

Taxonomy

Molecular and morphological data clarify the phylogenetic position of genera formerly classified in *Oenochrominae sensu lato* (Lepidoptera: Geometridae)

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Subject Editor: Stephen Baca

Oenochrominae sensu stricto (*s. s.*) are a group of robust-bodied geometrid moths found in the Australasian region. However, over the years, there has been a tendency to relegate genera that are difficult to classify under other subfamilies of Geometridae into a taxonomic “trash bin,” referred to as *Oenochrominae sensu lato* (*s. l.*). Here, we examine this assemblage of moths, focusing on Australasian genera, with the aim of making the classification of *Oenochrominae s. s.* consistent with phylogeny. We do this by reconstructing a molecular phylogeny that includes 24 of 40 genera and 49 of 183 species traditionally assigned to *Oenochrominae s. l.* These are analyzed using a dataset of 1,398 taxa from all geometrid subfamilies worldwide, with up to 11 gene markers per terminal taxon. Using a maximum likelihood approach, we show that some *Oenochrominae s. l.* taxa belong to other subfamilies (Desmobathrinae, Ennominae), or are *incertae sedis*, and adjust classification so that *Oenochrominae s. s.* represents a monophyletic lineage. We also examine the morphology of the reclassified taxa, and discuss and illustrate their characters for taxonomic clarity. Our results also show that several genera within *Oenochrominae s. s.* are polyphyletic, highlighting the need for a modern revision.

Keywords: Australian moth, Geometridae, *Oenochrominae*, phylogeny, systematic

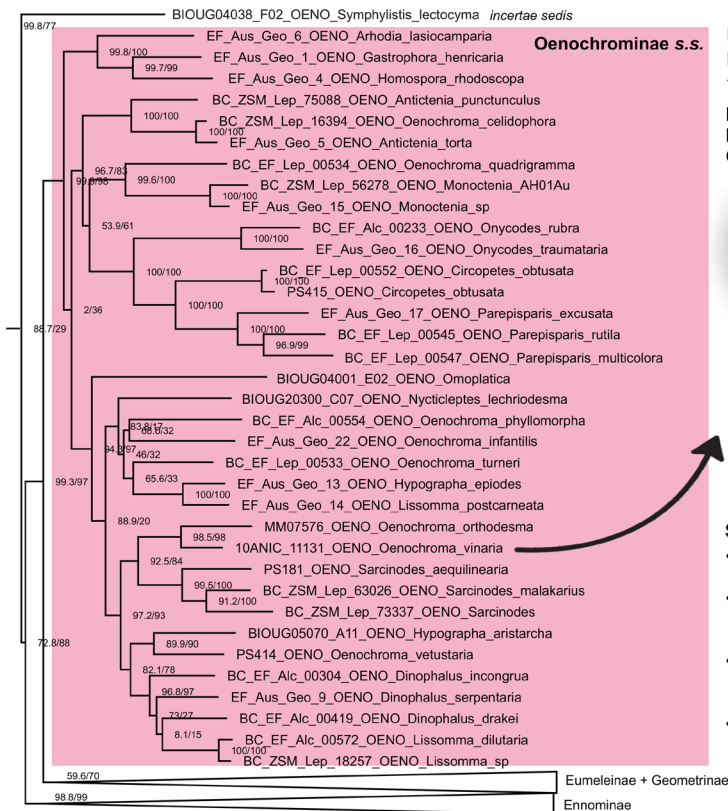
Received: 24 July 2025. Revised: 3 January 2026. Accepted: 25 January 2026

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Version of Record, first published online March 6, 2026, with fixed content and layout in compliance with Art. 8.1.3.2 ICZN.

Graphical abstract



Molecular and morphological data reveal the phylogenetic position of genera classified earlier in Oenochrominae sensu lato (Lepidoptera: Geometridae)

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Oenochroma vinaria
Type species of subfamily Oenochrominae

Summary

- Australasian moth lineage Oenochrominae sensu lato has been an unnatural assemblage of geometrid species
- We used molecular and morphological data to create a phylogenetic hypothesis and to understand the needs for reclassification
- After several species were reclassified to other subfamilies, Oenochrominae sensu stricto (tree on the left) became a monophyletic entity
- We illustrate the reclassified taxa for taxonomic clarity

Introduction

Molecular phylogenies have come to play an important role in revealing the taxonomic misplacement of many lineages in the tree of life and are an increasingly important tool for understanding the diversity and evolution of life, at a time when threats to ecosystems are an existential problem for the world. Improved classifications create taxonomic stability, which is essential when the diversity is represented and indexed in online taxonomic backbone classifications such as GBIF <https://www.gbif.org>, data repositories such as GenBank <https://www.ncbi.nlm.nih.gov/genbank> and BOLD <https://v5.boldsystems.org/>, global and regional checklists, and most importantly, in scientific literature in which correct names and classifications form the basis for applied research.

The combination of DNA sequences and statistical phylogenetic inference often leads to more stable natural classifications (Prance 2011). When combined with morphology and life histories, we can often more confidently assign taxa to the Linnaean hierarchical classification system. Significant progress in understanding evolutionary patterns in Lepidoptera has generally resulted from multi-gene approaches, leading to major rearrangements of the group (eg Mitter et al. 2017). In particular, molecular data have yielded phylogenetic hypotheses that have helped to resolve deep divergences and some of the most enigmatic phylogenetic relationships at all levels of Lepidoptera clades (Regier et al. 2009; Mutanen et al. 2010; Bazinet et al. 2013; Regier et al. 2013; Wahlberg et al. 2013; Bazinet et al. 2017; Kawahara et al. 2019; 2023), but see Rota et al. (2022) for the methodological challenges.

The phylogenetic relationships of the higher-level taxa of geometrid moths, the second most species-rich family of Lepidoptera with approximately 24,000 described species,

have been comprehensively studied (eg Sihvonen et al. 2011; Murillo-Ramos et al. 2019; 2023; Rajaei et al. 2022; Öunap et al. 2024), and the resulting topologies have been used as a framework to classify numerous taxa (eg Brehm et al. 2019; Murillo-Ramos et al. 2021; Sihvonen et al. 2020; Öunap et al. 2024).

Despite the progress, taxonomic challenges remain. Such is the case of the subfamily Oenochrominae, a group of robust-bodied geometrid moths occurring in the Australasian region. Over the years, there has been a tendency to place genera that did not fit into any other geometrid subfamilies into Oenochrominae, resulting in a taxonomic “trash bin” referred to as Oenochrominae sensu lato (*s. l.*). This taxonomic history is explained elsewhere (Scoble and Edwards 1989), but briefly, confusion arose when the original Oenochrominae concept of Guenée (1857) was expanded by Meyrick (1889) into Oenochrominae *s. l.* based on the form of veins Sc + R1 and Rs in the hindwing. Scoble and Edwards (1989, p. 372) explained this as follows: “The variation expressed in [Meyrick’s diagnostic] passage immediately suggests that the [wing venation] character is of dubious value...”. Although Meyrick’s concept was acknowledged as problematic for natural classification, it was applied extensively (eg Prout 1910, 1920, Turner 1929, 1930a, 1930b, Nielsen et al. 1996), probably to avoid classifying taxa as *incertae sedis*. In more recent years, some publications have made a distinction between Oenochrominae *s. s.* and Oenochrominae *s. l.* (eg Cook and Scoble 1992, Nielsen et al. 1996, Young 2008).

Recent studies have already clarified the taxonomic position of several misplaced oenochromine genera, placing them, for instance, in Sterrhinae (Sihvonen and Staude 2020, Sihvonen

et al. 2021), Ennominae (Hausmann and Sihvonen 2019), Desmobathrinae (Murillo-Ramos et al. 2019, Staude et al. 2023) and in the recently described Epidesmiinae (Murillo-Ramos et al. 2019, 2021).

Currently, Oenochrominae s. s. includes about 20 genera and 150 species found mostly in the Australasian realm (Nielsen et al. 1996, Rajaei et al. 2022), while Oenochrominae s. l. comprises approximately 40 genera and 185 species, mostly in Australasia, but also a few taxa in the Neotropic, Afrotropic and Indo-Malay realms (Nielsen et al. 1996, Rajaei et al. 2022). Many species are structurally isolated, and this is reflected in the classification, as 15 out of 40 genera are monotypic. Host associations of the Oenochrominae s. s. genera are available for nine genera (McFarland 1988, Lepidoptera Butterfly House <https://lepidoptera.butterflyhouse.com.au/chro/chro-cats.html>). Based on the limited data, host associations do occur on Myrtaceae and on Proteaceae. Little is known about the biology of Oenochrominae s. l. species, and generalisations are impossible because they are not a natural group. Most species are presumed nocturnal, including all Afrotropical species, but *Antasia flavicapitata* (Guenée, 1859) and several *Taxeotis* Guest, 1887 species are diurnal (Marriott 2012). The caterpillars of *Taxeotis* nr *reaserata* (Walker, 1861) have been reported to subsist briefly on dead and dry eucalyptus leaves (Marriott 2012). The Afrotropical–South Asian genera *Conolophia* Warren, 1894 and South African *Panagropsis* Warren, 1894 seem to feed exclusively on fresh leaves of trees in the family Sapotaceae, and South African *Barrama impunctata* feeds exclusively on *Vitex* spp. (Lamiaceae) (Staude et al. 2020).

Molecular phylogenetic analyses have confirmed a close relationship among Oenochrominae, Epidesmiinae, and Desmobathrinae (Sihvonen et al. 2011; Murillo-Ramos et al. 2019), and several Oenochrominae s. l. taxa were recently classified in Epidesmiinae and Desmobathrinae (Murillo-Ramos et al. 2019, 2021). To better understand the phylogenetic position of Australasian Oenochrominae s. l. genera and the boundaries of Oenochrominae s. s., we expanded the large, global molecular Geometridae dataset of Murillo-Ramos et al. (2023), with Australasian genera and with additional samples from Desmobathrinae and Epidesmiinae. We used this dataset to reconstruct a phylogenetic hypothesis based on up to 11 genetic markers for terminal taxa. After this, we investigated the morphological characters (eg female and male genitalia, wing venation, tympanal organ) of Oenochrominae s. l. taxa that were recovered in other geometrid subfamilies. Based on molecular and morphological data, we propose new classifications for several Oenochrominae s. l. genera to advance the natural classification of, and further research on, Geometridae.

