, V. Maicher, S. Delabye	917	
ISEA PAS	DL_2964	1	F	*Melanonaclia*	*trimacula*	7km NW Vohiparara	21.2.1995		1150	
ISEA PAS	MAD_081	1	F	*Melanonaclia*	*trimacula*	Andasibe-Mantadia National Park, Eulopia Trail	1.12.2019		970	
ISEA PAS	DL_06-975	1	F	*Melanonaclia*	*trimacula*	Kalambatritra, Befarara	14.12.2006		1507	
ISEA PAS	MAD_130	1	F	*Melanonaclia*	*trimacula*	path along river, N ad Mandraka Park	7.12.2019		1270-1310	
ISEA PAS	MAD_126	1	M	*Melanonaclia*	*trimacula*	path along river, N ad Mandraka Park	7.12.2019		1270-1310	
ISEA PAS	ISEZ-DNA_540, ISEZ-DNA_541, ISEZ-DNA_543, ISEZ-DNA_544	4	F	*Melanonaclia*	*trimacula*	Ranomafana National Park, ValBio Centre	10.4.2018		900-970	
ISEA PAS	ISEZ-DNA_539, ISEZ-DNA_542	2	M	*Melanonaclia*	*trimacula*	Ranomafana National Park, ValBio Centre	10.4.2018		900-970	
ISEA PAS	ISEZ-DNA_545, ISEZ-DNA_546	2	F	*Melanonaclia*	*trimacula*	Ranomafana National Park, ValBio Centre	11.4.2018		900-970	
ISEA PAS	MAD_211	1	F	*Melanonaclia*	*trimacula*	Ranomafana Region, 3.5 km SW ad Vorondolo	9.3.2020		1180	
ISEA PAS	DL_05-424	1	F	*Melanonaclia*	*trimacula*	Ranomafana, Sahamahalaotra	5.12.2004		1124	
ISEA PAS		1	F	*Melanonaclia*	*trimacula*	Ranomafana, ValBio	8-9.4.2018	H. Staude	896	
ISEA PAS	DL_14Z-002	1	F	*Melanonaclia*	*trimacula*	Saha Forest Camp	22.10.2014			

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
ISEA PAS	DL_1796	1	M	*Melanonaclia*	*trimacula*	Vohiparara	20.2.1995		1150	
Joel Minet MNHN	P9223085	1	F	*Melanonaclia*	*trimacula*	Madagascar Est, Ifanadiana, Ambodikimba	17.4.1966	P. et J. Minet		
Joel Minet MNHN	P9223086	1	F	*Melanonaclia*	*trimacula*	Madagascar Est, Ifanadiana, Ambodikimba	25.3.1967	P. et J. Minet		
MNHN	EL65169	1	F	*Melanonaclia*	*trimacula*	Madagascar Centre, dct. Ambohimahasoa, foret Tsarafidy	12.1959 - 1.1960	P. Griveaud	1450	
MNHN	, EL82800, EL82801, EL82806, EL82804, EL82803, EL82802, EL82805, EL82797, EL82798, EL82793, EL82794, EL82792, EL82791, EL82820, EL82822	15	F	*Melanonaclia*	*trimacula*	Madagascar Centre, Pays Betsileo, route du Sud, km 292	14-15.2.1974	P. Viette, A. Peyrieras	1700	
MNHN	, EL82790, EL82781, EL82816, EL82813, EL82821, EL82818, EL82819, EL82817, EL82815, EL82814, EL74859	11	M	*Melanonaclia*	*trimacula*	Madagascar Centre, Pays Betsileo, route du Sud, km 292	14.2.1974 - 15.2.1974	P. Viette, A. Peyrieras	1700	
MNHN	EL82808	1	F	*Melanonaclia*	*trimacula*	Madagascar Centre, route d' Ambositra a Ambohimanga du Sud, km 39	6.11.1963	P. Viette		

Coll.	**Specimen code**	**N**	**S**	**Genus**	**Species**	**Locality**	**Collecting date (d/m/yyyy)**	**Collector**	**Altitude m a.s.l.**	**Remarks**
MNHN	EL82789	1	M	*Melanonaclia*	*trimacula*	Madagascar Centre, s/préf. Ambositra, P.K. 192, 150-route Fianarantsoa, Ambatofitorahama	12-13.5.1973	A. Peyrieras, A. Rakotoarisolo	1300(1800?)	
MNHN	EL82785	1	M	*Melanonaclia*	*trimacula*	Madagascar E., Fort-Carnot		R. Decary		
MNHN	EL82795	1	F	*Melanonaclia*	*trimacula*	Madagascar Est, N.O. de Fort-Dauphin, massif d' Andohahelo, foret d' Andranomangara, R.N.I. no 11	20-25.1.1974	A. Peyrieras	1750	
MNHN	EL82812	1	F	*Melanonaclia*	*trimacula*	Madagascar Nord, Montagne d'Ambre, Les Roussettes	3.11.1958	P. Viette		
MNHN	EL82786	1	M	*Melanonaclia*	*trimacula*	Madagascar Nord, Montagne d'Ambre, Les Roussettes	3.11.1958	P. Viette	1000	
MNHN	EL82784	1	M	*Melanonaclia*	*trimacula*	Madagascar, Ikongo	1902(?)	G. Grandidier		
MNHN	EL82799, EL82810, EL82807, EL82809	4	F	*Melanonaclia*	*trimacula*	Madagascar-Centre, dct. Manjakandriana, La Mandraka	2.1961	P. Griveaud		
MNHN	, EL82788, EL82787, EL82783, EL82782, EL82780, EL82779	6	M	*Melanonaclia*	*trimacula*	Madagascar-Centre, dct. Manjakandriana, La Mandraka	2.1961	P. Griveaud		
MNHN	EL82811	1	F	*Melanonaclia*	*trimacula*	M'car Centre, La Mandraka	16.11.1968	Turlin		
MNHN	EL82796	1	F	*Melanonaclia*	*trimacula*	M'car Sud, Tulear, Rte de Sarondrana	4.1971	P. Brondel		
NHMUK	DL1794	1	F	*Melanonaclia*	*trimacula*	Ranomafana PN, Vohiparara MBG	19.2.1995		1150	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
NHMUK	NHMUK015109732	1	F	*Melanonaclia*	*trimacula*	Ranomafana PN, Park Vohiparara at broken bridge	4-12.2.2002	D.C. Lees	1110	MA-02-09A-15, malaise trap
NHMUK		3	F	*Melanonaclia*	*trimacula*	Sud de Madagascar	4.1922(?)	Lamberton		
NHMUK		1	M	*Melanonaclia*	*trimacula*	Sud de Madagascar	4.1922(?)	Lamberton (?)		
NHMUK	NHMUK015109730	1	F	*Melanonaclia*	*trimacula*	Madagascar Est, Mantadia, Mahanara River	15.3.1993 -	D.C. Lees	1100	
NHMUK	NHMUK015109731	1	F	*Melanonaclia*	*trimacula*	Madagascar SE, Ranomafana PN, Sahamalaotra	7.12.2004 -	D.C. Lees	1104-1204	
NHMUK		2	F	*Melanonaclia*	*trimacula*	Madagascar				
NHMUK		1	M	*Melanonaclia*	*trimacula*	Madagascar	-			
NHMUK		3	F	*Melanonaclia*	*trimacula*	Madagascar, Fianarantsoa	2e Semestre 1892	Perrot Freres		
NHMUK		1	M	*Melanonaclia*	*trimacula*	Madagascar, Fianarantsoa	2e Semestre 1892	Perrot Freres		
NHMUK		1	F	*Melanonaclia*	*trimacula*	Madagascar, Fianarantsoa	1922(?)	Lamberton(?)		
NHMUK		5	F	*Melanonaclia*	*trimacula*	Madagascar, S.-E. de Fianarantsoa, Mahasoabe	1923(?)	Lamberton(?)		
NHMUK		1	M	*Melanonaclia*	*trimacula*	Madagascar, S.-E. de Fianarantsoa, Mahasoabe	1923(?)	Lamberton(?)		
NHMUK		3	F	*Melanonaclia*	*trimacula*	Madagascar, Tamatave et forets d'Alahakato	1er Semestre 1888	Edouard Perrot		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
NHMUK		10	F	*Melanonaclia*	*trimacula*	Madagascar, Tananarive				
NHMUK		8	M	*Melanonaclia*	*trimacula*	Madagascar, Tananarive				
PZBT		1	F	*Melanonaclia*	*trimacula*					
PZBT		1	F	*Melanonaclia*	*trimacula*	Beparasy	5.1969	Dujardin, Delacour C.		
PZBT		1	F	*Melanonaclia*	*trimacula*	R. Anosibe	6(?).1966	Dujardin, Delacour C.		
PZBT		1	F	*Melanonaclia*	*trimacula*	Madagascar Centre, dct. Ambohimahasoa, foret Tsarafidy	1.1961	P. Griveaud	1450	
PZBT		1	M	*Melanonaclia*	*trimacula*	Madagascar Centre, dct. Ambohimahasoa, foret Tsarafidy	1.1961	P. Griveaud	1450	
PZBT		3	F	*Melanonaclia*	*trimacula*	Madagascar Centre, dct. Manjakandriana, La Mandraka	2.1961	P. Griveaud		
PZBT		10	M	*Melanonaclia*	*trimacula*	Madagascar Centre, dct. Manjakandriana, La Mandraka	2.1961	P. Griveaud		
PZBT		1	F	*Melanonaclia*	*trimacula*	Madagascar Centre, La Mandraka	15.2.1970	Turlin		
PZBT		1	F	*Melanonaclia*	*trimacula*	Madagascar Centre, Manjakandriana, La Mandraka	4.1972	P. Brondel		
PZBT		1	F	*Melanonaclia*	*trimacula*	Madagascar Centre, Tananarive, Parc Tsimbazaza	22.5.1973	A. Rakotoarisolo		
MNHN	EL65172, holotype	1	F	*Melanonaclia*	*dujardini*	Route Beparasy	4.1968	Collection Dujardin-Delacour		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL82777	1	M	*Melanonaclia*	*dujardini*	Marovato(?), Rogez	2(?).1941(/1943 ?)	Madie(?)	700	
PZBT		2	F	*Melanonaclia*	*dujardini*	Route Beparasy	4.1968	Collection Dujardin-Delacour		
PZBT		1	F	*Melanonaclia*	*dujardini*	R. Beparasy	6.1968	Collection Dujardin-Delacour		
PZBT		1	M	*Melanonaclia*	*dujardini*	Beparasy	5.1969	Dujardin, Delacour C.		
ISEA PAS	MAD_018, holotype	1	F	*Melanonaclia*	*ranomafana* sp. nov.	Ranomafana National Park, ValBio Centre	8.4.2018	H.S. Staude	896	
NHMUK	DL1769	1	F	*Melanonaclia*	*ranomafana* sp. nov.	Ranomafana National Park, Sahamalaotra	6.12.2004	D.C. Lees	991-991	
ISEA PAS	MAD_019	1	F	*Melanonaclia*	*ranomafana* sp. nov.	Ranomafana National Park, ValBio Centre	8.4.2018	H.S. Staude	896	
MNHN	EL65137, holotype	1	F	*Mortinaclia*	*perplexa*	Madagascar Est, Beondroka Marojejy	4.1960	P. Soga	1200	
ISEA PAS	DL_2985	1	M	*Mortinaclia*	*perplexa*	Masoala, R. Ambery	21.2.1993	D.C. Lees	10	
ISEA PAS	MAD_286	1	M	*Mortinaclia*	*perplexa*	Sava region, Andrakata, direction Andapa	23.10.2017	D.C. Lees	557	
MNHN	EL74948, EL74949	2	F	*Mortinaclia*	*perplexa*	Madagascar Est, 42 km N. de Sabava, foret d'Analabe	15-20.11.1958	P. Griveaud, J. Vadon et P. Viette	50	
MNHN	EL74947	1	M	*Mortinaclia*	*perplexa*	Madagascar Est, 42 km N. de Sabava, foret d'Analabe	15-20.11.1958	P. Griveaud, J. Vadon et P. Viette	50	

