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RESEARCH ARTICLE

An online taxonomic facility of Geometridae (Lepidoptera), with an overview of global species richness and systematics

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Abstract

We present a new, online, open access portal to the geometrid moths of the world (Lepidoptera: Geometridae). The portal provides access to the global database including data on classification, valid genera and species, synonyms and type localities, and to an online list of valid names. The value of this online facility, *inter alia*, is demonstrated by using the underlying data to update our understanding of the global and regional species richness of the family. We also review, clarify and list the family-group names (family, subfamily, tribe) of the Geometridae to provide users with a better understanding of the higher category framework when they access the database. Currently, the Geometridae database includes 34,897 available species-group names. Of these, 7,891 are considered synonyms (23% of available names), giving a total of 27,006 valid species-group names, which in turn comprise 23,872 species names and 3,134 subspecies names. The world fauna is classified into 2,019 genera, 92 tribes and 9 subfamilies. Our paper also includes an annotated list of all 202 subfamily, tribe and subtribe names in systematic order. One hundred family-group names (49.5%) are considered synonyms. Although most geometrid species were described in the 19th and 20th centuries, the average number of new species descriptions from 2000–2022 has been fairly constant at around 80 per year, implying there is still much more hidden geometrid diversity yet to be discovered.

Key words: biogeography, database, geometrid moths, global, review, website.

Zusammenfassung

Ein neues, frei zugängliches Online-Portal zu den Geometriden der Welt (Lepidoptera: Geometridae) wird hier vorgestellt. Das Portal bietet Zugang zu einer globalen Datenbank mit Informationen zur Klassifikation, zu sämtlichen validen Gattungs- und Artnamen, Synonymen und Typuslokalitäten. Die Bedeutung dieser öffentlich zugänglichen Datensammlung liegt darin, unsere Kenntnisse über den globalen und regionalen Artenreichtum der Familie Geometridae zu verbessern. Außerdem wurden die Namen der höherrangigen Taxa (Familie, Unterfamilie, Tribus) überarbeitet, ihr Status geklärt und aufgelistet, um den Benutzern ein besseres Verständnis der Phylogenie nach dem augenblicklichen Stand der Forschung zu vermitteln. Derzeit umfasst die Familie der Geometriden 23.872 beschriebene und valide Arten und 3.134 validierte Unterarten, während weitere 7.891 Namen als Synonyme betrachtet werden (23 % der verfügbaren Namen). Die weltweite Fauna ist in 2.019 Gattungen, 92 Triben und 9 Unterfamilien unterteilt. Unsere Arbeit enthält zudem eine kommentierte Liste aller 202 Unterfamilien-, Tribus- und Subtribusnamen in systematischer Reihenfolge. 100 dieser Namen (49,5 %) werden als Synonyme betrachtet. Während die meisten Geometriden-Arten im 19. und 20. Jahrhundert beschrieben wurden, liegt die durchschnittliche Zahl der neuen Artbeschreibungen von 2000 bis 2022 ziemlich konstant bei etwa 80 pro Jahr, was bedeutet, dass eine bedeutende Zahl von Geometriden noch darauf wartet, entdeckt zu werden.

Introduction

Card indexes of insect species exist in many museums, such as that in the Natural History Museum, London (GASTON et al. 1995; SCOBLE 1999). Some of the available published printed catalogues have evolved from such card indexes (e.g., Arctiinae: WATSON & GOODGER 1986; Geometridae: SCOBLE 1999) or were compiled otherwise (e.g., POOLE 1989; SOBczyk 2011). In recent years, several global Lepidoptera species databases have become available online, notably for Papilionoidea (HÄUSER et al. 2005), Pyraloidea (NUSS et al. 2022), Bombycoidea (KITCHING

et al. 2018), Tortricidae (GILLIGAN et al. 2018) and Gracilariidae (DE PRINS & DE PRINS 2006–2022) in addition to a growing number of regional online catalogues (e.g., DE PRINS & DE PRINS 2011–2022; DOMINICK et al. 1983; HOLLOWAY 1986–1999; KARSHOLT & NIEUKERKEN 2013).

Species catalogues vary somewhat in their content, but provide basic taxonomic information to many of the following fields: valid names and synonyms, homonyms, authors, dates, references, type specimens, type localities and distribution. Depending on their comprehensiveness, they also enable access to consolidated data on species richness and how species are arranged in higher

taxonomic categories. Ideally, phylogenetic relationships are also reflected. Such extensive and structured content means that species catalogues can provide the foundation for global species richness estimates, and information on patterns in species description over time (GASTON et al. 1995). The number of insect species in the world is unknown, but current estimates rely significantly on verifiable information about the richness of described species (GARCIA et al. 2020). Furthermore, species catalogues may help to identify collection biases and understudied regions of the world, indicating where future field campaigns exploring the biodiversity should take place.

Species catalogues are lacking for most insect groups for several reasons. First, taxonomic information is scattered across a wide spread of journals and other literature. Second, many articles are difficult to source (although the Biodiversity Heritage Library provides a major improvement in accessibility, <https://www.biodiversitylibrary.org/>). Third, articles may be written in languages that are not widely understood. Fourth, numerous regional classifications may conflict with each other, making a consensus difficult. Fifth, data included in original publications are often superficial and do not allow unambiguous identification, a point especially true for the early literature. Finally, and perhaps most importantly, compiling such diverse and scattered information into a single entity is a time-consuming and labour-intensive task, requiring expert knowledge of a particular taxon, often with few specialists who are usually suffering a high workload.

Apart from our personal interest in the Geometridae, we consider that the family is particularly suitable for an online facility, with more than 23,000 species accounting for nearly 15% of all Lepidoptera species (NIEUKERKEN et al. 2011). Geometrid moths are the second-largest lepidopteran family (after Erebidae) in terms of described species. Furthermore, this global diversity has been summarised in two species catalogues dating back 23 and 15 years, respectively: (1) “Geometrid Moths of the World: A Catalogue” (SCOBLE 1999) and (2) “Online list of valid and available names of the Geometridae of the World” (SCOBLE & HAUSMANN 2007). Geometrid moths have received considerable attention during the last decades, and the use of molecular data, in particular, has advanced our understanding of the family significantly, so both the catalogue and the online list need updating. Before describing the scope and content of the new database (“Online taxonomic facility of geometrid moths”), we summarise the contents of the two earlier works.

Geometrid Moths of the World: A Catalogue (SCOBLE 1999). The Catalogue is a massive two-volume printed monograph of 1,016 pages, plus a 129-page index, and it is based on the British Museum of Natural History’s card index to genera and species of Geometridae housed in the Natural History Museum, London (NHMUK) [pre-

viously known as the British Museum (Natural History)]. The Catalogue provides access to the available names of geometrid moths of the World, including approximately 35,000 species-group names (including synonyms). The following data for each species and subspecies were entered (called ‘Fields’ in the Global Taxonomic Facility): Subfamily, Genus, Original genus, Taxon name (species or subspecies), Author, Date, Title of reference, Volume number of reference, Series number of reference, Part number of reference, Page number of original citation, Whether original reference was checked (yes/no), Whether a junior synonym (yes / no), If a junior synonym, of what species/subspecies, Number of names synonymised, Drawer number in BMNH collection, Depository of type(s), Type status (holotype, syntype(s) etc.), Type sex (if known), Type locality (country, state, place), Zoogeographical region. The printed Catalogue does not include all above-mentioned fields.

Entries are ordered alphabetically by genus and, within each genus, by species. The Catalogue also includes genus names and genus synonyms, citing author(s), date, reference to the original description, and type species. It includes extensive unpublished data extracted from details in the card index, but these were not separated from the published data. For a small number of species, larval foodplant data are provided. The publication also includes a morphological diagnosis of the family, a summary of the patterns of species description in the Geometridae derived from GASTON et al. (1995) and a list of genera in systematic order, following the order in which the collection in the British Museum of Natural History was laid out.

Online list of valid and available names of the Geometridae of the world (SCOBLE & HAUSMANN 2007). The global species list is displayed as an Excel spreadsheet derived from the above-mentioned Catalogue (SCOBLE 1999), containing information on the subfamily, genus, species, author and year of description for all validated geometrid moth species up to 2007, covering 22,951 species. Unlike the Catalogue (SCOBLE 1999), it does not give information on the original publication, depository of type(s), type status (holotype, syntype(s), etc.), subspecies, junior synonyms, or type locality. This list is now available the new Forum Herbulot website at <https://geometroidea.smns-bw.org/>.

In the present paper, we: i) announce the forthcoming launch of an online facility on Geometridae, describe its structure and comment on its value and purpose; ii) complement this open access biodiversity data release with an up-to-date review of Geometridae species diversity and subfamily-level phylogeny; and iii) provide an updated systematic list of family-group names. Finally, we present our plans for the future development of the facility.

Material and methods

In order to update the printed and online world catalogues of geometrid moths (SCOBLE 1999; SCOBLE & HAUSMANN 2007), we searched the Zoological Record database (<https://clarivate.com/webofsciencegroup/solutions/webofscience-zoological-record/>) for all records published after 2005, using the keyword “Geometridae”, and compared the contents of each publication against the “Online list of valid and available names of the Geometridae of the World” (SCOBLE & HAUSMANN 2007). In addition, we included all publications available to us from 1998, which were not covered by the Zoological Record database. In total, data from 462 publications (journal articles, books, short communications and any other form of available and valid scientific publications) were extracted and entered in the Excel table. These 462 literature references are listed in Appendix 2. Additionally, all published taxonomic changes, including new synonymies, new combinations, new statuses, etc., in all hierarchical categories, were incorporated. The cut-off date for the data input was 23 May 2022.

Geographic coverage of the aforementioned 462 publications was examined by scoring the biogeographic region(s) each publication included. If the taxa in the paper were confined to one biogeographic region only, only one region was scored “1”. If the paper covered multiple regions, each covered region was scored “1”. The scoring is listed in Supplementary File 1.

Statistics in this paper (see “A summary of the species richness and systematics of Geometridae”), below, are based on the Excel table we created, which contains 34,897 species-group names of geometrid moths. The sub-section “Phylogeny, classification and species richness by subfamily” is based partially on our literature review and partially on the Excel table (see Supplementary File 1).

The geographic distribution of geometrid moths (Fig. 4) is based on 23,872 valid species names (see Supplementary File 1), excluding the subspecies and synonyms (see Fig. 4A). Biogeographic regions were coded for each species based on its type locality (type locality information was missing for 17 species, which were excluded from the analysis). The biogeographic regions used in the analysis and shown in Fig. 4B are based on the scheme employed in the NHMUK collection and in The Global Lepidoptera Names Index (<https://www.nhm.ac.uk/our-science/data/lepindex/lepindex/>). The details are available in GASTON & HUDSON (1994).

The online portal with the graphical user interface (GUI) to access the data was created by computer engineer HAMID LAGHA (Mashhad, Iran) using React.js and python programming languages. The portal’s interface was designed to enable easy, user-friendly updates (by approved contributors) to reflect new taxonomic changes after its initial publication.

The classification presented under “Family-group classification and names of Geometridae of the world” (Appendix 1) and in a forthcoming “Online list of valid names of geometrid moths” will be merged into the GBIF Backbone Taxonomy (GBIF Secretariat 2021) and into backbone systematics on BOLD (RATNASINGHAM & HEBERT 2007).

Results

“Online taxonomic facility of geometrid moths” and list of valid names of geometrid moths

The new online portal provides access to all available names of geometrid moths of the world. The data are freely

available and can be accessed at <https://geometroidea.smns-bw.org/>. The portal provides front-end access to a back-end Excel table, which includes 34,897 species-group names of geometrid moths. The table includes data from all published systematic literature on geometrid moths accessible to the authors, covering the period from the 10th edition of *Systema Naturae* (LINNAEUS 1758) to 23 May 2022.

The back-end Excel table includes the following fields for all species-group names: Superfamily, Family, Subfamily, Tribe, Genus, Author, Year, Senior species, Senior subspecies, Senior species year, Senior subspecies year, Species, Subspecies, Species author, Species year, Species in author, Original genus, Country, Locality, Elevation, Latitude, Longitude, Junior synonym (yes/no), BIN, ID holotype (BOLD), Type depository, Type status, Type sex, Type country, Type state, Journal, Series, Volume, Part, Page (first), Comments.

Fields are not completed for every species, nor is a fully updated list of genera with synonyms available. As such, the online portal allows users to search the following columns for 34,897 species-group names: Family, Subfamily, Genus, Species, Subspecies and any name, including synonyms. Fig. 1A shows a typical query result from the back-end Excel table, in this case at genus level using the term “*Archiearis*”. Note that the search also reports a full list of synonyms and type localities. All species and synonyms are hyperlinked to the relevant species-level page (Fig. 1B). The data can be queried by using search terms (quick search and advanced search options are available) or by using a hierarchy search.

Additionally, the online portal contains a downloadable Excel table, which lists all valid and available names of Geometridae of the world. The structure of the Excel table is similar to that of the “Online list of valid and available names of the Geometridae of the world” (SCOBLE & HAUSMANN 2007).

The database will be updated by the authors as new information is published on Geometridae, with once-yearly updates of the facility and a list of valid and available names. This approach has the advantage of providing a citable, static version of the database with a date for each update release.

A summary of the species richness and systematics of Geometridae

Our database of geometrid moths provides an ideal source of information for summarising knowledge of the species richness, distribution and systematics of the family globally, demonstrating more widely the value of compiling databases of species-rich taxa. The present world database includes 34,897 available species-group names. Of these, 7,891 are considered synonyms (23% of avail-

A

Family: Geometridae Leach, 1815 Subfamily: Archiearinae Fletcher, 1953 Tribe: will be updated Genus: *Archiearis* Hübner, [1823]

[↗](#) *Archiearis infans infans* (Möschler, 1862) (*Brephos*) T.L. in: [Canada] ←
[↗](#) = *hamadryas* (Harris, 1869) (*Brephos*) T.L. in: [North America]

[↗](#) *Archiearis infans oregonensis* (Swett, 1917) (*Brephos*) T.L. in: [U.S.A.]