Material and Methods

Molecular Data

For the present study, we expanded the molecular dataset from Murillo-Ramos et al. (2023) by including DNA sequence data for 190 additional species of Oenochrominae s. l. and other Geometridae subfamilies, including altogether 1,398 terminal taxa. The molecular data included 11 genes: 1 mitochondrial (cytochrome oxidase subunit I, COI) and 10 protein-coding nuclear gene regions, carbamoylphosphate synthetase (CAD), Ribosomal Protein S5 (RpS5), wingless (wgl), cytosolic malate

dehydrogenase (MDH), glyceraldehydes-3-phosphate dehydrogenase (GAPDH), Elongation factor 1 alpha (EF-1alpha), Arginine Kinase (ArgK), Isocitrate dehydrogenase (IDH), sorting nexin-9-like (Nex9) and sarco/endoplasmic reticulum calcium ATPase (Ca-ATPase). We worked with DNA extracts that were originally used for DNA barcoding at the Canadian Centre for DNA Barcoding, Guelph (Supplemental S1). We obtained DNA sequence data following the same PCR amplifications and Sanger-sequencing protocols as in Murillo-Ramos et al. (2023), which were based on Wahlberg and Wheat (2008) and Wahlberg et al. (2016); see Supplemental S1 for accession numbers.

Alignment and cleaning sequences follow the protocol presented in Murillo-Ramos et al. (2019). Briefly, multiple sequence alignments were carried out in MAFFT as implemented in Geneious v.11.0.2 (Biomatters, <http://www.geneious.com/>) for each gene based on a reference sequence of Geometridae downloaded from the database VoSeq (Peña and Malm 2012). To locate homologous positions for gene alignment, we checked the alignments by eye. Low-quality sequences (eg short or noisy reads) were removed. To check for possible errors or contaminations, we inferred maximum likelihood (ML) trees for each gene. After processing the samples, we retrieved the eleven-gene dataset from Murillo-Ramos et al. (2023) and created a concatenated dataset of 1,398 taxa with a total sequence length of 7,692 bp, including gaps, and with up to eleven markers per sample.

Phylogenetic Inference

To infer the phylogenetic trees, we conducted ML analyses in IQ-TREE2 V2.0.7 (Minh et al. 2020). We selected the best-fit substitution models for each gene and codon with ModelFinder (Kalyaanamoorthy et al. 2017). Gene trees were inferred to check for possible errors or contaminations. Final phylogenetic trees were inferred with the concatenated dataset partitioned by gene and then by codon. Branch support was evaluated with 1,000 ultrafast bootstrap (UFBoot2) approximations (Hoang et al. 2018), and SH-like approximate likelihood ratio tests (Guindon et al. 2010). Values of SH \geq 80 and UFBoot2 \geq 95 indicate well-supported clades.

To reduce the risk of overestimating branch supports in the UFBoot2 test, we implemented the *-bnni* option. We visualized and edited the trees in FigTree v1.4.3 and with the R package *ggtree* (Yu et al. 2017). For better visualization of our groups of interest, we removed outgroups using the *ape* v.5.2 R package (Paradis and Schliep 2019). Full trees are visualized in supplementary material (S2: phylogenetic inference by gene, S3: phylogenetic inference by codon).

Morphological Work

We examined and illustrated the morphology of those species proposed for reclassification. The morphological examination followed the methods described in Sihvonen (2005) and Murillo-Ramos, et al. (2021).

For the morphological examination, specimens were loaned from the Australian National Insect Collection, CSIRO Division of Entomology, Canberra, Australia (ANIC); the Natural History Museum, London, UK (NHMUK); the Finnish Museum of Natural History, Helsinki, Finland (ZMH) and from the private collections of Egbert Friedrich (Germany) and Pasi Sihvonen (Finland).

For taxonomic evaluation, we used the relationships in the molecular trees to guide a post hoc morphological reassessment of genera and subfamily classification, with emphasis on the characters used widely in Geometridae taxonomy (see, eg, Müller et al. 2019): (1) external morphology, (2) genitalia morphology, including male eighth sternite, (3) descaled abdomen, including tympanal organ, (4) wing venation, and (5) if available, ecology and distribution.

Dissected and Examined Material for Morphological Studies

Aglossophanes pachygramma (Turner, 1942). **Male:** Australia 40 miles S. of Balladonia, WA. 21 March 1968, I.F.B. Common & M.S. Upton; ANIC specimen Barcode of Life DNA voucher specimen Sample ID: 10ANIC-11637, BOLD Proc. ID: ANIC0642-10. Preparation number PMS2915. **Female:** Australia 7 miles ESE. Of Dongara, W.A., 17 April 1968, I.F.B. Common & M.S. Upton; ANIC specimen; Barcode of Life DNA voucher specimen Sample ID: 10ANIC-11638, BOLD Proc. ID: ANIC06643-10. Preparation number PMS2916. Both in ANIC.

Antasia flavicapitata (Guenée, 1858). **Male:** Australia 14 km SE. of Braidwood, NSW, 9 October 1990, I. F. B. Common; ANIC specimen. Preparation number LMR24. **Female:** Australia 41.50S 146.03E, Pelion Hut, 870 m Tasmania, 18 November 1991, E.S. Nielsen, M. Horak; Barcode of Life DNA voucher specimen Sample ID: 10ANIC-11579, BOLD proc. ID: ANICO584-10. Preparation number LMR25. Both in ANIC.

Axiagasta rhodobaphes Turner, 1930. **Male:** Australia 18.38S 138.11E, 8 km SE by E of Musselbrook Camp Q, 11 May 1995, GPS E.D. Edwards; ANIC Specimen; Barcode of Life DNA voucher specimen Sample ID: 10ANIC-12089 BOLD Proc. ID: ANICP093-10. Preparation numbers PMS2923 (abdomen and genitalia), PMS2936 (wings). **Female:** Australia 18.38S 138.11E, Holts Ck 8 km NE Musselbrook Camp Q, 15 May 1995, GPS E.D. Edwards; ANIC Specimen; Preparation number PMS2924. Both in ANIC.

Cathaemacta thermistis (Lower, 1894). **Male:** Australia Safety Bay, WA, 20 July 1968, K.T. Potts; V.J. Robinson Collection; ANIC Specimen. Preparation number PMS2920. **Female:** Australia Safety Bay, WA, 14 July 1968, K.T. Potts; V.J. Robinson Collection; ANIC Specimen; Barcode of Life DNA voucher specimen Sample ID: 10ANIC-11584 BOLD Proc.ID: ANIC0589-10. Preparation number PMS2921. Both in ANIC.

Symphylistis leptocyma Turner, 1930. **Male:** [Australia] 34.54S 117.55E, 14 km NNE of Albany, WA, 27 November 1996, E.D. Edwards; ANIC Specimen. Preparation numbers PMS2970 (genitalia, abdomen), PMS2972 (wings). **Female:** [Australia] 34.55S 117.56E, 12 km NNE of Albany, WA, 4 December 1996, E.D. Edwards; ANIC Specimen. Preparation number PMS2971. Both in ANIC.

Taxeotis near *intextata* (Guenée, 1858). **Male:** Australia WA, Warren National Park, Maidenbush Trail, Warren Lookout, 34°30'28"S 116°57'45"E, 26.12.2014 lux 100 m, leg. Egbert Friedrich; AUS20; Bild14161. Preparation numbers PMS2917 (abdomen and genitalia), PMS2937 (wings). **Female:** Australia WA, Shannon National Park, Dam Great Forest Trees Drive, 35°34'57"S 116°24'45"E, 25.12.2014 lux 162 m, leg. Egbert Friedrich. Preparation number PMS2918. Both in coll. Egbert Friedrich, Jena, Germany.

Thaumato-graphe singularis Warren, 1907. **Male:** [Indonesia: Western New Guinea] 55. 21 Mt. Kunupi, Menoo Valley, Weyland Mts., 6,000 ft., Dutch New Guinea. Nov.-Dec. 1920. C.F., & J. Pratt.; Rothschild Bequest B.M.1939-1.; NHMUK 015106792. Preparation numbers PMS2929 (genitalia), PMS2932 (abdomen), PMS2935 (wings). **Female:** [Indonesia: Western New Guinea] 55. 21 Mt. Kunupi, Menoo Valley, Weyland Mts., 6,000 ft., Dutch New Guinea. Nov.-Dec. 1920. C.F., & J. Pratt.; Rothschild Bequest B.M.1939-1.; NHMUK 015106792. Preparation number PMS2930. Both in NHMUK.

Xyridacma ustaria (Walker, 1863). **Male:** [New Zealand] DUNEDIN 26-8-1911; ustaria; NHMUK 015106791. Preparation numbers PMS2928 (abdomen and genitalia), PMS2934 (wings). In The Natural History Museum, London, UK. **Female:** New Zealand, surr. Of Palmerston North, M. Kozlov 1-9.XII.1994; *Xyridacma ustaria* (Walker) det: J.S. Dugdale 1997. Preparation number PMS2931. In ZMH.