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
MNHN	EL74610, EL74609	2	F	*Mortinaclia*	*perplexa*	Madagascar Est, Rte Sambava - Andapa, env. alt. Maroambihy, Belalono	25.11.1967	A. Peyrieras		EL74610: P.G. 577; "Disseque pour verification de l'armure ♀"
MNHN	EL74608	1	M	*Mortinaclia*	*perplexa*	Madagascar Est, Rte Sambava - Andapa, env. alt. Maroambihy, Belalono	25.11.1967	A. Peyrieras		
NHMUK	DL1770	1	F	*Mortinaclia*	*perplexa*	Montagne d'Ambre	17.11.2004	D.C. Lees	812-812	
NHMUK	NHMUK015109803	1	M	*Mortinaclia*	*perplexa*	Masoala, Antanandava, Antafononana River (survey site W7L2)	17.1.1994 -	D.C. Lees	20-60	
PZBT		1	M	*Mortinaclia*	*perplexa*	Madagascar Est, Analabe 42 kn. Nord, Sambava	15-20.11.1968	Griveaud Viette		
PZBT		6	F	*Mortinaclia*	*perplexa*	Madagascar Est, Foret Analalava, Vohemar	10-14.11.1968	Griveaud Viette		
PZBT		4	F	*Mortinaclia*	*perplexa*	Madagascar Est, Rte Sambava Andapa Belolona, env. Alt. Maroambihy	25.11.1967	Peyrieras		
PZBT		3	M	*Mortinaclia*	*perplexa*	Madagascar Est, Rte Sambava Andapa Belolona, env. Alt. Maroambihy	25.11.1967	Peyrieras		

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
iNaturalist	32362435	1		*Thyrosticta*	*sylvicolens*	Madagascar, Fianarantsoa, Ranomafana PN	7.8.2019			
iNaturalist	9677581	1		*Thyrosticta*	*sylvicolens*	Madagascar, Toamasina, Alaotra-Mangoro, Analamazoatra Reserve	29.1.2018			
iNaturalist	24993608	1		*Thyrosticta*	*sylvicolens*	Madagascar, Toamasina, Alaotra-Mangoro, Mantadia	20.2.2010			
iNaturalist	202802183	1		*Thyrosticta*	*sylvicolens*	Madagascar, Toamasina, Alaotra-Mangoro, Mantadia	5.3.2024			
iNaturalist	129840828	1		*Thyrosticta*	*sylvicolens*	Madagascar, Fianarantsoa, Ifanadiana	2.9.2017			
iNaturalist	171368012	1		*Kowalskinaclia*	*dilata*	Madagascar, Antananarivo, Analamanga, Ankazobe, Ambohitantely RS	4.7.2023			
iNaturalist	159152612	1		*Kowalskinaclia*	*dilata*	Madagascar, Antananarivo, Analamanga, Ankazobe, Ambohitantely RS	28.4.2023			
iNaturalist	159147024	1		*Kowalskinaclia*	*dilata*	Madagascar, Antananarivo, Analamanga, Ankazobe, Ambohitantely RS	28.4.2023			
iNaturalist	159145611	1		*Kowalskinaclia*	*dilata*	Madagascar, Antananarivo, Analamanga, Ankazobe, Ambohitantely RS	28.4.2023			
iNaturalist	159123489	1		*Kowalskinaclia*	*dilata*	Madagascar, Antananarivo, Analamanga, Ankazobe, Ambohitantely RS				

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
iNaturalist	152128603	1		*Kowalskinaclia*	*dilata*	Madagascar, Antananarivo, Analamanga, Ankazobe, Ambohitantely RS	18.3.2023			
iNaturalist	152117354	1		*Kowalskinaclia*	*dilata*	Madagascar, Antananarivo, Analamanga, Ankazobe, Ambohitantely RS	18.3.2023			
iNaturalist	149139074	1		*Kowalskinaclia*	*dilata*	Madagascar, Antananarivo, Analamanga, Ankazobe, Ambohitantely RS	15.2.2023			
iNaturalist	148046379	1		*Kowalskinaclia*	*dilata*	Madagascar, Antananarivo, Analamanga, Ankazobe, Ambohitantely RS	3.2.2023			
iNaturalist	148046378	1		*Kowalskinaclia*	*dilata*	Madagascar, Antananarivo, Analamanga, Ankazobe, Ambohitantely RS	3.2.2023			
iNaturalist	220220276	1		*Kowalskinaclia*	*vieui*	Madagascar, Antananarivo, Analamanga, Anjozorobe	2.6.2024			
iNaturalist	149281300	1		*Kowalskinaclia*	*cowani*	Madagascar, Toamasina, Alaotra-Mangoro, Moramanga Dst	29.1.2023			
iNaturalist	163698959	1		*Mauricenaclia*	*minuta*	Madagascar, Toamasina, Alaotra-Mangoro, Moramanga Dst	27.4.2023			
iNaturalist	146775327	1		*Mauricenaclia*	*minuta*	Madagascar, Fianarantsoa, Vatovavy Fitovinany	15.1.2023			
iNaturalist	139559024	1		*Mauricenaclia*	*minuta*	Madagascar, Toamasina, Alaotra-Mangoro, Ihofa	18.6.2021			

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
iNaturalist	138368656	1		*Mauricenaclia*	*minuta*	Madagascar, Toliary, Menabe, Mahabo	5.9.2022			
iNaturalist	138303546	1		*Mauricenaclia*	*minuta*	Madagascar, Toamasina, Alaotra-Mangoro, Ihofa	16.6.2021			
iNaturalist	101015162	1		*Mauricenaclia*	*minuta*	Madagascar, Toamasina, Alaotra-Mangoro, Ihofa	18.6.2021			
iNaturalist	81830029	1		*Mauricenaclia*	*minuta*	Madagascar, Toamasina, Alaotra-Mangoro, Ambany tanana	16.6.2016			
iNaturalist	40519269	1		*Mauricenaclia*	*minuta*	Madagascar, Mahajaga, Melaky, Tsingy de Bemaraha	22.8.2017			
iNaturalist	19363728	1		*Mauricenaclia*	*minuta*	Madagascar, Toamasina, Analanjirofo, Rainforests of the Atsinanana World Heritage Site	15.9.2018			
iNaturalist	9819763	1		*Mauricenaclia*	*minuta*	Madagascar, Fianarantsoa, Vatovavy Fitovinany	1.2.2018			
iNaturalist	225323159	1		*Mauricenaclia*	*minuta*	Madagascar, Fianarantsoa, Vatovavy Fitovinany	26.6.2024			
iNaturalist	194681214	1		*Melanonaclia*	*trimacula*	Madagascar, Fianarantsoa, Haute matsiatra, Lalangina	29.11.2023			
iNaturalist	104652670	1		*Melanonaclia*	*trimacula*	Madagascar, Toamasina, Alaotra-Mangoro, Perinet	26.12.2021			
iNaturalist	9173528	1		*Melanonaclia*	*trimacula*	Madagascar, Fianarantsoa, Haute matsiatra	8.12.2017			

Coll.	Specimen code	N	S	Genus	Species	Locality	Collecting date (d/m/yyyy)	Collector	Altitude m a.s.l.	Remarks
iNaturalist	5047833	1		*Melanonaclia*	*trimacula*	Madagascar, Fianarantsoa, Vatovavy Fitovinany	18.11.2016			
iNaturalist	38824347 / 38824346 / 38824345	1		*Mortinaclia*	*perplexa*	Madagascar, Antsiranana, Sava, Makirovana	4.5.2010			

Table S2. List of sequences used in molecular analyses, with GenBank accession numbers. The sequences which have not obtained accession numbers yet are marked with “X”, N of bases – sum of base pairs (sequences lengths) obtained for each sample.

Code	Genus	Species	CAD	COI-begin	COI-end	EF1a-begin	EF1a-center	EF1a-end	GAPDH	IDH	MDH	RpS5	Wgl400	N of bases
RZ398	*Cyana*	sp	JN401073	JN401285	JN401167	JN401400	JN401511	JN401511	JN401610	JN401712	JN401816	JN401876	JN400967	6401
RZ399	*Garudinia*	*simulana*	JN401071	JN401283	JN401165	JN401398	JN401509	JN401509	JN401609	JN401710	JN401814	JN401905	JN400965	6401
RZ30	*Creatonotos*	*transiens*	HQ006991	HQ006198	HQ006902	HQ006294	HQ006387	HQ006387	X	HQ006537	HQ006619	HQ006711	HQ006806	6401
MZ018	*Epidesma*	*ursula*	KX360779	KX360818	KX360818	KX360876	KX360876	KX360876	KX360917	KX360944	KX360986	KX361025	KX361077	6401
ISEZ-DNA_522	*Kowalskinaclia*	*cowani*	X	X	X	X	X	X	X	X		X	X	5994
RZ404	*Amerila*	*astreus*	X	JN401288	JN401170	JN401403	JN401514	JN401514	JN401612	JN401715		JN401910		5594
LN016	*Nacliodes*	*microsippia*	MK158595	MK158563	MK158563	MK158641	MK158641	MK158641	MK158686		MK158732	MK158778	MK158846	5679
DL_02-109	*Julienaclia*	*pauliani*	X	X	X	X	X	X	X			X	X	5272
MM00154	*Dysauxes*	*famula*	GU828120	GU828619	GU828417	GU828954		GU829244		GU830008	GU830328		GU829514	4914
MAD_241	*Pseudonaclia*	*puella*	X	MZ255003	X	MZ270190			X			X	MZ270509	3765
LN017	*Amata*	*leucerythra*	MK158596	MK158509	MK158509	MK158601						MK158779	MK158847	3882
CLV_7	*Skippernaclia*	*lacrimata*	X	X	X	X						X	X	3882
MA_16-6	*Julienaclia*	*pauliani*	X	X	X	X						X	X	3882
MAD_286	*Mortinaclia*	*perplexa*	X	X	X	X						X	X	3882
RZ8	*Amata*	*phegea*	X	HQ006238	HQ006941		HQ006425	HQ006425	HQ006492	X	HQ006656	HQ006749	HQ006846	5860
LN008	*Balacra*	*rubrostriata*	MK158593	MK158532	MK158532		MK158619	MK158619	MK158680	MK158715		MK158772	MK158840	5453
CLV_3	*Skippernaclia*	*lacrimata*	X	X	X							X	X	3341
LN012	*Meganaclia*	*sippia*	MK158594	MK158554		MK158635	MK158635	MK158635	MK158684	MK158718		MK158776	MK158844	5188
LN015	*Amerila*	*brunnea*		KX300223	KX300223	KX300346	KX300346	KX300346	KX300609	KX300688	KX300779	KX300895	KX301005	5416
MAD_018	*Melanonaclia*	*ranomafana* sp. nov.		X	X	X	X	X	X	X	X	X	X	5539
MAD_263	*Mauricenaclia*	*octopunctata*		X	X	X	X	X	X	X	X	X	X	5539
DL_SF11	*Melanonaclia*	*luctuosa*		X	X	X	X	X	X	X	X		X	4936

