A morphological appraisal of the new subfamily Epidesmiinae (Lepidoptera: Geometridae) with an overview of all geometrid subfamilies

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Our study revises Epidesmiinae, the first new Geometridae subfamily that has been described in 127 years. We studied the morphological characters of representatives from all genera currently classified into Epidesmiinae, and compared those with all other geometrid subfamilies. Epidesmiinae were found to have an Australasian distribution, with one species occurring in the Indo-Malayan realm. They compose a lineage diagnosable by a combination of the following morphological characters: male antennae unipectinate; labial palps elongated (particularly the second segment), vom Raths's organ with an elliptical invagination; forewing with two areoles; hindwing with one anal vein; gnathos arms fused, granulate or dentate apically; female genitalia with two signa, one stellate, another an elongated and spinose plate. We also present a summary of diagnostic characters of all geometrid subfamilies, which confirm the lack of single unique morphological characters. The limited information on the biology and ecology of Epidesmiinae species are summarized, indicating that some species fly during the day, most adult records are from the Southern Hemisphere summer months and larvae are found on Myrtaceae. We transfer *Arcina* Walker, 1863 from Oenochrominae *s.l.* to Epidesmiinae. Epidesmiinae includes 102 species that are now classified into nine genera: *Abraxaphantes*, *Adeixis*, *Arcina*, *Dichromodes*, *Ecphyas*, *Epidesmia*, *Phrataria*, *Phrixocomes* and *Systatica*.

ADDITIONAL KEYWORDS: Australian moths – Desmobathrinae – *Epidesmia* – Oenochrominae.

INTRODUCTION

The systematics of geometrid moths (Lepidoptera: Geometridae) have developed gradually and the classifications have mostly been based on morphological features until the beginning of the 21st century. Early classifications relied on external features such as wing pattern, wing venation and the morphology of larvae and pupae. These were complemented by morphological studies of the abdomen, reproductive organs and other sclerites. Perhaps surprisingly, only few papers exist on geometrid systematics that have examined morphological characters in an analytical phylogenetic context. Examples include the following: Oenochrominae, *Sarcinodes* Guenée, 1857 (Holloway, 1996); Larentiinae, Cidariini (Choi, 1997); Ennominae, Abraxini (Choi *et al.*, 1998); Larentiinae, *Eulithis* Hübner, 1821 (Choi, 2001); Sterrhinae (Sihvonen & Kaila, 2004); Sterrhinae, Scopulini (Sihvonen, 2005); Australian Ennominae (Young, 2006, 2008) and the entire Ditrysia, in which Geometridae morphology was examined for ten species (Heikkilä *et al.*, 2015). Morphology has been studied extensively in taxonomic papers, but despite this, all attempts have failed to find unique, synapomorphic characters common to all members of each geometrid subfamily. Instead, subfamilies are supported by a combination of characters and when applied together, they support monophyletic entities. The lack of unique

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characters could be explained by convergent/parallel evolution of characters in lineages (Scoble, 1989) leading to a high frequency of homoplasy. Within Lepidoptera, homoplasy has been found to be high in the entire Ditrysia (Heikkilä *et al.*, 2015).

The rapid development of molecular techniques, sophisticated analyses and coordinated efforts on extensive taxon sampling have allowed testing of phylogenetic hypotheses of geometrid moths. Such studies have largely agreed with earlier findings on the subfamily level and the monophyly of many morphologically diagnosed subfamilies were supported (Sihvonen *et al.*, 2011; Murillo-Ramos *et al.*, 2019). Although molecular data have distinct advantages over morphological data, they provide no insight into taxon morphology or diagnostic phenotypical features. It is evident that a holistic approach is needed, and molecular data should be supplemented with evidence from ecology, life history, distribution and phenology, to name a few.

The focus of this study is the Epidesmiinae, a subfamily of Geometridae recently described and diagnosed by molecular data (Murillo-Ramos *et al.*, 2019). Currently, this lineage comprises the following eight genera: *Abraxaphantes* Swinhoe, 1890, *Adeixis* Warren, 1897, *Dichromodes* Guenée, 1857, *Ecphyas* Turner, 1929, *Epidesmia* Duncan & Westwood, 1841, *Phrataria* Walker, 1863, *Phrixocomes* Turner, 1930 and *Systatica* Turner, 1904. These genera include 101 species, of which 70% belong to *Dichromodes*. Epidesmiinae have an Australasian distribution, except the monotypic genus *Abraxaphantes*, which occurs in the Indo-Malay realm. Many species are diurnal and fly in dry, shrubby or forested areas (Marriott, 2012). Apart from this sparse information, almost all aspects of their biology, structural morphology and classification below the level of subfamily are unknown. Epidesmiinae are defined by their type genus *Epidesmia* Duncan & Westwood, 1841, and the type species is the Australian *Epidesmia tricolor* Westwood, 1841.

Before the recent molecular diagnosis and description of the Epidesmiinae (Murillo-Ramos *et al.*, 2019), the included taxa were not classified as a monophyletic group but as part of the Oenochrominae–Desmobathrinae complex. Guenée (1857) described a group of taxa formed by the genera *Arhodia* Guenée, 1857, *Gastrophora* Guenée, 1857, *Hypographa* Guenée, 1857, *Monoctenia* Guenée, 1857, *Oenochroma* Guenée, 1857, *Phallaria* Guenée, 1857 and *Sarcinodes* as Oenochrominae. This group of robust-bodied genera that occurs mostly in Australia, together with a few others, have been repeatedly classified as Oenochrominae *s.s.* (Scoble & Edwards, 1989; Holloway, 1996; Murillo-Ramos *et al.*, 2019). Confusion arose when the original Oenochrominae concept of Guenée was expanded by Meyrick (1889)

into Oenochrominae *s.l.*, naming it Monoctenidae (currently a junior synonym of Oenochrominae; see, for instance: Holloway, 1996), based on the form of veins Sc + R1 and Rs in the hindwing. The classification history is summarized by Scoble & Edwards (1989), and as they pointed out (p. 372): 'The variation expressed in [Meyrick's diagnostic] passage immediately suggests that the [wing venation] character is of dubious value…'. Hence, Meyrick (1889) made the Oenochrominae into an unnatural group, and this may later have resulted in a tendency to place further genera into the subfamily that do not fit into any other geometrid subfamily [modified from Scoble & Edwards (1989); see also Sommerer (1995)]. Although Meyrick's concept was acknowledged as an unnatural assemblage, it was applied by Prout (1910, 1920) and Turner (1929; 1930a, 1930b), probably as a way to avoid classifying taxa as *incertae sedis*. In his revision, Turner described considerable variation in the wing venation of what he called the *Oenochroma* group (currently Oenochrominae) and the *Dichromodes* group (all now Epidesmiinae).

Cook & Scoble (1992) reviewed the tympanal organs of geometrid moths and suggested the circular form of the lacinia and its orientation parallel to the tympanum as a potential synapomorphy of the robust-bodied Oenochrominae *s.s.* The genera that did not fit the definition were listed as Oenochrominae *s.l.* and it contained among others *Abraxaphantes*, *Dichromodes* and *Epidesmia* (all now Epidesmiinae).

Holloway (1996), based on his earlier work (Holloway, 1984), revived Desmobathrinae to subfamily level to include delicately built genera with elongated, slender appendages, previously classified in the Oenochrominae. Desmobathrinae are globally distributed, but almost entirely tropical and subtropical. Desmobathrinae included the Bornean genera *Celerena* Walker, 1865, *Derambila* Walker, 1863 and *Ozola* Walker, 1862 and a few others, as summarized in the checklist of the moths of Borneo (Holloway, 2011).

In the Australian checklist, Holloway's Desmobathrinae were not recognized, and all relevant genera were classified as Oenochrominae *s.l.* (McQuillan & Edwards, 1996; Nielsen *et al.*, 1996). This group of 24 genera also included all Australian genera now classified in Epidesmiinae, and the matter was commented upon briefly (p. 68): 'Another group of slender-bodied moths is placed in the Oenochrominae in the broad sense also with many Australian genera including *Taxeotis* Guest [currently Oenochrominae *s.l.*] and *Dichromodes* Guenée [currently Epidesmiinae]'. Scoble (1999) classified all genera now included in Epidesmiinae as Oenochrominae. Beljaev (2008) transferred *Abraxaphantes*, *Dichromodes*, *Epidesmia* and *Heteralex* Warren, 1894 to Desmobathrinae as

'basal group of Desmobathrinae *s. l.*', and the abovementioned genus *Celerena* from Desmobathrinae to Geometrinae. Marriott (2012), in his *Moths of Victoria*, followed Scoble (1999) and classified genera now assigned to Epidesmiinae as Oenochrominae *s. l.*, noting that they did not form a fully coherent group.

The taxonomic impediment and the polyphyletic nature of Oenochrominae *s. l.* have been clarified partly in recent years by transferring relevant taxa into other subfamilies (e.g. Scoble, 1986; Sihvonen & Staude, 2011; Sihvonen *et al.* 2015, 2020). In addition to the confusing taxonomic history of this group, it is worth noting that the different classifications summarized above were justified briefly or not at all, i.e. they were authoritative without basis. Virtually nothing has been published on the morphology of genera now classified in Epidesmiinae. The only accounts we could find are schematic drawings of wing venations of the few genera (Turner, 1929; 1930a, 1930b), and descriptions and illustrations of four *Adeixis* species from New Caledonia, including male and female genitalia. In the latter, *Adeixis* was classified in Oenochrominae (Holloway, 1979). Beljaev (2008) provided schematic drawings of the male genitalia of *Epidesmia chilonaria* Herrich-Schäffer, 1855 and *Dichromodes ainaria* Guénée, 1858, both as Desmobathrinae *s. l.* Several *Dichromodes* adults were illustrated in a study that examined symmetry systems in the wings (Schachat, 2020), and a few type specimens of *Dichromodes*, *Ecphyas* Turner, 1929 and *Epidesmia* were illustrated in Schmidt (2012), classified as Oenochrominae *s.l.*

Our paper provides the first overview of Epidesmiinae as a valid and monophyletic geometrid subfamily. We provide a diagnosis for the clade, illustrations at genus-level within Epidesmiinae and compare the subfamily traits against all other Geometridae subfamilies in a global context. We summarize the distribution of Epidesmiinae and provide information on immature stages, life histories, habitats and phenology. We regard this as an important contribution because Epidesmiinae is the first new Geometridae subfamily that has been described in 127 years, and the molecular phylogenetic hypothesis (Murillo-Ramos *et al.*, 2019) should be accompanied by proper diagnoses, descriptions and illustrations. These will aid subsequent authors in deciding which oenochromine and other geometrid genera should be included in the Epidesmiinae.

MATERIAL AND METHODS

The morphological review included representatives and type species for all Epidesmiinae genera recognized by Murillo-Ramos *et al.* (2019), as well as representatives and type species of all Geometridae subfamilies for the comparisons. Furthermore, all Australian genera classified as Oenochrominae *s. l.* by McQuillan & Edwards (1996) were examined externally, and the ones that could potentially belong to Epidesmiinae, were dissected and their morphology was examined.

Specimens were loaned and examined 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). The authentic material and observations were supplemented by literature sources.

Dissected and examined Epidesmiinae material

Abraxaphantes perampla (Swinhoe, 1890). Thailand, Chiangmai, Thoeng Dang, 7.04.2006, M. J. Pellinen leg. Preparation numbers: PS2802 (♀), PS2801 (♂), PS2803 (♂) (coll. Sihvonen).

Adeixis inostentata (Walker, 1861) [identity of *A. inostentata* is after Holloway (1979)]. New Caledonia. Gran Lac. 250m. Site 4. 06980/15367. J. D. Holloway. 19.5.1971. B. M. 1971-507. NHMUK ID labels: 012832641 (♀), NHMUK 012832640 (♂). Preparation numbers: PS2807 (♀), PS2806 (♂) (coll. NHMUK).

Adeixis griseata (Hudson, 1903). (♀). New Zealand, 43.15S 170.12E, W. D. Okarito, 27 Jan 2009, Hoare, Kaila & Kullberg. https://kotka.luomus.fi/view?uri=http://id.luomus.fi/HV.134. Preparation number: PS2819 (coll. ZMH).

Dichromodes indicataria (Walker, 1866). (Australia) Victoria E. Anderson. L. B. Prout Coll. B.M. 1939-643. NHMUK ID labels: NHMUK 012832634 (♀), NHMUK 012832633 (♂). Preparation numbers: PS2810 (♀), PS2809 (♂) (coll. NHMUK).

Dichromodes haematopa Turner, 1906. (♂): 28.32S 114.39E. Howatharra. Nat Res. 35 km NE. Geraldton WA. 1 Oct 1999. L. Kaila. Preparation number: LMR7 (coll. ZMH).

Ecphyas holopsara Turner, 1929. (♀): Australia-WA. Leeuwin-Naturaliste NP Boranup Dr[ive] Anchor Rd 34º08'41"S 115º04'11"E. 5.1.2015 lux. 100 m. leg. Egbert Friedrich. Preparation number: LMR3 (coll. Friedrich). (♂): ANIC Specimen. 35.05 S 117.55 E. Torndirrup N. P. Albany WA 5 Jan 1993 GPS E. D Edwards, E. S. Nielsen. Preparation number: LMR29 (coll. ANIC).

Epidesmia tricolor Westwood, 1841. (♀): NHMUK ID label: 010612396. 58:124 Australia. Preparation number: PS2805 (coll. NHMUK); ANIC Specimen. 22.12.1974. Lindfield NSW M. Pulvertaft. Preparation number: LMR22 (coll. ANIC). (♂): NHMUK ID label: 012832635. Pres. by Lady Lochore. Coll. B. M. 1946-341. Preparation number: PS2805 (coll. NHMUK).

Epidesmia chilonaria (Herrich-Schäffer, 1855). (♀): Australia-Victoria. East Gippsland, 25 km SE. Cann River, N Thurra River 65m 37º46'25"S 149º18'44"E. 1.1.2012 lux. leg. Egbert Friedrich. Preparation number: LMR1 (coll. Friedrich). (♂): Australia-QLD. Brisb. Forest, Camp Mountain, 413m ü NN 27º24'46"S 152º52'39"E. 26.12.2005 a.L. [at light] leg. E. Friedrich. Preparation number: PS2799 (coll. Friedrich).

Phrixocomes ophiucha (Meyrick, 1890). (♂): NHMUK ID label: 012832632. L. B. Prout Coll. B.M. 1939-643. National P. K. Sydney. 27 Sept 25. Preparation number: PS2811 (coll. NHMUK).

Phrixocomes ptilomacra (Lower, 1892). ANIC Specimens. (Australia) 33.40 S 123.11 E. 37 km SW of Mt. Ragged WA. 2 Nov 1977. M. S. Upton. Preparation number: LMR27 (♀), LMR26 (♂) (coll. ANIC).

Phrataria transcissata Walker, 1863. (♂): Australia, 35.16S 149.06E, Black Mountain summit, Canberra, ACT, 17.2.1999 BL, L. Kaila; https://kotka.luomus.fi/view?uri=http://id.luomus.fi/HV.137. Preparation number: PS2797 (coll. ZMH).