Results

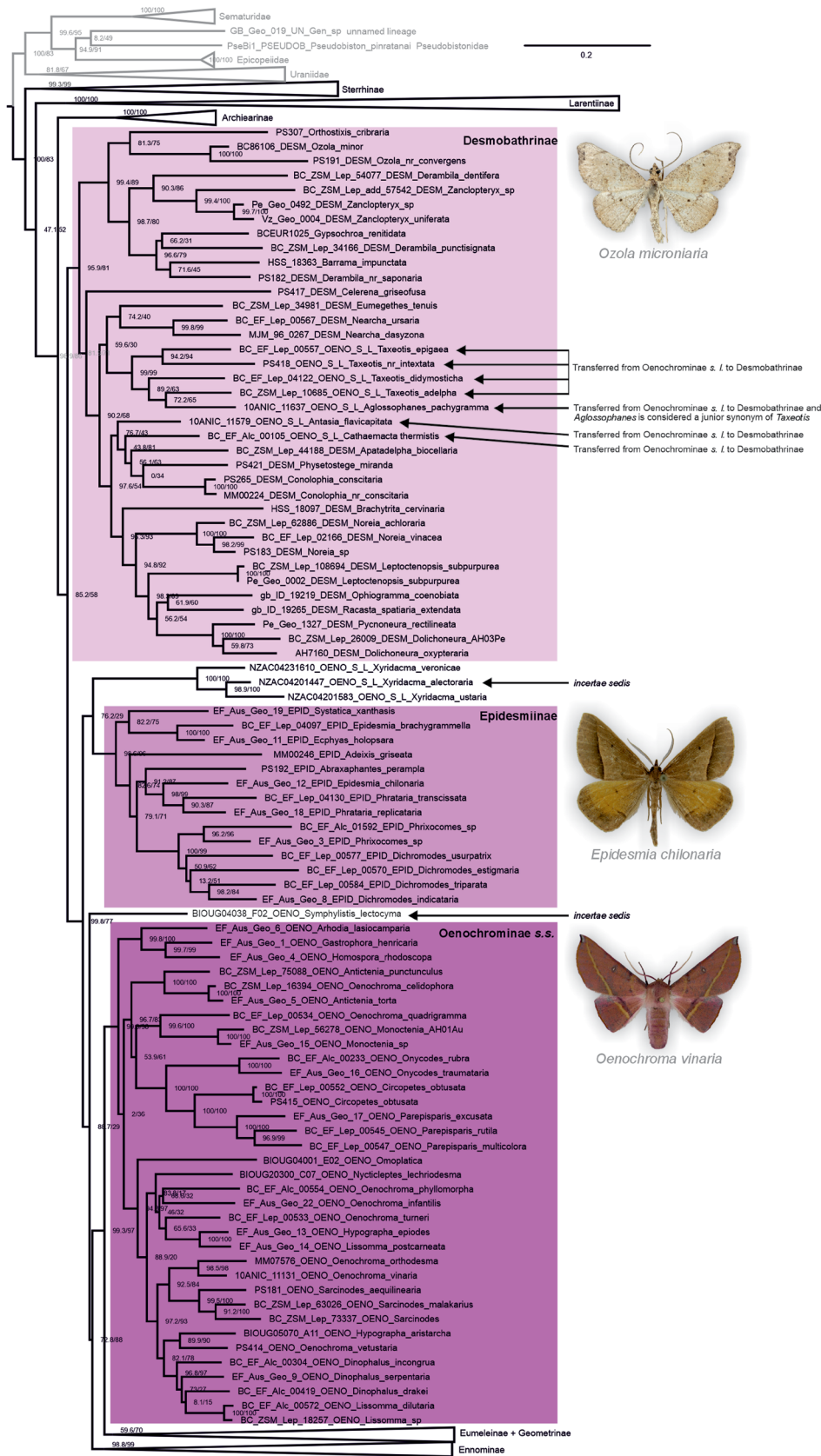
The Systematics of *Oenochrominae s. l.* and Their Relatives

Phylogenetic inference with partitions by gene (Fig. 1, Supplemental S2) and by codon (Supplemental S3) showed consistent global results, with minor differences as discussed below. Thus, we decided to discuss the topology below, following the data partitioned by gene (Fig. 1).

In line with previous phylogenetic hypotheses, *Oenochrominae s. s.* and *Geometrinae + Eumeleinae* (Murillo-Ramos et al. 2023), or *Geometrinae + Eumeleinae* (Murillo-Ramos et al. 2019), resolved as sister groups. *Desmobathrinae* were recovered as sister to *Epidesmiinae + remaining subfamilies*. Also, Öunap et al. (2024) recovered the same pattern, although *Eumeleinae* were not analyzed.

Oenochrominae s. s. is a monophyletic lineage occurring in the Australasian realm. *Oenochrominae s. l.* is polyphyletic, and the phylogenetic position of several taxa outside of *Oenochrominae* indicates that reclassifications are needed (Fig. 1). These include *Taxeotis* Guest, 1887, *Aglossophanes* Turner, 1942, *Cathaemacta* Turner, 1942 and *Antasia* Warren, 1894, which have been classified in *Oenochrominae* (eg Scoble 1999, Rajaei et al. 2022), but are intermixed within *Desmobathrinae* (Fig. 1; Supplemental S2). *Xyridacma* Meyrick, 1888 (*Oenochrominae* in Scoble 1999, Rajaei et al. 2022) is placed as sister to *Archierinae* in the analyses by codon (see Supplemental S3) but as sister to *Epidesmiinae* in the analyses by gene (Fig. 1; Supplemental S2). Three further genera, *Axiagasta* Turner, 1930, *Symphylistis* Turner, 1930 and *Thaumato-graphe* Warren, 1907, also earlier classified in *Oenochrominae* (eg Scoble 1999; Rajaei et al. 2022), were placed in unexpected positions. *Axiagasta* is placed in *Ennominae: Ennomini* and *Thaumato-graphe* in *Geometrinae: Chlorodontoperini*. *Symphylistis* Turner, 1930 is an unstable branch, and depending on the analysis, either resolves as sister to *Ennominae* or within *Oenochrominae s. s.* (Fig. 1, Supplemental S2 and S3).

The molecular phylogeny also recovered the genera *Oenochroma* Guenée, 1858, *Hypographa* Guenée, 1858 and *Lissomma* Warren, 1905 inside *Oenochrominae s. s.* respectively as non-monophyletic (Fig. 1). Members of the genus *Oenochroma*, for instance, appear in 4 different clades of the



Ozola micronaria



Epidesmia chilonaria



Oenochroma vinaria

Fig. 1. Phylogenetic hypothesis obtained under an ML approach in IQTREE2 for Oenochrominae, Epidesmiinae, and Desmobathrinae (trimmed topology, see Supplemental files S2 and S3 for full trees). Oenochrominae *sensu stricto* (s. s.) is at the bottom of the figure. Arrows indicate species that are here reclassified (many of them were classified in Oenochrominae *sensu lato*) and/or illustrated in the morphology plates (Figs 2 to 12). The displayed topology was recovered with data partitioned by gene, up to eleven markers and 1398 taxa. Numbers under the branches are support values SH-aLRT support (%) /ultrafast bootstrap support (%) from IQTREE2. Outgroups are marked with grey.

tree, and the genera *Dinophalus* Prout, 1910 and *Antictenia* Prout, 1910 are rendered paraphyletic by *Lissomma* and *Oenochroma*, respectively. Further, *Dinophalus oxystoma* (Turner, 1939) was recovered in Ennominae: Diptychini Janse, 1933, as sister to a South African lineage of robust-bodied species. This highlights the need for a modern generic revision of the Oenochrominae s. s., which is under preparation (Sihvonen et al., in prep.).

Our results also confirm the position of the monotypic sub-Saharan genus *Barrama* Warren, 1897 in Desmobaethrinae (Staudé et al. 2023), which was earlier classified in the Oenochrominae (Krüger 2020), and *Gypsochroa renitidata* Hübner, 1817 and *Eumegethes tenuis* Staudinger, 1898 (Hausmann and Sihvonen 2019) in Desmobaethrinae. The last 2 genera are among the few Desmobaethrinae species that occur in the Palearctic region.

The following 4 genera were included in a molecular phylogeny for the first time, with their position in Desmobaethrinae confirmed: *Celerena* Walker, 1862 from Indo-Malay realm (Holloway 1996, Rajaei et al. 2022, but classified as Oenochrominae s. l. in Nielsen et al. (1996)), *Physetostege* Walker, 1896 from Australasia (Rajaei et al. 2022, but classified as Oenochrominae s. l. in Nielsen et al. (1996)), *Apatadelpa* Prout, 1910 from West Africa (Holloway 1996, Rajaei et al. 2022) and *Brachytrita* Swinhoe, 1904 from East Africa (Holloway 1996, Rajaei et al. 2022).

The taxa reclassified here as part of Desmobaethrinae have morphologically typical diagnostic characters of the subfamily, including elongated legs and males with anteriorly pointing apophyses arising from the membrane between the second and third sternites (Murillo-Ramos et al. 2019). These morphological characters further support the molecular results, see Figs 2 to 5. In contrast, the Oenochrominae s. l. taxa reclassified here as Ennominae (*Axiagasta*) or *incertae sedis* (*Xyridacma*, *Thaumatographe*, *Symphylistis*) based on molecular data lack clear diagnostic morphological characters (as summarized in Murillo-Ramos et al. 2021) of the relevant subfamilies. Classification and morphology of each case are covered in “Discussion” section. Proposed taxonomic changes are listed in Table 1.

Discussion

The Taxonomic Treatment of Oenochrominae s. l. and Their Relatives

The topology of our phylogenetic hypothesis is similar to previous studies with Oenochrominae s. s. and Geometrinae + Eumeleinae (Murillo-Ramos et al. 2023), or Geometrinae + *Eumelea* (Murillo-Ramos et al. 2019), resolved as sister groups. Desmobaethrinae were recovered as sister to Epidesmiinae + remaining subfamilies. This similarity increases confidence that the molecular results are robust, given that the studies differed substantially in taxon sampling and gene coverage: the current study included 1,398 taxa and up to 11 genes with Oenochrominae s. s. represented by 49 species, whereas in Murillo-Ramos et al. (2023) the analysis included 39 taxa and up to 1,000 genes with Oenochrominae s. s. represented by only 2 species.

Our molecular hypotheses and morphological examination support the polyphyly of Oenochrominae s. l. and proposed taxonomic reclassifications. We also demonstrated that with

Table 1. Summary of the proposed taxonomic changes for taxa that were classified in Oenochrominae s. l. earlier

Explanation	Taxonomic change
<i>Aglossophanes</i> Turner, 1942, is considered a junior subjective synonym of <i>Taxeotis</i> Guest, 1887.	New synonym
<i>Aglossophanes</i> Turner, 1942, is transferred from Oenochrominae s. l. to Desmobaethrinae	New classification
<i>Antasia</i> Warren, 1894, is transferred from Oenochrominae s. l. to Desmobaethrinae	New classification
<i>Axiagasta</i> Turner, 1930, is transferred from Oenochrominae s. l. to Ennominae	New classification
<i>Cathaemacta</i> Turner, 1942, is transferred from Oenochrominae s. l. to Desmobaethrinae	New classification
<i>Symphylistis</i> Turner, 1930, classified in Oenochrominae earlier, is now classified as <i>incertae sedis</i>	Higher classification <i>incertae sedis</i>
<i>Taxeotis</i> Guest, 1887, is transferred from Oenochrominae s. l. to Desmobaethrinae	New classification
<i>Thaumatographe</i> Warren, 1907, classified in Oenochrominae earlier, is now classified as <i>incertae sedis</i>	Higher classification <i>incertae sedis</i>
<i>Xyridacma</i> Meyrick, 1888, classified in Oenochrominae earlier, is now classified as <i>incertae sedis</i>	Higher classification <i>incertae sedis</i>

Several genera in Oenochrominae s. s. were also found non-monophyletic (see “Results” section). Those will be treated in a separate paper (Sihvonen et al., in prep.).

an integrated taxonomic approach, several problematic taxa can be unambiguously classified in the tree of life, providing confidence that the classification of the yet missing taxa can be resolved also. Several of the non-Australian Oenochrominae s. l. taxa may eventually be treated under Desmobaethrinae, similar to our results and the findings of Murillo-Ramos et al. (2019, 2023). After our analysis, the systematic positions of 15 Oenochrominae s. l. genera and about 22 species have yet to be resolved (Rajaei et al. 2022).