Code	Genus	Species	CAD	COI-begin	COI-end	EF1a-begin	EF1a-center	EF1a-end	GAPDH	IDH	MDH	RpS5	Wgl400	N of bases
LN011	*Anapisa*	*monotica*		MK158519	MK158519	MK158608	MK158608	MK158608	MK158683	MK158717		MK158775	MK158843	5009
DL_06-291	*Riconaclia*	*bimacula*		X	X	X	X	X	X	X		X	X	5132
DL_2966	*Mauricenaclia*	*octopunctata*		X	X	X	X	X	X	X		X	X	5132
DL_2973	*Privatenaclia*	*seguyi*		X	X	X	X	X	X	X		X	X	5132
ISEZ-DNA_556	*Kowalskinaclia*	*cowani* (=*incerta*)		X	X	X	X	X	X	X		X	X	5132
MAD_218	*Riconaclia*	*bimacula*		X	X	X	X	X	X	X		X	X	5132
MAD_084	*Melanonaclia*	*toulgoeti*		X	X	X	X	X	X	X		X	X	5132
MAD_144	*Kowalskinaclia*	*dilata*		MW817639	X	X	X	X	X	X			X	4529
DL1790	*Fletcherinia*	*decaryi*		MK158546	MK158546	MK158629	MK158629	MK158629	MK158668		MK158726	MK158751	MK158817	4817
LN056	*Pseudothyretes*	*obscurus*		MK158570	MK158570	MK158648	MK158648	MK158648	MK158701		MK158741	MK158802	MK158875	4694
LN050	*Thyretes*	*negus*		MK158580	MK158580	MK158654	MK158654	MK158654	MK158698		MK158739	MK158798	MK158870	4817
DL1802	*Mauricenaclia*	*minuta*		MK158582	MK158582	MK158655	MK158655	MK158655	MK158672		MK158727	MK158758	MK158823	4817
DL1769	*Melanonaclia*	*ranomafana* sp. nov.		MK158585	MK158585	MK158658	MK158658	MK158658	MK158665		MK158725	MK158748	MK158814	4694
MAD_186	*Dysauxes*	*florida*		MZ255002	X	X	X	X	X		X	X	MZ270508	4817
DL_05-857	*Mauricenaclia*	*rothschildi*		X	X	X	X	X	X		X	X	X	4817
DL1799	*Dubianaclia*	*amplificata*		MK158539	MK158539	MK158624	MK158624	MK158624	MK158669			MK158755	MK158820	4287
DL1804	*Maculonaclia*	*leopardina*		MK158551	MK158551	MK158632	MK158632	MK158632	MK158673			MK158759	MK158824	4410
DL1800	*Maculonaclia*	*leopardina*		MK158552	MK158552	MK158633	MK158633	MK158633	MK158670			MK158756	MK158821	4287
DL1770	*Mortinaclia*	*perplexa*		MK158576	MK158576	MK158652	MK158652	MK158652	MK158666			MK158749	MK158815	4410
DL1788	*Julienaclia*	*pauliani*		MK158583	MK158583	MK158656	MK158656	MK158656	MK158667			MK158750	MK158816	4287
DL1801	*Melanonaclia*	*toulgoeti*		MK158584	MK158584	MK158657	MK158657	MK158657	MK158671			MK158757	MK158822	4287
DL1810	*Dubianaclia*	*amplificata*		MK158590	MK158590	MK158664	MK158664	MK158664	MK158674			MK158761	MK158826	4410
MAD_180	*Dysauxes*	*florida*		MZ255000	X	X	X	X	X			X	MZ270506	4410

Code	Genus	Species	CAD	COI-begin	COI-end	EF1a-begin	EF1a-center	EF1a-end	GAPDH	IDH	MDH	RpS5	Wgl400	N of bases
MAD_182	*Dysauxes*	*florida*		MZ255001	X	X	X	X	X			X	MZ270507	4410
DL_2968	*Privatenaclia*	*seguyi*		X	X	X	X	X	X			X	X	4410
DL_2974	*Privatenaclia*	*seguyi*		X	X	X	X	X	X			X	X	4410
ISEZ-DNA_540	*Melanonaclia*	*trimacula*		X	X	X	X	X	X			X	X	4410
ISEZ-DNA_543	*Melanonaclia*	*trimacula*		X	X	X	X	X	X			X	X	4410
ISEZ-DNA_546	*Melanonaclia*	*trimacula*		X	X	X	X	X	X			X	X	4410
ISEZ-DNA_558	*Kowalskinaclia*	*cowani*		X	X	X	X	X	X			X	X	4410
MAD_020	*Mauricenaclia*	*minuta*		X	X	X	X	X	X			X	X	4410
MAD_073	*Riconaclia*	*bimacula*		X	X	X	X	X	X			X	X	4410
DL_SG30	*Melanonaclia*	*nigra*		X	X	X	X	X	X			X	X	4410
DL_02-325	*Mauricenaclia*	*minuta*		X	X	X	X	X	X			X		4010
MAD_110	*Skippernaclia*	*ankaratra*		X	X	X	X	X	X				X	3807
DL1862	*Dubianaclia*	cf. *eleonora*		MK158538	MK158538	MK158623	MK158623	MK158623				MK158766	MK158833	3719
DL1816	*Tritonaclia*	*melania*		MK158587	MK158587	MK158661	MK158661	MK158661				MK158763	MK158828	3719
DL_06-975	*Melanonaclia*	*trimacula*		X	X	X	X	X				X	X	3719
MAD_081	*Melanonaclia*	*trimacula*		X	X	X	X	X				X	X	3719
DL_06-406	*Privatenaclia*	*seguyi*		X	X	X		X	X	X			X	4336
ISEZ-DNA_574	*Dysauxes*	*parvigutta*		MZ254999	X	MZ270189			X	X	X	X	MZ270505	4840
MAD_212	*Mauricenaclia*	*rothschildi*		X	X	X			X	X	X		X	4237
DL1863	*Tritonaclia*	*melania*		MK158588	MK158588	MK158662			MK158677		MK158729	MK158767	MK158834	4118
DL_05-424	*Melanonaclia*	*trimacula*		X	X	X			X			X	X	3711
DL_14Z-002	*Melanonaclia*	*trimacula*		X	X	X			X			X	X	3711
ISEZ-DNA_541	*Melanonaclia*	*trimacula*		X	X	X			X			X	X	3711
ISEZ-DNA_544	*Melanonaclia*	*trimacula*		X	X	X			X			X	X	3711

Code	Genus	Species	CAD	COI-begin	COI-end	EF1a-begin	EF1a-center	EF1a-end	GAPDH	IDH	MDH	RpS5	Wgl400	N of bases
ISEZ-DNA_545	*Melanonaclia*	*trimacula*		X	X	X			X			X	X	3711
MAD_019	*Melanonaclia*	*ranomafana* sp. nov.		X	X	X			X			X	X	3711
ISEZ-DNA_518	*Riconaclia*	*bimacula*		X	X	X			X				X	3108
ISEZ-DNA_542	*Melanonaclia*	*trimacula*		X	X	X			X				X	3108
DL1792	*Mauricenaclia*	*peyrierasi*		MK158547	MK158547	MK158630						MK158752	MK158818	3020
DL1811	*Mauricenaclia*	*bruneata*		MK158555	MK158555	MK158636						MK158762	MK158827	3020
DL_14R-218	*Kowalskinaclia*	*vieui*		X	X	X						X	X	3020
ISEZ-DNA_521	*Kowalskinaclia*	*cowani*		X	X	X						X	X	3020
MA_16-9	*Mauricenaclia*	*octopunctata*		X	X	X						X	X	3020
MAD_131	*Kowalskinaclia*	*vieui*		X	X	X						X	X	3020
MAD_287	*Mauricenaclia*	*minuta*		X	X	X						X	X	3020
MAD_288	*Mauricenaclia*	*minuta*		X	X	X						X	X	3020
DL1852	*Micronaclia*	sp1_cf_*imaitsa*		MK158562	MK158562	MK158640							MK158831	2417
MAD_075	*Kowalskinaclia*	*cowani*		X	X	X							X	2417
MAD_108	*Skippernaclia*	*ankaratra*		X	X	X							X	2417
ISEZ-DNA_519	*Melanonaclia*	*toulgoeti*		X	X	X								2017
DL1817	*Tritonaclia*	sp13		MK158589	MK158589		MK158663	MK158663	MK158675		MK158728	MK158764	MK158829	4276
MAD_153	*Kowalskinaclia*	*dilata*		MW817646	X		X	X				X	X	3178
MAD_282	*Mauricenaclia*	*minuta*		X	X		X	X				X	X	3178
DL_2985	*Mortinaclia*	*perplexa*		X	X			X				X	X	2985
DL1860	*Toulgoetinaclia*	*obliquipuncta*		MK158548	MK158548				MK158676			MK158765	MK158832	3047
DL_02-92	*Julienaclia*	*pauliani*		X	X				X			X	X	3170
LN068	*Dysauxes*	*famula*		MK158542	MK158542				MK158708				MK158885	2295
LN080	*Thyrogonia*	*efulensis*		MK158581	MK158581							MK158812	MK158891	2479

Code	Genus	Species	CAD	COI-begin	COI-end	EF1a-begin	EF1a-center	EF1a-end	GAPDH	IDH	MDH	RpS5	Wgl400	N of bases
DL_02-26	*Mauricenaclia*	*octopunctata*		X	X							X	X	2479
MAD_025	*Kowalskinaclia*	*cowani*		X	X							X	X	2479
MAD_029	*Kowalskinaclia*	*cowani*		X	X								X	1876
DL_SC3	*Melanonaclia*	*luctuosa*		X	X								X	1876
MAD_129	*Melanonaclia*	*toulgoeti*		X	X								X	1876
MAD_005	*Kowalskinaclia*	*vieui*		X	X									1476
MAD_126	*Melanonaclia*	*trimacula*		X	X									1476
MAD_157	*Kowalskinaclia*	*dilata*		MW817650	X									1476
MAD_211	*Melanonaclia*	*trimacula*		X	X									1476
ISEZ-DNA_538	*Melanonaclia*	*toulgoeti*		X	X									1476
MAD_009	*Melanonaclia*	*toulgoeti*		X	X									1476
ISEZ-DNA_539	*Melanonaclia*	*trimacula*		X		X	X	X	X			X		3204
DL_06-040	*Riconaclia*	*bimacula*		X		X			X	X		X	X	3627
DL1795	*Thyrosticta*	*sylvicolens*		MK158540		MK158625						MK158754	MK158819	2214
MAD_142	*Kowalskinaclia*	*dilata*		MW817637		X						X		1814
MAD_273	*Kowalskinaclia*	*cowani* (=*incerta*)		X									X	1070
DL_06-320	*Privatenaclia*	*seguyi*		X										670
DL_06-321	*Privatenaclia*	*seguyi*		X										670
DL_06-324	*Privatenaclia*	*seguyi*		X										670
DL_06-327	*Privatenaclia*	*seguyi*		X										670
DL_06-347	*Privatenaclia*	*seguyi*		X										670
MAD_008	*Privatenaclia*	*ratovosoni*		X										670
MAD_100	*Kowalskinaclia*	*cowani*		X										670
MAD_111	*Skippernaclia*	*ankaratra*		X										670
MAD_130	*Melanonaclia*	*trimacula*		X										670
MAD_145	*Kowalskinaclia*	*dilata*		MW817640										670

Code	Genus	Species	CAD	COI-begin	COI-end	EF1a-begin	EF1a-center	EF1a-end	GAPDH	IDH	MDH	RpS5	Wgl400	N of bases
MAD_146	*Kowalskinaclia*	*dilata*		MW817641										670
MAD_147	*Kowalskinaclia*	*dilata*		MW817642										670
MAD_169	*Skippernaclia*	*vestigii*		X										670
MAD_260	*Mauricenaclia*	*minuta*		X										670
MAD_272	*Mauricenaclia*	*octopunctata*		X										670
MAD_274	*Privatenaclia*	*triangulifera*		X										670
DL_2980	*Melanonaclia*	*luctuosa*		X										670
DL_SG29	*Melanonaclia*	*nigra*		X										670
MAD_074	*Melanonaclia*	*toulgoeti*		X										670
MAD_082	*Melanonaclia*	*toulgoeti*		X										670
MAD_085	*Melanonaclia*	*toulgoeti*		X										670
MAD_127	*Melanonaclia*	*toulgoeti*		X										670
MAD_128	*Melanonaclia*	*toulgoeti*		X										670
MAD_133	*Melanonaclia*	*toulgoeti*		X										670
MAD_134	*Melanonaclia*	*toulgoeti*		X										670

Table S3. List of all localities, where the species covered in the paper were recorded.