Phrataria replicataria Walker, 1866. NHMUK ID label: 012832639 (♀). (Australia) Gisborne, V. 10.3.1901. G. Lyell. L. B. Prout Coll. B. M. 1939-643. Lyell P.56. Seitz XII. Preparation number: PS2815 (coll. NHMUK). NHMUK ID label: 012832638 (♂). Rothschild Bequest B.M. 1939-I- (A. Simson). (Australia) Gisborne 17. 2.1901. Preparation number: PS2814 (coll. NHMUK).

Systatica xanthastis (Lower, 1894). Australia-Victoria. East Gippsland, 15 km W Cann River, Lind NP, Euchre Valley, 300m. 37º35'13"S 148º59'22"E. 2.1.2012 lux. leg. Egbert Friedrich. Preparation number: PS2798 (♂) (coll. Friedrich). (Australia) 28.11 S 153.11 E, Binna Burra, Lamington Nat, Park QLD 700m, 15 Nov. 1992, I. F. B. Common; ANIC Specimen. Preparation number: PS2826 (♀) (coll. ANIC).

Arcina fulgorigera Walker, 1863. ANIC specimens. BoldID ANICO645-10 (♀) and BoldID ANICO645-10 (♂). (Australia) 32.48 S 116.05 E. Icy Creek. Lane Poole Res. WA. 26 Oct 2005. A. Zwick. Preparation number: LMR23 (♀), PS2816 (♀) (coll. ANIC). (Australia) 34.26 S 116.38 E, Lake Muir Rd, Talling SF, WA, 200 m GPS, 3 Nov 2003, A. Zwick. Preparation number: PS2820 (♂) (coll. ANIC).

SPECIMEN PREPARATION AND PHOTOGRAPHY

Genitalia dissections were prepared according to the methods implemented in Sihvonen (2005). The abdomens were briefly put in 10% potassium hydroxide (KOH) solution and heated at 92 ºC for 5–7 min to remove fat and other soft tissue, and cleaned in water and ethanol with small brushes. Some structures were photographed during dissection *in situ*, to allow an optimal angle for observing and illustrating certain

structures. The male vesica was everted via the caecum that was cut open by placing the aedeagus inside a hypodermic syringe (Sihvonen, 2001, 2005). Before preparing the head and thorax, the wings were removed and prepared (as described below), or glued to a piece of plastic with original labels. The head and thorax, attached to the original pin, were placed in a 10% KOH solution and kept at room temperature for 12–15 h. Following this treatment, scales were removed with brushes. The metathorax was separated from the mesothorax at the intersegmental membrane using forceps. All structures were stained with Chlorazol black. Preparations of genital, abdominal and other structures were eventually mounted in Euparal. We used the terminology of Klots (1970) and Sibatani (1972) for genitalia descriptions, Wootton (1979) for wing venation, Brock (1971) and Fänger (1999) for thoracic sclerites and if homologies were in doubt, we used neutral descriptions.

Wings were removed from the dry specimen and submerged in 90% ethanol for a few seconds to remove the surface tension. Then wings were submerged in 2.7% sodium hypochlorite (NaClO) solution for a few minutes for scale removal and washed in water as in Murillo-Ramos *et al.* (2016). They were placed on an object-glass with a drop of ethanol, which was replaced by a drop of Euparal, and covered with a coverslip. The wing slides were left unstained.

Structural characters were examined and photographed using a Leica S9D stereomicroscope, Leica DM1000 LED microscope and Canon EOS 5D digital camera with MP-E 65 mm EF 100 mm macro lenses. Photos were taken with StackShot automated macro rail and focus stacked in Image Manager software (Zerene Stacker). Image files were edited in Photoshop (CC 2019) and the final plates arranged using CorelDraw (Graphics Suite, 2018).

PHENOLOGY AND LIFE HISTORY

Phenology data were retrieved from specimen labels by recording the month of each specimen, and from Marriott (2012). Some records were obtained from nightly monitoring using a mercury vapour lamp and light sheet at Bendigo in Central Victoria, Australia between 2009 and 2019. These records were added for each month (Fig. 17). Phenology data were available for 41 species representing all Epidesmiinae genera.

Females from the nightly monitoring were also collected and, where possible, eggs were obtained for rearing. The life history and host preferences for many of the species were unknown, so a spectrum of local hosts growing at the time of collection was presented to newly hatched larvae. These hosts were selected to represent a broad spread of plant families. When

larvae demonstrated an affinity to a plant, then other members of this plant genus were subsequently offered to larvae, to assist in refining understanding of host preferences. If there were no behavioural evidence for host preference, then a subsequent suite of different plants was offered. In some cases, an additional collection of eggs and rearing attempts were required. During rearing, photographs were taken at regular intervals to record the full life cycle from egg to adult. Also, notes were taken on larval behaviour.

RESULTS

Epidesmiinae, as here redefined, currently comprises nine genera and 102 species. According to the molecular hypothesis by Murillo-Ramos *et al.* (2019), the subfamily is the sister of a group formed by Oenochrominae *s.s.*, *Eumelea ludovicata* Guenee, (1858), Geometrinae and Ennominae. From a morphological point of view, Epidesmiinae are a diverse group, with numerous genus-specific characters. We thus did not manage to find a single synapomorphic character that would be shared by all of them and is not found in other geometrid subfamilies. This concerns both external characters, such as wing pattern, size and shape, other external characters, sclerites and internal structures. Despite this, and similar to all geometrid subfamilies (see below), members of Epidesmiinae can still be diagnosed and differentiated from the other geometrid subfamilies by the following combination of diagnostic characters (none of these are present in all Epidesmiinae): male antennae unipectinate (Fig. 12); labial palps elongated (particularly the second segment) in both sexes, up to five times diameter of eye (for instance Fig. 14), with vom Raths's organ an elliptical invagination (Fig. 6); forewing with two areoles (Figs 4, 5); hindwing with one anal vein (Fig. 4); gnathos arms fused, granulate, spinose or dentate apically (for instance Fig. 6); female genitalia with two signa, one stellate, the other an elongated and spinose plate (for instance Figs 13–15).

GENERAL DESCRIPTION OF EPIDESMIINAE

Head and thorax (Figs 1, 6–15)

Antennae unipectinate in males, shorter towards the apex (bipectinate in 2/5 *Adeixis* species and *Arcina*); filiform in females (shortly bipectinate in *Systatica* and *Abraxaphantes*). Labial palps elongated, second segment longest (less pronounced in *Systatica*); vom Raths's organ an elliptical invagination. Frons elongated in many species. Chaetosemata small.

Tegula large. Epiphysis small. Spur formula in male and female tibia 0–2–4 (hind leg with 2 + 2 spurs). Male hindleg hair-pencil absent (present in *Phrataria replicataria* Walker, 1866). Metathorax furca with well-developed apophyses; anterior and basal ventral laminas separate.

Abdomen (Figs 1, 6–15)

Abdomen slender. Tympanal organs large, almost meeting medially in a few species; tympanal organs approaching 45° angle relative to the abdomen; the posteromedial corner with narrow sclerotizations that extend into second sternite (pronounced in *Abraxaphantes* and *Epidesmia*). Ansa shape variable, ranging from evenly tapering and narrow rod to bottle-shaped with pickaxe-shaped apex. Second sternite often distinctly sclerotized, in few species with sternotympanal process with free end curved over tympanum (Figs 6, 14). Abdominal sternites and tergites of both sexes undifferentiated, with few exceptions (e.g. posterior margin of male eighth sternite bilobed and setose in *Epidesmia tricolor*). Male third sternite with a row of setae in few species (*Epidesmia, Dichromodes*).

Wings (Figs 1, 2, 4, 5)

Pattern, size and shape variable (Fig. 1). Colour varies from different shades of brown to yellowish, grey and white. Wingspan from 20 to 70 mm. Forewing outer margin distinctly convex (*Ecphyas* and *Systatica*), weakly convex or concave. Forewing apex acute or rounded. Forewing venation: two areoles formed by R + Rs1–4; Rs1–Rs3 often stalked; cross-veins between M1 and M3 reduced, weakly tubular. CuA1 not stalked with M3. Hindwing venation: Sc + R1 parallel for long-distance with Rs; cross-veins between M1 and M3 reduced, weakly tubular. M2 tubular. One tubular A vein. Frenulum small. Resting posture of wings varies from planiform (for instance *Systatica*) to tectiform (for instance *Phrixocomes*) and potentially veliform (the latter is supported by a distinctly coloured underside and frequent observations of specimens with the wings partly or fully vertically folded over the abdomen in *Phrataria*) (Fig. 2).

Male genitalia (Figs 6–15)

Uncus long, narrow (short in *Ecphyas*). Socii minute, setose (reduced, barely recognizable in *Adeixis*). Gnathos distinct, arms fused, apically granulate, spinose or dentate. Tegumen narrow. Opened valvae upright (but nearly horizontal in *Dichromodes*), mobile (fused in *Ecphyas*), setose ventrally, with narrow or
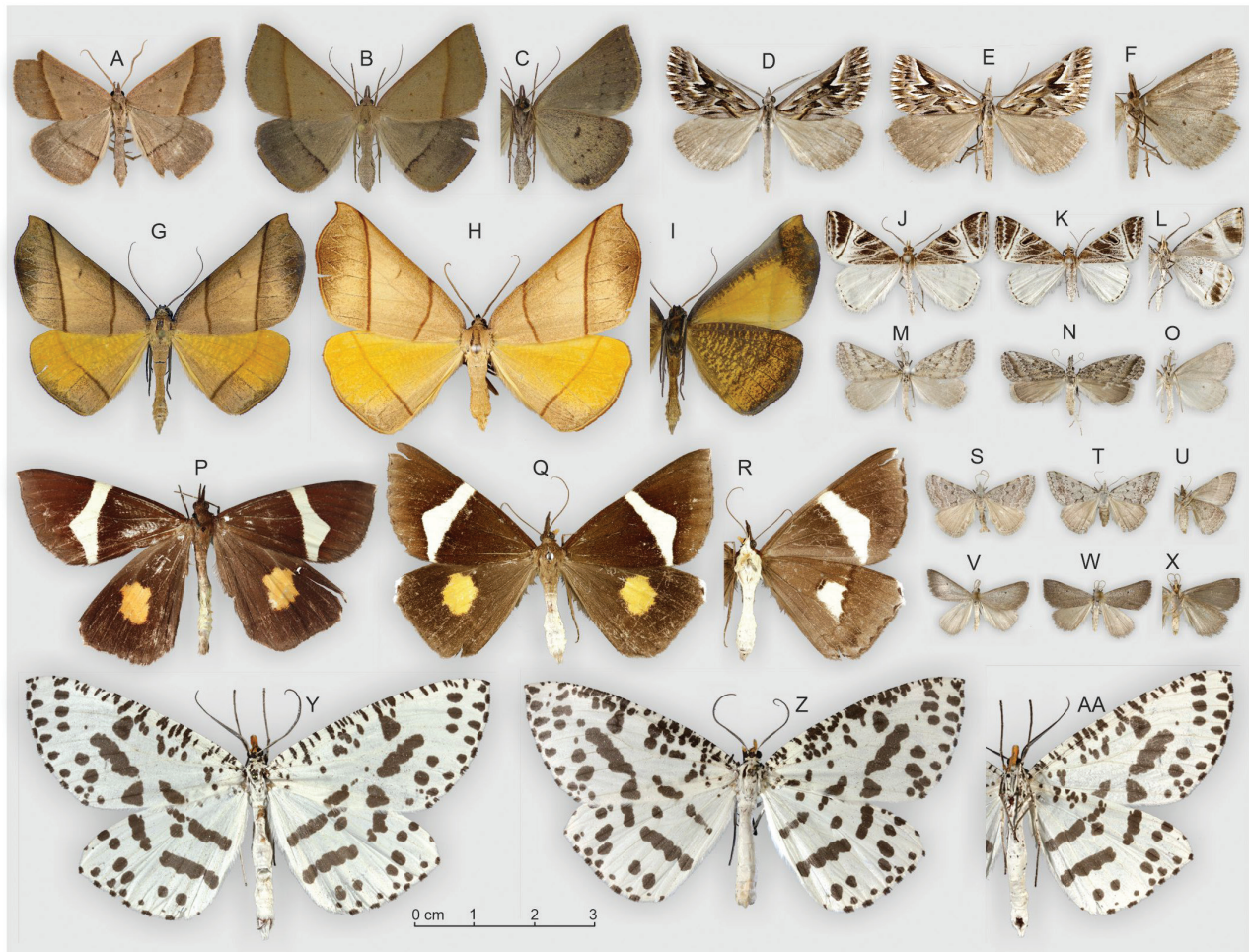
Figure 1. Adults of Epidesmiinae genera. Type species of each genus is illustrated, except in *Phrataria*, where a similar species is illustrated instead. A. *Ecphyas holopsara* male. Australia, WA, Albany, Torndirrup NP, 5.1.1993, coll. ANIC. B, C. *E. holopsara* female. Australia, WA, Leeuwin-Naturaliste NP, 5.1.2015, coll. Friedrich. D. *Arcina fulgorigera* male. Australia, WA, Talling, WA, 200 m, 3.11.2003, coll. ANIC. E, F. *A. fulgorigera* female. Australia, WA, Icy Ck, Lane Pool Res. 300 m, 6.11.2003, coll. ANIC. G, I. *Systatica xanthastis* male. Australia, Victoria, East Gippsland, 2.1.2012, 300 m, coll. Friedrich. H. *S. xanthastis* female. Australia, QLD, Binna Burra Lamington NP, 15.11.1992, 700 m, coll. ANIC. J, L. *Phrataria replicataria* male. Australia, Victoria, Gisborne, 17.2.1901, coll. NHMUK. K. *P. replicataria* female. Australia, Victoria, Gisborne, 10.3.1901, coll. NHMUK. M, O. *Phrixocomes ptilomacra* male. Australia, WA, 37 km SW of Mt. Ragged, 2.11.1977, coll. ANIC. N. *P. ptilomacra* female. Australia, WA, 37 km SW of Mt. Ragged, 2.11.1977, coll. ANIC. P. *Epidesmia tricolor* male. (without locality, without date) Pres. by Lady Lochore to B. M. 1946-341, coll. NHMUK. Q, R. *E. tricolor* female. Australia, NSW, Lindfield, 22.12.1974, coll. ANIC. S. *Dichromodes indicataria* male. Australia, Victoria (without date). coll. NHMUK. T, U. *D. indicataria* female. Australia, Victoria (without date). coll. NHMUK.. V. *Adeixis inostentata* male. New Caledonia, Grand Lac, 19.5.1971, 250 m, coll. NHMUK. W, X. *A. inostentata* female. New Caledonia, Grand Lac, 19.5.1971, 250 m, coll. NHMUK. Y, AA *Abraxaphantes perampla* male. Thailand, Chiangmai, Thoeng Dang, 7.4.2006, 500 m, coll. Sihvonen. Z. *A. perampla* female. Thailand, Chiangmai, Thoeng Dang, 7.4.2006, 500 m, coll. Sihvonen.

round projections (absent in *Systatica* and *Phrataria*, and projections present or absent in *Dichromodes*). Juxta variable, often sclerotized and bifurcate. Vinculum narrow. Transtilla often with two large, sclerotized, triangular lobes laterally, arms weakly sclerotized or membranous medially, barely fused. Saccus round (angled in *Systatica*). Coremata absent. Aedeagus variable, cornutus single (two cornuti in *Dichromodes confluaria, D. euscia* and *D. stilbiata* C. Byrne, pers. comm.) or absent, vesica surface often covered with sclerotized granules. Vesica large, with diverticula.