The previous misclassifications likely resulted from a regional rather than a global approach, the limited number of taxonomic studies focusing on Australian genera, the ambiguity of external characters of some groups, and a lack of information on the species’ biology. This is particularly true for monotypic genera, which would benefit from analysis in a global phylogenetic framework. However, morphological examinations and molecular data have continuously revealed that Oenochrominae s. s. is a well-defined clade of robust-bodied geometrids occurring in the Australasian biogeographic realm (Scoble and Edwards 1989; Murillo-Ramos et al. 2019). Our results support this monophyly. We are now working on a taxonomic revision of Oenochrominae s. s. to improve their classification and to document the diversity of this lineage (Sihvonen et al., in prep.).

The genera *Taxeotis* and *Aglossophanes* were recovered within Desmobaethrinae (Fig. 1). *Taxeotis* is a genus that currently comprises 48 species, while *Aglossophanes* consist of only 2 species (Rajaei et al. 2022). Most *Taxeotis* species are brownish with a uniform appearance and filiform antennae in both sexes. The body and abdomen are delicate, the forewings are triangular, and the hind wing margin is rounded (Turner 1929; Marriott 2012). In some species, there is an angulated line extending from the costa to the middle of the discal cell.

***Aglossophanes pachygramma* (Australia)**

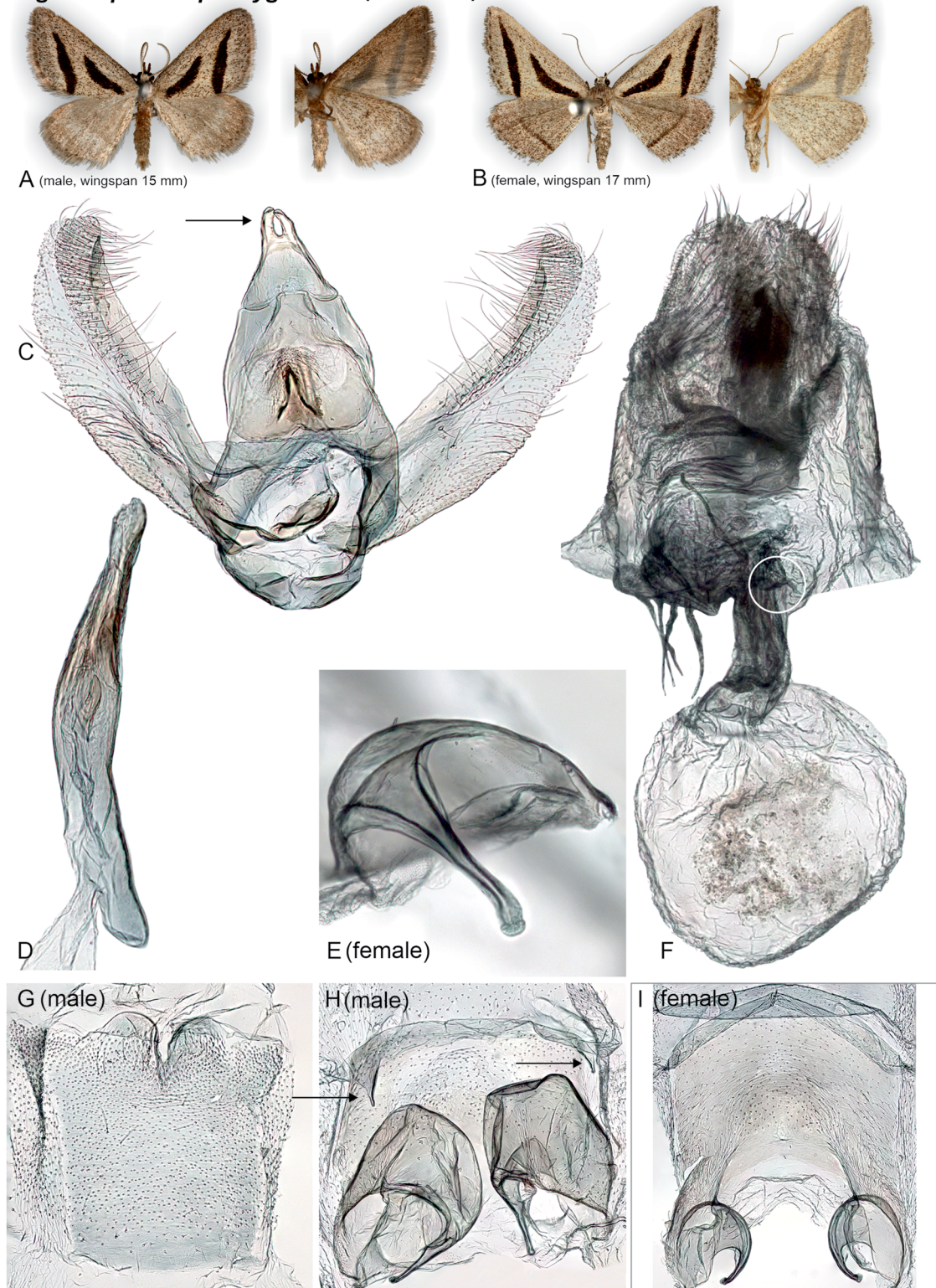


Fig. 2. Selected morphological structures of *Aglossophanes pachygramma* (Lower, 1893). *Aglossophanes* Turner, 1942, is considered a junior subjective synonym of *Taxeotis* Guest, 1887 (**new synonymy**) and here transferred from Oenochrominae s. l. to Desmobathrinae (**new subfamily classification**).

Adults of *Aglossophanes* are similar, but they lack a visible proboscis, which was considered a diagnostic generic character by Turner (1942).

In our molecular phylogeny (Fig. 1), *Aglossophanes* was found nested in *Taxeotis*, suggesting a genus-level synonymy. Both genera share two areoles on forewing (Fig. 10), but

otherwise, the examined morphology does not indicate a close relationship (Figs 2 and 3). For instance, *Taxeotis* nr. *intextata* has an acute uncus (bifurcate in *A. pachygramma*), spinose gnathos apex (acute and apex lacking spines in *A.*

pachygramma) in the male genitalia, and 2 signa in the female genitalia (signum absent in *A. pachygramma*).

The morphological dissimilarity could be explained by the limited morphological examination of the taxa, that is, the

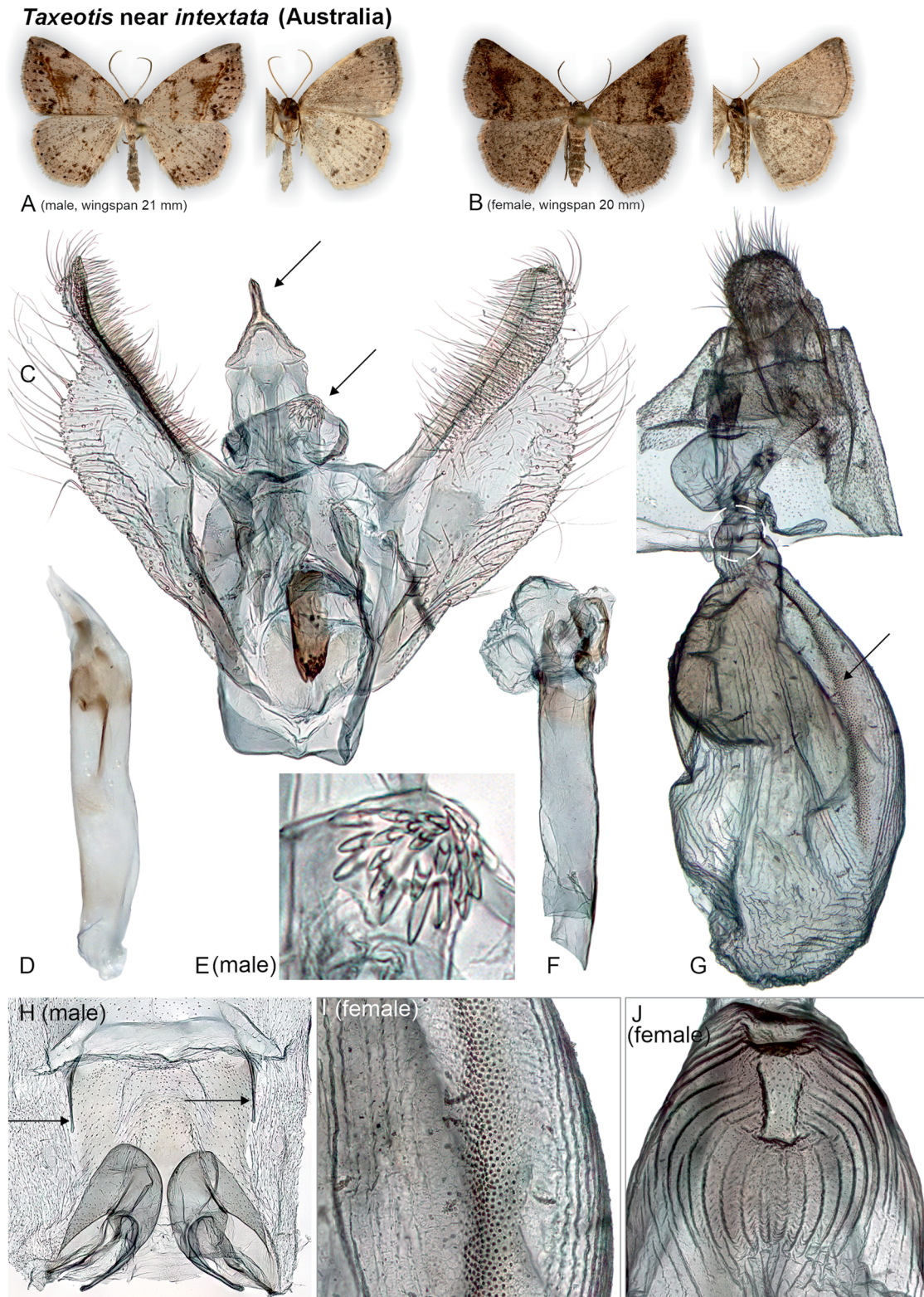


Fig. 3. Selected morphological structures of *Taxeotis* nr. *intextata* (Guenée, 1858). *Taxeotis* Guest, 1887, is transferred from Oenochrominae s. l. to Desmobathrinae (new subfamily classification).