Locality	Latitude	Longitude	Remarks
50 km W of Mahonoro, Ambinanindrano	-20.0928	48.483	
Ambahibe	-18.7419	44.7134	
Ambalavao	-21.832	46.9363	
Ambanja, Beangona Ambevy = N of Beangona-Ambevy, Andranomafana	-14.05	48.7	
Ambatolampy, Ampolomita, E of Belanitra	-18.89	47.76	
Ambatondrazaka	-17.8351	48.4104	
Ambatondrazaka, Andranomandevy (Didy)	-18.1533	48.6157	
Ambodiazomamy, W of Voloina	-15.5667	49.5	Coordinates of Ambodiazomamy, after Moat et Smith (2007).
Ambodiriana, route de Lakato km 10	-19.0317	48.3389	Coordinates of Ambodiriana, after Moat et Smith (2007).
Ambodivoanio	-16.1805	49.6618	Coordinates of Ambodivoanio, after Viette (1991).
Ambohitsitondroin' Mahalavona, ridge, primary forest	-15.4394	49.959	
Ambositra P.K. 192, 150-route Fianarantsoa, Ambatofitorahama	-20.817	47.1827	
Ambovombe	-25.1752	46.0906	
Analabey, 42 km N Sambava = forêt d'Analabe	-14.0117	49.8489	
Analalava, Beraty	-14.0093	48.244	
Analalava, Manongarivo	-15.1833	47.8833	Coordinates of Manongarivo after Moat et Smith (2007). Not to be confused with Manongarivo Massif listed in Vitte (1991), nor Manongarivo S.R.
Analamazaotra, Feony-ala	-18.9472	48.4179	
Analamazoatra PN = Forêt d' Analamazoatra	-18.9333	48.42	
Analamerana Forest ("Cote Nord-Ouest")	-12.7801	49.4947	Approximate locality in the middle of Analamerana S.R., after Viette (1991).

Locality	Latitude	Longitude	Remarks
Andapa, Ambatoarano	-14.6491	49.6374	Uncertain locality, coordinates of Andapa.
Andapa, Anjanaharibe = Anjanaharibe, 50 km W Andapa	-14.7226	49.4716	
Andrangoloaka, forest E of Mantasoa Lake ("Lac de Mantasoa")	-19.0339	48.4368	
Andranohinaly	-23.2833	43.9833	
Andranomena S.R.	-20.1663	44.5261	
Andranotobaka, Ambatolampy	-19.3867	47.442	
Andringitra	-14.0785	48.3201	
Anjozorobe (8 km SE of), Vanjamanitra Forest ("Forêt de Vanjamanitra")	-18.4499	47.9189	Approximate locality 8 km SE of Anjozorobe, after Viette (1991).
Anjozorobe, Betatao, Analavory	-18.2102	47.8778	Uncertain locality, coordinates of Betatao, after Viette (1991) and Moat et Smith (2007).
Anjozorobe, Vanjamanitra	-18.475	47.95	
Ankafina-Tsarafidy = Tsarafidy = Forêt de Tsarafidy = Forêt Tsarafidy = forêt d'Ankafina	-21.2	47.25	
Ankarafantsika = Ankarafantsika, Bevazaha	-16.2335	47.15	
Ankarafantsika, Ampijoroa	-16.2299	46.4737	
Ankarafantsika, Ampijoroa Lake ("Lac d'Ampijoroa")	-16.3	46.817	
Ankarana PN, Ankarana Lodge	-12.9611	49.1494	
Ankasina, Route Lakato	-19.048	48.36	
Ankasoka, route de Lakato = route de Lakato km 15 = 15 km Ankasoka	-18.9476	48.2285	
Ankazoabo, Hera (most probably misspelled "Herea")	-22.2897	44.5109	Coordinates of Ankazoabo after Viette (1991).
Ankazobe, Ambohitantely S.R. = Tampoketsa = Tampoketsa d'Ambohitantely	-18.1969	47.2847	
Antampona	-15.9704	49.2199	
Antanadavahely, Antalaha	-14.9058	50.2791	
Antananarivo (="Tananarive")	-18.8493	47.5055	
Antananarivo, Analamanga, Anjozorobe	-18.4136	47.9411	Observation from iNaturalist.
Antananarivo, Analamanga, Ankazobe, Ambohitantely S.R.	-18.1956	47.2855	Observation from iNaturalist.

Locality	Latitude	Longitude	Remarks
Antananarivo, Tsimbazaza Parc	-18.9312	47.5264	
Antongil Bay, Antanambe	-16.4448	49.8469	
Antongil Bay, Maroantsetra, Hiaraka	-15.4343	49.8478	
Antsiranana = Diego Suarez = Isokitra near Diego Suarez	-12.3141	49.2932	
Antsiranana, Manongarivo S.R., Mt. Betampona	-14.047	48.29	
Antsiranana, Sava, Makirovana	-14.1775	49.9442	Observation from iNaturalist.
Beparasy = Route Beparasy	-19.1696	48.0252	
Brickaville	-18.8188	49.0643	
Brickaville, Piste d' Ambodimanga, Anivorano-Kely	-18.35	48.883	
Causses de Kelifaly, Kasijy Forest ("Forêt de Kasijy")	-17.0667	45.8833	
contreforts du Tsaratanana, Haut Sambirano vallée de la Besanetribe	-14.15	48.7833	
E of Lake Mantasoa, Ambohiboatavo Forest	-19.0113	47.9583	
Fanovana	-18.9309	48.5097	
Fenerive = Fenoarivo Atsinanana	-17.3857	49.4092	
Fianarantsoa	-21.4467	47.0727	
Fianarantsoa (SE of), Mahasoabe	-21.5944	47.2203	
Fianarantsoa Vatovavy Fitovinany	#ARG!	47.5077	Observation from iNaturalist.
Fianarantsoa Vatovavy, Fitovinany	-21.2608	47.451	Observation from iNaturalist.
Fianarantsoa, Haute matsiatra	-21.2402	47.3945	Observation from iNaturalist.
Fianarantsoa, Haute matsiatra Lalangina	-21.2402	47.3938	Observation from iNaturalist.
Fianarantsoa, Ranomafana PN	-21.2296	47.4018	Observation from iNaturalist.
Fianarantsoa, Vatovavy Fitovinany	-21.2615	47.4605	Observation from iNaturalist.
Fito = Sahaviavy-Fito = Ifito	-18.083	48.9	"Sahaviavy-Fito" in Moat et Smith (2007), "Ifito" in Google Maps
Ifanadiana, Ambodikimba	-21.2546	47.4412	
Ifasy, Ambilobe	-13.1987	49.0491	
Ikongo = Fort-Carnot	-21.8833	47.4333	
Imerimandrosa, Lake Aloatra	-17.4976	48.4494	

Locality	Latitude	Longitude	Remarks
Kalambatritra, Befarara	-23.417	46.43	
Kirindy Nord	-20.0589	44.668	
Lac Alaotra	-17.47	48.52	
Lac Alaotra, Befody	-17.3167	48.6833	
Lakato = Lakato Forest	-19.1833	48.45	
Lake Mantasoa, Barrage d'Andrangoloaka	-19.033	47.917	
Madiorano, Vondrozo Forest ("Forêt de Vondrozo")	-22.8182	47.324	
Maevatanana	-16.9523	46.8327	
Mahafaly Plateau, 11/12 km W of Ankalirano	-24.2141	44.1664	
Mahajaga, Melaky, Tsingy de Bemaraha	-18.92	44.7944	
Mahitsy Arongana, Nord Maroantsetra, near Itsikiory (="Sikory") River	-15.1907	49.5309	
Maitsoarongana, just above camp	-15.1891	49.5159	
Majunga Airport ("Terrain d'Aviation Majunga")	-15.6674	46.3492	
Makira	-15.4802	49.4614	
Makira, Anjanaharibe Mt.	-15.1823	49.6214	
Makira, Bivontro	-15.3984	49.4477	
Makira, Maitsoarongana	-15.188	49.4951	
Makira, Vohitaly	-15.4379	49.5344	
Mananara-Nord, Seranambe	-16.247	49.8391	
Mananjara	-18.75	47.3167	Coordinates of Mananjara after Moat et Smith (2007). Viette (1991) did not list this locality. There are two places named Mananjara listed in Moat et Smith (2007), the one located closer to Antananarivo seems more probable.
Mananjary	-21.2209	48.3483	
Mandraka Park (N of), path along river	-18.9	47.9	
Manjakandriana, La Mandraka = Mandraka	-18.9129	47.9296	
Mantadia PN (="Andasibe-Mantadia PN" or "Andasibe PN")	-18.936	48.4189	

Locality	Latitude	Longitude	Remarks
Mantadia PN Parc Mitsinjo	-18.9361	48.4111	
Mantadia PN, Belakato Trail	-18.8167	48.4333	
Mantadia PN, Eulopia Trail	-18.8	48.4833	
Mantadia PN, Feon'ny Ala Hotel	-18.8811	48.42	
Mantadia PN, Rianasu Circuit	-18.825	48.4347	
Mantadia PN, Vakona Lodge	-18.8894	48.4372	
Mantadia, Mahanara River	-18.82	48.45	
Maroambihy, Route Sambava Andapa Belolona	-14.488	49.8787	
Maroantsetra, Ambodivoangy	-15.2799	49.6202	There are other places named Manombo, this one matches the species distribution the most.
Maroantsetra, Marogavo = Ambodigavo, at the edge of Maroantsetra airport	-15.4367	49.6894	
Maroantsetra, Tampanambo	-17.2796	49.3987	
Maroantsetra, Varigohitra	-15.4581	49.6953	
Marojejy PN	-14.4387	49.7506	
Marojejy PN, 10 km NW Manantenina, tributary Manantenina River	-14.4333	49.7617	
Marojejy PN, 11 km NW Manantenina, source of Andranomifototra R.	-14.4467	49.735	
Marojejy PN, Ambatosoratra	-14.5218	49.6913	
Marojejy PN, Ambinanitelo	-14.46	49.85	
Marojejy PN, Andasy II - Camp 2 in Marojejy Massif = Marojejia Camp = Marojejya Camp	-14.4346	49.7609	
Marojejy PN, Andrakata	-14.6167	49.7167	
Marojejy PN, Antsiranana = camp 3 trap 8 = camp 3 trap 9	-14.4367	49.7434	
Marojejy PN, Beondroka	-14.45	49.8	
Marojejy PN, Camp 2	-14.4344	49.759	
Marojejy PN, Ankobahina	-14.5473	49.6092	Approximate coordinates, after Andasibe-Kobahina in Viette (1991), and Andasibe-Kobaina in Moat et Smith (2007).