[↗](#) *Archiearis parthenias bella* (Inoue, 1955) (*Brephos*) T.L. in: Japan

[↗](#) *Archiearis parthenias elegans* (Inoue, 1955) (*Brephos*) T.L. in: Japan

[↗](#) *Archiearis parthenias hilara* (Sawamoto, 1937) (*Brephos*) T.L. in: Japan

[↗](#) *Archiearis parthenias lapponica* (Rangnow, 1935) (*Brephos*) T.L. in: [Sweden/Finland]

[↗](#) *Archiearis parthenias parthenias* (Linnaeus, 1761) (*Phalaena (Noctua)*) T.L. in: Sweden
[↗](#) = *fulvulata* (Pallas, 1773) (*Phalaena*) T.L. in: [Russia]
[↗](#) = *glaucescens* (Goeze, 1781) (*PhalaenaNoctua*) T.L. in:
[↗](#) = *glaucofasciata* (Goeze, 1781) (*PhalaenaGeometra*) T.L. in:
[↗](#) = *plebeja* (Linnaeus, 1761) (*PhalaenaNoctua*) T.L. in: Sweden
[↗](#) = *vidua* (Fabricius, 1775) (*Bombyx*) T.L. in: Anglia [England]

[↗](#) *Archiearis parthenias sajana* (Prout, 1912) (*Brephos*) T.L. in: [Russia]

B *Archiearis infans infans* (Möschler, 1862) (*Brephos*)

Family: Geometridae Leach, 1815 Subfamily: Archiearinae Fletcher, 1953
 Tribe: will be updated Genus: *Archiearis*
 Author: Hübner Year: [1823]
 Senior species: *infans* Senior sub species: *infans*
 Senior species author: Möschler Senior species year: 1862
 Species: *infans* Subspecies: *infans*
 Species author: Möschler Species year: 1862
 Species in author: Original genus: *Brephos*
 Country: [Canada]

SYNONYMS

= *hamadryas* (Harris, 1869) (*Brephos*)

CLASSIFICATION

Family	Geometridae Leach, 1815
Subfamily	Archiearinae Fletcher, 1953
Tribe	will be updated
Genus	<i>Archiearis</i>

Fig. 1. Examples of search results from the “Online taxonomic facility of geometrid moths”, available at <https://geometroidea.smns-bw.org/>. **A.** Genus-level result using the term “*Archiearis*”. **B.** Species-level result using the term “*Archiearis infans infans*”, or selecting the hyperlink in (A) (black arrow).

able names), giving a total of 27,006 valid species-group names, which in turn comprise 23,872 species names and 3,134 subspecies names. This diversity is classified into 2,019 genera and nine subfamilies (see “Phylogeny, classification and species richness by subfamily” for details).

Subspecific names are often controversial in systematics. The current version of the “Online taxonomic facility of geometrid moths” includes 3,134 such entries. A robust approach has been taken in checklists of other lepidopteran

taxa (e.g., POOLE 1989; NIELSEN et al. 1996), in which it was proposed that subspecies names should be treated as junior synonyms of the relevant species name. With respect to the Geometridae, SCOBLE (1999: xx–xxi) argued that “subspecies are inconsistently founded and usually they merely burden the taxonomy without adding anything to our understanding of natural divisions within a species”. The subspecies problem was also discussed by SKOU & SIHVONEN (2015: 37) in the European context, a continent

overwhelmed by subspecies and synonymies. Indeed, in “The Geometrid Moths of Europe” series (HAUSMANN 2001, 2004; MIRONOV 2003; HAUSMANN & VIDALEPP 2012; SKOU & SIHVONEN 2015; MÜLLER et al. 2019a, 2019b) hundreds of subspecies names were sunk into synonymy (see HAUSMANN & SIHVONEN 2019). We follow SCOBLE (1999) and encourage taxonomists using the online database to adopt the approach of synonymising subspecies if they do not merit the rank of species unless there are clear and consistent reasons for not doing so.

Phylogeny, classification and species richness by subfamily

Much research on the systematics of the Geometridae has been carried out from the time of LINNAEUS onwards, but more needs to be done to improve its current state. Specifically, many if not most genera outside the Palaearctic or Nearctic regions need revision. Many genera as currently accepted are not monophyletic and their systematic position remains unstudied, even for those that have been

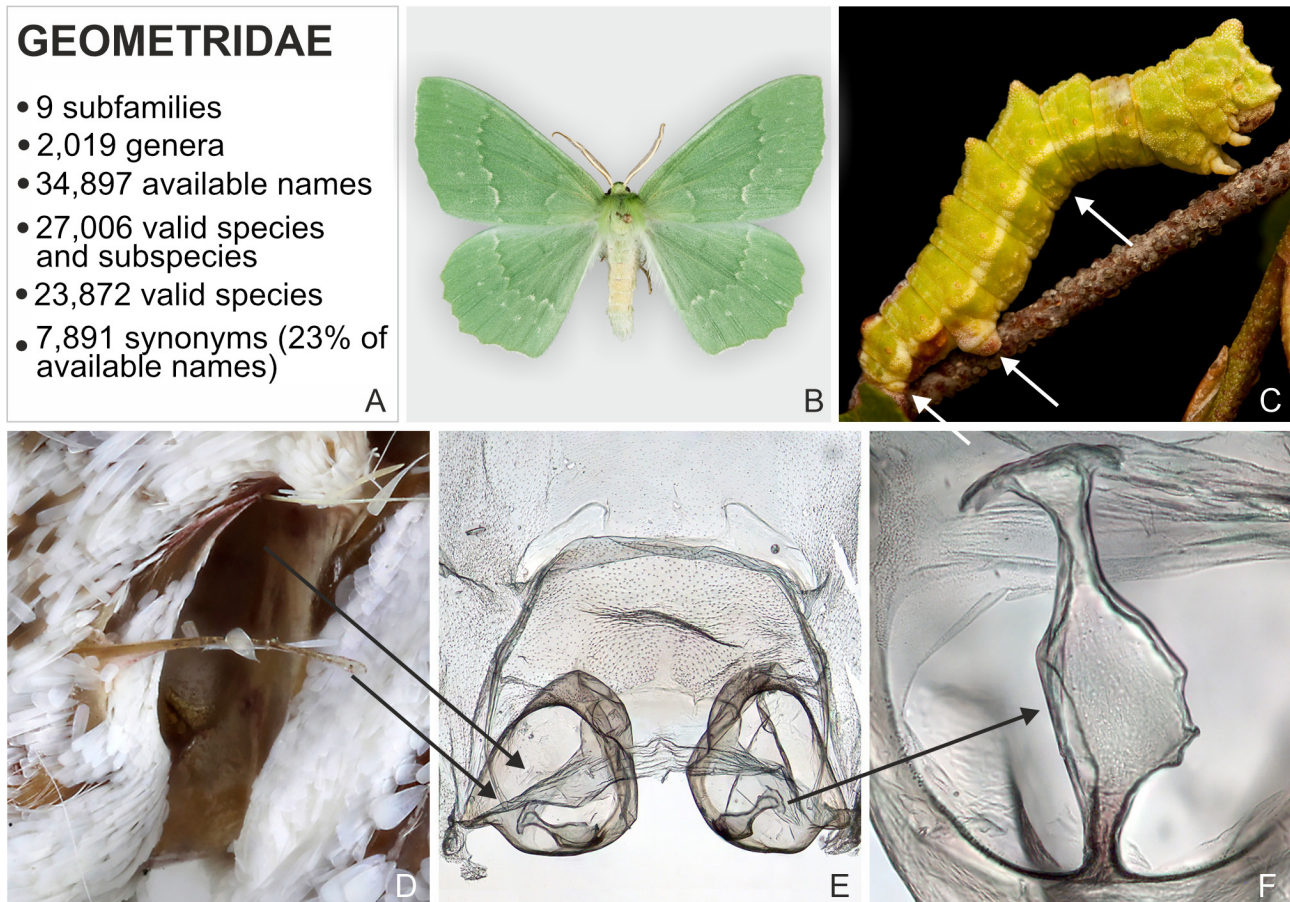


Fig. 2. Summary of species richness and classification of geometrid moths (based on data collected until 23.5.2022) and diagnostic morphological characters of the family. **A.** Summary of species richness and classification—see text for details. **B.** *Geometra papilionaria* Linnaeus, 1758 (photo: PEKKA MALINEN), adult male, the type species of the type genus of Geometridae. **C.** *Geometra papilionaria* caterpillar (photo: TAPIO KUJALA), showing diagnostic loss or reduction of ventral prolegs; prolegs are present only on segments 6 and 10, which causes the characteristic “looping” progression. Geometrid caterpillars also possess subprimary seta L4 on the abdominal segments (not visible on the photo due to the small size of the seta). **D–E.** *Phrataria replicataria* Walker, 1866 (photos: PASI SIHVONEN), showing the morphologically diagnostic tympanal organs on the ventral side of the second abdominal segment. **D.** Specimen with scales, arrows showing tympanal cavity and arched sclerotised rod curved over the tympanum. The ansa, which is visible in E and F, is inside the tympanal cavity and not visible in D. **E.** Specimen without scales, showing both tympanal organs. Arrows on left side of picture showing tympanal cavity and sclerotised rod. **F.** Tympanal organ’s ansa (arrow) enlarged. (B and C published under CC-BY-NC-SA-4.0 licence; original photos available on Finnish Biodiversity Info Facility <https://laji.fi/en>; D and E reproduced from MURILLO-RAMOS (2021), slightly modified)

collected and examined frequently from well-explored habitats and biomes. Moreover, numerous species remain undescribed.

A major impediment to achieving a more comprehensive and robust taxonomy for the Geometridae is the large number of species in the family compared with the limited resources for study—especially in terms of specialists and funding. The situation is further hindered by geographically and methodologically restricted approaches, which has resulted in classifications that are too narrow in outlook, lacking the necessary global overview of the family. In recent years, however, these shortcomings have been addressed, and with international collaboration and better geographic sampling, significant advances have been made. Notably, the higher-level classification has been rendered decidedly more robust. A summary of the main observations on the state of Geometridae systematics follows:

- Geometridae are a monophyletic family, being sister to Uraniidae within Geometroidea (Fig. 2A, B). The systematic position and monophyly of the family are supported by molecular and morphological data (e.g., HOLLOWAY 1997; MINET & SCOBLE 1999; SIHVONEN et al. 2011; REGIER et al. 2013; HEIKKILÄ et al. 2015; RAJAEI et al. 2015; KAWAHARA et al. 2019; MURILLO-RAMOS et al. 2019). The combination of presence of a central rod ('ansa') in the cavities of the paired tympanal organs and tympanal organs present on fused abdominal sternites 1–2 [Fig. 2D, E, F; for overview of structures see COOK & SCOBLE (1992)] is diagnostic, whereas in Uraniidae the tympanal organs differ in morphology and location, being on tergites 2–3 in males and on sternite 2 in females. Other geometroid families (Sematuridae, Epicopeiidae, Pseudobistonidae) lack tympanal organs [see RAJAEI et al. (2015) for other diagnostic characters] and other taxa with tympanal organs at the base of the abdomen, such as Pyraloidea and Drepanoidea, differ in structural details (MINET & SCOBLE 1999; MUNROE & SOLIS 1999). Tympanal organs are reduced in size in a few geometrid lineages, particularly in brachypterous females [see examples in MÜLLER et al. (2019a, 2019b)]. In Geometridae, larval prolegs are typically reduced to two pairs, causing these caterpillars to move by looping (Fig. 2C), whereas uraniid larvae have five pairs of well-developed prolegs (MINET & SCOBLE 1999). A few Geometridae species have more abdominal prolegs, e.g., species of Archiearinae (HAUSMANN 2001) and Oenochrominae (COMMON 1990) and in Ennominae this characteristic is almost exclusively confined to Diptychini as defined by MURILLO-RAMOS et al. (2019), including, for instance, Afrotropical *Callioratis* Felder, 1874 (DUKE & DUKE 1998; STAUDE 2001; SIHVONEN et al. 2015) and some Australian and South American taxa (PARRA & HENRIQUEZ-RODRIGUEZ 1993; YOUNG 2008). HAUSMANN (2001: 69) provided a summary for Ennominae. Geometridae larvae have an extra L seta (subprimary L4) on the abdominal segments, which is absent in other families (DUGDALE 1961) except in Thyatiridae (STEHR 1987), but mapping of this character needs wider taxon sampling. Externally, both adults and larvae of geometrids are very variable in size, pattern and colour.
- Nine subfamilies of Geometridae are usually accepted, and the relationships between eight of them (Sterrhinae, Larentiinae, Archiearinae, Desmobathrinae, Epidesmiinae, Oenochrominae s. str., Geometrinae and Ennominae) are well-established (Fig. 3). These subfamilies are supported by morphological characters (see MURILLO-RAMOS et al. 2021a) and molecular characters (MURILLO-RAMOS et al. 2019). The status of the ninth subfamily, Orthostixinae, needs more research, as it may be part of Desmobathrinae (MURILLO-RAMOS et al. 2021b). The phylogenetic position of the genus *Eumelea* Duncan & Westwood, 1841 remains uncertain. It has been considered variously as a sister group to Desmobathrinae: Desmobathrini (HOLLOWAY 1996), Geometrinae (BELJAEV 2008b), or the Ennominae genus *Plutodes* Guenée, 1858, depending on the analysis employed (MURILLO-RAMOS et al. 2019); as a result, MURILLO-RAMOS et al. (2019) treated it as *incertae sedis*. The most recent study, based on 329 genetic markers, placed *Eumelea* either as sister to Geometrinae (analysis based on nucleotides) or as sister to Oenochrominae s. str. (analysis based on a study of amino acids) (MURILLO-RAMOS et al. 2021b). The situation is under review, with a proposal to accept *Eumelea* as representing a separate lineage and giving it subfamily status (MURILLO-RAMOS et al., unpublished). If Orthostixinae becomes a junior synonym of Desmobathrinae and *Eumelea* is given subfamily rank, the total number of valid subfamilies in Geometridae would remain at nine.
- Sterrhinae alone (MURILLO-RAMOS et al. 2019) or Sterrhinae + Larentiinae are considered the sister group to the rest of Geometridae (e.g., YAMAMOTO & SOTA 2007; SIHVONEN et al. 2011). With regard to the phylogeny, many taxa, particularly in Desmobathrinae, Oenochrominae s. l., and Ennominae are still misplaced and will need transferring to other subfamilies.
- The most recent tribal-level classification based on a study benefitting from global taxon sampling included 1,206 geometrid species and 11 genes (MURILLO-RAMOS et al. 2019). The resultant phylogenetic analysis improved the systematics of geometrids significantly. The results revealed that many species are misplaced in tribes and in genera; that many genera are non-monophyletic; and that a great deal of research is needed