***Cathaemacta thermistis* (Australia)**

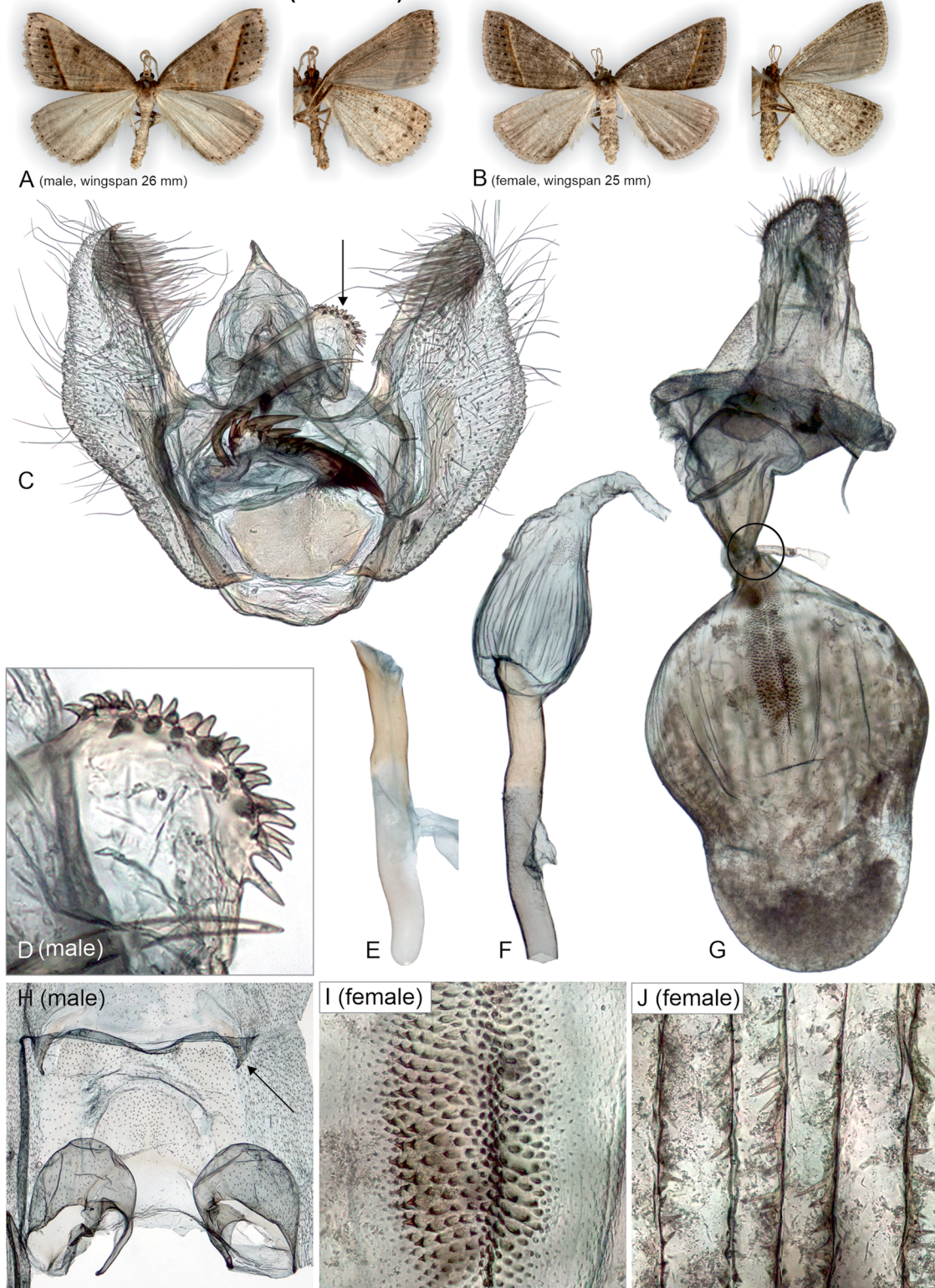


Fig. 4. Selected morphological structures of *Cathaemacta thermistis* (Lower, 1894). *Cathaemacta* Turner, 1942 is transferred from Oenochrominae s. l. to Desmobathrinae (**new subfamily classification**).

extent of morphological variation is not yet understood, or *Taxeotis* may be a heterogeneous lineage needing reclassification into several genera. Despite this, we propose *Aglossophanes* Turner, 1942 **syn. nov.** to be a junior synonym of *Taxeotis*

Guest, 1887, to highlight the close relationship and transfer both to Desmobathrinae (Table 1).

Two other Australian genera, which were classified in Oenochrominae s. l. earlier (Scoble and Edwards 1989;

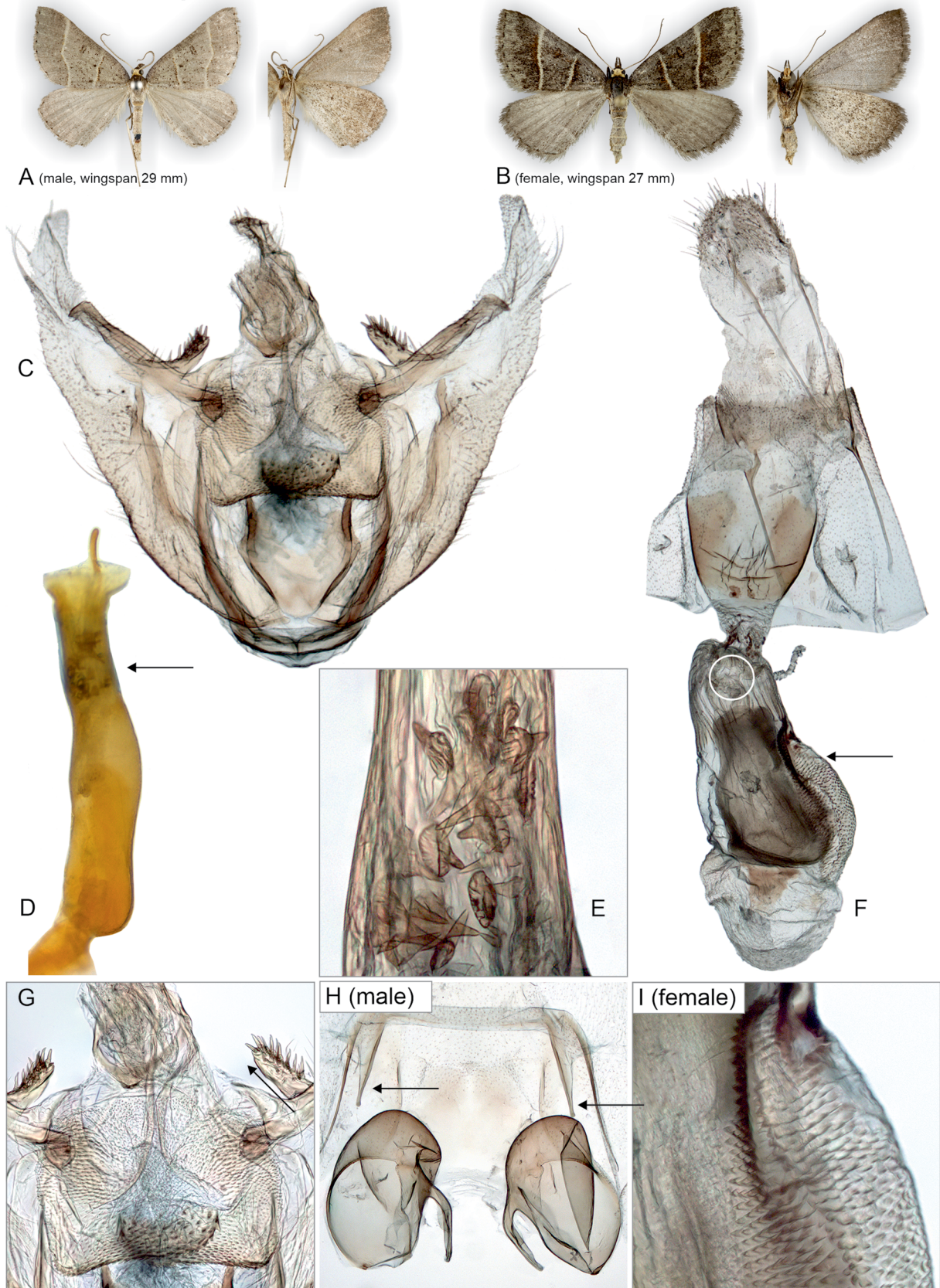
***Antasia flavicapitata* (Australia)**

Fig. 5. Selected morphological structures of *Antasia flavicapitata* (Guenée, 1858). *Antasia* Turner, 1930 is transferred from Oenochrominae s. l. to Desmobathrinae (new subfamily classification).