Locality	Latitude	Longitude	Remarks
Maromizaha Reserve de Ressources Naturelles	-18.9833	48.4833	
Masoala PN, Ambatoavy, near Masioposa River = Be Dinta, survey site W9L1, ridge	-15.67	49.98	
Masoala PN, Ambery River	-15.373	50.43	
Masoala PN, Andranomaloto River, towards Ambohitsitoindroina Mahalevona	-15.432	49.946	
Masoala PN, Antanandava, Antafononana River (survey site W7L2)	-15.747	50.186	
Masoala PN, coastal path S of Andranobe River	-15.666	49.958	
Masoala PN, Manosona	-15.786	50.217	
Masoala PN, Ratsiaranana	-15.4632	50.4338	
Masoala, Ambavony River	-15.282	50.288	
Midongy du Sud PN = Midongy du S. = Midongy-Atsimo	-23.5904	47.015	Cooridnates of Midongy-Atsimo, after Moat et Smith (2007).
Midongy du Sud PN, Befotaka Forest ("Forêt de Befotaka")	-23.5943	47.022	
Montagne d'Ambre	-12.564	49.16	
Montagne d'Ambre PN, 3 km SE Joffreville	-12.5139	49.1839	
Montagne d'Ambre PN, Forêt d' Ambre	-12.4753	49.217	
Montagne d'Ambre PN, Les Roussettes	-12.525	49.1722	
Moramanga, Andasibe Headquater NAT, near Hotel Feon n'y Ala, SW of Forêt de Analmazaotra (Analamazaotra PN)	-18.9566	48.42	
Moramanga, Andasibe, Anevoka, Maromizaha PN ("Forêt pluviale de Maromizaha PN")	-18.9731	48.4608	
Moramanga, Ankasoka	-18.8373	48.4657	
Moramanga, Perinet = Perinet, Forêt de l'est = Mange = Sahamalato	-18.9278	48.4151	
Moramanga, Route d'Anosibe Sandrangato	-19.1	48.2333	
Morondava Region, E of Kirindy Ecolodge	-20.0742	44.6697	
Morondava Region, N of Kirindy Ecolodge	-20.0589	44.6572	

Locality	Latitude	Longitude	Remarks
Morondava, forest S of Befasy ("Forêt sud de Befasy")	-20.59	44.38	
Namoroka PN, Namoroka, Deparapangi	-16.4591	45.2929	
Namoroka PN, Tsingy Massif	-16.41	45.3053	
Nosy Boraha (= Île Sainte-Marie), Ambodena	-16.8183	49.963	
Nosy Boraha (= Île Sainte-Marie), Forêt de Kalalao	-16.917	49.8826	
Nosy-Be, Lokobe Forest ("Forêt de Lokobe") = Lokobe	-13.4103	48.3149	
Nosy-Be, Oceanographic Station ("Station Oceanographique")	-13.4	48.3	
NW of Manantenina, Anosyennes Mountains ("Chaines Anosyennes"), northern massif	-24.1134	47.108	Very approximate locality in Anosyennes Mountains, NW of Manantenina.
NW of Tolanaro, Andohahelo = Andohahela ("N.O. de Fort-Dauphin, massif d' Andohahelo forêt d' Andranomangara, R.N.I. no 11")	-24.6228	46.6931	Approximate locality slightly SW of Trafonaomby, after Viette (1991), and Moat et Smith (2007).
Pays Betsileo, Route du Sud, km 292 = Ankazomivady	-20.7667	47.1833	
Piste Mandritsara, Bealanana, W of Rantabe (misspelled as "Beahanana")	-15.7333	49.45	Coordinated after Moat et Smith (2007) and Viette (1991), therein as "Beanana", W of Rantabe.
Ranomafana	-21.2763	47.3255	
Ranomafana PN Radar Station	-21.2603	47.4703	
Ranomafana PN Sahamahalaotra	-21.2381	47.3949	
Ranomafana PN, Sahamalaotra	-21.262	47.4212	
Ranomafana PN, ValBio = ValBio Centre	-21.2528	47.4269	
Ranomafana region, 3.5 km SW Vorondolo	-21.2697	47.355	
Ranomafana, km 402	-21.1481	47.4801	
Ranomafana, Vohiparara = Vohiparara MBG = 7km NW Vohiparara	-21.233	47.386	
Rogez = Andekaleka	-18.8	48.6	
Route d'Ambositra a Ambohimanga du Sud, km 39	-20.5396	47.2458	
Route Nationale 6, 40 km N of Port-Bergé	-15.5707	47.6415	

Locality	Latitude	Longitude	Remarks
Route nationale 7, 64 km E of Tulear, forêt d'Andranovory = Andranovory	-23.1398	44.1446	Coordinates of Andranovory.
Route Sambava-Andapa, Belalono = Belalona	-14.8833	49.35	
Sadjoavato, Sahafary Forest ("Forêt de Sahafary")	-12.7659	49.2891	Approximate coordinates of a locality 53 km S in a straight line from Antsiranana = Diego Suarez, after Viette (1991).
Saha Forest Camp	-18.4101	47.9387	
Sakaraha, Lambomakandro	-22.911	44.5293	
Sakaraha, Zombitsy	-22.9	43.632	
Sava, Ambodiala, direction Antalaha	-14.413	50.089	
Sava, Andrakata, direction Andapa	-14.647	49.71	
Ste Marie de Madagascar = Nosy Boraha = Île Sainte-Marie	-16.898	49.9023	
Toamasina, Alaotra-Mangoro, Ambany tanana	-17.4356	48.5841	Observation from iNaturalist.
Toamasina, Alaotra-Mangoro, Ihofa	-18.7552	48.4109	Observation from iNaturalist.
Toamasina, Alaotra-Mangoro, Moramanga 1	-18.939	48.4062	Observation from iNaturalist.
Toamasina, Alaotra-Mangoro, Moramanga 2	-18.9638	48.59	Observation from iNaturalist.
Toamasina, Alaotra-Mangoro, Perinet	-18.9193	48.424	Observation from iNaturalist.
Toamasina, Analanjirofo, Rainforests of the Atsinanana World Heritage Site	-15.7282	49.9668	Observation from iNaturalist.
Tolanaro = Fort Dauphin = Fort Dauphin, Isaka Forest ("Forêt d'Isaka")	-25.0246	46.9632	
Toliara (= Tulear), Route de Sarondrana = Sarodrano, near Sarodrano Cave	-23.5168	43.7534	
Toliary, Menabe, Mahabo	-20.7472	45.5405	Observation from iNaturalist.
Tsaratanana massif (1)	-14.2034	48.9532	
Tsaratanana massif (2), descent	-14.1898	48.9452	
Tsaratanana massif, versant W of Andilambe	-14.0009	48.9869	
Tsingy de Bemaraha PN, Analamanitsy, eastern cliff	-18.7292	44.9591	

Locality	Latitude	Longitude	Remarks
Vohemar, Analalava Forest = 37 km S. de Vohémar, forêt d'Analalava	-13.6767	49.8603	
Vohemar, Route Milanoa, Bevitsika Forest	-13.5825	49.7852	Coordinates of Milanoa.
Vondrozo	-22.8108	47.33	
W of Mitanoka, Onibe Valley	-17.7705	48.8974	
Zahamena PN	-17.5131	48.7269	
Zahamena PN (="Reserve Naturelle III"), Ambatovositra, Andranomalaza	-17.6538	48.6192	Coordinates after Moat et Smith (2007), in OpenStreetMap as "Andranomalaza Sud".
Zahamena PN (="Reserve Naturelle III"), Andranomalaza, Ivelona Valley ("vallée d'Ivelona")	-17.65	48.617	
Zahamena PN, near cascade	-17.5411	48.7219	

SUPPLEMENTARY FIGURES

Figure S1. Phylogenetic tree of the taxa included in the study, based on Maximum Likelihood analysis in RAxML.

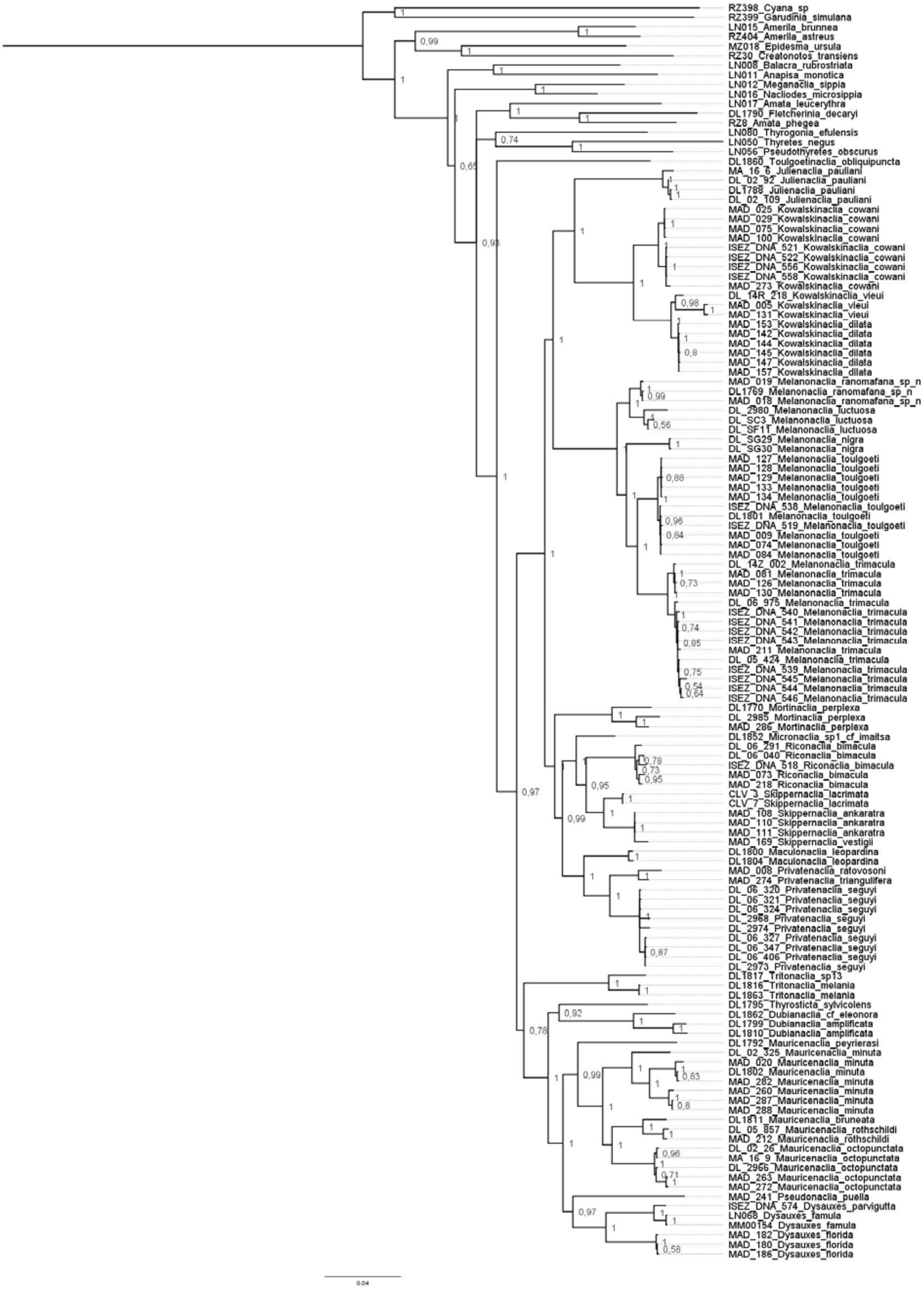


Figure S2. Phylogenetic tree of the taxa included in the study, based on Bayesian Inference analysis in MrBayes.