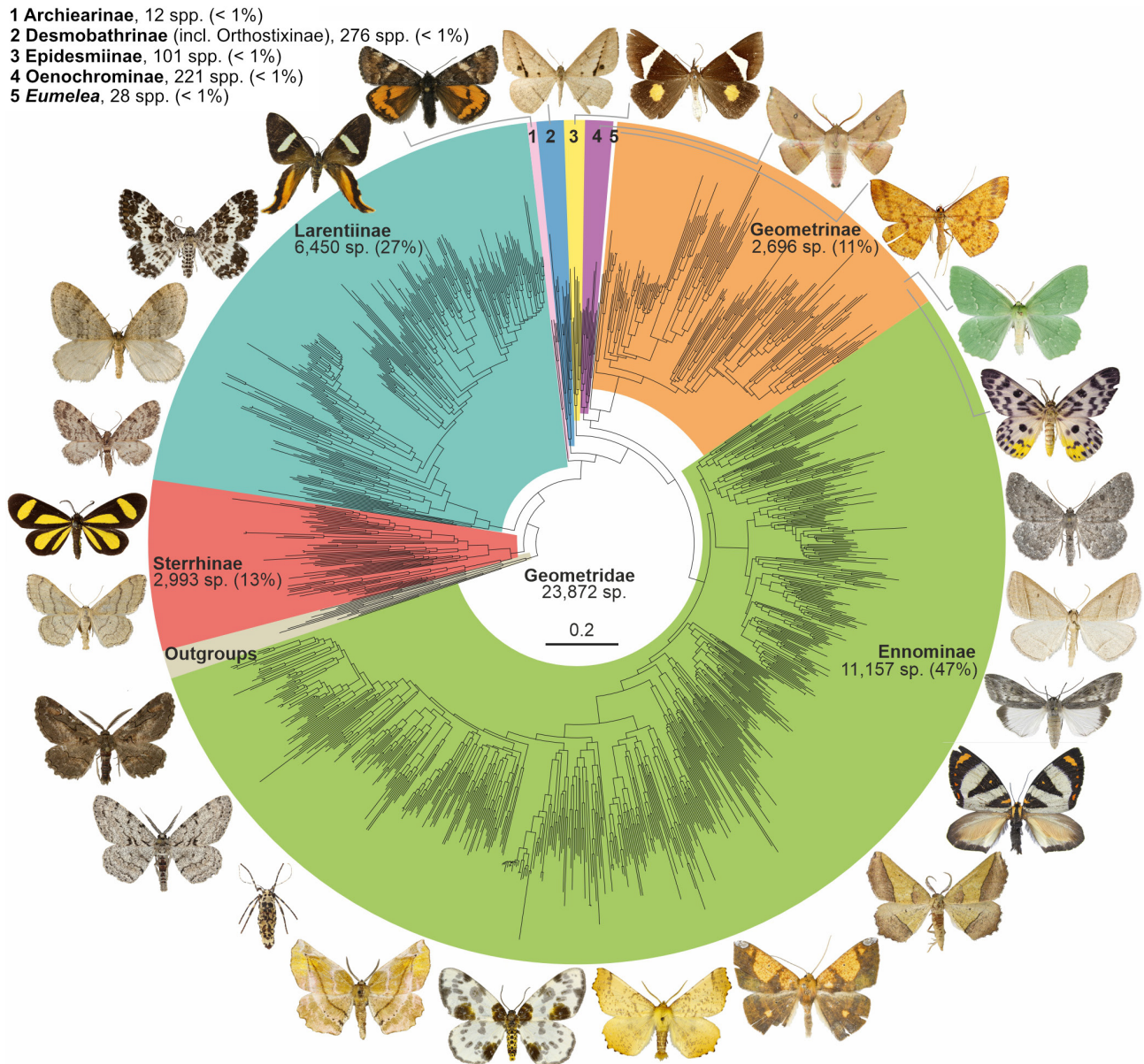


Fig. 3. Summary of Geometridae phylogeny, classification and species richness by subfamily. Non-ultrametric phylogeny and classification based on MURILLO-RAMOS et al. (2019) and MURILLO-RAMOS (2021); species richness in each subfamily based on data presented in the current paper. The size of the coloured subfamilies in the tree is representative of the taxon sampling in MURILLO-RAMOS et al. (2021b), not the species richness. The figured moths (not in scale relative to each other) represent selected species in each subfamily, both nocturnal and diurnal, to highlight the diversity of wing patterns, shapes and colours.

at these taxonomic levels. Subtribal classification is rarely applied in Geometridae systematics, except to Geometrinae (BAN et al. 2018).

Our understanding of the phylogenetic relationships and classification of geometrids varies greatly geographically and by taxon. The most intensively studied areas are the Nearctic (e.g., MCGUFFIN 1987; FERGUSON 2008;

POHL et al. 2016) and the West Palearctic (e.g., MÜLLER et al. 2019a, 2019b and references therein), yet much work remains to be done even in these areas. The taxonomic impediment is highest in the tropics, which are known to be the most species-rich areas (HILLEBRANDT 2004; BREHM et al. 2016). Significant parts of these faunas have not been included in modern taxonomic studies, and often nothing else exists than the original, usually very superficial

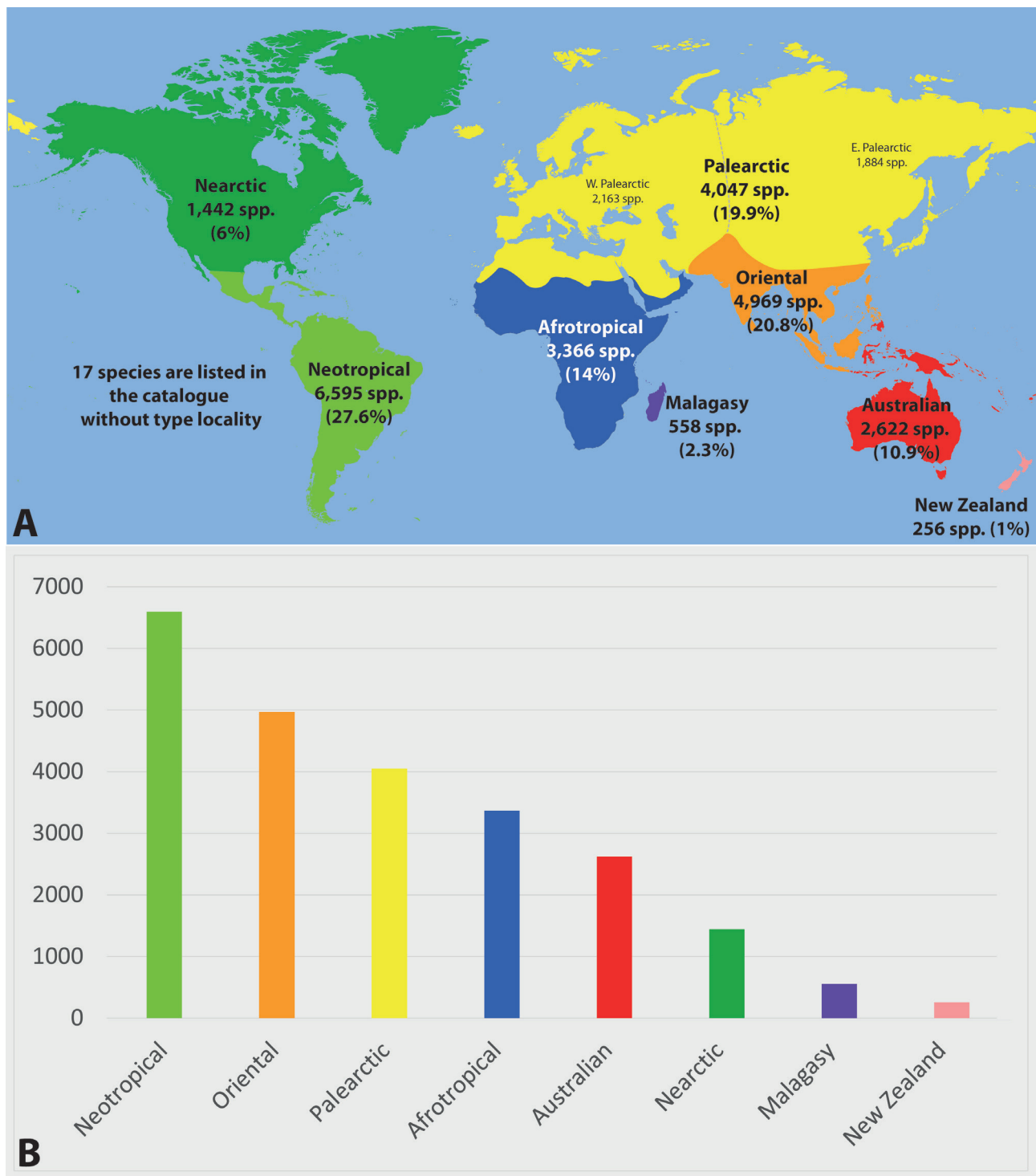


Fig. 4. Species richness in different biogeographic regions based on the analysis of the type localities of 23,872 valid species, showed on world map (A) and as a bar graph (B). The Neotropics are the most species-rich biogeographic region.

species and genus descriptions from late 1800s and early 1900s. Exceptions do exist, for instance *The Moths of Borneo* series (see HOLLOWAY 2011 and references therein).

Species richness and geographic distribution of type localities

Species richness of Geometridae in different biogeographic regions of the world is mapped in Fig. 4, a graphic that is based on an analysis of type localities. As regards the biogeographic regions, the highest described species richness is in the Neotropics, with 6,595 species, followed by the Oriental Region with 4,969 described species. The Palearctic Region, specifically the West Palearctic Region, is the most explored and its fauna has been the target of extensive taxonomic studies for several centuries. In total, 4,047 valid species are known from this region, 53% of them from the West Palearctic. The Afrotropical Region has 3,366 described species, followed by the Australian Region with 2,622 species. Of note is that the Oriental Region is considerably smaller in land area than the Nearctic, but the number of described species is much higher: 4,969 in the Oriental and 1,442 in the Nearctic. Madagascar and New Zealand are the smallest in terms of

described species, but many of the species are endemic to these islands.

Patterns of species description in the Geometridae

The annual pattern of species description in Geometridae (Fig. 5) shows a peak roughly between the years 1860 and 1950, with the highest numbers in the early 1900s. In seven years, the annual number of new species described exceeded 600: 1897 (1,137 species), 1858 (968 species), 1904 (807 species), 1907 (658 species), 1901 (645 species), 1893 (641 species) and 1916 (603 species). Altogether 1,854 new species and subspecies have been described by various authors since 2000, after publication of “Geometrid Moths of the World: A Catalogue” (SCOBLE 1999). From 2000–2022, the average number of new species descriptions has been 80 per year.

Most productive authors describing Geometridae

Analysis of all published species-level names of the geometrid moths shows that two English lepidopterists, namely WILLIAM WARREN (1839–1914) and LOUIS BEETHOVEN PROUT (1864–1943), described together 8,961 taxa, which

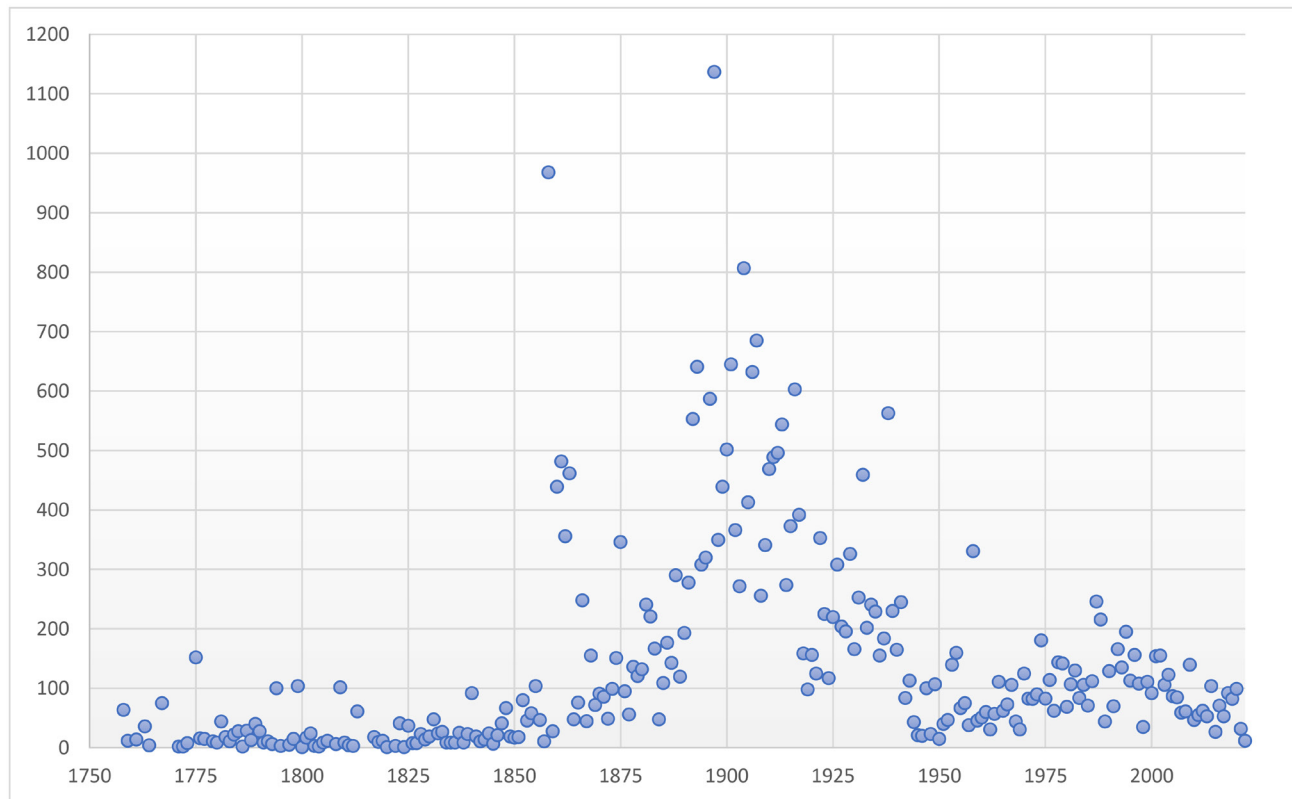


Fig. 5. Annual pattern of species description in Geometridae from 1758 to 2022. Similar data until 1995, but summarised by decade, were published by GASTON et al. (1995).