Figure 2. Adults of Epidesmiinae, showing different resting positions (A–E) and a 'dancing' specimen of *Phrataria bijugata*, see text for details. Photos printed with permission, see Acknowledgements for details. A, *Systatica xanthastis*, Australia, Queensland, Tamborine Mtn., 8 Oct. 2016, photo Nicholas Fisher. B, *Dichromodes atrosignata*, Australia, Victoria, Wilsons Promontory, 22 Sept. 2006, photo Peter Marriott. C, *Phrixocomes ophiuca*, Australia, Victoria, Davis Creek, Mallacoota, 1 Nov. 2010, photo Marilyn Hewish. D, *Abraxaphantes perampla*, Thailand, 19 Feb. 2012, photo Tim Stratford. E, *Epidesmia tricolor*, Australia, New South Wales, 16 Feb. 2009, photo Denis Wilson. F, *Phrataria bijugata*, Australia, Victoria, Eppalock, 24 Jan. 2012, photo Steve Williams.

Female genitalia (Figs 6–15)

Two signa (in 5/9 genera), one stellate or granulate wide plate, another long, granulate or spinose narrow plate, both in mid-part of corpus bursae either ventrally or laterally; or one stellate or irregular-shaped signum (in 4/9 genera) in mid-part of corpus bursae either ventrally or laterally. Corpus bursae pyriform or constricted and narrower before anterior end, posterior part with sclerotized striations (in 5/9 genera). Ductus bursae length and degree of sclerotization variable. Shape and degree of sclerotization of lamella antevaginalis and lamella postvaginalis variable. Papillae anales round or weakly elongated, setose.

Morphology of individual Epidesmiinae genera (Figs 6–15)

Morphology of each genus was studied using the type species, and in species-rich genera other material was studied also. We are aware that as more material is examined, in particular in *Dichromodes*, we will gain a more accurate understanding of variation within each genus. Therefore, we do not provide detailed descriptions of genera, but instead illustrate relevant morphological structures in the colour plates provided. Selected structures are highlighted with arrows. The highest variation in the morphological structures are found in wing pattern and size; the number, position and shape of signa; shape of corpus bursae and its sclerotizations; tympanal organs; valva shape and its ornamentations; and in labial palps. Variation and similarities in these are useful in diagnosing the Epidesmiinae genera, and other groups within Epidesmiinae, for instance, if a tribe-level classification within the subfamily is needed later. The morphological variation should be compared against the molecular phylogenetic hypothesis of Epidesmiinae (Murillo-Ramos *et al.*, 2019) to see if correlations exist.

Distribution, biology and immature stages (Fig. 3)

Epidesmiinae have an Australasian distribution with species recorded from Australia, New Zealand, New Caledonia and eastern Papua New Guinea. Monotypic *Abraxaphantes* is the only Indo-Malayan representative, recorded from Thailand and southern China. *Dichromodes* is the most diverse genus with 67 described species (Scoble & Hausmann, 2007), but potentially over 200 additional species await description (Marriott, 2012). Several species fly commonly during the day and fly a short distance when disturbed in heath and grassy areas, but are also attracted to light during the night (Marriott, 2012). Little information is available on immature stages. Eggs are laid singly by *Phrataria bijugata* (Walker, 1863) and *Epidesmia hypenaria* (Guenée, 1857). Those are turquoise blue when laid and darken as they develop. The first instar larva of *P. bijugata* is faint pink, and its abdomen is curved when resting. *Epidesmia tricolor* larvae have been recorded feeding on tea tree (*Leptospermum* J.R.Forst. & G.Forst.; Myrtaceae) (Scoble, 1999) and *Dichromodes* have been reared on *Eucalyptus* L'Hér. (also Myrtaceae). *Dichromodes* larvae are characteristically long and thin, and camouflaged to resemble small dead twigs of the hosts. *Dichromodes anelictis* Meyrick, 1890 showed high host specificity and was successfully reared on *Eucalyptus viridis* R.T.Baker (green mallee). This moth occurs in autumn and can be prevalent at that time in 'mallee areas' but is absent in different habitats. In contrast, the larva of *Epidesmia chilonaria* is polyphagous and was easily raised on *Eucalyptus melliodora* A.Cunn. ex Schauer and that of *Epidesmia hypenaria* fed on *Eucalyptus camaldulensis* Dehnh. (river red gum) and *Eucalyptus macrorhyncha* F. Muell. ex Benth. (red stringybark). Small and fully grown larvae of *Ep. chilonaria* are shown in Figure 3E, F. Larvae of *P. bijugata*, shown in Figure 3B, proved difficult to rear and it took several attempts to identify host preferences. Feeding was eventually observed on *Eucalyptus polyanthemos* Schauer and *Eu. melliodora*, where leaves were skeletonized from the edge. These larvae did not survive beyond the second instar, probably indicating that the preferred eucalypt host has yet to be identified. The first instar larvae of *Phrixocomes hedrasticha* Turner, 1936 showed some interest in a number of the local shrubs of Victoria but did not establish. The larvae of *Dichromodes*, *Epidesmia* and *Phrixocomes* that have been reared, show a propensity to remain rigid, stationary and often in plain sight during the day and actively feed at night.

Adeixis inostentata occurs in herbaceous marsh association in Australia, three *Adeixis* species were found on *Baeckea*-sedge maquis on sedimentary rock in New Caledonia and *A. griseata* occurs in characteristic 'pakihi' country, poorly drained acid areas with sedges and scattered low shrubs in New Zealand (Holloway, 1979). Larvae of *Adeixis baeckeae* Holloway, 1979 have been reared on Myrtaceae: *Baeckea ericoides* (Holloway, 1979). This species pupates in loosely constructed cocoons in the terminal leaves of *Baeckea*, and emerges about 25 days after pupation (Holloway, 1979). Structural details of pupa, such as the arrangement of cremaster setae, are not available. The habitus of *Ep. chilonaria* pupa is shown in Figure 3F. Adults of *Epidesmia tricolor* fly in or near wet forests in south-eastern Australia. For more information on phenology, see Figure 17.

Figure 3. Immature stages of Epidesmiinae. All photos by Steve Williams. A, *Phrataria bijugata*, eggs, Australia, Queensland, 5 January 2015. B, *Phrataria bijugata*, 1st instar larva in lateral view, Australia, Victoria, 30 January 2015. C, *Phrataria bijugata*, 1st instar larva in dorsal view, Australia, Victoria, 7 January 2020. D, *Epidesmia hypenaria*, eggs, Australia, Victoria, 6 December 2015. E, *Epidesmia chilonaria*, small larvae, Australia, Victoria, 6 February 2013. F, *Epidesmia chilonaria*, fully grown larva, Australia, Victoria, 6 April 2013. G, *Epidesmia chilonaria*, pupa, Australia, Victoria, 22 December 2013.
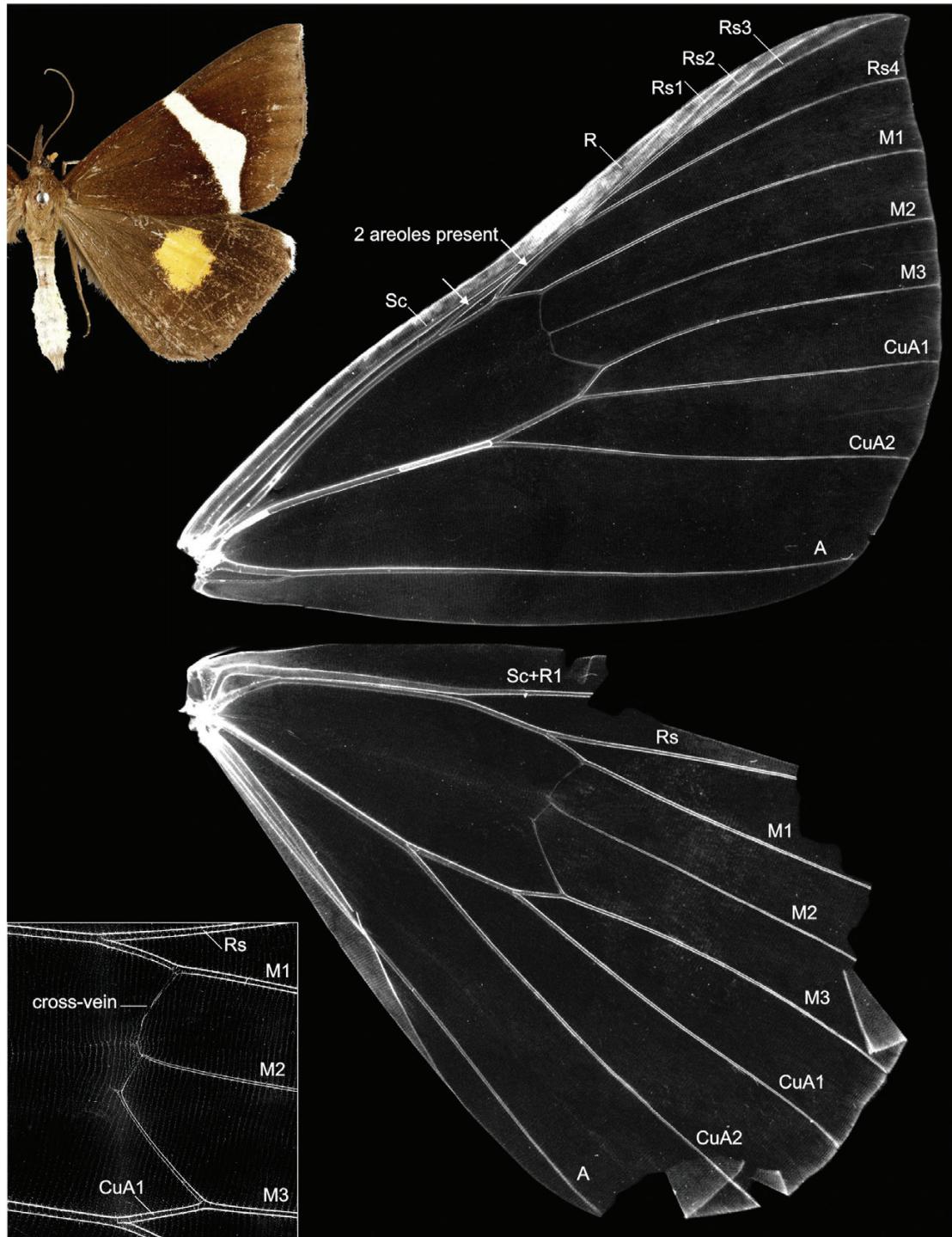
Figure 4. Female wing venation of *Epidesmia tricolor* Westwood, 1841. Part of hindwing is shown enlarged. Australia, NSW, Lindfield, 22.12.1974. Preparation number: LMR22 (coll. ANIC).
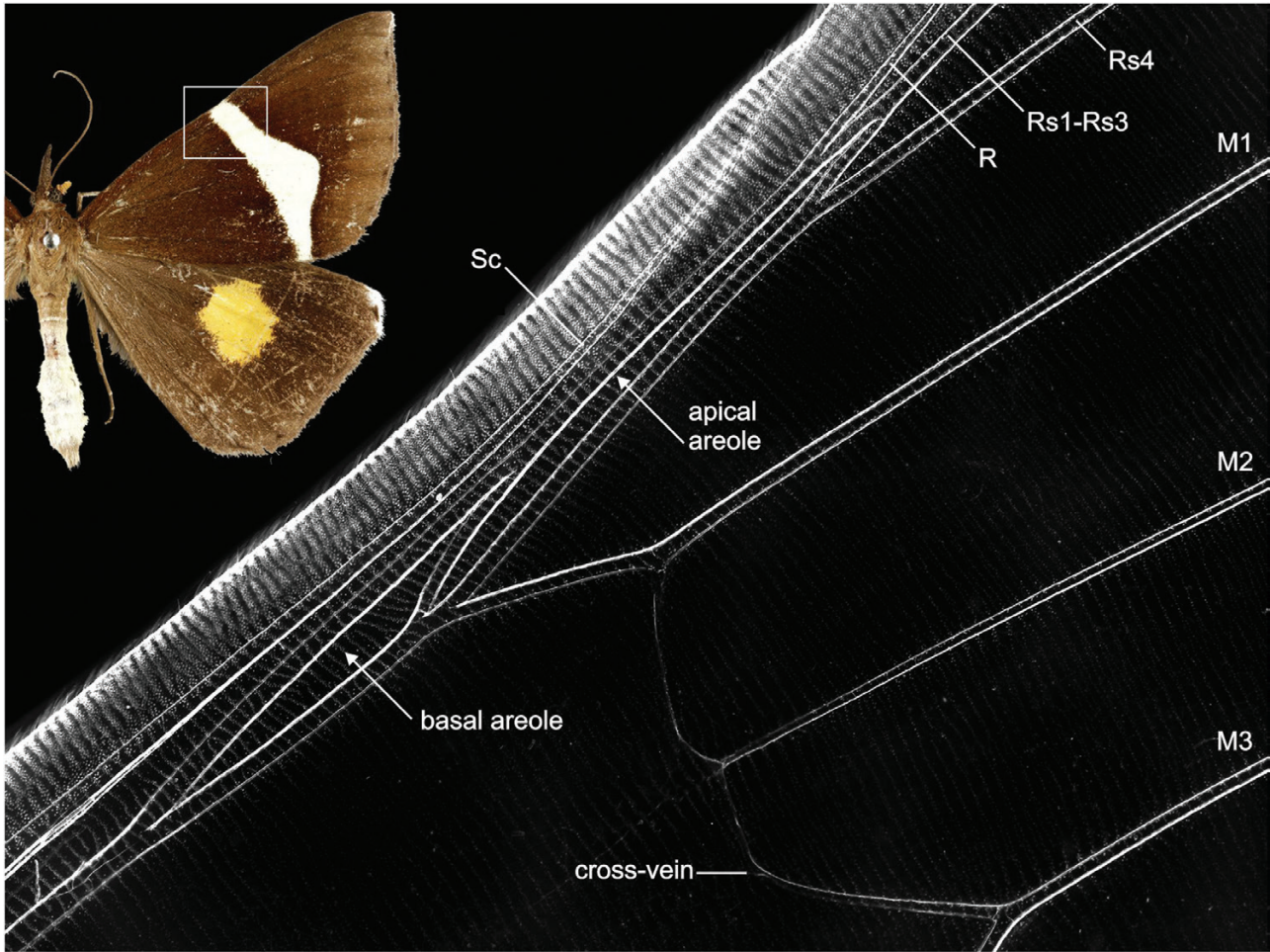
Figure 5. Detail of female fore wing venation of *Epidesmia tricolor* Westwood, 1841. Australia, NSW, Lindfield, 22.12.1974. Preparation number: LMR22 (coll. ANIC).