***Axiagasta rhodobaphes* (Australia)**

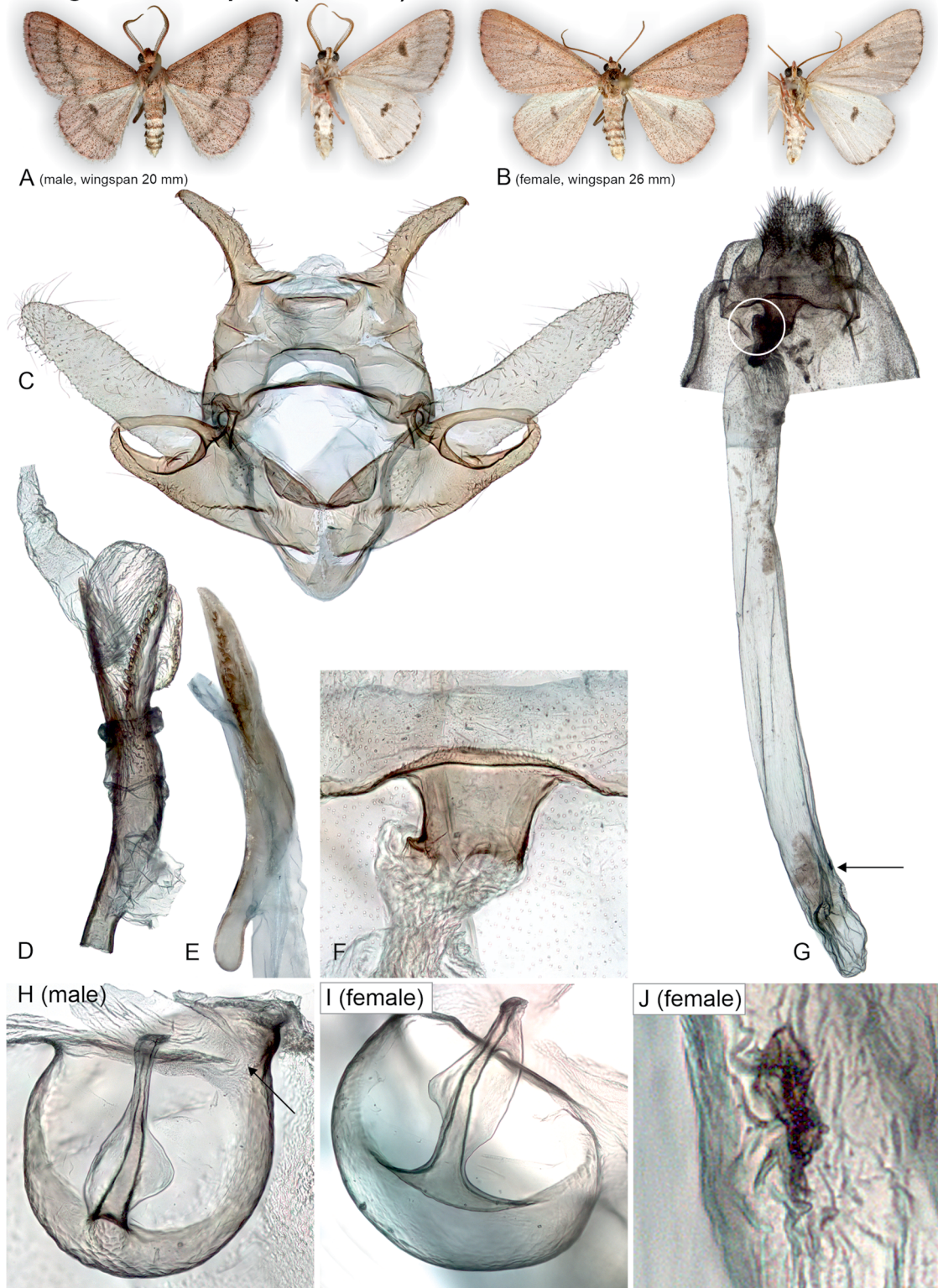


Fig. 6. Selected morphological structures of *Axiagasta rhodobaphes* Turner, 1930. *Axiagasta* Turner, 1930, is transferred from Oenochrominae s. l. to Desmobathrinae (**new subfamily classification**).

McQuillan and Edwards 1996; Rajaei et al. 2022), also fall within Desmobathrinae in this study: *Antasia* and *Cathaemacta*. *Antasia* is a monotypic genus, while *Cathaemacta* currently

comprises 2 species. Both genera have the diagnostic desmobathrine character, namely the male apophyses arising from the membrane between the second and third sternites (Figs 4

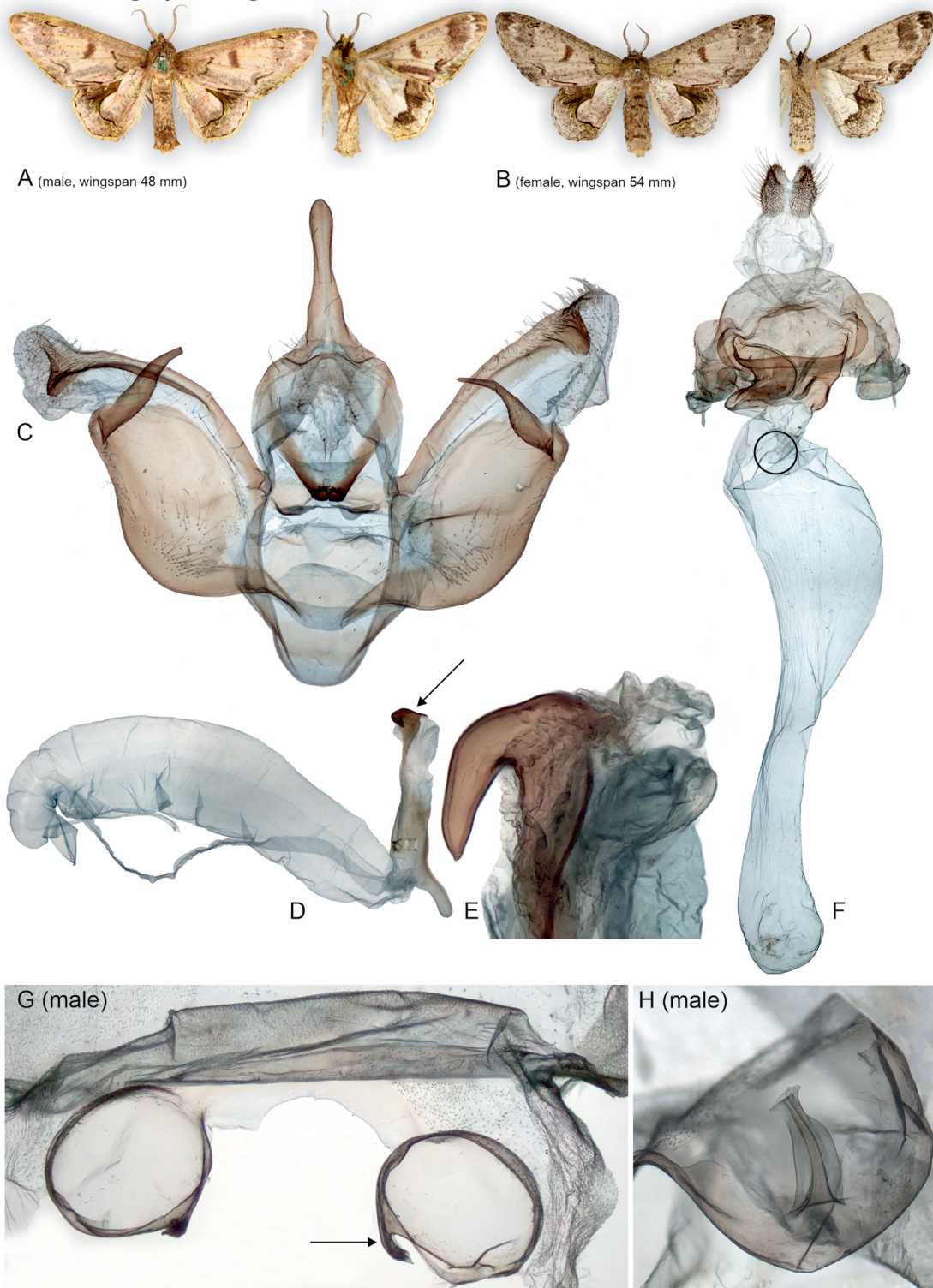
***Thaumatographe singularis* (Papua New-Guinea)**

Fig. 7. Selected morphological structures of *Thaumatographe singularis* Warren, 1907. *Thaumatographe* Warren, 1907, classified in Oenochrominae earlier, is now classified as *incertae sedis*.

and 5). Given the phylogenetic position of these genera in our analyses, we propose to also transfer these lineages to Desmobathrinae (see Table 1).

Axiagasta was nested within the Ennominae: Ennomini (Supplement S2). This position is unexpected from a

morphological point of view (Fig. 6), because hindwing vein M2 is present as fully developed, while the vast majority of Ennominae lack tubular M2 (see Pitkin 2002, Sihvonen et al. 2015 for other exceptions). Otherwise, the adult morphology is not particularly informative on subfamily-level classification.

***Xyridacma ustaria* (New Zealand)**

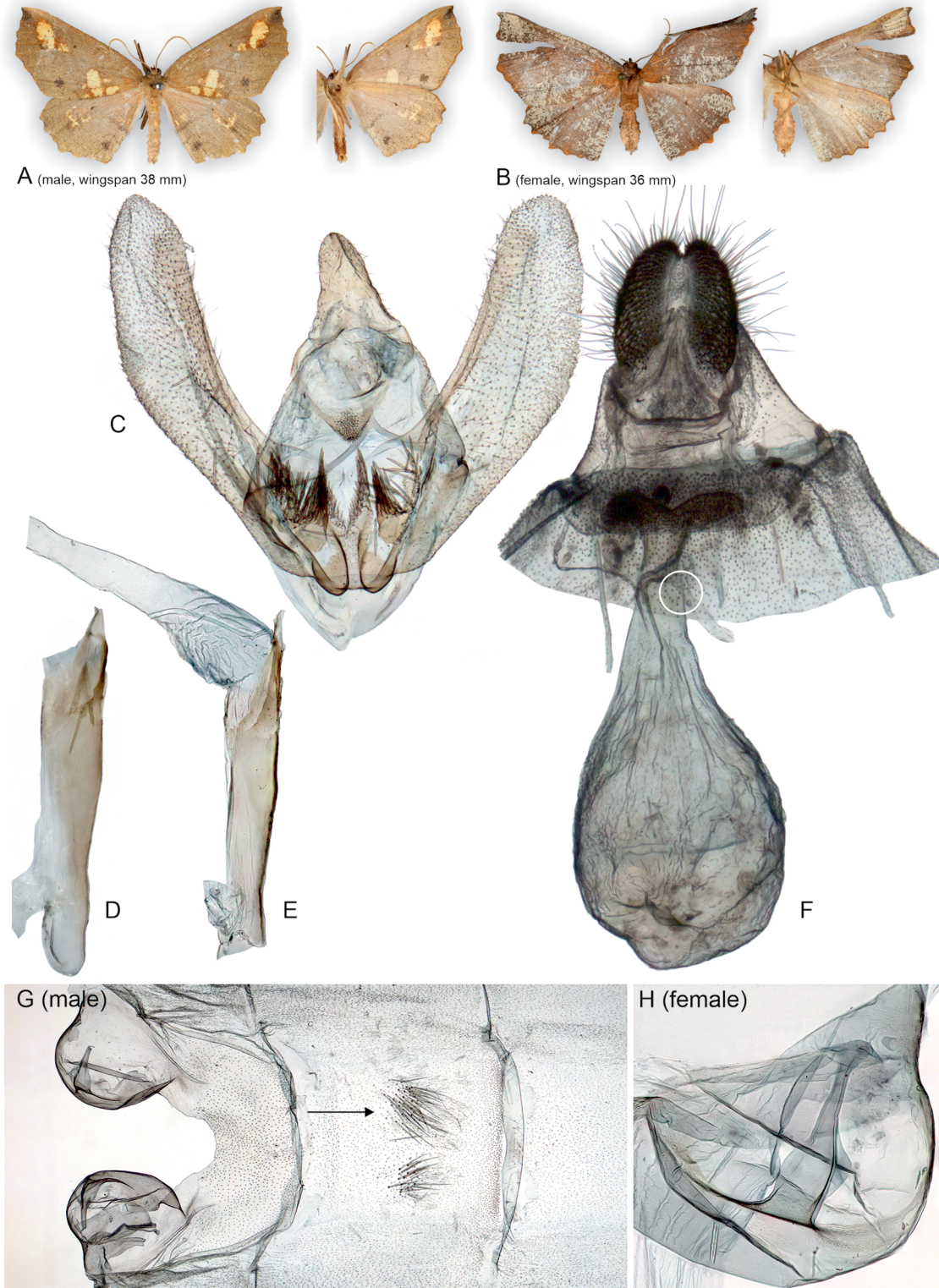


Fig. 8. Selected morphological structures of *Xyridacma ustaria* (Walker, 1863). *Xyridacma* Meyrick, 1888, classified in Oenochrominae earlier, is now classified as *incertae sedis*.