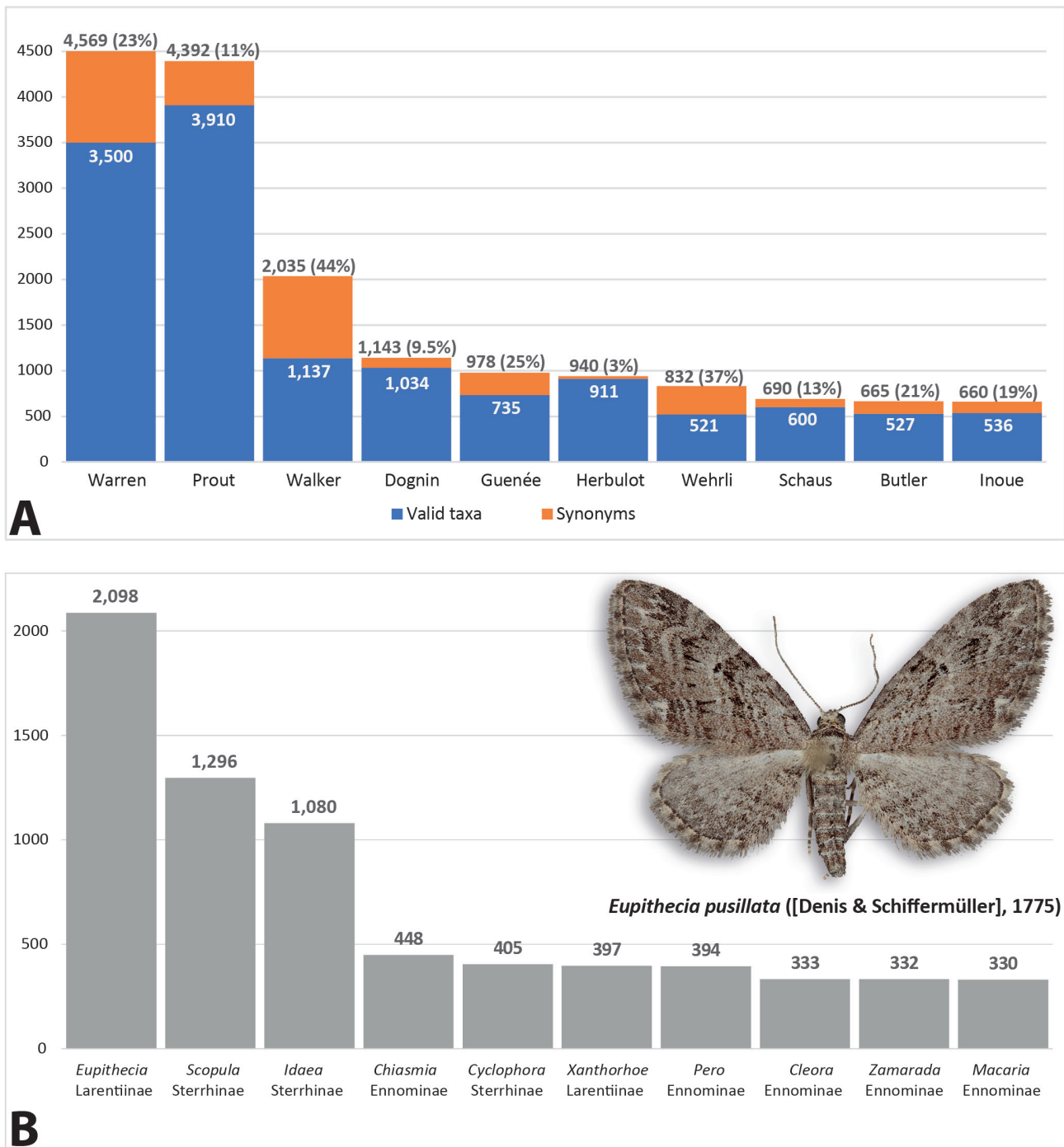


Fig. 6. Ten most prolific authors and ten most species-rich genera. **A.** Ten most prolific authors in Geometridae systematics and number of species-level taxa described by each, including taxa currently considered as synonyms (see also GASTON et al. 1995). Numbers above the bars are absolute numbers of described taxa, with percentages of synonymised names in parentheses; numbers of currently valid taxa are shown on the blue bars. **B.** Ten most species-rich genera of Geometridae. Number of valid species on y-axis. (Photo of *Eupithecia pusillata* by PEKKA MALINEN, published under CC-BY-NC-SA-4.0 licence and available on Finnish Biodiversity Info Facility <https://laji.fi/en>)

is roughly 25% of all described names in the family Geometridae. The top ten authors describing the most species-level taxa in Geometridae are shown in Fig. 6A. All have passed away, most recently French lepidopterist CLAUDE HERBULOT (19.2.1908–19.1.2006) and Japanese lepidopterist HIROSHI INOUE (8.7.1917–2.6.2008).

Most species-rich genera in Geometridae

The ten most species-rich genera are shown in Fig. 6B. The three most species-rich genera [*Eupithecia* Curtis, 1825 (Larentiinae), *Scopula* Schrank, 1802 (Sterrhinae) and *Idaea* Treitschke, 1825 (Sterrhinae)] are cosmopolitan. These genera have a large number of small species relative to the Geometridae in general, with a wingspan of usually much less than 30 mm. While Geometridae larvae typically consume fresh leaves, many *Eupithecia* caterpillars feed on flowers, and most *Idaea* and numerous *Scopula* larvae feed on withered plant debris.

Geographic coverage of taxonomic literature during the last two decades (2003–2022)

The geographic coverage of taxonomic literature on Geometridae during 2003–2022 is shown in Fig. 7. The taxonomic literature is uneven between biogeographic

regions for that period, and out of 462 papers, the majority deal with the Palearctic (36%) and Oriental faunas (30%). Together, 353 publications cover the fauna of these regions, which is 66% of the world total. The fauna of China, which includes Palearctic and Oriental elements, has been intensively studied during 2003–2022; 46 papers focus on this fauna, and Chinese authors have prepared the majority of these. Fifty-four papers (10% of total) deal with the Neotropical fauna, which hosts the highest number of described species. The majority of taxonomic papers were published in *Zootaxa* (93), *Tinea* (74) and *SHILAP Revista de Lepidopterologia* (23).

Taxa excluded from Geometridae after 1999

After “Geometrid Moths of the World: A Catalogue” (SCOBLE 1999) was published, three species have been transferred from Geometridae to other families:

- *Pseudobiston pinratanae* Inoue, 1994 was tentatively assigned to Geometridae: Geometrinae (INOUE 1994), but the absence of antero-abdominal tympanal organs, among other characters, raised doubts about its systematic position (STÜNING 2001). Based on molecular and morphological data, *P. pinratanae* was included in a new family, Pseudobistonidae Minet, Rajaei &

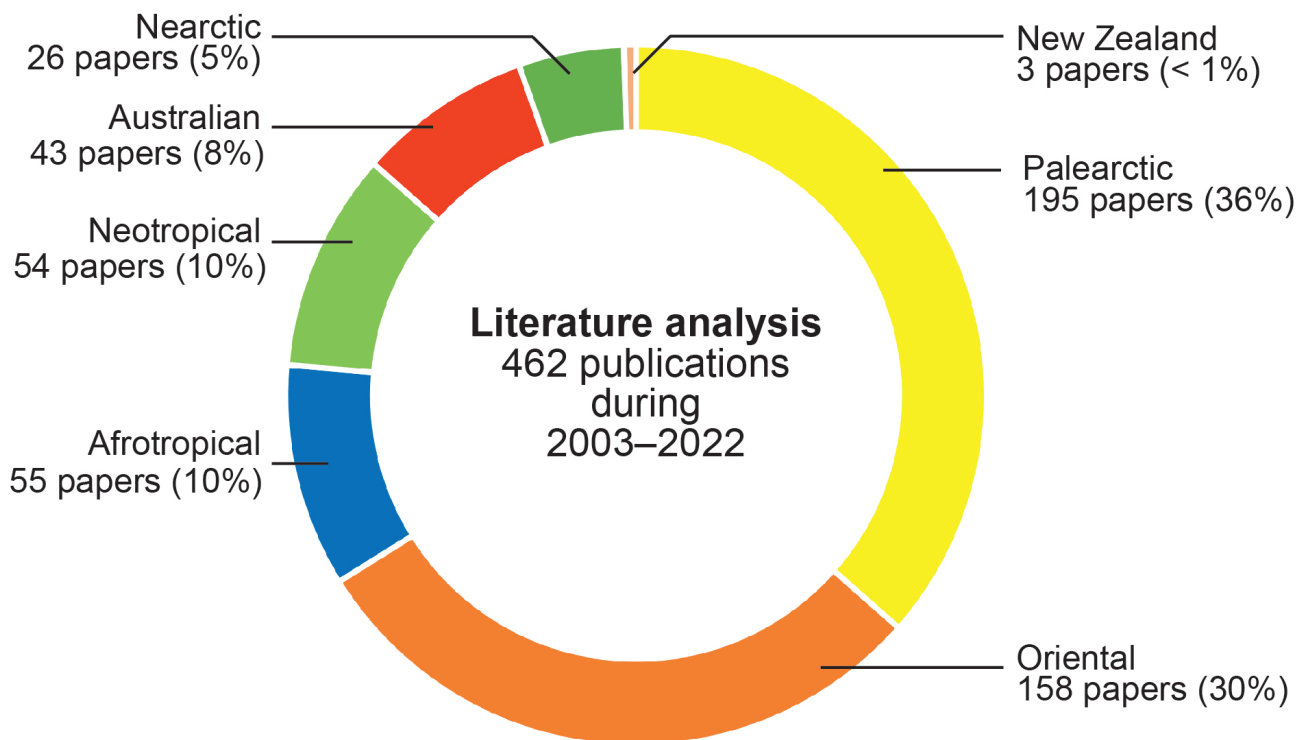


Fig. 7. Geographic coverage of taxonomic literature on Geometridae during 2003–2022. Colours align with biogeographic regions shown in Fig. 4. Details of examined literature listed in Supplementary File 1.

Stüning, 2015, as sister to Epicopeiidae, both families being part of Geometroidea (RAJAEI et al. 2015). This oriental moth is known from North Thailand and North Vietnam, and it is the only species included in Pseudobistonidae.

- *Cartaletis dargei* Herbulot, 2003 was originally placed in Geometridae: Sterrhinae (HERBULOT 2003). Recently, it was shown that the moth only superficially resembles true *Cartaletis* Warren, 1894 [the genus name is currently considered a junior synonym of *Aletis* Hübner, 1820, see SIHVONEN et al. (2020)], and it was transferred to Noctuidae: Agaristinae as *Aletopus dargei* (SIHVONEN et al. 2021).
- *Probolaea robiginosa* Turner, 1943 from Australia: Queensland was originally placed in Geometridae: Larentiinae (TURNER 1943). FLETCHER (1979) proposed an objective generic replacement name for *Probolaea*, namely *Ecphysis* Fletcher, 1979, because *Probolaea* Turner, 1943 is a junior homonym of *Probolaea* Meyrick, 1885. The species *robiginosa* is, however, a noctuid moth and was assigned to Erebidae: Cato-calinae by NIELSEN et al. (1996). This information was overlooked and *P. robiginosa* was listed as a Larentiinae in SCOBLE (1999). The original transfer from Geometridae to Erebidae may have been done earlier than NIELSEN et al. (1996), but we have not traced such literature. NIELSEN et al. (1996: 372, note 613) also explained that the original species name was misspelled as *robiginosa*, and that it should be *robigonosa* instead. We note that *robigonosa* is misspelled also, justifying this by the etymology note in TURNER (1943: 106), who wrote that the species name was based on “robiginosus, rusty” and emended it to *robiginosa* (ICZN 1999, Articles 32.5.1, 33). The classification in Erebidae was also missed by ÖZDIKMEN (2009), who proposed a new generic replacement name in Geometridae for *Ecphysis* Fletcher, 1979, which is a junior homonym of *Ecphysis* Townes, 1969 in Hymenoptera. Accordingly, this Australian species is currently named *Aslihana robiginosa* (Turner, 1943) and is assigned to Noctuoidea: Erebidae. DNA barcodes also support this assignment (BIN: BOLD:AAE0689).

*Taxa transferred, after 1999,
from other families to Geometridae*

Crambometra Prout, 1915 with type species *C. derelicta* Prout, 1915 from South Africa, is a genus originally classified in Ennominae (as Geometrinae) with the note “Affinities very obscure, apparently rather a primitive form, perhaps verging on the Oenochrominae” (PROUT 1915: 376). *Crambometra* was later transferred to Noto-dontidae (JANSE 1920) without explanation, and this was potentially the reason why geometrid researchers over-

looked the taxon and it was not included in the relevant geometrid literature anymore, including the geometrid catalogues (SCOBLE 1999; SCOBLE & HAUSMANN 2007). SCHINTLMEISTER (2013) re-examined the type species of *Crambometra* and transferred it and its three species back to Geometridae. KRÜGER (2015) treated *Pachyncnemoides* Krüger, 1999 as a junior synonym of *Crambometra* Prout, 1915 and listed two further genus synonyms established earlier by KIRIAKOFF (1970). *Crambometra* was analysed in a multi-gene molecular phylogeny study and found to be nested within Ennominae: Diptychini, within the *Callioratis* Felder, 1874 and *Veniliodes* Warren, 1894 complex of genera (MURILLO-RAMOS et al. 2019). Currently, *Crambometra* includes 14 species (KRÜGER 2015).

Family-group classification and
names of Geometridae of the world

A list of Geometridae family-group names is presented in Appendix 1, to provide a higher classificatory context to the online facility. Many annotations are included to allow readers to gain a perspective on the way that the nomenclature and systematic ordering has evolved. The current list of family-group names is based on the “Moths of Borneo” publications (HOLLOWAY 1994, 1996, 1997), as well as FLETCHER (1979) and has been expanded and updated in line with recent studies, particularly molecular phylogenetic work (e.g., SIHVONEN et al. 2011; ÖUNAP et al. 2016; JIANG et al. 2017; BAN et al. 2018; BREHM et al. 2019; MURILLO-RAMOS et al. 2019; SIHVONEN et al. 2020). The morphology of the subfamilies was reviewed by MURILLO-RAMOS et al. (2021a) and the overall systematic order is based on the latest extensive molecular phylogeny [MURILLO-RAMOS et al. (2019), presented in full in BREHM et al. (2019; supplement 1)] and supplemented by more focused systematic studies as indicated in the text. We emphasise the point that there are numerous ways to render a phylogenetic hypothesis as a linear classification, and thus encourage the readers to study the original tree-form hypotheses in parallel.

Names of a few tribes that were not included in the molecular analyses are listed, some of them considered valid by BELJAEV (2008b), who discussed their relationships based on morphology. The list, which does not include incorrect subsequent spellings, will be updated and refined, and we expect to publish new versions with future updates in the “Online taxonomic facility [and list of valid names] of geometrid moths”.

In Appendix 1, all available family-group names (family, subfamily, tribe, subtribe) are shown in bold. The numbers of subordinated family-group names are given in brackets in the headline of each subfamily. Names in brackets are those given by the original author.

Discussion

What is the real species richness of geometrid moths?