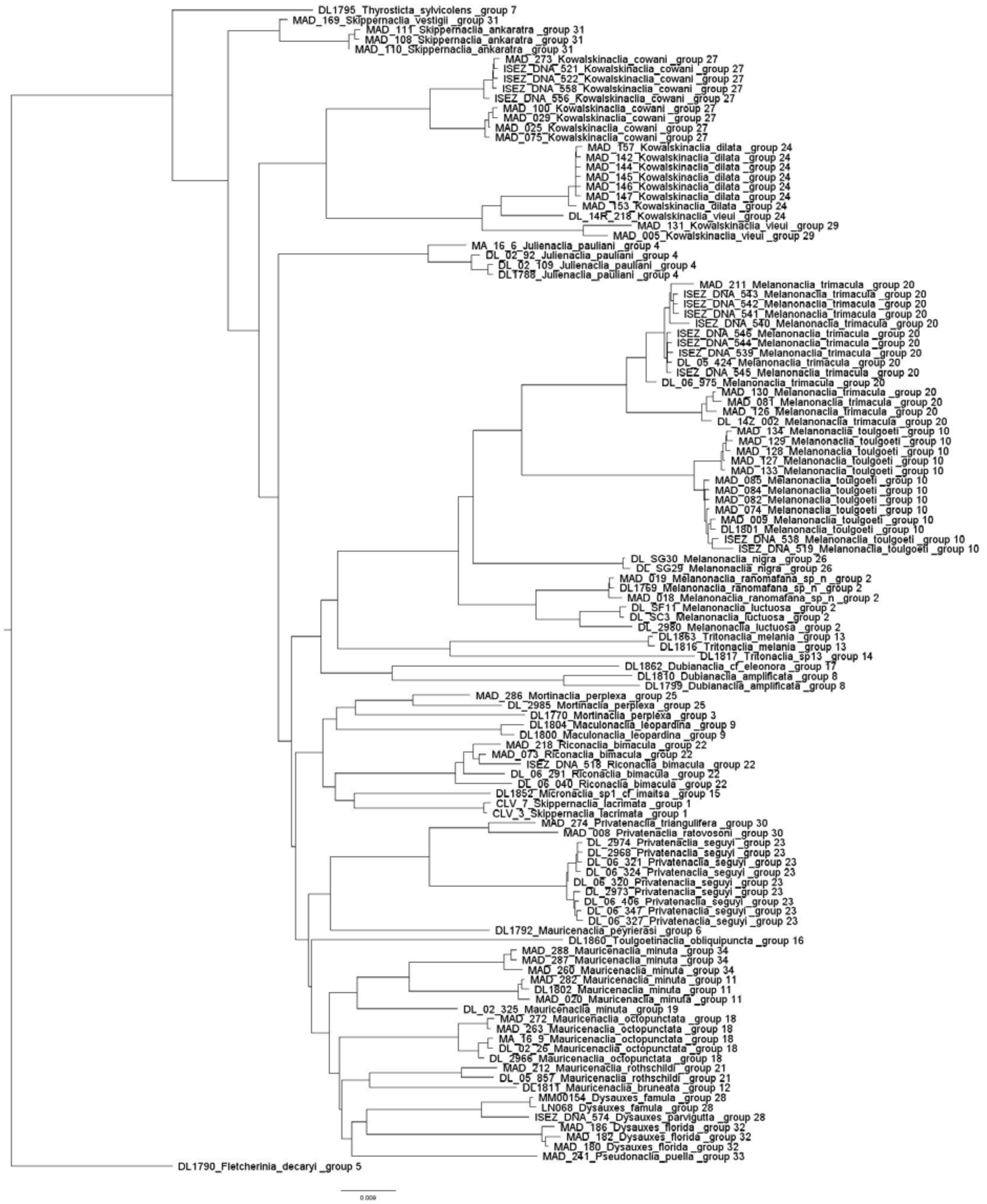


Figure S3. Results of Automatic Barcode Gap Discovery (ABGD) analysis based on COI-begin (barcode region), with 34 initial partitions.

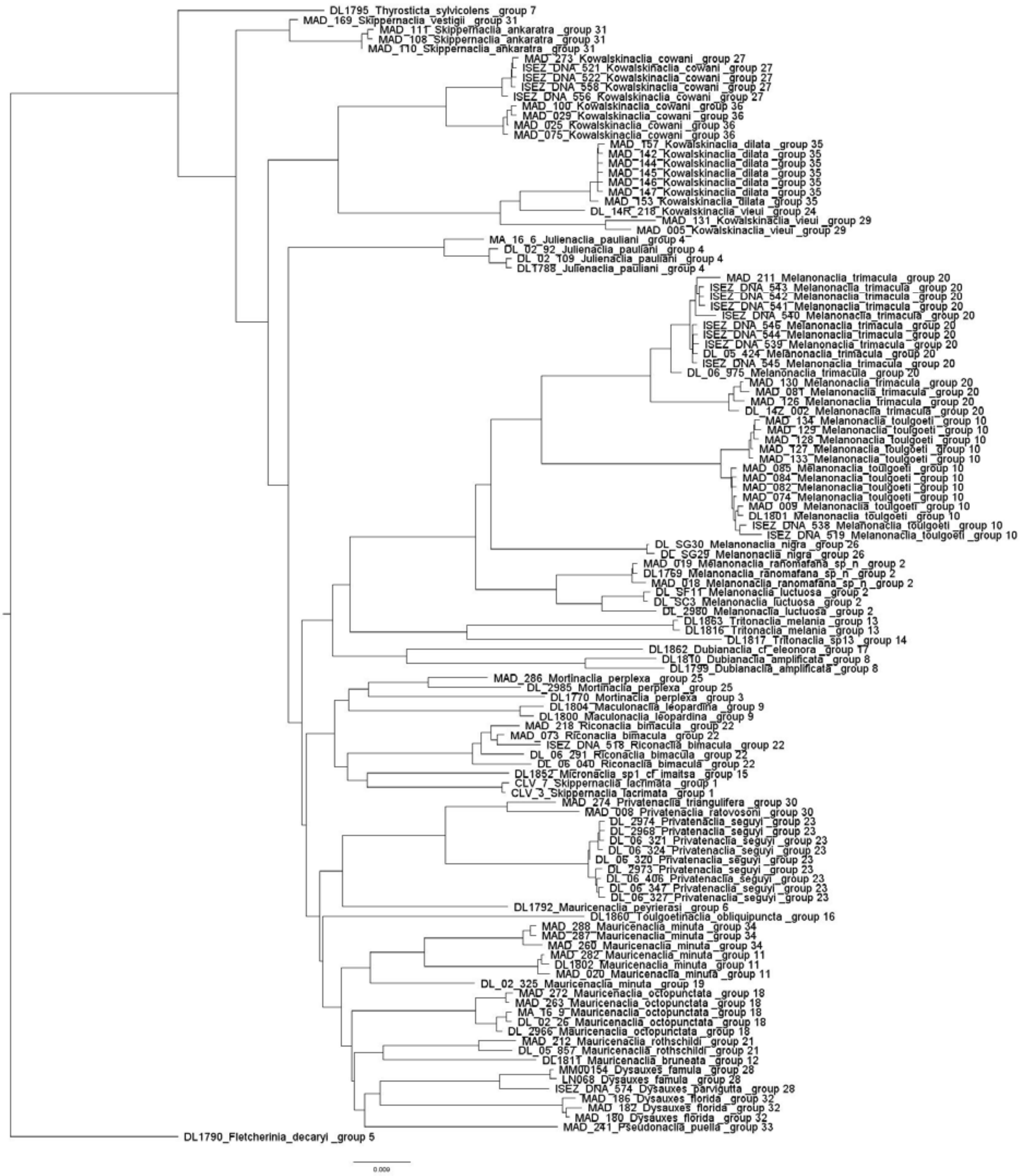


Figure S4. Results of Automatic Barcode Gap Discovery (ABGD) analysis based on COI-begin (barcode region), with 36 recursive partitions.

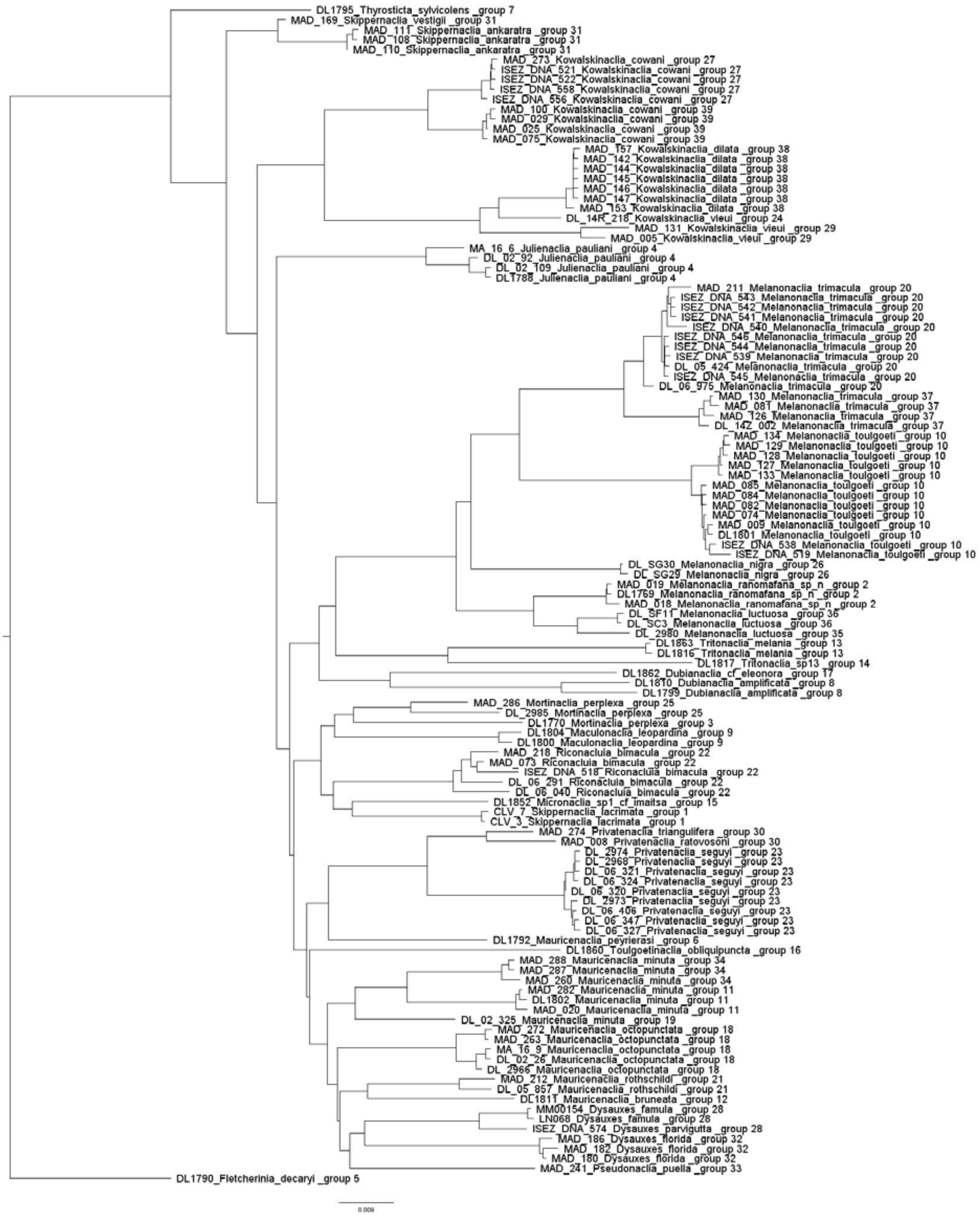


Figure S5. Results of Automatic Barcode Gap Discovery (ABGD) analysis based on COI-begin (barcode region), with 39 recursive partitions.