DISCUSSION

EPIDESMIINAE + DESMOBATHRINAE + OENOCHROMINAE *S. S.*

After carefully studying representatives of the different genera, reviewing the relevant published taxonomic literature and the structure of the molecular phylogenetic hypothesis of Murillo-Ramos *et al.* (2019), our results show that Oenochrominae *s.s.*, Desmobathrinae and Epidesmiinae display considerable variation (Table 1) and each is supported by diagnostic characters. Selected differences in traits among these three subfamilies include the following (Fig. 16). Adults of Desmobathrinae possess forewings with one areole (or none), formed by R veins; cross-veins between M1 and M3 are reduced. In Oenochrominae *s.s.*, the areole is present but the areoles are extremely long and narrow, and they result from the stalking between R_2 and R_3; the cross-veins between M1 and M3 are tubular in all oenochromines. In Epidesmiinae, the areoles are wider and formed by the R + Rs1–4, cross-veins between M1 and M3 are reduced, as in Desmobathrinae. The male genitalia are similar among the subfamilies with no unique synapomorphies, but in Desmobathrinae the structure of the tegumen has a characteristic thickening loop; the uncus is modified and has a 'broom' shape. In Oenochrominae *s.s.*, the valvae are simple or include spine-like or digitate processes. Many species have a pair of processes arising from the base of each valvae; the uncus is mostly simple, long and finger-shaped or short and acuminate. In Epidesmiinae, the tegumen is narrow, the uncus is long and the valva is simple with no conspicuous traits. Female genitalia show great variation. The signa in Desmobathrinae consist of longitudinal
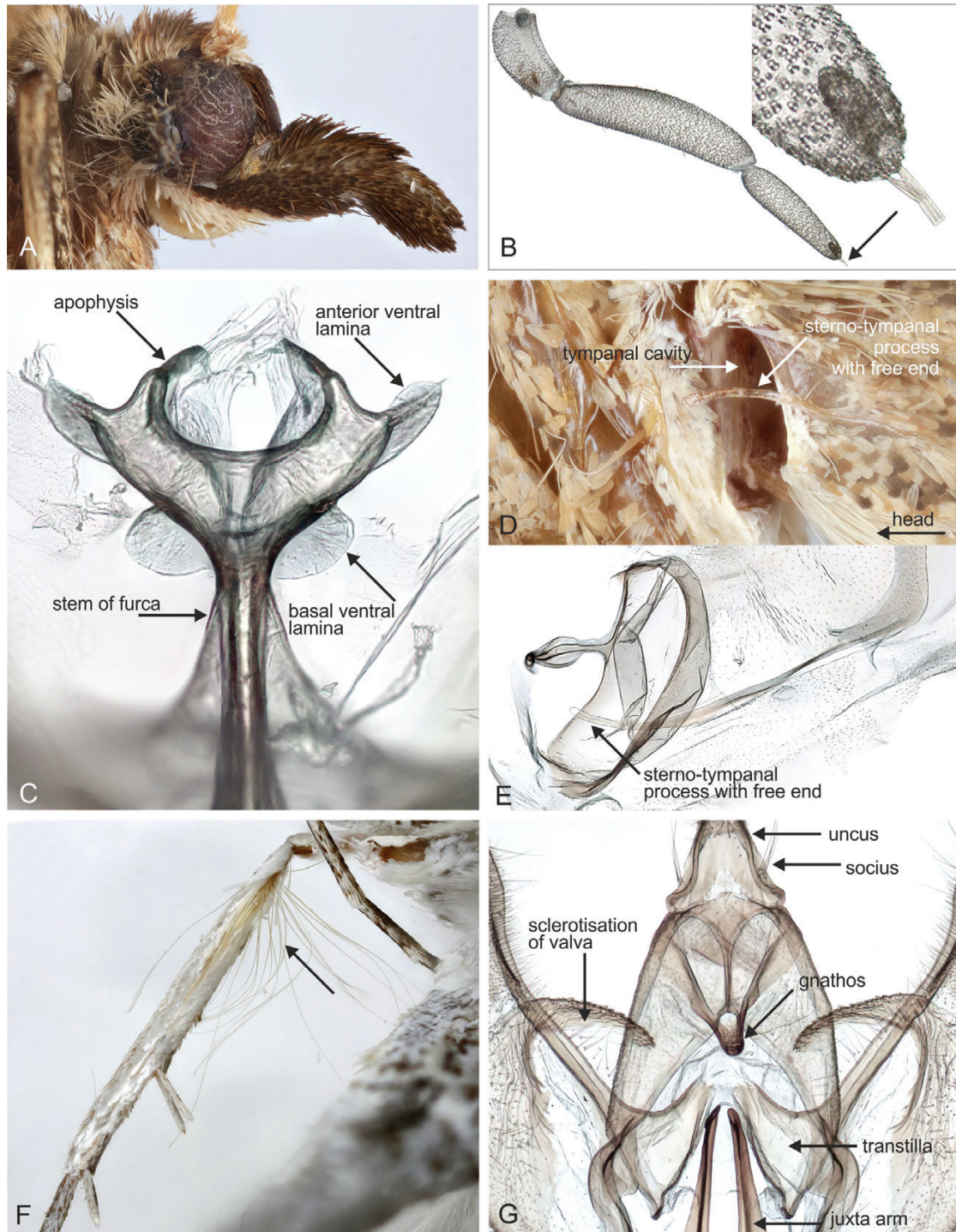
Figure 6. Selected male structures of *Epidesmiinae species*. A, labial palps with scales. B, labial palps descaled and pit-organ (vom Rath's organ) enlarged (*Epidesmia chilonaria*). C, metathorax furca, dorsal view (*E. chilonaria*). D, E, tympanal organ with scales and descaled (*E. chilonaria*). F, hind leg with hair-pencil (*Phrataria replicataria*). G, part of male reproductive organ (*E. chilonaria*). Specimen metadata are given in Supporting Information, File S1.

Figure 7. Adults and selected structures of *Ecphyas holopsara* Turner, 1929. A, adult female, wingspan 35 mm. B. male reproductive organ. C, aedeagus. D, male tympanal organ. E, male head and labial palps. F, female reproductive organ. G, elongated signum. H, roundish signum. Specimen metadata are given in Supporting Information, File S1.

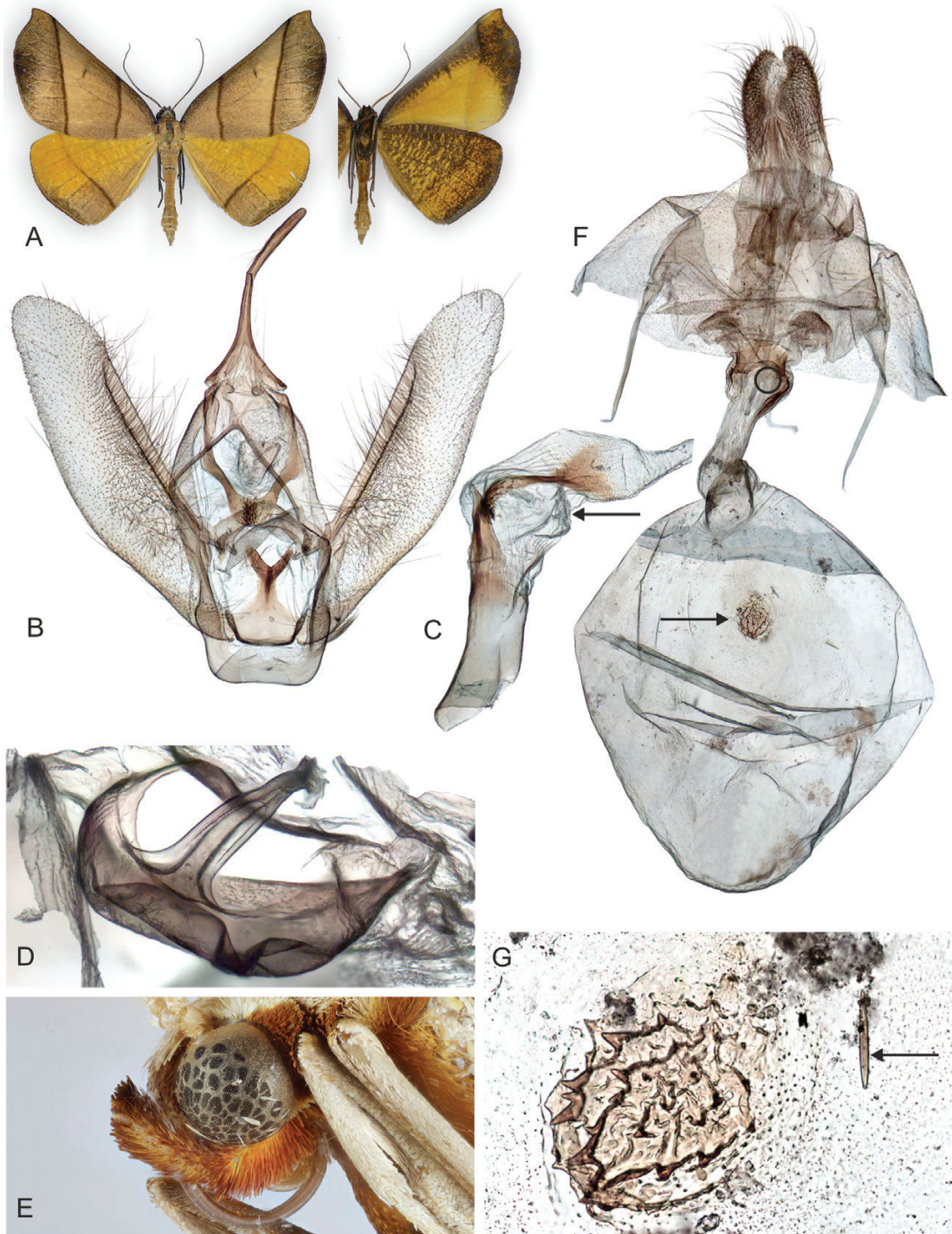**Figure 8.** Adults and selected structures of *Systatica xanthastis* (Lower, 1894). A, adult male, wingspan 41 mm. B, male reproductive organ. C, aedeagus with everted vesica. D, female tympanal organ. E, male head and labial palps. F, female reproductive organ. G, signum. Specimen metadata are given in Supporting Information, File S1.
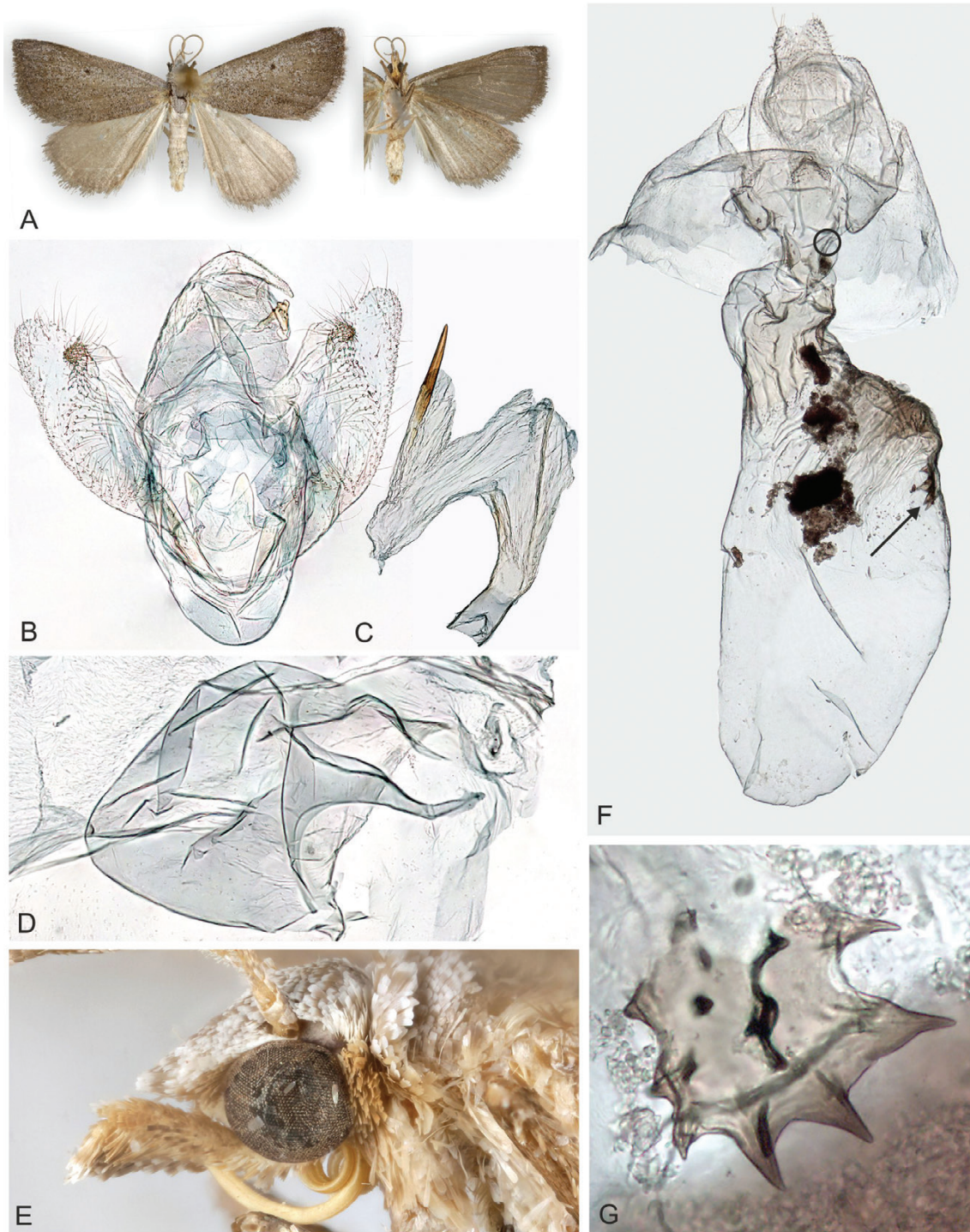
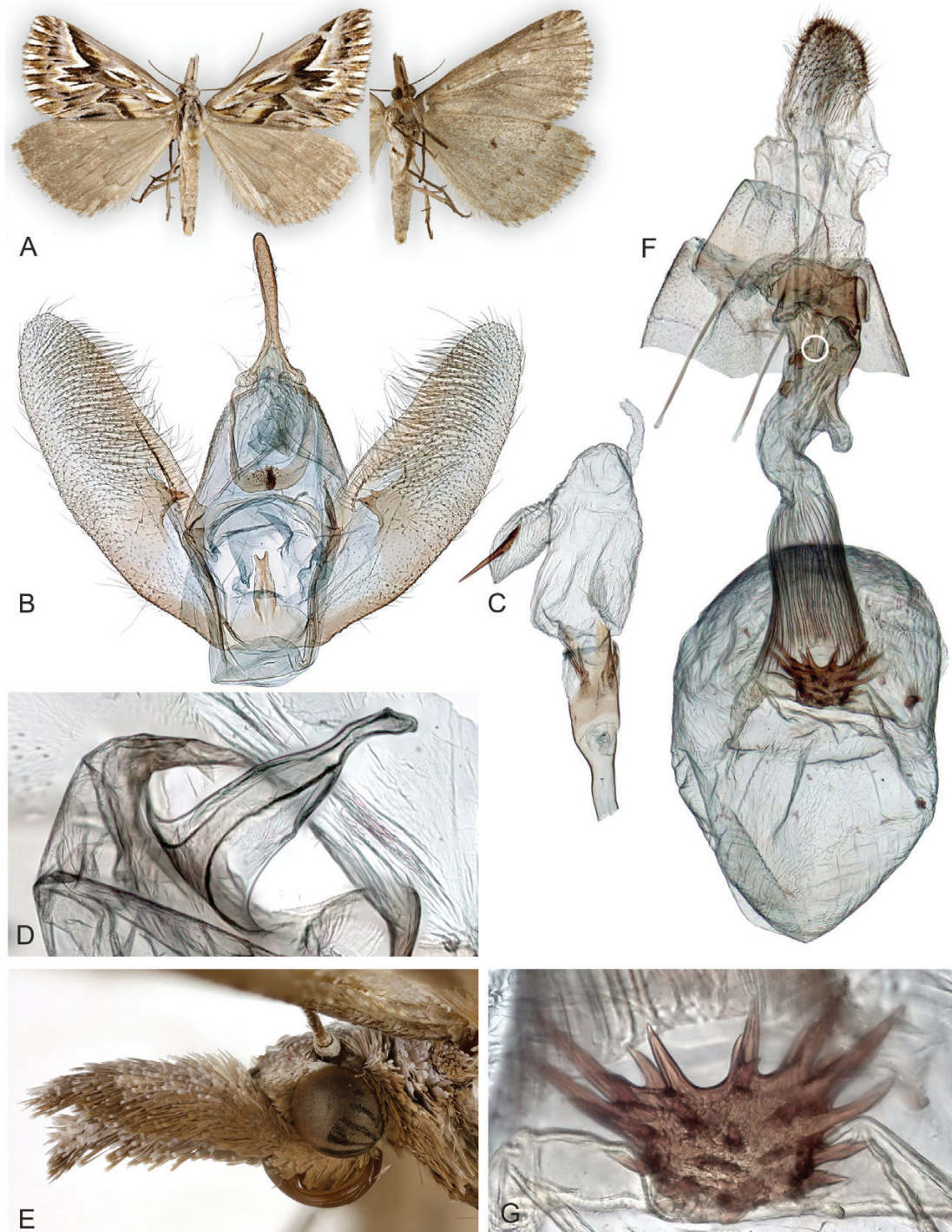**Figure 9.** Adults and selected structures of *Adeixis inostentata* (Walker, 1861). A, adult female, wingspan 18 mm. B, male reproductive organ. C, aedeagus with everted vesica. D, male tympanal organ. E, female head and labial palps. F, female reproductive organ. G, signum. Specimen metadata are given in Supporting Information, File S1.