In many insect groups the real species richness is estimated to be considerably higher than the described fauna (ØDEGAARD 2000; GARCIA et al. 2020). The indirect data available suggests this is the case in Geometridae also. We estimate that the real species richness on the global scale is likely to rise from the current 23,872 valid species to 40,000–50,000 species. We try to justify this estimate by a few examples:

- Geometridae have been among the target groups in the Global Campaign of DNA barcoding (iBOL Lepidoptera). Within this project, numerous unnamed genetic clusters have emerged and in Ennominae, for instance, which is the most species-rich geometrid lineage with about 11,100 described species worldwide, the genetic data on BOLD suggests that at least 7,000 additional species await description (see Preface in MÜLLER et al. 2019a). Available DNA barcode data suggest a large amount of cryptic diversity in Lepidoptera in general (GARCIA et al. 2020) and a considerable percentage of tropical species are not even represented yet in databases such as BOLD systems.
- Some of the tropical genera might easily be as species-rich as the genera illustrated in Fig. 6B. For example, BREHM et al. (2011) concluded that *Eois* Hübner, 1818 could easily comprise more than 1,000 species, given the low rate of matches (10%) with described species of material collected in southern Ecuador.
- Regional diversity estimates in tropical regions also strongly suggest that a high number of species still need to be described. For example, BREHM et al. (2016) estimated regional species richness of geometrid moths at 2,350 species in an area of only 40 km² in the southern Andes. This corresponds to more than one third of the richness of the entire Neotropical Region (6,595 species), a far higher percentage than appears likely for a very small area that did not even include elevations below 1,000 m.
- Beta diversity along environmental gradients could currently be still underestimated. In montane areas, closely related species (currently regarded as one species) occur at different elevational bands (e.g., BREHM et al. 2003, 2016). Similar examples exist along the latitudinal gradient (e.g., PAKNIA & RAJAEI 2015).
- Several recent revisions based on both museum and fresh materials show a clear trend that the actual species richness is considerably higher than historically thought. An integrative revision of the genus *Prasinocyma* Warren, 1897 (Geometrinae), which focused on Ethiopia only, revealed that just 52% of the 40 Ethiopian species had been described (HAUSMANN et al. 2016).

The revision of the same genus at a continental scale (Africa) will raise the validated species number from 86 (in SCOBLE 1999) to more than 300 (HAUSMANN, unpublished), i.e., by more than 350%. In the Indo-Australian genus *Ziridava* Walker, 1863 (Larentiinae), the increase was 33% (SCHMIDT & TAUTEL 2022); in the Afrotropical *Trimetopia* Guenée, 1858 (Larentiinae) the increase was 70% (STADIE & FIEBIG 2019); and in the Chinese *Timandra* Duponchel, 1829 (Sterrhinae) the increase was 140% (CUI et al. 2019). On the other hand, there is a tendency of finding synonyms in better explored faunas, for example in Europe (see Conclusions).

Assuming a real number of at least 40,000 geometrid species on our planet, including at least 16,128 undescribed species, and assuming a linear continuation of the current pace of 80 descriptions per year, traditional taxonomic research will need another ca. 200 years to complete the task. However, detection of undescribed species may be fostered by DNA barcoding and descriptions may be accelerated by automated, modern tools of data transfer and manuscript templates.

Future development of the “Online taxonomic facility of geometrid moths”

We wish, in time and depending on resources, to expand the “Online taxonomic facility of geometrid moths” in its current format to a more comprehensive knowledge base. Specifically, it is our long-term aim to:

- Expand coverage to include the entire superfamily Geometroidea, namely the families Geometridae, Epicopeidae, Pseudobistonidae, Sematuridae and Uraniidae.
- Supplement the database with photographs of type specimens. Progress is already being made by the project “Geometridae Mundi” (coordinated by AXEL HAUSMANN and HANS LÖBEL from Germany). It is intended to photograph not only type specimens but selected other material for all species. The number of photographs taken already exceeds 50,000 and covers ca 50% of the described species.
- Add information for each taxon on original descriptions, type localities, type specimens and their depositories, and genera and their synonyms, as in SCOBLE (1999).
- Forge links with the data on the BOLD website, particularly to type specimens.
- Add, if possible, information on immature stages and their hostplants, global and elevational distribution and habitats.
- Add, if possible, photographs of morphological traits (e.g., male and female genitalia, wing length, size).

Conclusions

We have noted already the geographical bias in Geometridae systematics and conclude that there is an evident need to encourage a greater effort on species-rich but understudied regions if we are to make significant progress. Yet how might this be achieved? The universal and frequent plea for funding for taxonomy of the magnitude needed is unlikely to materialise, so finding ways of accelerating progress must rely on the community of geometrid taxonomists. DNA barcoding (HEBERT et al. 2003) has been used for rapid, mass description of species of braconid wasps (SHARKEY et al. 2021; FERNANDEZ-TRIANA 2022) and weevils (RIEDEL et al. 2014; RIEDEL & NARAKUSUMO 2019), as well as for descriptions and monographs of Geometridae (e.g., HAUSMANN et al. 2016; MÜLLER et al. 2019a, 2019b). Although extensive use of DNA barcoding without complementary evidence bears a risk of taxonomic instability [see MEIER et al. (2021) for a criticism of a minimalist, barcode-only-based approach to species description], molecular methods are an invaluable tool for developing taxonomic hypotheses, especially for mega-diverse taxa in the tropics. While this approach should be used ideally in conjunction with morphological evidence, the catastrophic loss of biodiversity requires more haste in species description, and thus some relaxation in selecting the perfect methodology. Therefore, we regard an accelerated integrative approach as the best practical option for promoting the taxonomy of geometrid moths in tropical countries, where species diversity is at its highest.

A further approach is to encourage geometrid taxonomists to concentrate on reviews and revisions at the level of genus, sampling as many species as possible. Past examples include studies on the Neotropical Geometrinae (PITKIN 1996), Ennominae (PITKIN 2002), Macariini (SCOBLE & KRÜGER 2002) and Scopulini (SIHVONEN 2005) and numerous papers dealing with the Chinese fauna (see Supplementary File 1), which created a framework to help those dealing with species descriptions. Such works would need to be centred at institutions with large collections with significant global coverage, but undertaken in a highly collaborative way among taxonomists, parataxonomists and collectors in species-rich regions.

Combined, these two approaches might be an effective means of making progress. A collaborative approach is exemplified in this paper, with authors from five countries contributing and benefitting from e-communication, although we note that only one country (Colombia) falls among those regions with high species richness.

If the description of new species is the major challenge in the tropics (e.g., BREHM 2018), that of synonymy is a greater issue in well-studied but relatively species-poor regions. As many as 23% of available names in “Online taxonomic facility of geometrid moths” are synonyms

($n = 7,891$). This percentage is likely to increase significantly, considering that many of the 3,134 subspecies are likely to be synonymised in future. In Volume 6, Part 1 of the “The Geometrid Moths of Europe” (MÜLLER et al. 2019a), merely four new species were described, while 111 new synonymies, new statuses and new combinations were proposed, many of the proposed synonymies benefiting from DNA barcode data. The point raised years ago by SCOBLE (1999: xiv) is still valid, at least for well-known faunas: “We need to take careful account of the magnitude of synonymy besides the description of new species if we are to have ... a better understanding of species richness in the Geometridae”.

Finally, we were astonished by how difficult it sometimes is to find taxonomic literature on geometrid moths, despite the fact that we work in an era where funding bodies and institutions are encouraging or requiring open access publishing. While much of the older taxonomic literature is now available via the Biodiversity Heritage Library, even today, some taxonomists publish in journals that are not accessible online. Indeed, we encountered a few cases where even university librarians could not gain access to papers with data we wished to source. Furthermore, a few papers were published in journals lacking peer review and editorial standards. We encourage geometrid taxonomists to publish their manuscripts in peer-reviewed journals that are easily accessible and preferably open access.

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Supplementary File 1: Examined literature between 2003 and 23.5.2022, with biogeographic coverage (Excel file).

Appendix 1. Family-group classification and names of Geometridae of the world.Family **Geometridae** Stephens, 1829 (202 names)

Declared as the correct name by the International Commission on Zoological Nomenclature (ICZN 1957, Opinion 450).

Currently validated: 9 subfamilies (see text for details on problems in subfamily classification), 93 tribes and 11 subtribes.

Subfamily **Sterrhinae** Meyrick, 1892 (Sterrhidae) (23 names)

Although there are several senior synonyms of this name, the name Sterrhinae should be maintained for nomenclatural stability [as proposed by HOLLOWAY (1997: 15)]. For justification, see below under the tribe Sterrhini. Validity and order of tribes based on HOLLOWAY (1997), HAUSMANN (2004), MURILLO-RAMOS et al. (2019) and SIHVONEN et al. (2020).

Tribe **Mecoceratini** Guenée, 1858 (Mecoceridae)

Mecoceras is a junior objective synonym of *Ametris*. Validated at tribe level and transferred from Desmobathrinae to Sterrhinae by SIHVONEN et al. (2020).

= **Ametridini** Prout, 1910 (Ametridicae), junior synonym (SIHVONEN et al. 2020).

Tribe **Cosymbiini** Prout, 1911 (Cosymbiinae)

Although there are senior synonyms of this name (see below), the name should be retained to maintain nomenclatural stability [as proposed by HOLLOWAY (1997: 23)]; see also ICZN (1999, Art. 40.2).

= **Ephyrini** Guenée, 1858 (Ephyridae), based on a junior homonym of a genus-group name outside Lepidoptera. Invalid according to ICZN (1999, Art. 39).

= **Zonosomini** White, 1876 (Zonosomatidi), based on *Zonosoma*, thus emended, senior synonym (HOLLOWAY 1997).

= **Cyclophorini** Moore, 1887 (Cyclophoridae), senior synonym (HOLLOWAY 1997). As the name Cyclophoridae is in common usage in Mollusca, based on the genus *Cyclophorus*, HOLLOWAY (1997: 15) proposed that it should be “gracefully conceded” to malacologists.

Tribe **Timandrini** Stephens, 1850 (Timandridi)

= **Calothysanini** Herbulot, 1963 (Calothysanini), based on (misinterpreted) genus name *Calothysanis*, a synonym of *Scopula* (Scopulini) (HOLLOWAY 1997).

Tribe **Rhodometrini** Agenjo, 1952 (Rhodometrinae)

= **Lythriini** Herbulot, 1962 (Lythriini), transferred from Larentiinae to Sterrhinae by ÖUNAP et al. (2008), synonymised with Rhodometrini by SIHVONEN et al. (2020).

Tribe **Cylopodini** Kirby, 1892 (Cylopodidae)

= **Micropinini** Kirby, 1912 (Micropinidae), junior synonym, based on an unnecessary genus-group replacement name (HOLLOWAY 1997).

= **Rhodostrophiini** Prout, 1935 (Rhodostrophiicae), junior synonym (SIHVONEN et al., 2020).

Tribe **Sterrhini** Meyrick, 1892 (Sterrhidae)

Although senior synonyms of this name exist (see below), Sterrhini should be maintained for nomenclatural stability, as proposed by HOLLOWAY (1997: 15) and in accordance with the intention and spirit of the concept of “prevailing usage” of ICZN (1999, cf. Art. 40.2).

= **Goniacidalini** Packard, 1876 (Goniacidalinae), senior synonym (HODGES et al. 1983).

= **Idaeni** Butler, 1881 (Idaeidae), senior synonym (HOLLOWAY 1997).

= **Ptychopodini** Pierce, 1914 (Ptychopodinae), junior synonym (HOLLOWAY 1997).

Tribe **Haemaleini** Sihvonen & Brehm, 2020 (Haemaleini)Tribe **Lissoblemmini** Sihvonen & Staude, 2020 (Lissoblemmini)Tribe **Scopulini** Duponchel, 1845 (Scopulites)

= **Acidaliini** Duponchel, 1845 (Acidalites). The original Latin word stem Acidal- (with the suffix -ites) needs to be emended to Acidali- (being based on the type genus *Acidalia*), leading to “Acidaliini” rather than to Acidalini; junior synonym, based on a junior homonym of a genus-group name outside the Lepidoptera (HOLLOWAY 1997).

= **Aletini** Hampson, 1918 (Aletinae), junior synonym (HOLLOWAY 1996).

= **Problepsini** Wiltshire, 1990 (Problepsini), junior synonym (HOLLOWAY 1997).

Subfamily **Larentiinae** Duponchel, 1845 (Larentites) (47 names)

The original Latin word stem Larent- (with the suffix -ites) needs to be emended to Larenti- (being based on the type genus *Larentia*), leading to “Larentiinae” rather than to Larentinae. Validity and order of tribes mainly follow HOLLOWAY (1997), VIIDALEPP (2011), HAUSMANN & VIIDALEPP (2012), ÖUNAP et al. (2016), BREHM et al. (2019) and MURILLO-RAMOS et al. (2019). BREHM et al. (2019), in their phylogenetic hypothesis, highlighted four lineages, each marked as “unnamed clade”. If further data substantiate these clades, they will need description at the level of tribe, but at this stage they are excluded from the list.

Tribe **Dyspteridini** Hulst, 1896 (Dyspteridinae)

Dyspteridini were removed from synonymy with Trichopterygini and given tribal rank by VIIDALEPP (2011), an action confirmed by ÖUNAP et al. (2016) and MURILLO-RAMOS et al. (2019).

Tribe **Brabirodini** Brehm, Murillo-Ramos & Öunap, 2019 (Brabirodini)

Tribe **Trichopterygini** Warren, 1894 (Trichopteryginae)

= **Lobophorini** Tutt, 1896 (Lobophorinae), junior synonym (HODGES et al. 1983).

Tribe **Chesiadini** Stephens, 1850 (Chesiadi)

The Latin word stem is Chesiad- (genitive of the type genus name *Chesias* = Chesiadis). Authorship of tribe name “Pierce, 1914” according to VIIDALEPP (2011).

= **Eucestiini** Warren, 1894 (Eucestiinae). Based on *Eucestia*, which is a junior objective synonym of *Chesias*; junior synonymy of tribe name: HOLLOWAY (1997: 97).

= **Odeziini** Exposito, 1978 (Odeziini), junior synonym (HAUSMANN & VIIDALEPP 2012: 442).

Subtribe **Aplocerina** Viidalepp, 2011 (Aplocerina)

Rank of subtribe adopted here, based on the findings of MURILLO-RAMOS et al. (2019).

Tribe **Chrismopterygini** Brehm, Murillo-Ramos & Öunap, 2019 (Chrismopterygini)

Tribe **Eudulini** Warren, 1897 (Eudulinae)

Tribe **Asthenini** Warren, 1894 (Astheninae)

Tribe **Perizomini** Herbulot, 1961 (Perizomini)

Tribe **Melanthiini** Duponchel, 1845 (Melanthites)

Emended by reasons of grammar: based on *Melanthia*.

Tribe **Eupitheciini** Tutt, 1896 (Eupitheciinae)

Preferred over the senior name Tephroclystini, following ICZN (1999, Art. 40.2) (prevailing usage of the pre-1961 replacement substitute name of the type genus).

= **Tephroclystiini** Warren, 1895 (Tephroclystiinae), senior synonym. Based on *Tephroclystia*, now treated as a junior synonym of *Eupithecia* (ICZN 1999, Art. 40.2.1).