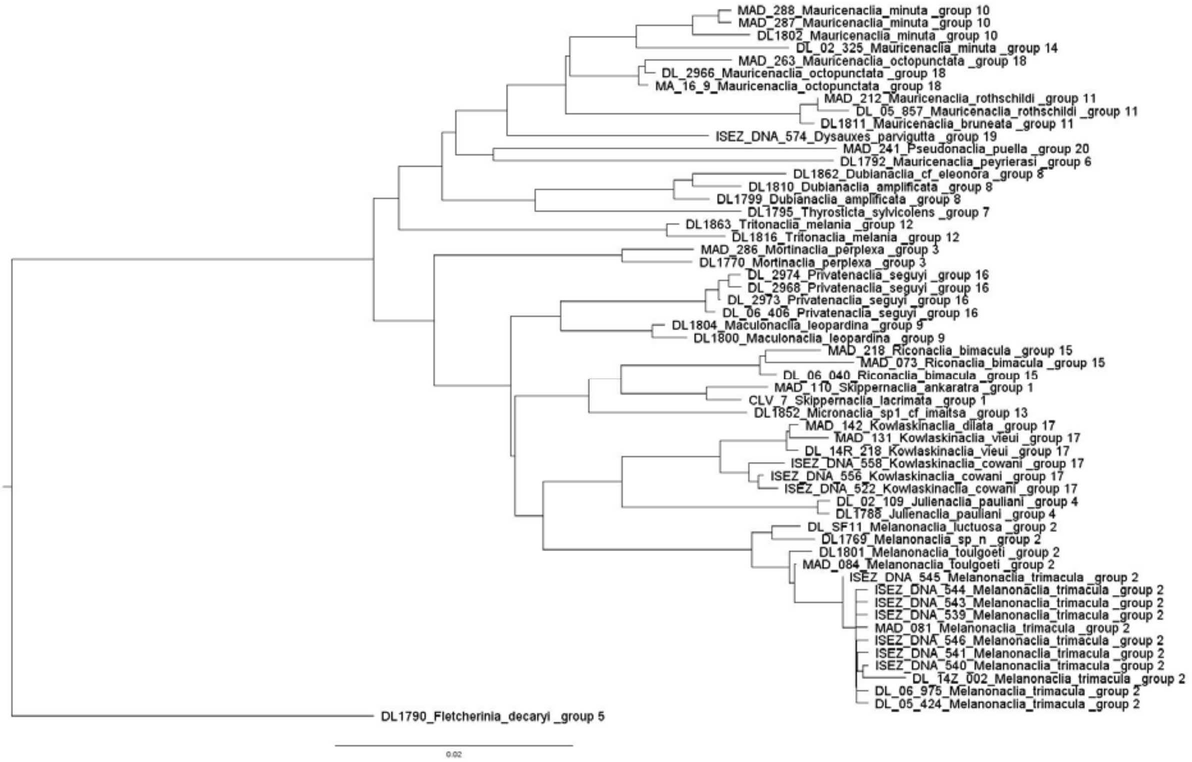


Figure S6. Results of Automatic Barcode Gap Discovery (ABGD) analysis based on EF1a-begin gene region.

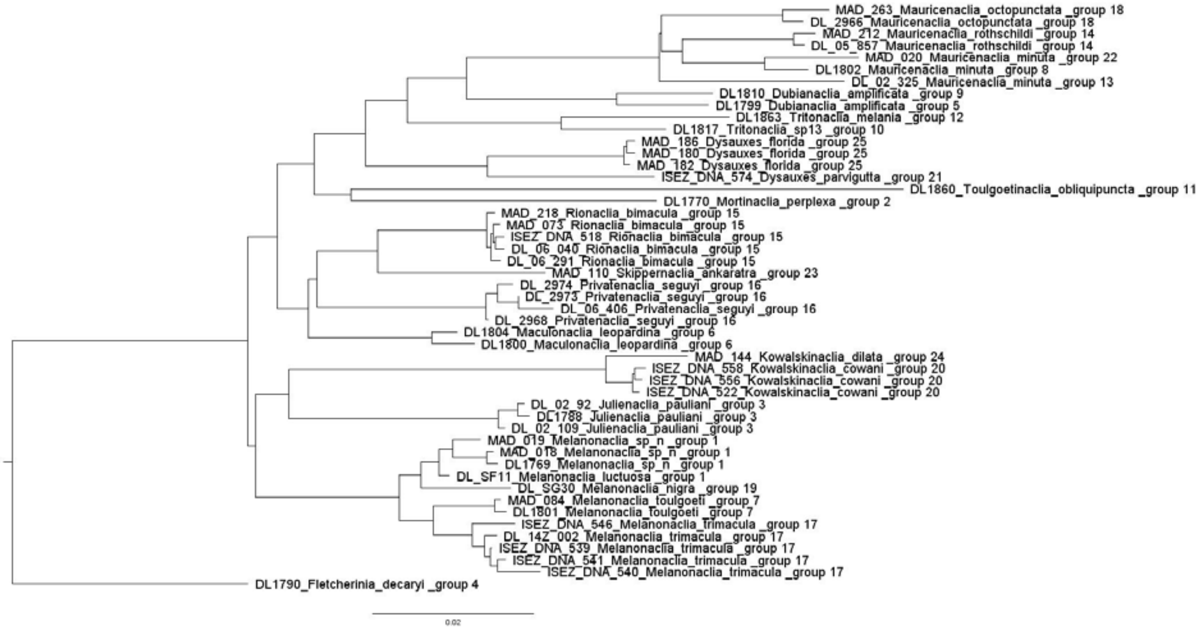


Figure S7. Results of Automatic Barcode Gap Discovery (ABGD) analysis based on GAPDH gene.

SUPPLEMENTARY FILE

File S1. Input parameters for Automatic Barcode Gap Discovery (ABGD) analyses, and results of Poisson Tree Processes (PTP) analyses with Maximum Likelihood support for partitions.

1. **Parameters used in the Automatic Barcode Gap Discovery analyses.**

1.1. COI-begin (barcode region):

Pmin: 0.001, Pmax 0.15, steps 30, X = 1, simple distance; Nb bins: 35

1.2. EF1a-begin region:

Pmin: 0.001, Pmax 0.12, steps 30, X = 1, simple distance, Nb bins: 40

1.3. GAPDH region:

Pmin: 0.002, Pmax 0.14, steps 35, X = 1, simple distance, Nb bins: 45

2. Results of Poisson Tree Processes (PTP) with Maximum Likelihood support values of the partitions.

2.1. COI-begin (barcode region):

Species 1 (support = 1.000)
    DL1790_Fletcherinia_decaryi
Species 2 (support = 1.000)
    DL1860_Toulgoetinaclia_obliquipuncta
Species 3 (support = 1.000)
    DL1795_Thyrosticta_sylvicolens
Species 4 (support = 0.488)
    DL1816_Tritonaclia_melania,DL1863_Tritonaclia_melania
Species 5 (support = 1.000)
    DL1817_Tritonaclia_sp13
Species 6 (support = 1.000)

DL1862_Dubianaclia_cf_eleonora

Species 7 (support = 0.451)

DL1788_Julienaclia_pauliani,DL_02_109_Julienaclia_pauliani,DL_02_92_Julienaclia_pauliani,MA_16_6_Julienaclia_pauliani

Species 8 (support = 1.000)

DL1770_Mortinaclia_perplexa

Species 9 (support = 1.000)

DL1792_Mauricenaclia_peyrierasi

Species 10 (support = 1.000)

MAD_241_Pseudonaclia_puella

Species 11 (support = 0.688)

MAD_180_Dysauxes_florida,MAD_186_Dysauxes_florida,MAD_182_Dysauxes_florida

Species 12 (support = 0.589)

DL_02_26_Mauricenaclia_octopunctata,MA_16_9_Mauricenaclia_octopunctata,DL_2966_Mauricenaclia_octopunctata,MAD_263_Mauricenaclia_octopunctata,MAD_272_Mauricenaclia_octopunctata

Species 13 (support = 0.494)

DL_SG29_Melanonaclia_nigra,DL_SG30_Melanonaclia_nigra

Species 14 (support = 0.588)

DL_06_040_Riconaclia_bimacula,ISEZ_DNA_518_Riconaclia_bimacula,MAD_218_Riconaclia_bimacula,MAD_073_Riconaclia_bimacula,DL_06_291_Riconaclia_bimacula

Species 15 (support = 0.907)

DL1800_Maculonaclia_leopardina,DL1804_Maculonaclia_leopardina

Species 16 (support = 0.993)

DL1811_Mauricenaclia_bruneata

Species 17 (support = 0.739)

DL_05_857_Mauricenaclia_rothschildi,MAD_212_Mauricenaclia_rothschildi

Species 18 (support = 0.182)

DL_06_320_Privatenaclia_seguyi,DL_06_321_Privatenaclia_seguyi,DL_06_324_Privatenaclia_seguyi,DL_2968_Privatenaclia_seguyi,DL_2974_Privatenaclia_seguyi,DL_06_327_Privatenaclia_seguyi,DL_2973_Privatenaclia_seguyi,DL_06_406_Privatenaclia_seguyi,DL_06_347_Privatenaclia_seguyi

Species 19 (support = 0.521)

DL1801_Melanonaclia_toulgoeti,MAD_009_Melanonaclia_toulgoeti,MAD_074_Melanonaclia_toulgoeti,MAD_084_Melanonaclia_toulgoeti,MAD_085_Melanonaclia_toulgoeti,MAD_082_Melanonaclia_toulgoeti,ISEZ_DNA_519_Melanonaclia_toulgoeti,ISEZ_DNA_538_Melanonaclia_toulgoeti,MAD_127_Melanonaclia_toulgoeti,MAD_134_Melanonaclia_toulgoeti,MAD_133_Melanonaclia_toulgoeti,MAD_128_Melanonaclia_toulgoeti,MAD_129_Melanonaclia_toulgoeti

Species 20 (support = 0.183)

DL_05_424_Melanonaclia_trimacula,ISEZ_DNA_539_Melanonaclia_trimacula,ISEZ_DNA_544_Melanonaclia_trimacula,ISEZ_DNA_546_Melanonaclia_trimacula,ISEZ_DNA_545_Melanonaclia_trimacula,DL_06_975_Melanonaclia_trimacula,MAD_211_Melanonaclia_trimacula,ISEZ_DNA_540_Melanonaclia_trimacula,ISEZ_DNA_542_Melanonaclia_trimacula,ISEZ_DNA_543_Melanonaclia_trimacula,ISEZ_DNA_541_Melanonaclia_trimacula,DL_14Z_002_Melanonaclia_trimacula,MAD_081_Melanonaclia_trimacula,MAD_126_Melanonaclia_trimacula,MAD_130_Melanonaclia_trimacula

Species 21 (support = 0.181)

MAD_108_Skippernaclia_ankaratra,MAD_110_Skippernaclia_ankaratra,MAD_111_Skippernaclia_ankaratra,MAD_169_Skippernaclia_vestigii

Species 22 (support = 0.485)

CLV_3_Skippernaclia_lacrimata,CLV_7_Skippernaclia_lacrimata

Species 23 (support = 1.000)

DL1852_Micronaclia_sp1_cf_imaitsa

Species 24 (support = 0.345)