Figure 10. Adults and selected structures of *Arcina fulgorigera* (Walker, 1863). A, adult female, wingspan 29 mm. B, male reproductive organ. C, aedeagus with everted vesica. D, ansa of male tympanal organ. E, female head and labial palps. F, female reproductive organ. G, signum. Specimen metadata are given in Supporting Information, File S1.
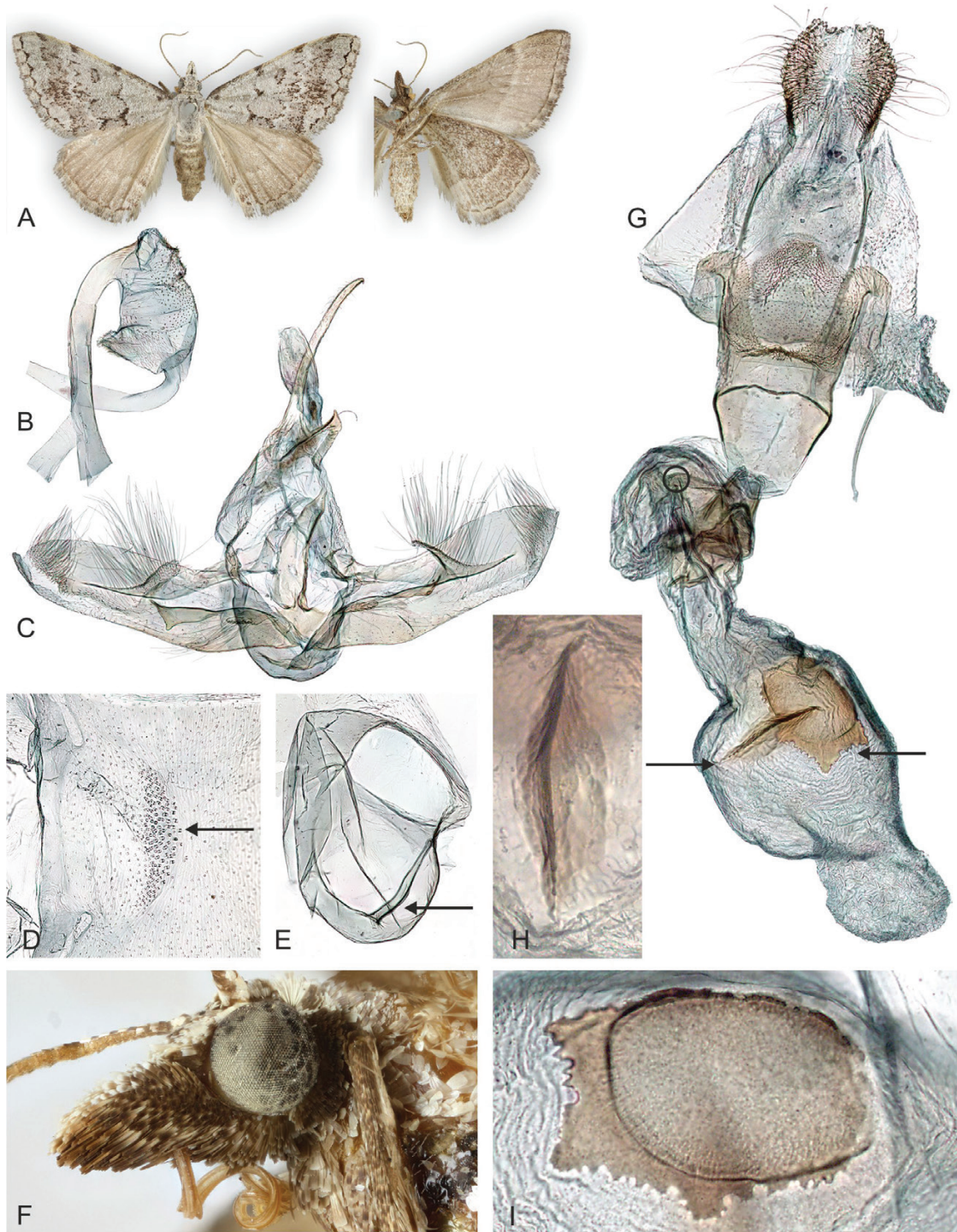
Figure 11. Adults and selected structures of *Dichromodes indicataria* (Walker, 1866). A, adult female, wingspan 19 mm. B, aedeagus with everted vesica. C, male reproductive organ. D, male third abdominal segment. E, female tympanal organ. F, female head and labial palps. G, female reproductive organ. H, elongated signum. I, roundish signum. Specimen metadata are given in Supporting Information, File S1.
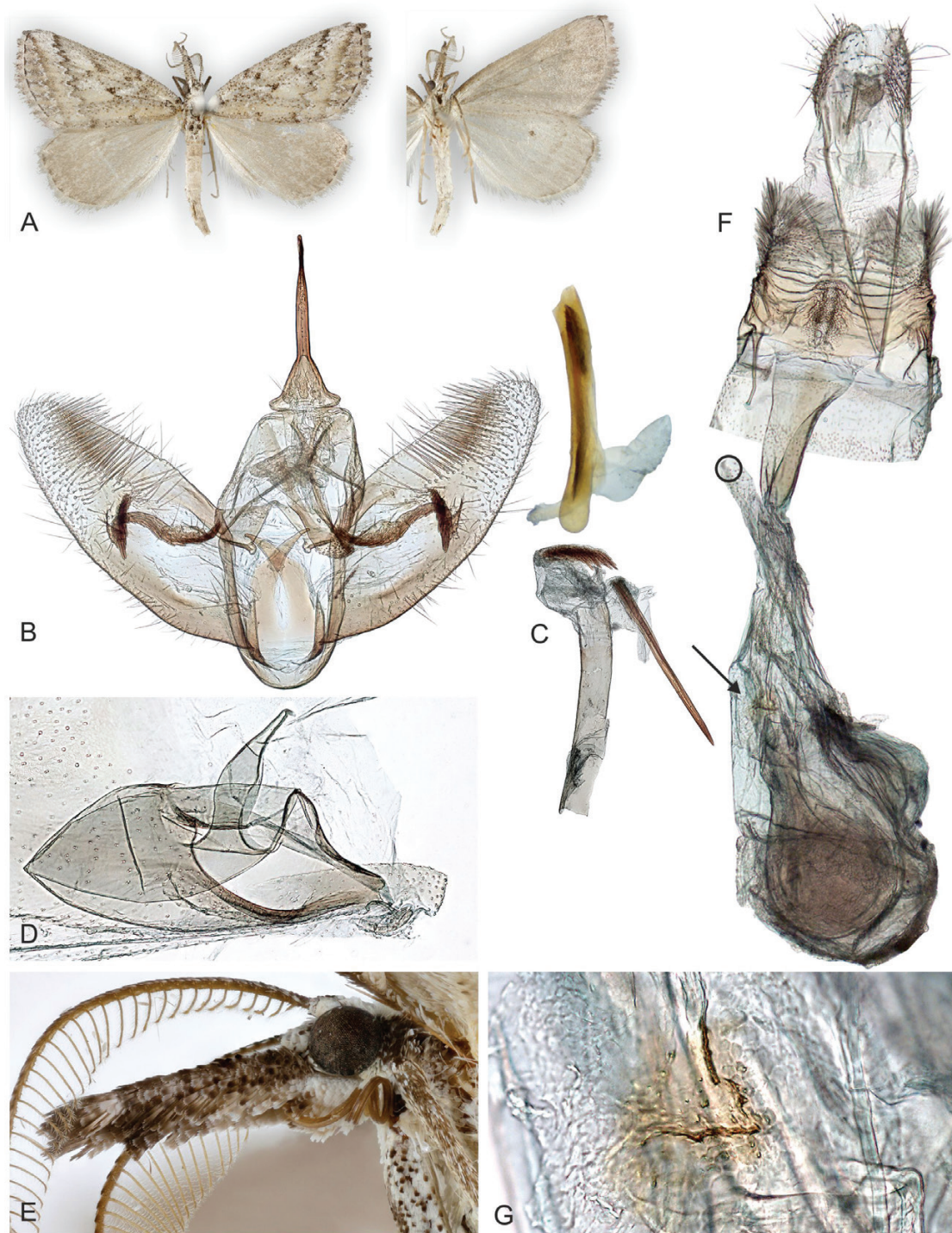
Figure 12. Adults and selected structures of *Phrixocomes ptilomacra* (Lower, 1892). A, adult male, wingspan 23 mm. B, male reproductive organ. C, aedeagus, vesica partly everted (below). D, male tympanal organ. E, male head and labial palps. F, female reproductive organ. G, signum. Specimen metadata are given in Supporting Information, File S1.
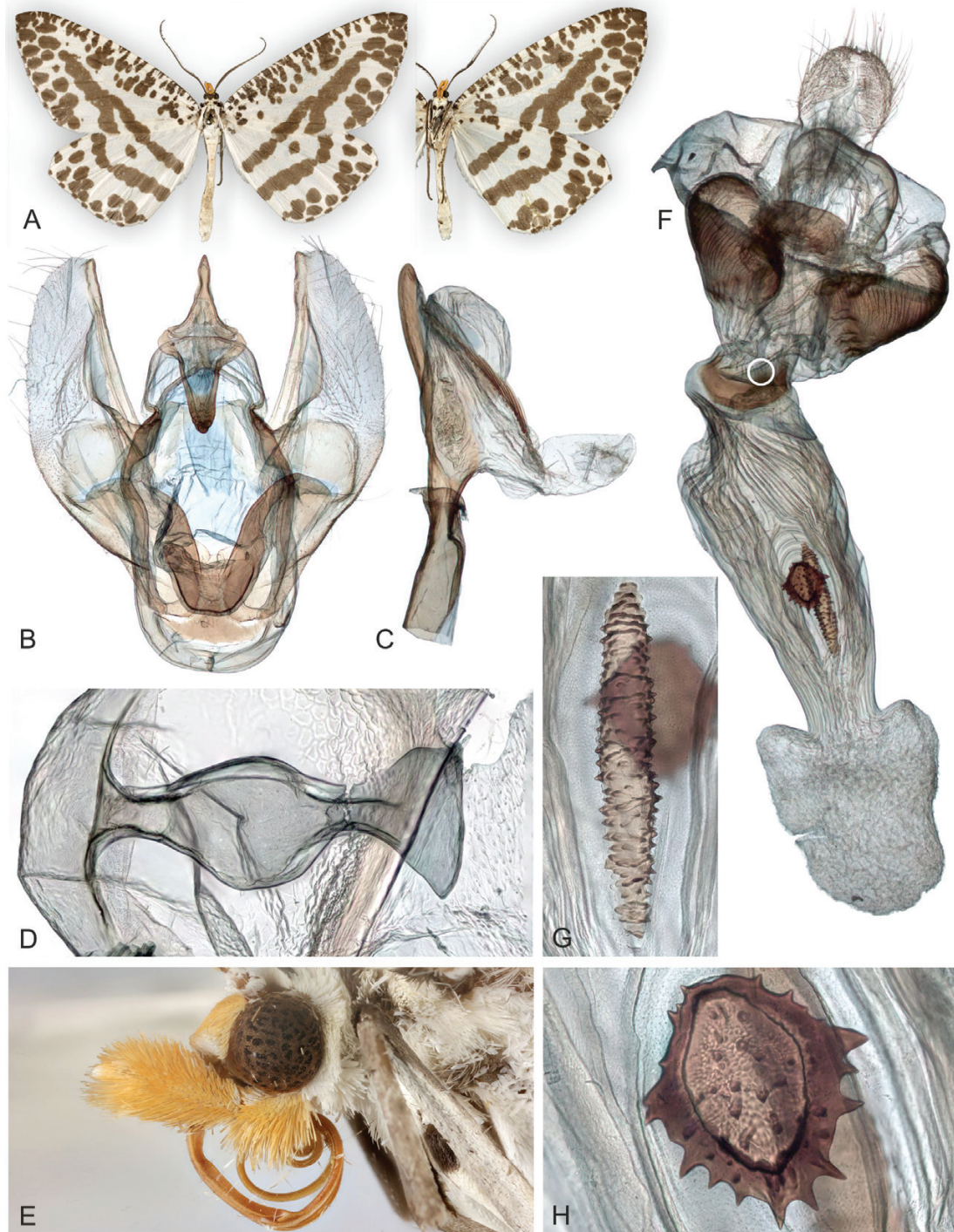
Figure 13. Adults and selected structures of *Abraxaphantes perampla* (Swinhoe, 1890). A, adult male, wingspan 72 mm. B, male reproductive organ. C, aedeagus with everted vesica. D, ansa of male tympanal organ. E, Female head and labial palps. F, female reproductive organ. G, elongated signum. H, stellate signum. Specimen metadata are given in Supporting Information, File S1.
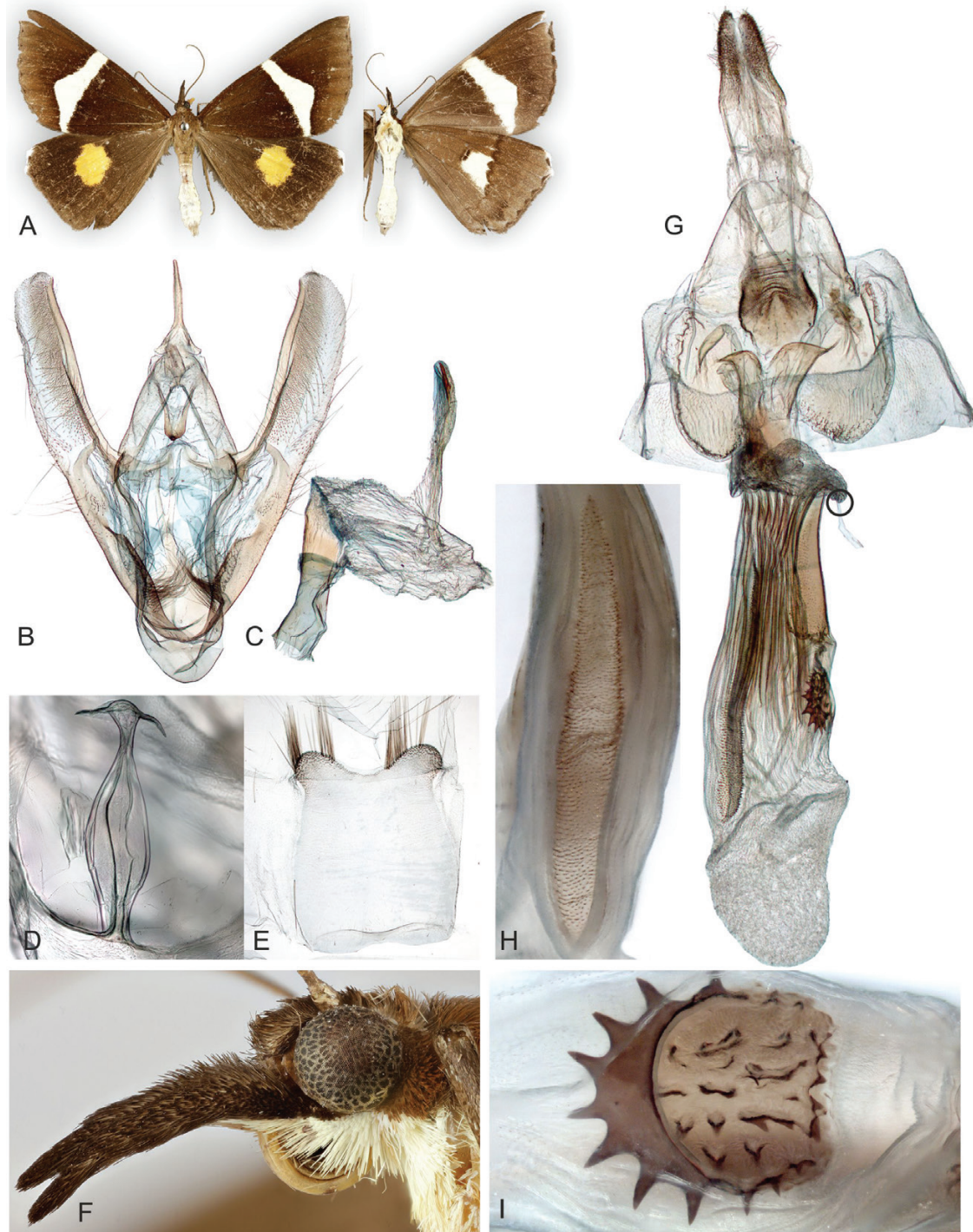