= **Chloroclystini** Mironov, 1990 (Chloroclystina), junior synonym, originally proposed as a subtribe of Eupitheciini (HOLLOWAY 1997).

Tribe **Operophterini** Packard, 1876 (Operophterinae)

HOLLOWAY (1997) noted that Operophterinae should probably take precedence over Oporiniini as in VIVES MORENO (1994). Following this, Oporiniini is treated here as junior synonym.

= **Oporiniini** Pierce, 1914 (Oporiniinae), junior synonym (HOLLOWAY 1997).

Tribe **Solitaneini** Leraut, 1980 (Solitaneini)

Tribe **Triphosini** Tutt, 1896 (Triphosidi)

Subordinated under Rheumapterini in HAUSMANN & VIIDALEPP (2012), but validated at tribe level by VIIDALEPP (2011), SCHMIDT (2015), ÖUNAP et al. (2016) and MURILLO-RAMOS et al. (2019). The three tribes Triphosini, Phileremini and Rheumapterini resolved as a single cluster in BREHM et al. (2019), but these authors did not feel ready to synonymise the tribes without further study.

Tribe **Phileremini** Pierce, 1914 (Philereminae)

See comment under Triphosini

Tribe **Rheumapterini** Herbulot, 1961 (Rheumapterini)

See comment under Triphosini.

= **Melanippini** Bruand, 1846 (Melanippidae), senior synonym. Based on *Melanippe*, a junior synonym of *Rheumaptera*. It is proposed not to apply this name, as Rheumapterini is accepted widely.

= **Eucosmiini** Gumpenberg, 1887 (Eucosmiinae), senior synonym. It is proposed not to apply this name, as Rheumapterini is widely accepted in the literature and Eucosmiinae was never used after the original description. Emended by reasons of grammar (based on *Eucosmia*, a junior synonym of *Hydria*).

Tribe **Psaliadini** Brehm, Murillo-Ramos & Öunap, 2019 (Psaliadini)

Tribe **Cidariini** Duponchel, 1845 (Cidarites)

The original Latin word stem Cidar- (with the suffix -ites) needs to be emended to Cidari- (being based on the type genus *Cidaria*), leading to “Cidariini” rather than to Cidarini.

= **Therini** Pierce, 1914 (Therinae), junior synonym (HOLLOWAY 1997). Based on *Thera*. Theriini (based on *Theria*) is a family-group name in Ennominae.

Tribe **Scotopterygini** Warren, 1895 (Scotopteryginae)

Subordinated under Xanthorhoini in HAUSMANN & VIIDALEPP (2012), but treated as a tribe by VIIDALEPP (2011), SCHMIDT (2015) and, using molecular data, by ÖUNAP et al. (2016) and MURILLO-RAMOS et al. (2019).

= **Euboliini** Duponchel, 1845 (Eubolites), senior synonym, but not applied, as Scotopterygini is now largely accepted in the literature over Euboliini. Emended by reasons of grammar: based on *Eubolia*, a junior synonym of *Scotopteryx*.

= **Ortholithini** Tutt, 1896 (Ortholithinae), senior synonym, but not applied, as Scotopterygini is now largely accepted in the literature over Ortholithinae. Based on *Ortholitha*, a junior synonym of *Scotopteryx*.

= **Phasianini** Gumpfenberg, 1897 (Phasianinae). Based on *Phasiane*, a junior synonym of *Scotopteryx*. Senior synonym, but junior homonym of a family-group name in common use in Aves (*Phasianus*) (HOLLOWAY 1997: 98).

Tribe **Euphyiini** Herbulot, 1961 (Euphyiini)

Tribes Euphyiini, Pterocyphini, Cataclysmiini, Xanthorhoini and Epirrhoini form a complex of tribes (BREHM et al. 2019), potentially requiring synonymy. More research is needed.

Tribe **Pterocyphini** Brehm, Murillo-Ramos & Öunap, 2019 (Pterocyphini)Tribe **Cataclysmiini** Herbulot, 1962 (Cataclysmiini)

Treated as a tribe by HAUSMANN & VIIDALEPP (2012) and ÖUNAP et al. (2016), but lumped with Xanthorhoini in MURILLO-RAMOS et al. (2019) and classified as part of the Euphyiini-Xanthorhoini complex by BREHM et al. (2019).

Tribe **Xanthorhoini** Pierce, 1914 (Xanthorhoinae)

= **Psychophorini** Hampson, 1918 (Psychophorinae), treated as a junior synonym in HAUSMANN & VIIDALEPP (2012). VIVES-MORENO (1994) considered Psychophorini a junior synonym of Larentiini. *Psychophora* Kirby, 1824 has not been included in molecular phylogenetic analysis yet.

Tribe **Epirrhoini** Pierce, 1914 (Epirrhoini)

Subordinated under Xanthorhoini in VIIDALEPP (2011) and HAUSMANN & VIIDALEPP (2012), but raised to tribe level by BREHM et al. (2019; misspelled as “Epirhoini” in fig. 2).

Tribe **Rhinurini** Brehm, Murillo-Ramos & Öunap, 2019 (Rhinurini)Tribe **Larentiini** Duponchel, 1845 (Larentites)

Emended by reasons of grammar (see under subfamily name).

= **Entephrini** Pierce, 1914 (Entephrinae), emended by reasons of grammar (based on *Entephrina*), junior synonym.

Tribe **Ennadini** Brehm, Murillo-Ramos & Öunap, 2019 (Ennadini)Tribe **Hydriomenini** Meyrick, 1872 (Hydriomenidae)Tribe **Heterusiini** Warren, 1897 (Heterusiinae)Tribe **Cophoceratini** Brehm, Murillo-Ramos & Öunap, 2019 (Cophoceratini)Tribe **Erateiniini** Guenée, 1858 (Erateinidae)

Sometimes misspelled as Erateiniini.

Tribe **Erebochlorini** Brehm, Murillo-Ramos & Öunap, 2019 (Erebochlorini)Tribe **Stamnodini** Forbes, 1948 (Stamnodini)Subfamily **Geometrinae** Stephens, 1829 (Geometrinae) (33 names)

Validity and order of tribes mainly based on PITKIN (1996), HOLLOWAY (1996), HAUSMANN (1996a, 1996b, 2001), BAN et al. (2018), BREHM et al. (2019) and MURILLO-RAMOS et al. (2019). BREHM et al. (2019), in their phylogenetic hypothesis, highlighted four lineages, each marked as “unnamed clade”. These may require formal description at the category of tribe when more data are available.

Tribe **Ornithospilini** Ban, Jiang, Cheng, Yue & Han, 2018 (Ornithospilini)Tribe **Agathiini** Ban, Jiang, Cheng, Yue & Han, 2018 (Agathiini)

Tribe **Chlorodontoperini** Murillo-Ramos, Sihvonen & Brehm, 2019 (Chlorodontoperini)

Tribe **Aracimini** Inoue, 1961 (Aracimini)

Tribe **Neohipparchini** Holloway, 1996 (Neohipparchiti)

Relationship of ‘Neohipparchiti’ to ‘Geometriti’ noted by HOLLOWAY (1996: 193). Treated as a tribe by BAN et al. (2018) and supported by MURILLO-RAMOS et al. (2019).

Tribe **Timandromorphini** Inoue, 1961 (Timandromorphini)

Tribe **Geometrini** Stephens, 1829 (Geometrinae)

Tribe **Comibaenini** Inoue, 1961 (Comibaenini)

= **Euchlorini** Herbulot, 1963 (Euchlorini), junior synonym; based on genus name *Euchloris*, which is a junior homonym of a generic name in Coleoptera.

Tribe **Nemoriini** Gumpfenberg, 1887 (Nemorinae)

The original Latin word stem Nemor- (with the suffix -inae) needs to be emended to Nemori- (being based on the type genus *Nemoria*) leading to “Nemoriini” rather than to Nemorini.

= **Ochrognesiini** Inoue, 1961 (Ochrognesiini), junior synonym (HOLLOWAY 1996: 151; HAUSMANN 1996b: 31).

= **Synchlorini** Ferguson, 1969 (Synchlorini), relations to Comibaenini discussed in HOLLOWAY (1996: 196) and PITKIN (1996: 322), but subordinated under Nemoriini in MURILLO-RAMOS et al. (2019) and BREHM et al. (2019) based on molecular evidence.

Tribe **Archeobalbini** Viidalepp, 1981 (Archeobalbini [sic!])

Emended, as based on *Archeobalba*. Synonymised with Pseudoterpnini by HOLLOWAY (1996: 149), raised again to tribe rank by MURILLO-RAMOS et al. (2019) and BREHM et al. (2019).

Tribe **Dysphaniini** Warren, 1895 (Dysphaniinae)

= **Hazini** Guenée, 1858 (Hazidae), junior synonym; based on *Hazis*, a junior objective synonym of *Euschema*, junior synonym of *Dysphania* (HOLLOWAY 1996).

= **Euschemini** Walker, 1862 (Euschemidae), junior synonym; based on *Euschema*, a junior synonym of *Dysphania* (HOLLOWAY 1996).

Tribe **Pseudoterpnini** Warren, 1893 (Pseudoterpninae)

PITKIN et al. (2007) commented the taxonomic history of the tribe.

= **Terpnini** Inoue, 1961 (Terpnini), junior synonym; based on *Terpne* (misspelled as *Terpna*), a junior synonym of *Geometra*, but referring to *Terpne* auctorum (= *Pachyodes*) (HAUSMANN 1996a: 96; HOLLOWAY 1996).

= **Pingasini** Heppner & Inoue, 1992 (Pingasini), junior synonym (HOLLOWAY 1996).

Tribe **Dichordophorini** Ferguson, 1969 (Dichordophorini)

Validity and potential subordination under another tribe awaiting study of molecular data.

Tribe **Hemitheini** Bruand, 1946 (Hemitheidae)

Reasons for tribal rank were given by HAUSMANN (1996; 2001). HOLLOWAY (1996: 196) proposed a broad concept of the tribe to include Thalerini, Comostolini, Hemistolini, Jodini and Thalassodini, a view supported by recent molecular analyses, e.g., BAN et al. (2018), BREHM et al. (2019) and MURILLO-RAMOS et al. (2019).

= **Thalerini** Herbulot, 1963 (Thalerini), given the rank of tribe by HAUSMANN (1996b; 2001), but synonymised as subtribe Hemitheina (misspelled as Hemitheiti) by BAN et al. (2018).

= **Chlorochromini** Duponchel, 1845 (Chlorochromites), senior synonym, based on *Chlorochroma*, a junior objective synonym of *Thalera*. Chlorochromini is not applied here, as Hemitheini is accepted widely (cf. HAUSMANN 1996a: 101).

The following taxa might have been treated as synonyms of Hemitheini (see above), but we list them as subtribes. Many further lineages revealed by molecular analysis, but not yet named, are likely to belong here.

Subtribe **Heliotheina** Exposito, 1978 (Heliothinae)

Based on *Heliothea*. Considered to belong to Geometrinae: Rhomboristini (as Rhomboristiti) by HOLLOWAY (1996: 150, 195), see also HAUSMANN (1996b: 12; 2001: 110). Treated as Hemitheini by BAN et al. (2018; misspelled as “Heliotheiti”) and MURILLO-RAMOS et al. (2019) based on molecular evidence.

Subtribe **Rhomboristina** Inoue, 1961 (Rhomboristini)

Relationship to both Comostolini and Jodini suggested by HAUSMANN (1996b: 41). Subordination under Hemitheini proposed by BAN et al. (2018; misspelled as “Rhomboristiti”) based on molecular evidence, confirmed by MURILLO-RAMOS et al. (2019).

Subtribe **Hemistolina** Inoue, 1961 (Hemistolini)

Treated as a tribe by HAUSMANN (1996b; 2001). HOLLOWAY (1996: 196) proposed a wider concept (including Thalerini, Comostolini, Hemistolini, Jodini and Thalassodini). Subordination under Hemitheini proposed by BAN et al. (2018; misspelled as “Hemistoliti”) based on molecular evidence and supported by MURILLO-RAMOS et al. (2019).

Subtribe **Comostolina** Inoue, 1961 (Comostolini)

Treated as a tribe by HAUSMANN (1996b; 2001), related to Jodini (HAUSMANN 1996b: 41). HOLLOWAY (1996: 196) proposed a wider concept (including Thalerini, Comostolini, Hemistolini, Jodini and Thalassodini). Subordination under Hemitheini proposed by BAN et al. (2018; misspelled as “Comostoliti”) based on molecular evidence and supported by MURILLO-RAMOS et al. (2019).

Subtribe **Microloxiina** Hausmann, 1996 (Microloxiini)

Originally published on 21.11.1996 at tribe rank (HAUSMANN 1996). Subordination under Hemitheini proposed by BAN et al. (2018; misspelled as “Microloxiiti”) based on molecular evidence and supported by MURILLO-RAMOS et al. (2019). = **Hierochothoniini** Viidalepp, 1996, published without exact date (= 31.12.1996)

Subtribe **Lophochoristina** Ferguson, 1969 (Lophochoristini)

Treated as a tribe by Pitkin (1996: 322). Subordination under Hemitheini proposed by BAN et al. (2018; misspelled as “Lophochoristiti”) based on molecular evidence and supported by MURILLO-RAMOS et al. (2019).

Subtribe **Jodina** Inoue, 1961 (Jodiini)

Emended by reasons of grammar (based on *Jodis* with the Latin word stem Jod-). Treated as a tribe by HAUSMANN (1996b; 2001), suggesting a relationship with Comostolini (HAUSMANN 1996b: 41). HOLLOWAY (1996: 196) proposed a wider concept (including Thalerini, Comostolini, Hemistolini, Jodini and Thalassodini). Subordination under Hemitheini proposed by BAN et al. (2018; misspelled as “Joditi”) based on molecular evidence and supported by MURILLO-RAMOS et al. (2019).

Subtribe **Thalassodina** Inoue, 1961 (Thalassodini)

Treated as a tribe by HAUSMANN (1996b). HOLLOWAY (1996: 196) proposed a wider concept (including Thalerini, Comostolini, Hemistolini, Jodini and Thalassodini). Subordination under Hemitheini proposed by BAN et al. (2018; misspelled as “Joditi”) based on molecular evidence and supported by MURILLO-RAMOS et al. (2019).

Subfamily **Archiearinae** Fletcher, 1953 (Archiearinae) (2 names)

The analyses of SIHVONEN et al. (2011) and MURILLO-RAMOS et al. (2019) suggest that Archiearinae are the sister group to all Geometridae except the Sterrhinae + Larentiinae lineage.

= **Brephinae** auct. nec Hübner, 1826 (Brephidae), based on *Brephos* Ochsenheimer, 1816, a junior homonym of *Brephos* Hübner, 1813.