Unfortunately, only 2 genes (Ca-ATPase and COI-begin) were successful for *Axiagasta*, so molecular data are limited. We transfer *Axiagasta* Turner, 1930 from Oenochrominae (eg [Rajaei et al. 2022](#)) to Ennominae, but note that more research is needed.

Other Oenochrominae *s. l.* analyzed in this study were *Xyridacma*, *Symphylistis* and *Thaumatographe*. Surprisingly, *Xyridacma*, which is an endemic genus from New Zealand, was recovered sister to Epidesmiinae in analyses partitioned by gene and the sister to Archearinae in analyses partitioned by codon.

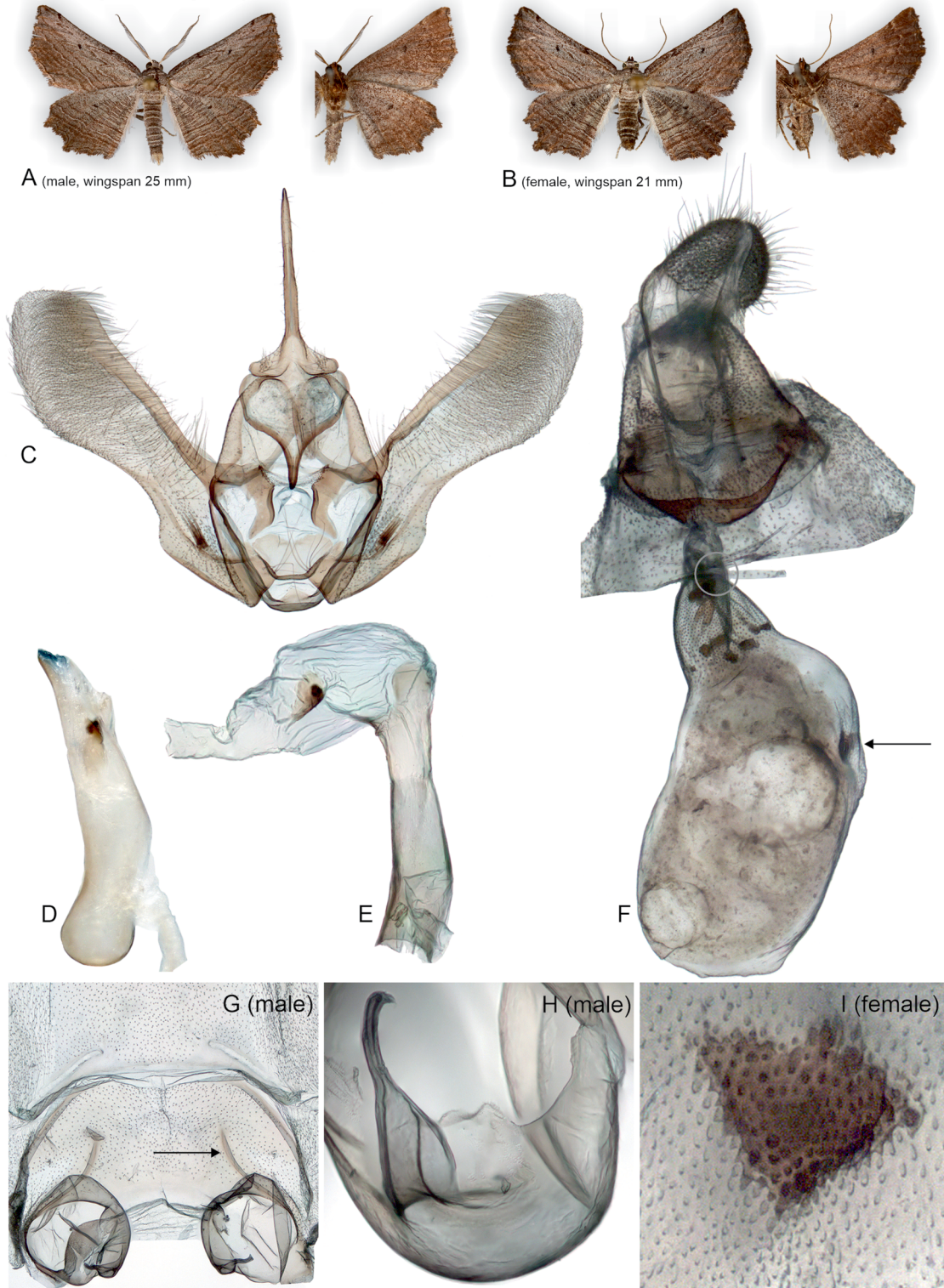
***Symphylistis leptocyma* (Australia)**

Fig. 9. Selected morphological structures of *Symphylistis leptocyma* Turner, 1930. *Symphylistis* Turner, 1930, classified in Oenochrominae earlier, is now classified as *incertae sedis*.

Regardless of the cause, further analyses are needed to clarify the taxonomic position of *Xyridacma*. Regarding the morphology (Fig. 8), the examined structures do not offer firm support for subfamily-level classification. The overall external appearance and the setae on the third male sternite support

classification in Ennominae, whereas the developed tubular hindwing vein M2 contradicts classification in Ennominae. Furthermore, typical Epidesmiinae structures, such as the double signum in the female genitalia, and elongated labial palpi, are absent in *Xyridacma*. The putative association with Archearinae

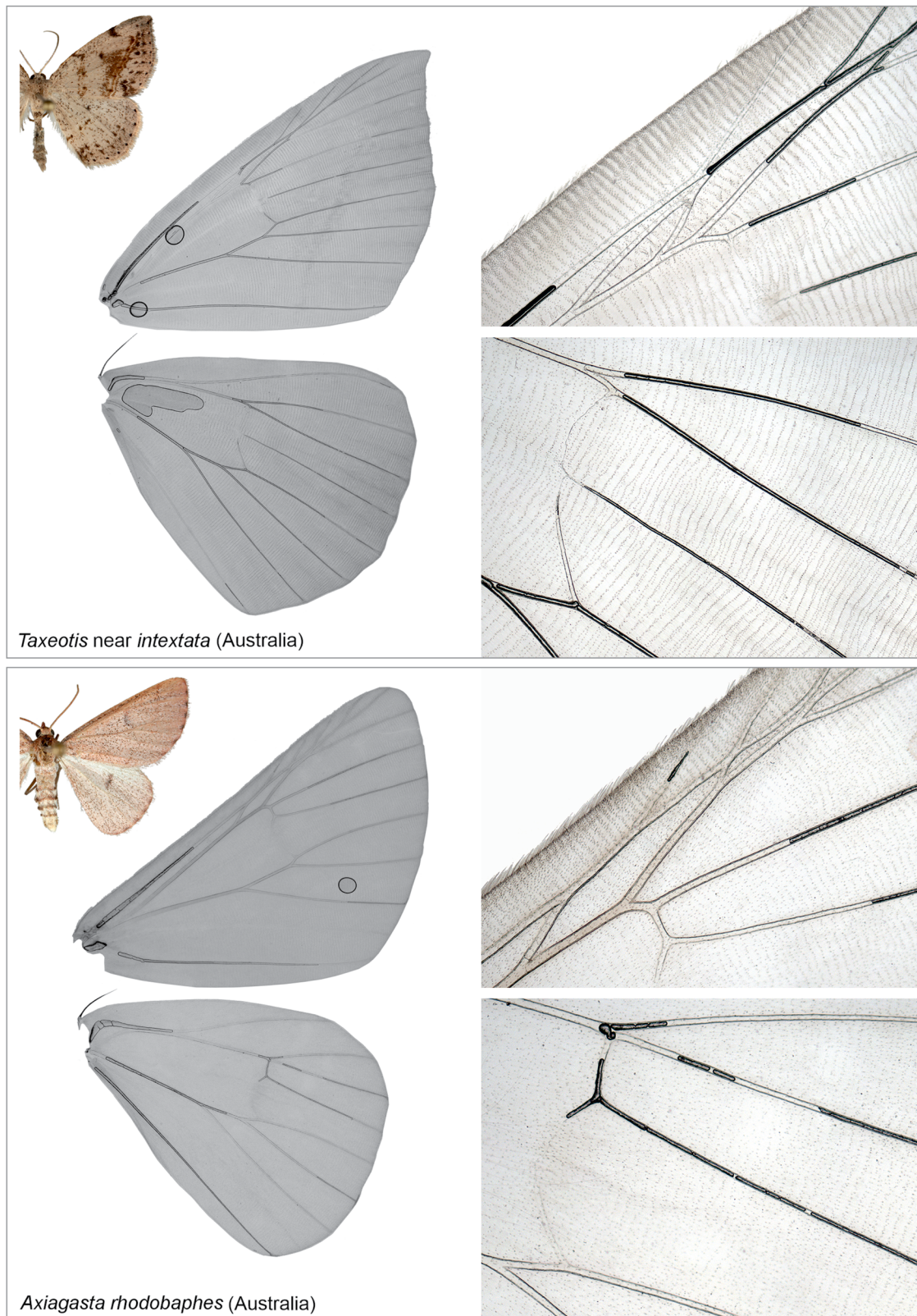


Fig. 10. Wing venation of *Taxeotis* nr. *intextata* and *Axiagasta* *rhodobaphes*. Left panel shows the entire wings and venation, the right panel shows parts of the venation enlarged. *Taxeotis* is now classified in Desmobaethrinae and *Axiagasta* in Ennominae. See text for details.

is unlikely due to biogeography, and the caterpillar of *X. ustaria* <https://inaturalist.nz/taxa/410463-Xyridacma-ustaria> does not have the additional prolegs on segments A3 to A6, which are

characteristic in the Holarctic Archiearinae (Hausmann 2001). As with many other Oenochrominae s. l. genera, we lack detailed natural history data on *Xyridacma*. The species are commonly