Figure 14. Adults and selected structures of *Epidesmia tricolor* Westwood, 1841. A, adult female, wingspan 52 mm. B, male reproductive organ. C, aedeagus with everted vesica. D, ansa of tympanal organ. E, male eighth abdominal segment. F, female head and labial palps. G, female reproductive organ. H, elongated signum. I, stellate signum. Specimen metadata are given in Supporting Information, File S1.
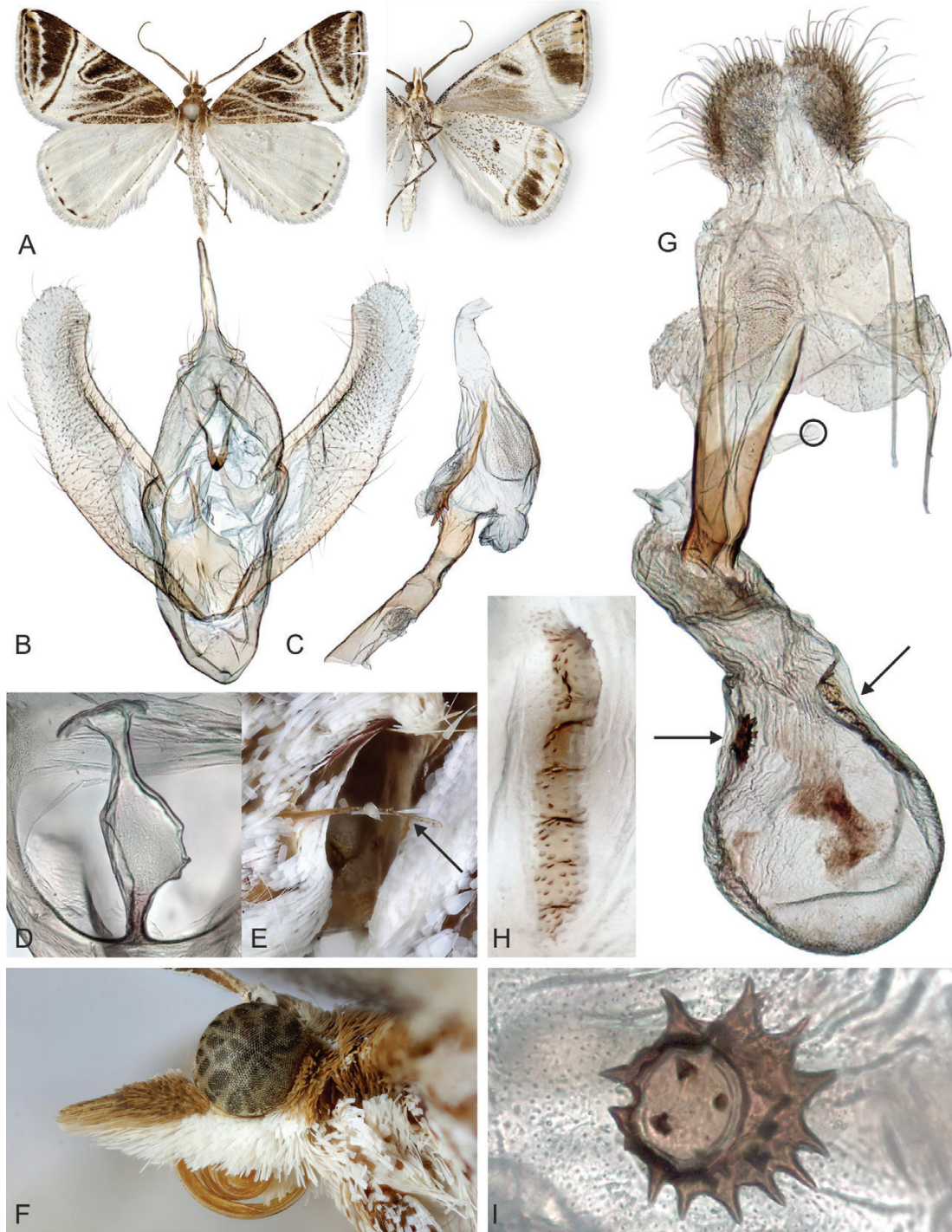
Figure 15. Adults and selected structures of *Phrataria replicataria* Walker, 1866. A, adult male, wingspan 27 mm. B, male reproductive organ. C, aedeagus with everted vesica. D, ansa of male tympanal organ. E, rod extending beyond male tympanal organ. F, male head and labial palps. G, female reproductive organ. H, elongated signum. I, stellate signum. Specimen metadata are given in Supporting Information, File S1.
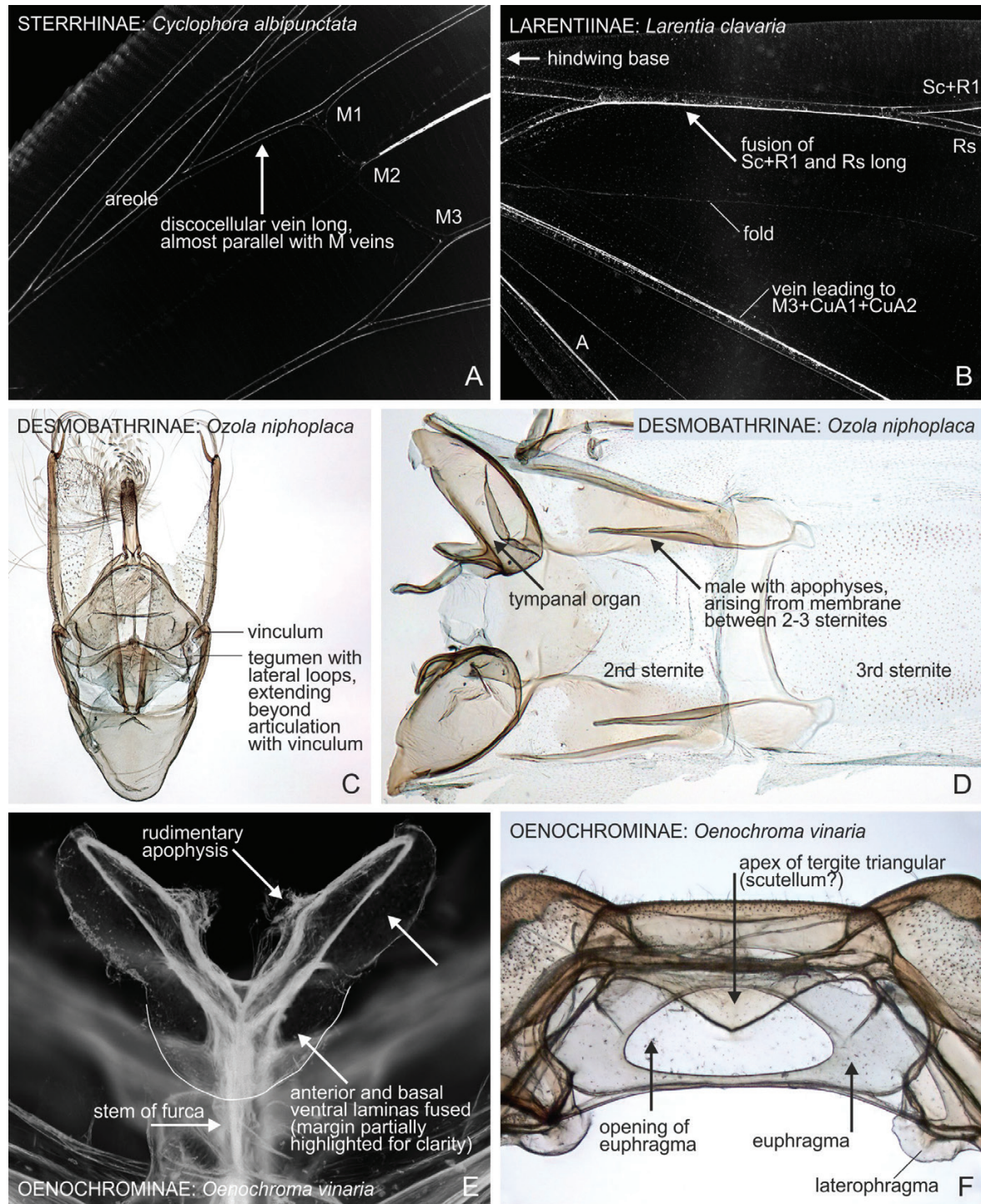
Figure 16. Diagnostic morphological structures of different geometrid subfamilies. A, Sterrhinae: *Cyclophora albipunctat*a, detail of forewing venation. B, Larentiinae: *Larentia clavaria*, detail of hindwing venation. C, Desmobathrinae: *Ozola niphoplaca*, male genitalia. D, Desmobathrinae: *O. niphoplaca*, sternite A2–A3. E, Oenochrominae: *Oenochroma vinaria*, metafurca (ventral view, compare against Fig. 6C). F, Oenochrominae: *O. vinaria*, dorsal part of metathorax (dorsal view). Specimen metadata are given in Supporting Information, File S1.
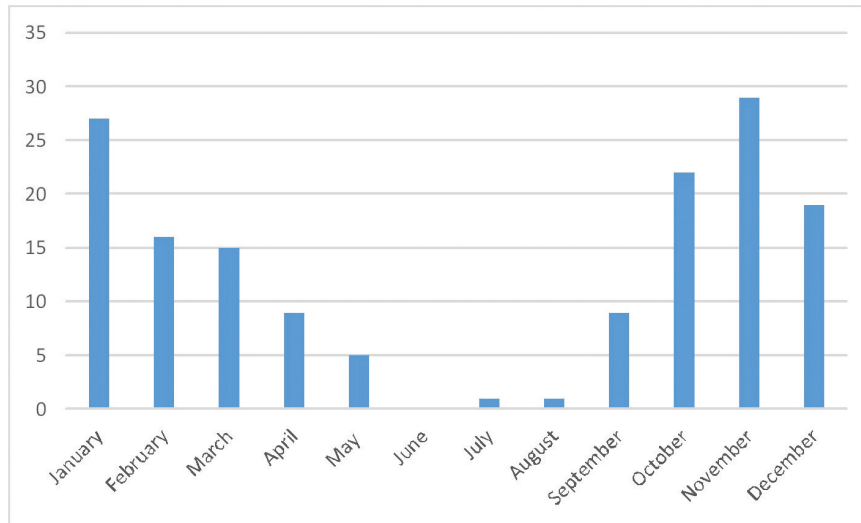
Figure 17. Phenology for Epidesmiinae moths, summarizing the number of flight time records per month (42 species, nine genera). The most records are from the Southern Hemisphere summer months, highest numbers being between October and January. The adult records in many species occur within 2–4-month periods, indicating these may have only one generation per year. *Abraxaphantes perampla* has been taken in Thailand in March–April, but there is a single record in July.