Subfamily **Desmobathrinae** Meyrick, 1886 (Desmobathridae) (2 names)

Based on *Desmobathra* Meyrick, 1886 (junior synonym of *Ozola* Walker, 1861). For validity at subfamily rank see HOLLOWAY (1996: 152, 159). See Orthostixinae for more information on Desmobathrinae–Orthostixinae relationship.

Tribe **Desmobathrini** Meyrick, 1886 (Desmobathridae)Tribe **Eumeleini** Warren, 1894 (Eumeleinae)

The position and classification of Eumeleini have proven difficult to elucidate. Based on molecular data, MURILLO-RAMOS et al. (2019) suggested a sister-group relationship with the subfamily Geometrinae, provisionally placing the genus as “incertae sedis”. Recently, *Eumelea* Duncan & Westwood, 1841 was included in a whole-genome shotgun sequencing analysis and the name-bearing genus *Eumelea* was reconstructed as sister to Geometrinae (based on nucleotide analysis) or Oenochrominae s. str. (based on amino acid analysis). The authors proposed to raise Eumeleini to subfamily rank, but the publication and names and nomenclatural acts therein are not available for purposes of zoological nomenclature in accordance with ICZN (2012, Arts. 8.2, 8.3), and MURILLO-RAMOS and collaborators will formalise the new classification in a forthcoming publication.

Subfamily **Orthostixinae** Meyrick, 1892 (Orthostixidae) (1 name)

Subfamily rank questioned (HOLLOWAY 1996: 151), possibly subordinated to Ennominae. HAUSMANN (1996a, 1996b) recognized the subfamily but noted that the genera *Derambila* and *Ozola* seem to link with *Myinodes/Eumegethes*, *Orthostixis/Naxa* and *Gypsochroa*. The validity at subfamily rank was maintained by HAUSMANN (2001: 70, 89). Tentative molecular information on the genus *Naxa* suggests subordination under Ennominae (SIHVONEN 2011; MURILLO-RAMOS et al. 2019) despite several contradicting morphological characters. Recently, the name-bearing genus *Orthostixis* was included in a whole-genome shotgun sequencing analysis and *Orthostixis* was reconstructed as sister to *Ozola* (MURILLO-RAMOS et al. 2021b). Therefore, the authors proposed Orthostixinae as a junior synonym of Desmobathrinae, but the publication and names and nomenclatural acts therein are not available for purposes of zoological nomenclature in accordance with ICZN (2012, Arts. 8.2, 8.3), and MURILLO-RAMOS and collaborators will formalise the synonymy in a forthcoming publication.

Subfamily **Epidesmiinae** Murillo-Ramos, Brehm & Sihvonen, 2018 (Epidesmiinae) (1 name)

Epidesmiinae were recognised as a valid subfamily by Murillo-Ramos et al. (2019). Epidesmiinae have an Australasian distribution, with one species occurring in the Indo-Malayan realm. The lineage includes 102 described species that are classified into nine genera. Those are not classified into tribes thus far, and no family-level synonyms have been recognised (MURILLO-RAMOS et al. 2021a).

Subfamily **Oenochrominae** Guenée, 1858 (Oenochromidae) (3 names)

Oenochrominae s. str. has been recovered as sister to Geometrinae in molecular phylogenetic analyses (SIHVONEN et al. 2011; MURILLO-RAMOS et al. 2019).

= **Lyrceini** Meyrick, 1883 (Lyrceini), based on *Lyrcea*, a junior homonym of a name outside Lepidoptera; junior subjective synonym. Invalid according to ICZN (1999, Art. 39).

= **Monocteniini** Meyrick, 1889 (Monocteniadae), emended, junior subjective synonym (HOLLOWAY 1996: 151).

Subfamily **Ennominae** Duponchel, 1845 (Ennomites) (93 names)

Validity and order of tribes mainly based on MURILLO-RAMOS et al. (2019), supplemented by information from HOLLOWAY (1994), PITKIN (2002), BELJAEV (2008b), SKOU & SIHVONEN (2015), JIANG et al. (2017) and BREHM et al. (2019). BREHM et al. (2019), in their phylogenetic hypothesis, highlighted four lineages, marked as “unnamed clade”, which may need to be formally described at tribe level when more data become available. Those are not included in the current list.

Tribe **Euangeronini** Brehm, Murillo-Ramos & Sihvonen, 2019 (Euangeronini)

Type genus *Euangerona*, previously assigned to Nacophorini (PITKIN 2002).

Tribe **Gonodontini** Forbes, 1948 (Gonodontini)

See remarks in HOLLOWAY (1994: 8, 111). Gonodontini needs to be referred to the Commission for a ruling (ICZN 1999, Arts. 41 and 65.2.), because of the misidentification of the generic type species (see SKOU & SIHVONEN 2015).

Tribe **Gnophini** Duponchel, 1845 (Gnophites)

Earlier suggested to fall, probably, under the wide concept of Boarmiini by HOLLOWAY (1994: 7), but recent molecular phylogenies have recovered Gnophini as a monophyletic lineage sister to Gonodontini (MURILLO-RAMOS et al. 2019).

= **Aspilatini** Duponchel, 1845 (Aspilatites), senior subjective synonym (HOLLOWAY: 1994: 5), but based on a misspelled genus group name (*Aspitates*) (HOLLOWAY: 1994: 5). See SKOU & SIHVONEN (2015) for further information.

= **Dasydini** Duponchel, 1845 (Dasydites), based on *Dasydia* Guenée, 1845, a junior objective synonym of *Sciadia*.

= **Sionini** Duponchel, 1845 (Sionites). Included in Gnophini by HERBULOT (1961–1963), confirmed repeatedly, for instance by VIIDALEPP et al. (2007), WAHLBERG et al. (2010), SKOU & SIHVONEN (2015) and MURILLO-RAMOS et al. (2019).

= **Angeronini** Forbes, 1948 (Angeronini). Considered valid at tribal rank (e.g., by MCGUFFIN 1981; VIIDALEPP 1996; HAUSMANN et al. 2011; VIVES MORENO 2014), but included as a junior synonym of Gnophini by SKOU & SIHVONEN (2015) and BELJAEV (2016). Synonymy also confirmed by molecular data (YAMAMATO & SOTA 2007; SIHVONEN et al. 2011; MURILLO-RAMOS et al. 2019).

= **Psodini** Povolný & Moucha, 1955: 155, [Fig.] 1 (Psodinae). Not an available name because description is absent (Psodini is only mentioned on the figure). Included in Gnophini by BELJAEV (2016).

= **Diaprepesillini** Kuznetsov & Stekolnikov, 1982: 369 (Diaprepesillini). Included in Gnophini by VIIDALEPP (1996) and BELJAEV (2016).

Tribe **Odontoperini** Tutt, 1896 (Odontoperinae)

See HOLLOWAY (1994: 8, 111). Related to Nacophorini s. l. (MURILLO-RAMOS et al. 2019).

= **Crocallini** Tutt, 1896 (Crocallidi), junior subjective synonym according to BELJAEV (2016). Limited molecular data suggest relationships to *Ennomos* and *Opisthograptis* (ÖUNAP et al. 2011). SKOU & SIHVONEN (2015) classified *Crocallis* in Ennomini of uncertain association. More research is needed.

= **Azelinini** Forbes, 1948 (Azelinini). A junior subjective synonym, proposed on the basis of molecular data (BREHM et al. 2019). In the phylogenetic analysis, Azelinini (represented by *Pero*) nested within Odontoperini (BREHM et al. 2019). Earlier, based on functional morphology of the male genitalia, relationships to Ennomini s. l. and Prosoplophini were suggested by BELJAEV (2009).

Tribe **Nacophorini** Forbes, 1948 (Nacophorini)

Relationship to Odontoperini (= Azelinini [= junior synonym of Odontoperini]) suggested by HOLLOWAY (1994: 8). This view is further supported by molecular data (MURILLO-RAMOS et al. 2019). The North American fauna was revised by RINDGE (1983).

Tribe **Ennomini** Duponchel, 1845 (Ennomites)

= **Odopterini** Stephens, 1850 (Odopteridi), based on *Odoptera*, an unnecessary replacement name for *Ennomos*.

= **Ouraapterygini** Bruand, 1846 (Uraapteridae). Emended by FORBES (1848), HOLLOWAY (1996: 6). Subordinated under Ennomini by SIHVONEN et al. (2011), as earlier suggested by morphology (BELJAEV 2008a). Ourapterygini was subordinated under Ennomini based also on extensive molecular data (MURILLO-RAMOS et al. 2019).

= **Emplociini** Guenée, 1858 (Emplocidae). Emended by reasons of grammar. Junior subjective synonym (PITKIN 2002: 135).

= **Oxydiini** Butler, 1886 (Oxydiidae). Junior subjective synonym (PITKIN 2002: 135).

= **Pantherini** Moore, 1887 (Pantheridae); based on a junior homonym of a genus-group name outside Lepidoptera (HOLLOWAY 1994: 9); invalid according to ICZN (1999, Art. 39).

= **Nephodiini** Warren, 1894 (Nephodiinae). Junior subjective synonym (BELJAEV 2008a), further supported by molecular data (MURILLO-RAMOS et al. 2019; BREHM et al. 2019).

= **Leuculini** Hulst, 1896: 249 (Leuculinae), 317 (Leuculidae). Type genus: *Leucula* Guenée, 1858. Male genitalia are typical for Ourapterygini (see PITKIN 2002). However, the description of the tribe is based on “*Leucula lacteolata* Hulst”, a taxon situated outside Geometridae (E. BELJAEV, pers. comm.). *Leucula* subordinated under Ennomini in molecular analyses (MURILLO-RAMOS et al. 2019, BREHM et al. 2019).

= **Cingiliini** Forbes, 1948 (Cingiliini). Junior subjective synonym (HOLLOWAY 1994: 6; PITKIN 2002: 135).

Tribe **Rumiini** Tutt, 1896 (Rumiinae)

Based on *Rumia*, which is a junior objective synonym of *Opisthograptis*. Junior subjective synonym of Ennomini according to LERAUT (1997). Phylogenetic position still under investigation. In the molecular analysis of SIHVONEN et al. (2011), reconstructed as sister to *Epirranthis diversata*; in the analysis of ÖUNAP et al. (2011), as sister to *Crocallis elinguaris*.

Tribe **Thinopterygini** Holloway, 1994 (Thinopterygini)

Tribe **Campaeini** Forbes, 1948 (Campaeini)

= **Metrocampini** Tutt, 1896 (Metrocampidae), senior synonym. Based on *Metrocampa*, which is a junior objective synonym of *Campaea*. It is proposed not to apply this name, as Campaeini is largely accepted (see HOLLOWAY 1994: 6). In MURILLO-RAMOS et al. (2019), Campaeini lumped into a single cluster with Campaeini, Alsophilini and Prosoplophini.

Tribe **Alsophilini** Herbulot, 1963 (Alsophilinae)

Treated as a subfamily by HAUSMANN (2001), despite earlier doubts about subfamily rank and the suggestion of subordination under Ennominae (HOLLOWAY 1996: 149). Evidence from molecular analyses, however, supports the rank of tribe under Ennominae (e.g., SIHVONEN et al. 2011; MURILLO-RAMOS et al. 2019). In SIHVONEN et al. (2011) and MURILLO-RAMOS et al. (2019), classified as a tribe and Alsophilini united into a single cluster with Campaeini, Wilemaniini and Prosoplophini.

Tribe **Cheimoptenini** Kuznetsov & Stekolnikov, 1982: 347 (Cheimoptenini)

Position of tribe unclear. It has been placed in Ennominae (BELJAEV 2006) and in Desmobaethinae (BELJAEV 2008b), but has not been subjected to studies on molecular phylogeny.

Tribe **Wilemaniini** Wehrli, 1941 (**Wilemaninae [sic!]**)

The original Latin word stem Wileman- (with the suffix -inae) needs to be emended to Wilemani- (being based on the type genus *Wilemania*), leading to “Wilemaniini” rather than to Wilemanini. In MURILLO-RAMOS et al. (2019), Wilemaniini united into a single cluster with Campaeini, Alsophilini and Prosoplophini. BELJAEV (2016) listed Wilemaniini as a junior synonym of Prosoplophini.

Tribe **Prosoplophini** Warren, 1894: 464 (Prosoplophinae)

In MURILLO-RAMOS et al. (2019), Prosoplophini was united into a single cluster with Campaeini, Alsophilini and Wilemaniini.

= **Ligiini** Guenée, 1858 (Ligidae), emended, based on *Ligia*. Senior synonym, but based on a junior homonym of a genus-group name outside Lepidoptera. Invalid according to ICZN (1999, Art. 39).

= **Colotoini** Wehrli, 1940: 345 (Colotoinae). Synonymy proposed in BELJAEV (2016). In the molecular phylogeny of Brehm et al. (2019), the Holarctic *Colotois pennaria* (Colotoini) grouped next to the Central American species *Himeromima aulis* Druce, 1892, which was assigned to Prosoplophini.

= **Compsopterini** Herbulot, 1963 (Compsopterini). The genus *Compsoptera* Blanchard, 1845 has not been included in a molecular phylogeny yet. *Compsoptera* was listed under Prosoplophini in BELJAEV (2016) and HAUSMANN & SIHVONEN (2019).

= **Zamacrini** “Meyrick nec Agassis”: cf. VIIDALEPP (1989: 102) and ZOOLOGICAL RECORD (1990/1991, 13D: 326): “Apochimini nom. nov. Viidalepp ... for Zamacrini Meyrick nec Agassis”. Listed under Prosoplophini in BELJAEV (2016).

= **Apochimini** VIIDALEPP, 1989: 102 (Apochimini) (an unnecessary replacement name for Zamacrini). Listed under Prosoplophini in BELJAEV (2016).

Tribe **Onychorini** Herbulot, 1963 (Onychorini)

Hausmann & Sihvonen (2019) listed *Onychora* Meyrick, 1892 in “Genera of uncertain tribus association”. Not included in a molecular phylogeny yet.

Tribe **Diptychini** Janse, 1933 (Diptychini)

Historically, Diptychini was considered as an intermediate group between Geometrinae [Geometrini] and Larentiinae [Larentiini] by JANSE (1933: 2) and as part of Oenochrominae by PROUT (1931: 120, in: PROUT 1929–1935). For subordination under Ennominae and supposed relationships to Nacophorini and Ourapterygini, see HOLLOWAY (1996: 150–151) and PITKIN (2002: 135). In the most recent and most extensive molecular dataset to date, Diptychini is nested within Ennominae and classified as a tribe, being sister to an unnamed clade and the Campaeini + Alsophilini + Wilemaniini + Prosoplophini complex. It does not show close relationship to Nacophorini (MURILLO-RAMOS et al. 2019).

= **Lithinini** Forbes, 1948 (Lithinini). Synonymised with Diptychini by MURILLO-RAMOS et al. (2019). Close relationship with Caberini according to ABRAHAM et al. (2001; fig. 5b), not confirmed subsequently.