MAD_005_Kowalskinaclia_vieui,MAD_131_Kowalskinaclia_vieui

Species 25 (support = 0.354)

MAD_142_Kowalskinaclia_dilata,MAD_146_Kowalskinaclia_dilata,MAD_144_Kowalskinaclia_dilata,MAD_147_Kowalskinaclia_dilata,MAD_157_Kowalskinaclia_dilata,MAD_145_Kowalskinaclia_dilata,MAD_153_Kowalskinaclia_dilata

Species 26 (support = 0.982)

DL_14R_218_Kowalskinaclia_vieui

Species 27 (support = 0.606)

DL1802_Mauricenaclia_minuta,MAD_282_Mauricenaclia_minuta,MAD_020_Mauricenaclia_minuta

Species 28 (support = 0.863)

MAD_260_Mauricenaclia_minuta,MAD_287_Mauricenaclia_minuta,MAD_288_Mauricenaclia_minuta

Species 29 (support = 0.999)

DL_02_325_Mauricenaclia_minuta

Species 30 (support = 0.853)

DL_2985_Mortinaclia_perplexa

Species 31 (support = 0.853)

MAD_286_Mortinaclia_perplexa

Species 32 (support = 0.859)

DL1799_Dubianaclia_amplificata

Species 33 (support = 0.859)

DL1810_Dubianaclia_amplificata

Species 34 (support = 0.715)

DL_2980_Melanonaclia_luctuosa

Species 35 (support = 0.353)

DL_SC3_Melanonaclia_luctuosa,DL_SF11_Melanonaclia_luctuosa

Species 36 (support = 0.622)

DL1769_Melanonaclia_ranomafana_sp_n,MAD_019_Melanonaclia_ranomafana_sp_n,MAD_018_Melanonaclia_ranomafana_sp_n

Species 37 (support = 0.693)

MAD_008_Privatenaclia_ratovosoni

Species 38 (support = 0.693)

MAD_274_Privatenaclia_triangulifera

Species 39 (support = 0.414)

ISEZ_DNA_521_Kowalskinaclia_cowani,ISEZ_DNA_522_Kowalskinaclia_cowani,ISEZ_DNA_558_Kowalskinaclia_cowani,MAD_273_Kowalskinaclia_cowani,ISEZ_DNA_556_Kowalskinaclia_cowani

Species 40 (support = 0.250)

MAD_025_Kowalskinaclia_cowani,MAD_029_Kowalskinaclia_cowani,MAD_100_Kowalskinaclia_cowani,MAD_075_Kowalskinaclia_cowani

Species 41 (support = 0.696)

ISEZ_DNA_574_Dysauxes_parvigutta

Species 42 (support = 0.333)

LN068_Dysauxes_famula,MM00154_Dysauxes_famula

2.2. EF1a-begin region:

Species 1 (support = 1.000)

DL1790_Fletcherinia_decaryi

Species 2 (support = 1.000)

DL1792_Mauricenaclia_peyrierasi

Species 3 (support = 0.605)

DL1816_Tritonaclia_melania,DL1863_Tritonaclia_melania

Species 4 (support = 0.635)

DL1770_Mortinaclia_perplexa,MAD_286_Mortinaclia_perplexa

Species 5 (support = 0.997)

MAD_241_Pseudonaclia_puella

Species 6 (support = 0.078)

DL1769_Melanonaclia_ranomafana_sp_n,DL_SF11_Melanonaclia_luctuosa,DL1801_Melanonaclia_toulgoeti,DL_05_424_Melanonaclia_trimacula,DL_06_975_Melanonaclia_trimacula,DL_14Z_002_Melanonaclia_trimacula,ISEZ_DNA_541_Melanonaclia_trimacula,ISEZ_DNA_546_Melanonaclia_trimacula,MAD_081_Melanonaclia_trimacula,ISEZ_DNA_545_Melanonaclia_trimacula,ISEZ_DNA_539_Melanonaclia_trimacula,ISEZ_DNA_543_Melanonaclia_trimacula,ISEZ_DNA_540_Melanonaclia_trimacula,ISEZ_DNA_544_Melanonaclia_trimacula,MAD_084_Melanonaclia_toulgoeti

Species 7 (support = 0.415)

DL_14R_218_Kowalskinaclia_vieui,MAD_131_Kowalskinaclia_vieui,MAD_142_Kowalskinaclia_dilata,ISEZ_DNA_522_Kowalskinaclia_cowani,ISEZ_DNA_556_Kowalskinaclia_cowani,ISEZ_DNA_558_Kowalskinaclia_cowani

Species 8 (support = 0.609)

DL1800_Maculonaclia_leopardina,DL1804_Maculonaclia_leopardina

Species 9 (support = 0.302)

DL_06_406_Privatenaclia_seguyi,DL_2968_Privatenaclia_seguyi,DL_2974_Privatenaclia_seguyi,DL_2973_Privatenaclia_seguyi

Species 10 (support = 0.987)

ISEZ_DNA_574_Dysauxes_parvigutta

Species 11 (support = 0.696)

MA_16_9_Mauricenaclia_octopunctata

Species 12 (support = 0.918)

DL1795_Thyrosticta_sylvicolens

Species 13 (support = 0.594)

DL1799_Dubianaclia_amplificata,DL1810_Dubianaclia_amplificata,DL1862_Dubianaclia_cf_eleonora

Species 14 (support = 0.405)

DL_2966_Mauricenaclia_octopunctata

Species 15 (support = 0.405)

MAD_263_Mauricenaclia_octopunctata

Species 16 (support = 0.517)

DL1788_Julienaclia_pauliani

Species 17 (support = 0.517)

DL_02_109_Julienaclia_pauliani

Species 18 (support = 0.574)

DL1811_Mauricenaclia_bruneata

Species 19 (support = 0.343)

DL_05_857_Mauricenaclia_rothschildi,MAD_212_Mauricenaclia_rothschildi

Species 20 (support = 0.488)

EL1802_Mauricenaclia_minuta,MAD_287_Mauricenaclia_minuta,MAD_288_Mauricenaclia_minuta

Species 21 (support = 0.771)

DL_02_325_Mauricenaclia_minuta

Species 22 (support = 0.918)

DL1852_Micronaclia_sp1_cf_imaitsa

Species 23 (support = 0.276)

DL_06_040_Riconaclia_bimacula,MAD_073_Riconaclia_bimacula,MAD_218_Riconaclia_bimacula

Species 24 (support = 0.639)

CLV_7_Skippernaclia_lacrimata,MAD_110_Skippernaclia_ankaratra

2.3. GAPDH region:

Species 1 (support = 1.000)

DL1790_Fletcherinia_decaryi

Species 2 (support = 1.000)

DL1770_Mortinaclia_perplexa

Species 3 (support = 0.216)
DL1801_Melanonaclia_toulgoeti,MAD_084_Melanonaclia_toulgoeti,DL_14Z_002_Melanonaclia_trimacula,ISEZ_DNA_539_Melanonaclia_trimacula,ISEZ_DNA_540_Melanonaclia_trimacula,ISEZ_DNA_541_Melanonaclia_trimacula,ISEZ_DNA_546_Melanonaclia_trimacula,DL_SG30_Melanonaclia_nigra,DL_SF11_Melanonaclia_luctuosa,MAD_019_Melanonaclia_ranomafana_sp_n,DL1769_Melanonaclia_ranomafana_sp_n,MAD_018_Melanonaclia_ranomafana_sp_n

Species 4 (support = 0.570)

DL1788_Julienaclia_pauliani,DL_02_92_Julienaclia_pauliani,DL_02_109_Julienaclia_pauliani

Species 5 (support = 0.997)

DL1860_Toulgoetinaclia_obliquipuncta

Species 6 (support = 0.970)

ISEZ_DNA_574_Dysauxes_parvigutta

Species 7 (support = 0.312)

MAD_180_Dysauxes_florida,MAD_186_Dysauxes_florida,MAD_182_Dysauxes_florida

Species 8 (support = 0.827)

DL1800_Maculonaclia_leopardina,DL1804_Maculonaclia_leopardina

Species 9 (support = 0.422)
DL_06_406_Privatenaclia_seguyi,DL_2973_Privatenaclia_seguyi,DL_2968_Privatenaclia_seguyi,DL_2974_Privatenaclia_seguyi

Species 10 (support = 0.396)
DL_06_040_Riconaclia_bimacula,MAD_218_Riconaclia_bimacula,MAD_073_Riconaclia_bimacula,ISEZ_DNA_518_Riconaclia_bimacula,DL_06_291_Riconaclia_bimacula

Species 11 (support = 0.958)

MAD_110_Skippernaclia_ankaratra

Species 12 (support = 0.838)

MAD_144_Kowalskinaclia_dilata

Species 13 (support = 0.570)

ISEZ_DNA_522_Kowalskinaclia_cowani

Species 14 (support = 0.771)

DL_2966_Mauricenaclia_octopunctata,MAD_263_Mauricenaclia_octopunctata

Species 15 (support = 0.901)

DL_02_325_Mauricenaclia_minuta

Species 16 (support = 0.903)

DL1817_Tritonaclia_sp13

Species 17 (support = 0.903)

DL1863_Tritonaclia_melania

Species 18 (support = 0.455)

DL1802_Mauricenaclia_minuta,MAD_020_Mauricenaclia_minuta

Species 19 (support = 0.607)

DL_05_857_Mauricenaclia_rothschildi,MAD_212_Mauricenaclia_rothschildi

Species 20 (support = 0.677)

DL1799_Dubianaclia_amplificata

Species 21 (support = 0.677)

DL1810_Dubianaclia_amplificata

Species 22 (support = 0.311)

ISEZ_DNA_556_Kowalskinaclia_cowani

Species 23 (support = 0.311)

ISEZ_DNA_558_Kowalskinaclia_cowani

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As co-author of the paper
Wiorek M., Malik K., Lees D., Przybyłowicz Ł. 2021. Malagasy Polka Dot Moths (Noctuoidea: Erebidae: Arctiinae: Syntomini) of Ambohitantely—endemism in the most important relict of Central Plateau rainforest in Madagascar. PeerJ 9:e11688 DOI 10.7717/peerj.11688. (published)
I confirm, that my contributions were gathering and analysing Syntomini species distributional data, map preparation, and writing discussion. I estimate my participation in the preparation of the publication as 10%.

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I confirm, that my contributions were as follows: consultation of molecular analyses, interpreting the results, making additions and comments to the manuscript, and its linguistic verification. I estimate my participation in the preparation of the publication as 10%.

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I confirm, that my contributions were as follows: collecting Syntomini specimens in the field, data obtaining in museum collections, consultation of the results, and writing comments on the manuscript. I estimate my participation in the preparation of the publication as 10%.

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DOCTORAL CANDIDATE STATEMENT

Marcin Wiorek

DOCTORAL CANDIDATE STATEMENT

I declare, that:

- I wrote the doctoral thesis entitled: **“Taxonomy and phylogeny of selected genera of Malagasy Syntomini (Lepidoptera: Erebidae: Arctiinae)” / “Taksonomia I filogeneza wybranych rodzajów madagaskarskich Syntomini (Lepidoptera: Erebidae: Arctiinae)”** on my own. I did not use the help of third parties, and I did not borrow content from other works. All fragments of the thesis, such as quotes, figures, tables, programs, etc., which are not of my authorship, have been appropriately indicated, and their sources of origin have been included in the work, within the meaning of the Act of February 4, 1994, on Copyright and Related Rights (Journal of Laws of 1994, No. 24, Item 83);

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30.09.2024, Marcin Wiorek
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date, signature

Kraków, 30.09.2024