rows of slender spines, a small arc or spiral or a longitudinal scobinate band (Holloway, 1996), while in Oenochrominae *s.s.* the signum is a small circular patch, absent or not easily visible in some species. In Epidesmiinae, there are either two signa, one circular-stellate and another long plate, or a single signum of small circular patch. Many of the morphological characters included in our review may be the result of homoplasy, but assuming the homology concept is understood, one of the main characters separating these subfamilies is the shape and number of signa. Although signa in Geometridae are variable in shape and position, Epidesmiinae is the first subfamily bearing two distinctly differently shaped signa, or at least this character has not been published so far in any other geometrid group.

THE SYSTEMATIC POSITION OF *ARCINA*

We are aware, and highlight, that there are many genera, currently classified in Oenochrominae *s.l.* in the Australasian realm (Nielsen *et al.* 1996), which were not included in molecular studies or this review, but which eventually need to be classified in Epidesmiinae or other geometrid subfamilies. This unnatural assemblage of taxa (Oenochrominae *s. l.*) needs a thorough modern revision.

The monotypic *Arcina* Walker, 1863 (**new classification**) is among those and, based on morphological evidence, we transfer it from Oenochrominae *s.l.* (Nielsen *et al.*, 1996) to Epidesmiinae. The position of *Arcina* in Epidesmiinae

is supported by the combination of the following characters: elongated labial palps; the forewing has two areoles; the hindwing veins Sc + R1 and Rs are parallel for a long distance; the hindwing vein M2 is tubular; the structures of the uncus + socii + gnathos are typical; the juxta is bifurcate; the valva is in upright projection, and the tympanal organs have narrow sclerotization on the posteromedial corner that extends into the second sternite. *Arcina* shares with *Adeixis* bipectinate male antenna, tapering of the ansa of the tympanal organ, and a single stellate signum. The classification of *Arcina* in other subfamilies is excluded by comparing the structures, as summarized in Table 1.

SYNAPOMORPHIES IN GEOMETRIDAE SUBFAMILIES

Our literature survey on synapomorphies that define geometrid subfamilies revealed, as expected, that none of the subfamilies have unique synapomorphic characters common to all members of each subfamily (Table 1). Instead, subfamilies are supported by a combination of characters and, when applied together, these support monophyletic entities. These morphologically diagnosed subfamilies have largely been confirmed by molecular phylogenetic data, most recently by Murillo-Ramos *et al.* (2019). The survey of diagnostic subfamily features also revealed that these characters represent only a subset of the morphological characters available. Most frequently used characters are taken from wing venation, the abdominal structures, the number of larval prolegs and, to a lesser degree, the chaetotaxy of larvae and characters of the pupa. It is not known if these are

Table 1. Diagnostic morphological characters of geometrid subfamilies, based on the literature and on the present study. Currently, nine subfamilies are recognized, but the validity of Orthostixinae has not been tested in a phylogenetic context (see comments below). None of the listed characters is unambiguous at subfamily level and all of them show exceptions, but when considered together, they allow delimitation of subfamilies as monophyletic groups. A diurnal lifestyle, accompanied by atypical coloration compared to nocturnal relatives, has evolved independently in several lineages. This is one the reasons why wing colour and pattern are of limited value in diagnosing subfamilies. Structural characters show less variation and homologies are easier to interpret, but homoplasy is frequent in Geometridae (e.g. Sihvonen & Kaila, 2004) and Lepidoptera (Heikkilä *et al.*, 2015). Diagnoses for the entire Geometridae are available in the literature (Minet & Scoble, 1999; Hausmann, 2001)

Subfamily	Diagnostic (synapomorphic) characters	Remarks
Sterrhinae	Most anterior discocellular vein (vein between the base of M1 and areole) in forewing long and oriented almost parallel with M veins (Forbes, 1948, our wording) (Fig. 16A); forewing fasciae single (e.g. Minet & Scoble, 1999); hindwing discal spot with pale marking in darker surround (Holloway, 1997); one or two areoles in forewings (absent in Mecoceratini); in forewing point of origin of vein M1 is either proximal or distal areole; absence of anterolateral extensions on male 2nd abdominal sternite (Sihvonen & Kaila, 2004; Sihvonen *et al.* 2020).	The first three characters were not included in a morphological phylogeny (Sihvonen & Kaila, 2004), because it was not possible to code the observed variation into discontinuous character states. Most Sterrhinae species have one or two forewing areoles, the character is absent in only a few species (Hausmann, 2004) and Mecoceratini (Sihvonen *et al.* 2020). Forewing fasciae are single in many Sterrhinae (e.g. Minet & Scoble, 1999), but the wing pattern characters are variable. Sterrhinae and Larentiinae share a hammer-headed tip in tympanal organ's ansa (Cook & Scoble, 1992, see also Viidalepp, 2011) and a few other characters (summarized in Hausmann, 2004). McGuffin (1967, 1987) provided diagnostic larva and pupa characters, but those were based on limited Canadian material.
Larentiinae	Hindwing veins Sc + R1 and Rs *fused* for long-distance (Meyrick, 1892, Hausmann & Viidalepp, 2012) (Fig. 16B); forewing fasciae are multiple (= composed of bands of closely juxtaposed lines) (e.g. Minet & Scoble, 1999); forewing radial veins Rs1–Rs4 or Rs2–Rs4 arising from the areole and are stalked or connate with M1, or, if separate, M1 proceeds in line with the anterior margin of the discal cell (Õunap *et al.*, 2008); subcostal accessory cell (between veins Sc and R) missing; vein M2 thinner concerning M1 and M3 on both wings; socii absent (Hausmann & Viidalepp, 2012); gnathos generally strongly reduced (Schmidt, 2015).	*Fusion* of hindwing veins Sc + R1 and Rs is a typical feature of Larentiinae (in other families these veins may be *parallel* or *connected* via short cross-vein). These veins can be separate in Larentiinae also, for instance in monotypic *Amygdaloptera testaria* and *Dyspteris* (Hausmann & Viidalepp, 2012), the latter taxon being among the most basal Larentiinae (Murillo-Ramos *et al.* 2019). A long *fused* condition of the hindwing veins Sc + R is found in the Sterrhinae tribe Rhodometrini also (Õunap *et al.* 2008, Sihvonen *et al.* 2020). Forewing fasciae are multiple in many Larentiinae (e.g. Minet & Scoble, 1999), but the wing pattern characters are variable. Hausmann (2004) lists further diagnostic characters, but none of them is without exceptions in Larentiinae. Contrary to the historical view, gnathos or remnants of gnathos are found in Larentiinae (Hausmann, 2004, Schmidt, 2015). Sterrhinae and Larentiinae share hammer-headed tip in the tympanal organ's ansa (Cook & Scoble, 1992, see also Viidalepp, 2011) and a few other characters (summarized in Hausmann, 2004). McGuffin (1987) provided diagnostic larva and pupa characters, but those were based on limited Canadian material.

Table 1. Continued

Subfamily	Diagnostic (synapomorphic) characters	Remarks
Archiearinae	Accessory tympanum lacking in metapostnotum and fenestra media narrow (Minet, 1983); larva with prolegs on segments A3–A6; hindwing M2 weak (Minet & Scoble, 1999); hindwing veins A2–A3 present and A1 present but not tubular (Hausmann, 2001); head with hair-like scales on the front of the head (Minet & Scoble, 1999).	Additional larval prolegs are also present in few Ennominae and Oenochrominae s.s. The Australian genera *Dirce* and *Acalyphes*, which were previously classified in Archiearinae (McQuillan & Edwards, 1996), are currently classified in Ennominae (Young, 2006; Murillo-Ramos *et al.* 2019). The systematic position of Mexican and Neotropical taxa, classified in Archiearinae, awaits further studies.
Desmobathrinae	Tegumen with lateral loops, extending beyond the articulation with vinculum (Fig. 16C); male 3rd sternite with pair of longitudinally elongated patches; male 8th sternite often with a finely corrugate zone laterally; often with complex structures at the junction of male 3rd and 4th sternites; delicate moths with elongated appendices (Holloway, 1996); forewing with one areole or areole absent (our observation); hindwing veins Sc + R1 and Rs parallel for long-distance or separate and connected with a short cross-vein (our observation); male with apophyses arising from membrane between the 2nd and 3rd sternites (our observation); pupa cremaster with four hooked shaftlets (= setae) (Holloway, 1996).	The characters listed here for Desmobathrinae are based on Desmobathrini only (see the composition of this clade in Murillo-Ramos *et al.* (2019)). Male apophyses arising from membrane between 2nd and 3rd sternite (found widely in Desmobathrinae, our observation) have not been mentioned as a diagnostic character earlier (Fig. 16D). Many Ennominae and Sterrhinae have similar-looking sternotympanal processes, but those originate from the posterior margin of the 2nd sternite and they are outside the abdomen (see for instance *Ekboarmia* in Skou *et al.* (2017)). No diagnostic Desmobathrinae characters have been found in the female structures. The corpus bursae have longitudinal rows of spines in the type genus *Ozola*, but there is great variation between genera (Holloway, 1996). Hausmann (2001) reports that Desmobathrinae has one or two areoles present in the forewing. Areoles are absent in *Ozola*, type genus of Desmobathrinae (our observation).
Epidesmiinae	Male antennae unipectinate, labial palps (2nd segment) elongated; two signa (one stellate, one elongated); hindwing with one anal vein (A); fore wing with two areoles; cross-veins between M veins reduced in both wings; gnathos arms fused, granulate or dentate apically; vom Rath's organ elliptical.	Epidesmiinae are diverse externally and structurally, but some characters are shared by genus-groups such as the shape of the ansa, a planiform or tectiform resting posture, and valvae with or without dorsally directed ampulla.
Oenochrominae s.s.	Robust-bodied; lacinia of tympanal organ circular, lying parallel to the tympanum; fultura superior fused with the transtilla, forming a rigid plate (Cook & Scoble, 1992); larva often with prolegs on A4–A6 (Scoble & Edwards, 1989); pupa cremaster with two hooked shaftlets (= setae) (Holloway, 1996).	Oenochrominae s.s. refers to the robust-bodied species that occur in Australasia and Indo-Malay realms, approximating Guenée's original concept (Guenée, 1857). The female signum, when present, is a single, small, circular patch of sclerotization (Holloway, 1996). The cremaster hooks (or setae) in pupa are reduced to a single apical pair in the Australian genera (McFarland, 1988). We illustrate here two additional structures from the metathorax of *Oenochroma vinaria*, which are unique among the material examined, but more material is needed to confirm their diagnostic value. The anterior and basal laminas of the metafurca are fused (Fig. 16E) and dorsal tergite is triangular extending to the opening of the euphragma (Fig. 16F).

Table 1. Continued

Subfamily	Diagnostic (synapomorphic) characters	Remarks
Geometrinae	The green pigment, (geoverdin) is predominant (Cook *et al.* 1994; the hindwing vein M2 arises closer to M1 than to M3 (Minet & Scoble, 1999); the ansa is narrow at the base, widening medially and tapered towards the apex (Cook & Scoble, 1992), the female pheromone glands are long (Bendib, 2001).	Although green pigment is found widely in Geometrinae, there are several non-green Geometrinae taxa, and green moths are in other subfamilies also. Other defining, widely present characters include: reduction of the frenulum; paired setal patches on the male 3rd sternite; socii well developed often with parallel reduction of uncus; aedeagus with sclerotization reduced to a ventral strip along the length; oblique, papillate ovipositor lobes; a bicornute signum (Holloway, 1996). Beljaev (2008) added further characters from the skeleto-muscular system of the male genitalia. The systematic position of Eumeleini has remained controversial, see discussion under Desmobathrinae and in Holloway (1996) and Murillo-Ramos *et al.* (2019). Beljaev (2008) classified Eumeleini in the Geometrinae.
Ennominae	Loss (or reduction to a fold) of hindwing vein M2; transverse setae on the 3rd male sternite; stellate signum, often with spiked concavity medially (e.g. Holloway, 1994, our wording).	Numerous molecular studies have provided support for a monophyletic Ennominae (e.g. Sihvonen *et al.* 2011, Murillo-Ramos *et al.* 2019), but the morphology-based definition of this species-rich subfamily is weak. For instance, hindwing vein M2 is present as tubular in numerous Ennominae lineages, e.g. *Melanolophia* (Boarmiini), *Alsophila* (Alsophilini), *Epirranthis* (Epirranthini), *Zerenopsis* (Diptychini) (Pitkin, 2002; Skou & Sihvonen, 2015; Sihvonen *et al.* 2015; Müller *et al.* 2019). Several lineages have additional prolegs on larva. Numerous other adult and larva characters define smaller groupings within Ennominae (Holloway, 1994; Young, 2008).
Orthostixinae	Putative characters: larva with prolegs on A5 (and occasionally on A4); hindwing veins Sc + R1 and Rs connected with short cross-vein; hindwing veins A2–A3 present; hindwing vein M2 tubular (Hausmann, 2001).	Subfamily status needs more research. Taxon shows similarities with Ennominae (Holloway, 1996) and Desmobathrinae (Hausmann, 1996b). It was noted as a 'putative tribe of Ennominae' (Hausmann & Sihvonen, 2019), based partly on the position of the tentative orthostixine genus *Naxa* (Sihvonen *et al.* 2011). Beljaev (2008) included Orthostixinae in Desmobathrinae based on skeleto-muscular structure. We find this position also to be possible (current study), because *Orthostixis cribraria* shares, with Desmobathrinae the following characters: male apophyses arising from membrane between 2nd and 3rd sternites; a tapering ansa, tegumen with weakly developed lateral loops; and presence of A2–A3 veins in the hindwing. Ecological features also support a relationship with Desmobathrinae (Hausmann, 2001).

the most diverse structures and, therefore, useful in classification, or whether they have been chosen because they are easy to observe and code in discrete character states. Thoracic sclerites and other internal structures are also diverse but these have not been used in subfamily classification. We observed the following potential diagnostic characters among these, which have not been previously mentioned in the literature: male with apophyses arising from membrane between second and third sternites in Desmobathrinae (Fig. 16D) and metathorax structures in Oenochrominae *s.s.* (Fig. 16E, F; Table 1). This illustrates that morphology of geometrid moths should be studied more extensively, beyond the routinely used characters.

Concerning Epidesmiinae synapomorphies, the situation is the same; no unique synapomorphies were found, but the subfamily is diagnosable by a combination of characters (Table 1). Among those structures, the bisignate condition of one stellate and one elongated signum, which are adjacent, is potentially unique in Geometridae. This is shared by 5/9 of Epidesmiinae genera. This bisignate condition is rare overall in the Geometridae. Structurally different examples include, for instance, in the Ennominae (*Hypoplectis* Hübner, 1823, *Mimomma* Warren, 1907 and *Nepitia* Walker, 1866) (Pitkin, 2002) and in the Sterrhinae (*Cyllopoda* Dalman, 1823, *Orthoserica* Warren, 1896 and *Rhodostrophia* Hübner, 1823; e.g. Hausmann, 2004; Lewis & Covell, 2008; Sihvonen *et al.* 2020). However, in most of these, the signa are similar in shape, parallel and adjacent, unlike in the Epidesmiinae.