= **Pachynemiini** Kirby, 1903 (Pachynemiidae). The structure of the male and female genitalia fit that of the Lithinini of Rindge (1986). Synonymy confirmed by MURILLO-RAMOS et al. (2019).

= **Epirrhanthini** Forbes, 1948 (Epirrhanthini). In a molecular analysis, the group was included in Ennominae (SIHVONEN et al. 2011), but tribal status was not given. Relationships to Ennomini and Desmobjathrininae were discussed in HAUSMANN (2001: 99). Treated under Ennominae in HOLLOWAY (1994: 7) and under Lithinini in BELJAEV (2016). HAUSMANN & SIHVONEN (2019) recognised Epirrhanthini as a valid tribe, listing it after Lithini in the sequence of tribes.

= **Lacariini** Orfila & Schajovskoy, 1959 (Lacariini), emended, based on *Lacaria*. For possible synonymy to Lithinini, see Holloway (1994: 7, 92).

Tribe **Oenoptilini** Brehm, Murillo-Ramos & Sihvonen, 2019 (Oenoptilini)

The genera *Neobapta* and *Oenoptila*, currently classified in Oenoptilini, were previously assigned to Caberini (PITKIN 2002).

Tribe **Baptini** Forbes, 1948 (Baptini)

Closely related to Palyadini (ABRAHAM et al. 2001; fig. 5b) and subordinated under Caberini in PITKIN (2002: 131). In MURILLO-RAMOS et al. (2019) and Brehm et al. (2019), treated as a tribe and included in a genetic cluster with Theriini.

= **Aleucini** Djakonov, 1936: 484 (Aleucini). Treated as a junior synonym of Baptini in HAUSMANN et al. (2011), but more recently classified in Theriini (SKOU & SIHVONEN 2015; HAUSMANN & SIHVONEN 2019). The name-bearing genus *Aleucis* Guenée, 1845 has not been included in molecular phylogenetic analysis yet. Aleucini is the senior synonym if included in the concept of Baptini or Theriini.

= **Lomographini** Wehrli, 1940: 381, 382 (Lomographinae). The original concept was based on the genus *Stegania* (possibly *Abraxini*), because of the misidentification of the generic type species. It needs to be referred to the ICZN Commission for a ruling (ICZN 1999, Arts. 41, 65.2.) (E. BELJAEV, pers. comm.).

Tribe **Theriini** Herbulot, 1963 (Theriini)

Falls into the broad conception of Boarmiini according to Holloway (1994: 13, 167). In MURILLO-RAMOS et al. (2019) and BREHM et al. (2019), treated as a tribe and included in a genetic cluster with Baptini. See Aleucini under Baptini.

= **Cheimatobiini** Tutt, 1896 (Cheimatobiidi), senior synonym. Based on *Cheimatobia* Stephens, 1829, which is a junior objective synonym of *Theria*. It is proposed not to apply this name, as Theriini is widely accepted (see HOLLOWAY 1994: 6).

Tribe **Plutodini** Warren, 1894 (Plutodinae)

In MURILLO-RAMOS et al. (2019) and BREHM et al. (2019), treated as a tribe, clustering separately from the Baptini/Theriini complex and more closely related to Palyadini.

Tribe **Palyadini** Guenée, 1858 (Palyadae)

Earlier subordination under Baptini rejected by HOLLOWAY (1994: 59), but accepted by ABRAHAM et al. (2001: fig. 5b). PITKIN (2002: 132) suggested status as a subtribe of Caberini/Baptini. In MURILLO-RAMOS et al. (2019) and BREHM et al. (2019), treated at tribe rank, closely related to Plutodini.

Tribe **Epionini** Bruand, 1846 (Epionidae)

= **Hypochrosini** Guenée, 1858 (Hypochrosinae). Hypochrosini sensu HOLLOWAY (1994). Potential synonymy suggested also by MURILLO-RAMOS et al. (2019), but there and in BREHM et al. (2019) formally still treated as a separate tribe because of limited taxon sampling.

= **Scardamiini** Warren, 1894 (Scardamiinae), based on *Scardamia*. Treated as a junior synonym of Epionini by BELJAEV (2016).

= **Anagogini** Forbes, 1948 (Anagogini), junior synonym (HOLLOWAY: 1994: 5). Potential synonymy suggested also by MURILLO-RAMOS et al. (2019), but there and in BREHM et al. (2019) formally still treated as a separate tribe because of limited taxon sampling.

= **Seleniini** Tutt, 1896 (Seleniidi), suggested as a junior synonym in HOLLOWAY (1994: 9).

= **Apeirini** Kuznetsov & Stekolnikov, 1982: 358 (Apeirini). Potential synonymy with Epionini suggested (but not formally established) by MURILLO-RAMOS et al. (2019) as well as by BREHM et al. (2019). Treated as a valid tribe by SIHVONEN & SKOU (2015), BELJAEV (2016) and HAUSMANN & SIHVONEN (2019). Apeirini is a morphologically isolated group (SIHVONEN & SKOU 2015). More research and, particularly, more extensive taxon sampling in this complex are needed.

Tribe **Drepanogynini** Murillo-Ramos, Sihvonen & Brehm, 2019 (Drepanogynini)

Genus *Drepanogynis* earlier subordinated under a wider concept of Nacophorini.

Tribe **Pyriniini** Brehm, Murillo-Ramos & Sihvonen, 2019 (Pyriniini)

Unassigned by PITKIN (2002), who suggested relationships with Caberini/Baptini. Sister lineage relationship to Caberini supported in MURILLO-RAMOS et al. (2019).

Tribe **Caberini** Duponchel, 1845 (Caberites)

Sister lineage relationship to Pyriiniini supported in MURILLO-RAMOS et al. (2019).

= **Erastrini** Herrich-Schäffer, 1845 (Erastridae), junior synonym (HOLLOWAY 1996: 7; 98). Emended, based on *Erastria*, with the Latin word stem *Erastr-*. The original concept referring to Noctuidae: Acontiinae. Classification of the generic type species (see FLETCHER 1979) leaves this family-group name applicable within Ennominae (HOLLOWAY 1994: 7).

= **Brotini** Grote, 1882 (Brotiinae). Emended, based on *Brotis*, with the Latin word stem *Brot-*, which is a junior homonym to a genus-group name in Noctuidae. Invalid according to ICZN (1999, Art. 39). Junior synonym in the broad concept of Caberini/Baptini of PITKIN (2002: 131).

= **Deiliniini** Warren, 1894 (Deiliniinae), based on *Deilinia*, a junior synonym of *Cabera* (HOLLOWAY 1996: 6; 98).

= **Catopyrrhini** Warren, 1894 (Catopyrrhinae), junior synonym (HOLLOWAY 1996: 6; 98).

= **Sphacelodini** Forbes, 1948 (Sphacelodini), retained as a synonym in the broad concept of Caberini/Baptini of PITKIN (2002: 131). Based on illustrations in PITKIN (2002), this group could be close to BELJAEV's concept of Deviniliini (E. BELJAEV, pers. comm.). In molecular phylogenies, *Sphacelodes vulneraria* (Hübner, 1823) grouped within Caberini (MURILLO-RAMOS et al. 2019; BREHM et al. 2019).

Tribe **Deveniliini** Beljaev, 1998: 440 (Deveniliini)

Subordinated under Baptini by STÜNING (2000), maintained valid as a tribe by BELJAEV (2016). Not included in molecular phylogenetic studies so far.

Tribe **Cassymini** Holloway, 1994 (Cassymini)

The molecular analysis of MURILLO-RAMOS et al. (2019) revealed two clearly distinct genetic clusters, with Cassymini clustering together with Abraxini, Eutoeini and Macariini.

Tribe **Abraxini** Warren, 1893 (Abraxinae)

= **Zerenini** Duponchel, 1845 (Zerenites), based on a junior homonym of a genus-group name outside Lepidoptera; junior synonym (HOLLOWAY 1994: 9). Invalid according to ICZN 1999, Art. 39). Abraxini clustered together with Cassymini, Eutoeini and Macariini in the analyses of MURILLO-RAMOS et al. (2019).

Tribe **Eutoeini** Holloway, 1994 (Eutoeini)

Eutoeini clustered together with Abraxini and Cassymini in the analyses of MURILLO-RAMOS et al. (2019).

Tribe **Macariini** Guenée, 1858 (Macaridae)

The original Latin word stem *Macar-* (with the suffix *-idae*) needs to be emended to *Macari-* (being based on the type genus *Macaria*), leading to "Macariini" rather than to *Macarini*. Macariini clustered with Cassymini, Abraxini and Eutoeini in MURILLO-RAMOS et al. (2019).

= **Atomorphini** Wehrli, 1953: 642 (Atomorphinae). Originally part of Semiothisinae, treated similarly in WILTSHIRE (1990), but later classified in Gnophini (e.g., VIIDALEPP 1996). The type genus *Atomorpha* Staudinger, 1901 was considered a junior synonym of *Isturgia* Hübner, 1823 by SKOU & SIHVONEN (2015) in Macariini. The name-bearing genus *Atomorpha* has not been included in molecular phylogenetic studies.

= **Semiothisini** Warren, 1894 (Semiothisinae), junior synonym (HOLLOWAY 1994: 9).

= **Fernaldellini** Hulst, 1896 (Fernaldellinae), junior synonym (HOLLOWAY 1994: 7).

Tribe **Boarmiini** Duponchel, 1845 (Boarmites)

A very broad concept of this tribe was proposed by HOLLOWAY (1994: 167), confirmed by recent molecular analyses (MURILLO-RAMOS et al. 2019; MURILLO-RAMOS et al. 2021c). JIANG et al. (2017) presented a detailed molecular analysis of the tribe, identifying 14 monophyletic lineages (potential subtribes) within it.

= **Cleorini** Duponchel, 1845 (Cleorites), junior synonym (HOLLOWAY: 1994: 6). Synonymy further supported by molecular analyses (e.g., MURILLO-RAMOS et al. 2019, 2021c).

= **Fidoniini** Duponchel, 1845 (Fidonites), emended by reasons of grammar; based on *Fidonia*, a junior synonym of *Eurranthis* (Leraut 1997: 214). Synonymy further supported by molecular analyses (e.g., MURILLO-RAMOS et al. 2019, 2021c).

= **Ascotini** Warren, 1893 (Ascotinae), junior synonym (HOLLOWAY: 1994: 5). Synonymy further supported by molecular analyses (e.g., MURILLO-RAMOS et al. 2019, 2021c).

= **Bistonini** Stephens, 1850 (Bistonidi). Falling into the broad concept of Boarmiini according to HOLLOWAY (1994: 13, 167). Synonymy further supported by molecular analyses (e.g., SIHVONEN et al. 2011; MURILLO-RAMOS et al. 2019, 2021c).

= **Amphidasini** Duponchel, 1845 (Amphidasites), senior synonym. Based on *Amphidasis*, a junior objective synonym of *Biston*. It is proposed not to apply this name (neither for a potential subtribe), as *Bistonini/Bistonina* is widely accepted (see HOLLOWAY 1994: 5).

= **Hyberniini** Duponchel, 1845 (Hibernites), senior synonym. Emended. Based on *Hybernia*, a junior objective synonym of *Erannis*. It is proposed not to apply this name, as *Bistonini/Bistonina* is widely accepted (see HOLLOWAY 1994: 5, 7).

= **Eubyjini** Warren, 1893 (Eubyjinae), based on *Eubyja*, which is a junior synonym of *Biston* (HOLLOWAY 1994: 7).

= **Erannini** Tutt, 1896 (Eranniinae), junior synonym (HOLLOWAY 1994: 7). Synonymy further supported by molecular analyses (e.g., MURILLO-RAMOS et al. 2019, 2021c). Emended, based on *Erannis*, with the Latin word stem *Erann-*.

= **Desertobiini** Viidalepp, 1989: 104 (Desertobiini). Subordinated under Boarmiini by BELJAEV (2000).

= **Dalimini** Wehrli, 1940 (Daliminae), junior synonym (HOLLOWAY 1996: 150).

- = **Selidosemini** Meyrick, 1892 (Selidosemidae), junior synonym (HOLLOWAY 1994: 9). Synonymy further supported by molecular analyses (e.g., MURILLO-RAMOS et al. 2019, 2021c).
- = **Braccini** Warren, 1894 (Braccinae), junior synonym (HOLLOWAY 1994: 167).
- = **Melanchroiini** Hulst, 1896 (Melanchroiinae), junior synonym (PITKIN 2002: 130). Synonymy further supported by molecular analyses (e.g., MURILLO-RAMOS et al. 2019, 2021c).
- = **Phaseliini** Wehrli, 1941 (Phaseliinae), suggested as falling into the wide concept of Boarmiini. Synonymy further supported by molecular analyses (e.g., MURILLO-RAMOS et al. 2019, 2021c).
- = **Melanolophini** Forbes, 1948 (Melanolophini), junior synonym (HOLLOWAY 1994: 8; PITKIN 2002: 131). Synonymy further supported by molecular analyses (e.g., MURILLO-RAMOS et al. 2019, 2021c).
- = **Glaucinini** Rindge, 1959: 265 (Glaucinini). Boarmiini synonymy supported by molecular analysis (MURILLO-RAMOS et al. 2019, 2021c).
- = **Bupalini** Herbulot, 1963 (Bupalini), junior synonym (HOLLOWAY 1994: 6; 167). Synonymy further supported by molecular analyses (e.g., MURILLO-RAMOS et al. 2019, 2021c).
- = **Milioniini** Holloway, 1994 (Milioniini). First mentioned by Inoue (1992), but without description and thus unavailable. Junior synonym (HOLLOWAY 1994: 8, 302). Synonymy further supported by molecular analyses (e.g., MURILLO-RAMOS et al. 2019, 2021c).

Tribe **Cystidiini** Kuznetsov & Stekolnikov, 1982: 344 (Cystidiini)

Not included in molecular phylogenetic analysis so far. The tribe cannot be subordinated to Boarmiini because the vinculum and tegumen are separated one from another by a deep narrowing. Lateral lobes of anellus in *Cystidia* completely reduced; in *Obeidia*, the mentioned structures possibly remained, but homologies are difficult to interpret [cf. Inoue's (1992) revision of *Obeidia*] (E. BELJAEV, pers. comm.).

- = **Obeidiini** Holloway, 1994 (Obeidiini). First mentioned by INOUE (1992), but without description and thus unavailable. Junior synonym (HOLLOWAY 1994: 8, 302).

Appendix 2. List of literature examined for the preparation of the “Online taxonomic facility of Geometridae”, spanning 1998 to 23.5.2022 and only including references not already listed in SCOBLE (1999) or SCOBLE & HAUSMANN (2007).

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