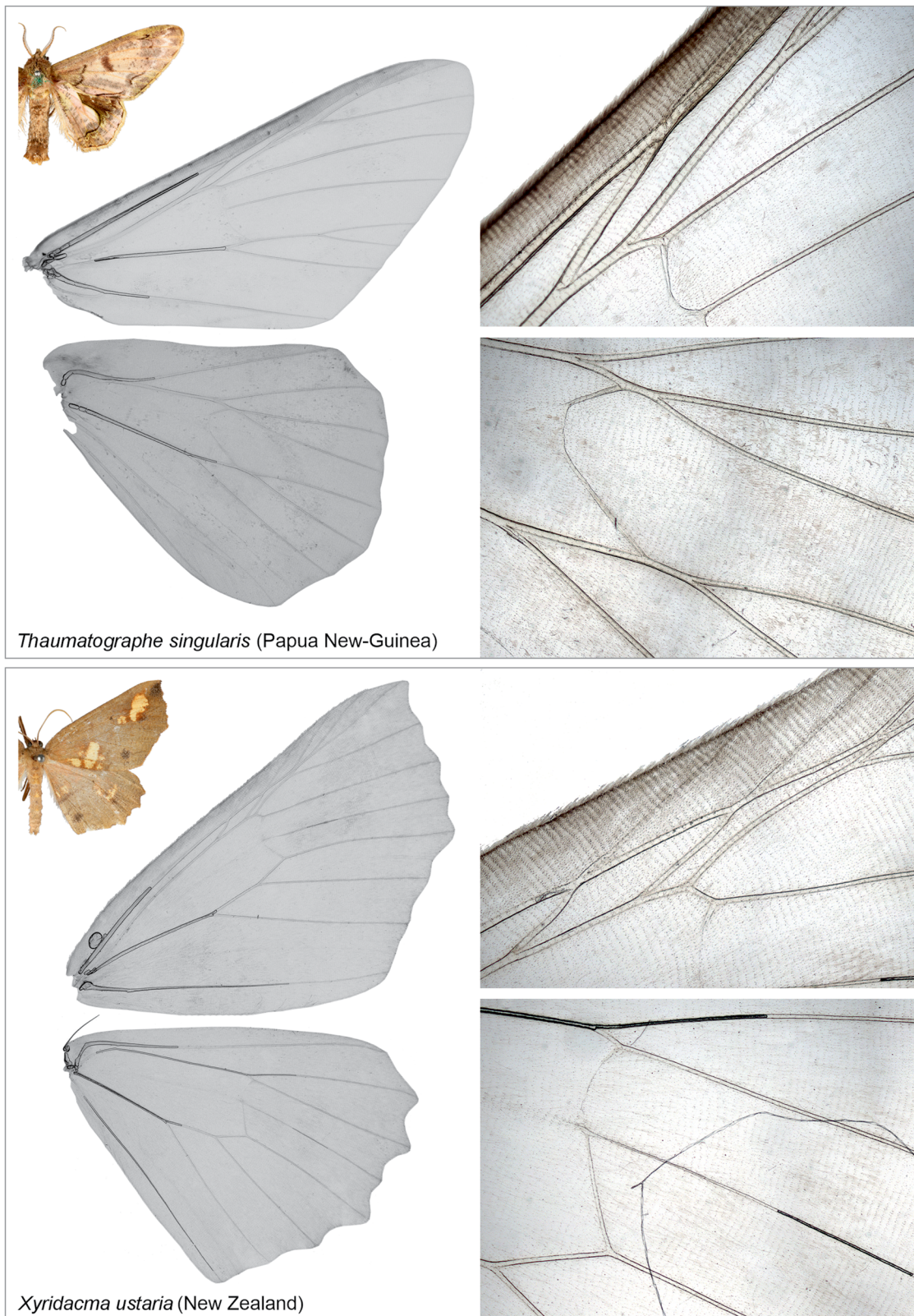


Fig. 11. Wing venation of *Thaumatographe singularis* and *Xyridacma ustaria*. Left panel shows the entire wings and venation, the right panel shows parts of the venation enlarged. Both *Thaumatographe* and *Xyridacma* are now classified as *incertae sedis*. See text for details.

known as 5-finger looper moths because caterpillars feed on the leaves of native 5-finger species (Araliaceae). The adults are rarely observed, but there is some data on caterpillar activity from November to January <https://www.citscihub.nz/>.

Thaumatographe is morphologically an isolated, monotypic genus, and its only species *T. singularis* Warren, 1907 is known to occur only in New Guinea (Figs 7 and 11). It has been classified in Oenochrominae based on the hindwing venation,



Symphylistis leptocyma (Australia)

Fig. 12. Wing venation of *Symphylistis leptocyma* Turner, 1930. *Symphylistis* Turner, 1930, classified in Oenochrominae earlier, is now classified as *incertae sedis*.

which resembles the oenochromine genus *Sarcinodes* Guenée, 1858 (Warren 1907, Prout 1920–1941). In our molecular analysis *Thaumatographe* grouped in the Geometrinae: Chlorodontoperini (Supplemental S2), a recently described tribe (Murillo-Ramos et al. 2019). This position is unexpected because *Chlorodontopera* (see, eg Holloway 1996) and *Thaumatographe* (Supplemental S2) do not resemble each other externally, and other morphological characters including those of the abdomen, genitalia and wing venation are not similar. Structurally *Thaumatographe* shows similarities with the oenochromine genus *Sarcinodes* in wing venation, with *Parepisparis* (see Scoble and Edwards 1989) and relatives such as *Homospora* Turner, 1904 and *Antictenia* Prout, 1910 (our observation). The latter for instance has small and round tympanal organs, divided valvae, elongated and melanized papillae anales, a strongly sclerotized and complex ostium bursae region and a long and narrow corpus bursae (Fig. 7). The resting position, with forewings rolled and hindwings partially folded over the abdomen, resembles Uraniidae, subfamily Epipleminae (see <https://www.inaturalist.org/observations/135300253>), but this association is not supported by morphology (eg Minet and Scoble 1999), nor our molecular phylogeny. We classify *Thaumatographe* as *incertae sedis*, noting that molecular data supports placement into Geometrinae, while morphological data indicates an affinity with Oenochrominae s. s.

Symphylistis is a monotypic Australian genus (Turner, 1930). Morphology (Figs 9 and 12) does not give clear indications on its phylogenetic position. The moths are slenderly built, with wide triangular forewings, unlike the majority of Oenochrominae s. s., which are robust, with forewings narrower and elongated. Further, the sclerotized grooves on the second male sternite are unique among the examined taxa,

while some structures like the uncus-socii-gnathos complex and cristate hairs are found widely in Ennominae, occurring, for instance, in the Diptychini of the Southern Hemisphere (Young 2008 [as Nacophorini], Krüger 2014). The ansa of the tympanal organ is like several Desmobaethrinae, and the one areole condition on the forewing is widespread in Geometridae. Female genitalia are rather simple, without distinct sclerotizations, except small, plate-like signum. Only 3 genes were successfully sequenced (ArgK, Ca-ATPase and COI-begin), so we classify *Symphylistis* as *incertae sedis*, highlighting that more research is needed.

Conclusions

We demonstrate that the systematics of Oenochrominae s. l., which are known to be an unnatural assemblage of geometrid moths, can be resolved by integrating molecular and morphological data. Oenochrominae s. s. occur mostly in the Australian realm, and therefore, our focus on the *sensu lato* concept focused on Australian taxa. The majority of reclassified Oenochrominae s. l. taxa from Australia were classified in Desmobaethrinae. More research is needed to test the placement of the non-Australian genera that were not included here.

With a better understanding of the evolutionary relationships among these moths and their classification into monophyletic groups, other biological aspects, such as host plant associations and biogeography, can be studied within an evolutionary framework. We emphasize that our conclusions are based on limited data; however, this is common in taxonomy. In many studies, especially within species-rich groups like Geometridae, achieving complete certainty regarding relationships and classification is rarely possible.

We acknowledge that future research will likely refine or revise our findings, either by us or others. Nonetheless, we hope our article serves as an inspiration and encourages further investigation into these fascinating moths.

Nomenclature

This paper and the nomenclatural act it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:0533B2D3-A677-45A0-8ED8-330C6079C9B2.

Acknowledgements

Andreas Zwick and You Ning Su (Australian National Insect Collection, Canberra, Australia) and Geoff Martin (The Natural History Museum, London, UK) are thanked for loaning the material for our study, Suresh Naik, Evgeny V. Zakharov and Vanessa Bouwer (CCDB Canadian Centre for Biodiversity Genomics, University of Guelph, Canada) are thanked for arranging the DNA extracts for our study.

Author Contributions

Pasi Sihvonen (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Funding acquisition [lead], Investigation [equal], Methodology [equal], Project administration [equal], Supervision [equal], Validation [equal], Visualization [equal], Writing—original draft [equal]), Hamid R. Ghanavi (Data curation [equal], Methodology [equal], Writing—review & editing [equal]), Kyung Min Lee (Data curation [equal], Investigation [equal], Methodology [equal], Project administration [equal], Writing—review & editing [equal]), Elina Laiho (Data curation [equal], Methodology [equal], Writing—review & editing [equal]), Axel Hausmann (Data curation [equal], Methodology [equal], Resources [equal], Writing—review & editing [equal]), Hermann Staudé (Data curation [equal], Investigation [equal], Resources [equal], Writing—review & editing [equal]), Friedrich Egbert (Data curation [equal], Resources [equal], Writing—review & editing [equal]), Gunnar Brehm (Data curation [equal], Resources [equal], Writing—review & editing [equal]), Hossein Rajaei (Data curation [equal], Resources [equal], Validation [equal], Writing—review & editing [equal]), and Leidys del Carmen Murillo-Ramos (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Investigation [equal], Methodology [equal], Resources [equal], Software [equal], Supervision [equal], Validation [equal], Visualization [equal], Writing—original draft [equal])

Supplementary Material

Supplementary material is available at *Insect Systematics and Diversity* online.

Funding

Pasi Sihvonen acknowledges funding from the Research Council of Finland (decision number 331995). Research visits of Pasi Sihvonen to the Natural History Museum, London, in 2021 and Leidys Murillo Ramos to Finnish Museum of Natural

History, University of Helsinki in 2019 were funded by SYNTHESYS+ project (EU Horizon2020, INFRAIA-2018-2020).

Conflicts of Interest

None declared.

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