Elongated labial palps (particularly the second segment) are another notable character of many Epidesmiinae. Although this character is quantitative, it easily sets apart the Epidesmiinae species from other geometrid subfamilies. Long labial palps are present in several non-related lineages, such as the Oecophoridae: Pleurotinae (Kaila *et al.*, 2019), the Gelechiidae (Huemer & Karsholt, 2018) and the Erebidae: Hypeninae, but the structural details of these are different. Also, the bi-areolar condition in the forewings of Epidesmiinae is commonly found in Geometridae, but are not necessarily formed by the same veins in other subfamilies. Currently, the homologies of relevant veins are not understood. Additionally, in Epidesmiinae the areoles are wide, whereas for instance in Oenochrominae *s.s.*, the areoles are narrow and elongated.

REFERENCES

Beljaev EA. 2008. *Phylogenetic relationships of the family Geometridae and its subfamilies (Lepidoptera), Vol. 60*. St. Petersburg: Meetings in memory of NA Cholodkovsky.

Brock JP. 1971. A contribution towards an understanding of the morphology and phylogeny of the Ditrysian Lepidoptera. *Journal of Natural History* **5:** 29–102.

Bendib A. 2001. Dorsal sex pheromone glands in female Geometridae (Lepidoptera: Geometroidea): a new apomorphy of the family. *European Journal of Entomology* **98:** 195–199.

Choi SW. 1997. A phylogenetic study on genera of Cidariini from the holarctic and the Indo-Australian areas (Lepidoptera: Geometridae: Larentiinae). *Systematic Entomology* **22:** 287–312.

Choi SW. 2001. Phylogeny of *Eulithis* and related genera (Lepidoptera: Geometridae), with an implication of wing pattern evolution. *American Museum Novitates* **3318:** 1–37.

Choi SW, **Kim SS**, **Shin Y-H. 1998.** Systematics of the tribe Abraxini (Lepidoptera: Geometridae, Ennominae) in South Korea. *Insecta Koreana* **15:** 41–76.

Cook MA, **Scoble MJ. 1992.** Tympanal organs of geometrid moths – a review of their morphology, function, and systematic importance. *Systematic Entomology* **17:** 219–232.

Cook MA, **Harwood LM**, **Scoble MJ**, **McGavin GC. 1994.** The chemistry and systematic importance of the green wing pigment in emerald moths (Lepidoptera: Geometridae, Geometridae). *Biochemical Systematics and Ecology* **22:** 43–51.

Fänger H. 1999. Comparative morphology of tergal phragmata occurring in the dorsal thoraco-abdominal junction of ditrysian Lepidoptera (Insecta). *Zoomorphology* **119:** 163–183.

Forbes WTM. 1948. Lepidoptera of New York and neighbouring States. *Memoirs of the Cornell University Agricultural Experimental Station* **2:** 1–274.

Guenée A. 1857. *Histoire Naturelle des Insectes. Species Général des Lépidoptéres.* Paris: Atlas.

Hausmann A. 1996a. The geometrid moths of the Levant and its neighbouring countries: systematic list and prodromus

of fauna (Part 1: Orthostixinae-Geometrinae). *Nota Lepidopterologica* **19:** 91–106.

Hausmann A. 1996b. The morphology of the geometrid moths of the Levant and its neighbouring countries (Part 1: Orthostixinae-Geometrinae). *Nota Lepidopterologica* **19:** 3–90.

Hausmann A. 2001. *The geometrid moths of Europe.* Stenstrup: Apollo Books.

Hausmann A. 2004. Sterrhinae. In: Hausmann A, ed. *The geometrid moths of Europe.* Stenstrup: Apollo Books, 1–600.

Hausmann A, **Sihvonen P. 2019.** *Revised, annotated systematic checklist of the Geometridae of Europe and adjacent areas Ennominae II. Geometrid moths of Europe.* Leiden: Brill, 795–871.

Hausmann A, **Viidalepp J. 2012.** *Larentiinae I. The geometrid moths of Europe.* Vester Skerninge: Apollo Books.

Heikkilä M, **Mutanen M**, **Wahlberg N**, **Sihvonen P**, **Kaila L. 2015.** Elusive ditrysian phylogeny: an account of combining systematized morphology with molecular data (Lepidoptera). *BMC Evolutionary Biology* **15:** 260.

Holloway JD. 1979. *A survey of the Lepidoptera, biogeography and ecology of New Caledonia. Series Entomologica 15.* The Hague: W. Junk.

Holloway JD. 1984. Lepidoptera and the Melanesian Arcs. In: Radovsky FJ, Raven PH, Sohmer SH, eds. *Biogeography of the Tropical Pacific. Bishop Museum Special Publication 129.* Honolulu: Bernice P. Bishop Museum, 169.

Holloway JD. 1993. Biological images of geological history: through a glass darkly or brightly face to face. *Journal of Biogeography* **30:** 165–179.

Holloway JD. 1996. The moths of Borneo, part 9: family Geometridae (incl. Orthoxtixini), subfamilies Oenochrominae, Desmobathrinae and Geometrinae. *Malayan Nature Journal* **49:** 179.

Holloway JD. 1997. The moths of Borneo: family Geometridae, subfamilies Sterrhinae and Larentiinae. *Malayan Nature Journal* **51:** 242.

Holloway JD. 2011. The moths of Borneo, part 2: Phaudidae, Himantopteridae, Zygaenidae, complete checklist, checklist notes, historical appendix, index. *Malayan Nature Journal* **63:** 1–548.

Huemer P, **Karsholt O. 2018.** Revision of the genus *Megacraspedus* Zeller, 1839, a challenging taxonomic tightrope of species delimitation (Lepidoptera, Gelechiidae). *Zookeys* **800:** 1–278.

Kaila L, **Mutanen M**, **Sihvonen P**, **Tyllinen J**, **Tabell J. 2019.** Characterization of Pleurotinae, with review of *Pleurota* species close to *P. aristella* (Linnaeus) from Morocco (Lepidoptera: Gelechioidea: Oecophoridae). *Zootaxa* **4545:** 451–477.

Klots AB. 1970. Lepidoptera. In: Tuxen SL, ed. *Taxonomists' glossary of genitalia in insects.* Copenhagen: Munksgaard, 115–130.

Lewis DS, **Covell CV. 2008.** A review of the Neotropical genus *Cyllopoda* (Lepidoptera: Geometridae: Sterrhinae: Cyllopodini). *Tropical Lepidoptera Research* **18:** 88–101.

Marriott P. 2012. *Moths of Victoria.* Watsonia North: Entomological Society of Victoria.

McFarland N. 1988. *Portraits of South Australian geometrid moths.* Lawrence: Allen Press.

McGuffin WC. 1967. Guide to the geometridae of Canada. Subfamily Sterrhinae. *Memoirs of the Entomological Society of Canada* **50:** 3–67.

McGuffin WC. 1987. Guide to the geometridae of Canada. Subfamily Ennominae. *Memoirs of the Entomological Society of Canada* **138:** 1–182.

McQuillan PB, **Edwards ED. 1996.** Geometroidea. In: Nielsen ES, Edwards ED, Rangsi TV, eds. *Checklist of the Lepidoptera of Australia.* Canberra: CSIRO.

Meyrick E. 1889. Revision of Australian Lepidoptera. *Proceedings of the Linnean Society of New South Wales* **4:** 1117–1216.

Minet J. 1983. Etude morphologique et phylogénétique des organes tympaniques des Pyraloidea. 1. généralités et homologies (Lep. Glossata). *Annales de la Société Entomologique de France* **19:** 175–207.

Minet J, **Scoble MJ. 1999.** The drepanoid/geometroid assemblage. In: Kristensen NP, ed. *Lepidoptera: evolution, systematics and biogeography.* Berlin: Walter de Gruyter, 301–320.

Müller B, **Erlacher S**, **Hausmann A**, **Rajaei H**, **Sihvonen P**, **Skou P. 2019.** Ennominae II. In Hausmann A, Sihvonen P, Rajaei H, Skou P, eds. *Geometrid Moths of Europe,* vol. 6. Leiden: Brill, 906.

Murillo-Ramos L, **Hernández-Mejía C**, **Llorente-Bousquets J. 2016.** The phylogenetic position of *Aphrissa* (Lepidoptera: Pieridae: Coliadinae) within its relatives the ancient American Catopsilias. *Zootaxa* **4147:** 538–550.

Murillo-Ramos L, **Brehm G**, **Sihvonen P**, **Hausmann A**, **Holm S**, **Reza Ghanavi H**, **Õunap E**, **Truuverk A**, **Staude H**, **Friedrich E**, **Tammaru T**, **Wahlberg N. 2019.** A comprehensive molecular phylogeny of Geometridae (Lepidoptera) with a focus on enigmatic small subfamilies. *PeerJ* **7:** e7386.

Nielsen ES, **Edwards ED**, **Rangsi TV. 1996.** *Checklist of the Lepidoptera of Australia. Monographs on Australian Lepidoptera.* Collingwood: CSIRO.

Õunap E, **Vidalepp J**, **Saarma U. 2008.** Systematic position of Lythriini revised: transferred from Larentiinae to Sterrhinae (Lepidoptera, Geometridae). *Zoologica Scripta* **37:** 405–413.

Pitkin LM. 2002. Neotropical ennomine moths: a review of the genera (Lepidoptera: Geometridae). *Zoological Journal of the Linnean Society* **135:** 121–401.

Prout LB. 1910. Lepidoptera Heterocera, fam. Geometridae, subfam. Oenochrominae. In: Wytsman, P, ed. *Genera insectorum fasc. 104.* Brussels: V. Verteneuil & L. Desmet, 119.

Prout LB. 1920. The Indoaustralian Geometridae, subfamily Oenochrominae. In: Seitz A, ed. *The Macrolepidoptera of the world.* Stuttgart: Fritz Lehmann Verlag, 5–43.

Schachat SR. 2020. Symmetry systems on the wings of *Dichromodes* Guenée (Lepidoptera: Geometridae) are unconstrained by venation. *PeerJ* **8:** e8263.

Schmidt O. 2012. An annotated and illustrated list of the primary type specimens of geometrid moths deposited in the Queensland Museum (Australia, Brisbane). *Spixiana* **35:** 79–100.

Schmidt O. 2015. One century after: a reappraisal of the gnathos (*sensu* Pierce, 1914) in Larentiinae (Lepidoptera: Geometridae). *Zootaxa* **3974:** 328–340.

Scoble MJ. 1986. The structure and affinities of the Hedyloidea: a new concept of the butterflies. Bulletin of the British Museum (Natural History). *Entomology Series* **53:** 251–286.

Scoble MJ. 1999. *Geometrid moths of the world: a catalogue (Lepidoptera, Geometridae).* Collingwood: CSIRO.

Scoble MJ, **Edwards ED. 1989.** *Parepisparis* Bethune-Baker and the composition of the Oenochrominae (Lepidoptera, Geometridae). *Entomologica Scandinavica* **20:** 371–399.

Scoble MJ, **Hausmann A. 2007.** *Online list of valid and nomenclaturally available names of the Geometridae of the world.* Available at: http://www.lepbarcoding.org/cl_geometridae.php (accessed 12 February 2014).

Sibatani A. 1972. Male genitalia of Lepidoptera: morphology and nomenclature IV. Notes on Tuxen's 'Taxonomist's glossary of genitalia in insects': second enlarged edition. *Journal of the Lepidopterists' Society* **26:** 117–122.

Sihvonen P. 2001. Everted vesicae of the *Timandra griseata* group: methodology and differential features (Geometridae, Sterrhinae). *Nota Lepidopterologica* **24:** 57–63.

Sihvonen P. 2005. Phylogeny and classification of the Scopulini moths (Lepidoptera: Geometridae, Sterrhinae). *Zoological Journal of Linnean Society* **143:** 473–530.

Sihvonen P, **Kaila L. 2004.** Phylogeny and tribal classification of Sterrhinae with emphasis on delimiting Scopulini (Lepidoptera: Geometridae). *Systematic Entomology* **29:** 324–358.

Sihvonen P, **Staude H. 2011.** Geometrid moth *Afrophyla vethi* (Snellen, 1886) transferred from Oenochrominae to Sterrhinae (Lepidoptera: Geometridae). *Metamorphosis* **22:** 102–113.

Sihvonen P, **Mutanen M**, **Kaila L**, **Brehm G**, **Hausmann A**, **Staude HS. 2011.** Comprehensive molecular sampling yields a robust phylogeny for geometrid moths (Lepidoptera: Geometridae). *PLoS One* **6:** e20356.

Sihvonen P, **Staude HS**, **Mutanen M. 2015.** Systematic position of the enigmatic African cycad moths: an integrative approach to a nearly century old problem (Lepidoptera: Geometridae, Diptychini). *Systematic Entomology* **40:** 606–627.

Sihvonen P, **Murillo-Ramos L**, **Brehm G**, **Staude H**, **Wahlberg N. 2020.** Molecular phylogeny of Sterrhinae moths (Lepidoptera: Geometridae): towards a global classification. *Systematic Entomology* **45:** 606–634.

Skou P, **Sihvonen P. 2015.** Ennominae I. In: Hausmann A, ed. *Geometrid moths of Europe.* Leiden: Brill, 657.

Skou P, **Stüning D**, **Sihvonen P. 2017.** Revision of the West-Mediterranean geometrid genus Ekboarmia, with description of a new species from Portugal (Lepidoptera, Geometridae, Ennominae). *Nota lepidopterologica* **40:** 39–63. Available at: https://doi.org/10.3897/nl.40.10440

Sommerer M. 1995. *The Oenochrominae (auct.) of Sumatra (Lep. Geometridae).* Pematang Siantar: Heterocera Sumatrana Society.

Turner AJ. 1929. Revision of Australian Oenochromidae (Lepidoptera). I. *Proceedings of the Linnean Society of New South Wales* **54:** 463–504.

Turner AJ. 1930a. Revision of Australian Oenochrominae (Lepidoptera). II. *Proceedings of the Linnean Society of New South Wales* **55:** 1–40.

Turner AJ. 1930b. Revision of Australian Oenochrominae (Lepidoptera). III. *Proceedings of the Linnean Society of New South Wales* **55:** 191–220.

Wootton RJ. 1979. Function, homology and terminology in insect wings. *Systematic Entomology* **4:** 81–93.

Young C. 2006. Molecular relationships of the Australian Ennominae (Lepidoptera: Geometridae) and implications for the phylogeny of the Geometridae from molecular and morphological data. *Zootaxa* **1264:** 1–147.

Young C. 2008. Characterisation of the Australian Nacophorini using adult morphology and phylogeny of the Geometridae based on morphological characters. *Zootaxa* **1736:** 1–141.

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