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Molecular phylogeny, classification, biogeography and diversification patterns of a diverse group of moths (Geometridae: Boarmiini)

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ABSTRACT

Understanding how and why some groups have become more species-rich than others, and how past biogeography may have shaped their current distribution, are questions that evolutionary biologists have long attempted to answer. We investigated diversification patterns and historical biogeography of a hyperdiverse lineage of Lepidoptera, the geometrid moths, by studying its most species-rich tribe Boarmiini, which comprises ca. 200 genera and ca. known 3000 species. We inferred the evolutionary relationships of Boarmiini based on a dataset of 346 taxa, with up to eight genetic markers under a maximum likelihood approach. The monophyly of Boarmiini is strongly supported. However, the phylogenetic position of many taxa does not agree with current taxonomy, although the monophyly of most major genera within the tribe is supported after minor adjustments. Three genera are synonymized, one new combination is proposed, and four species are placed in *incertae sedis* within Boarmiini. Our results support the idea of a rapid initial diversification of Boarmiini, which also implies that no major taxonomic subdivisions of the group can currently be proposed. A time-calibrated tree and biogeographical analyses suggest that boarmiines appeared in Laurasia ca. 52 Mya, followed by dispersal events throughout the Australasian, African and Neotropical regions. Most of the transcontinental dispersal events occurred in the Eocene, a period of intense geological activity and rapid climate change. Diversification analyses showed a relatively constant diversification rate for all Boarmiini, except in one clade containing the species-rich genus *Cleora*. The present work represents a substantial contribution towards understanding the evolutionary origin of Boarmiini moths. Our results, inevitably biased by taxon sampling, highlight the difficulties with working on species-rich groups that have not received much attention outside of Europe. Specifically, poor knowledge of the natural history of geometrids (particularly in tropical clades) limits our ability to identify key innovations underlying the diversification of boarmiines.

1. Introduction

The moth family Geometridae is a hyperdiverse insect group with more than 24,000 described species worldwide (Mitter et al., 2017). As with other lineages of Lepidoptera, geometrids show a suite of traits, such as host-plant shifts, as well as good camouflage, that could have played an important role in their evolutionary radiation (Ehrlich and Raven, 1964; Fordyce, 2010). Nevertheless, key components leading to their evolutionary success are unclear, and the diversification dynamics of the main lineages within geometrids remain unexplored. The lack of

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robust phylogenies based on broad and dense taxon sampling, a phylogenetically derived global classification, and a shortage of reliable fossil information have restricted our ability to answer many evolutionary questions on this group.

Within Geometridae, the tribe Boarmiini, in the subfamily Ennominae, is by far the most species-rich tribe, with ca. 200 genera and ca. 3000 known species (Scoble and Hausmann, 2007). However, the actual numbers are certainly higher, with rough estimates suggesting that Boarmiini may comprise 5000 or more species (Jiang et al., 2017; Müller et al., 2019). As a result, the evolutionary relationships among boarmiines have been difficult to resolve, further complicated by numerous conflicting regional classifications and the paucity of molecular data.

Adult boarmiines are medium-sized to large nocturnal moths, most frequently with a typical geometrid body plan (broad wings and slender body). However, several genera are – rather atypically for the family – characterized by stout bodies and narrow wings, and moths from some genera are known to have adopted a diurnal lifestyle. The majority of boarmiines have a mottled, brownish-greyish wing pattern providing camouflage against tree bark, which is the typical resting surface of these forest insects (Pitkin, 2002). The external similarity of the typical boarmiines has made it difficult to distinguish the natural subdivisions within the group.

A great proportion of the boarmiines are forest dwellers with larvae feeding on foliage of trees, and many are highly polyphagous (Holm et al., 2019; Müller et al., 2019). Some genera have nevertheless been proposed as specialists of particular plant families (Holloway 1994). Several species are economically important, including, for instance, tea pests such as *Ectropis grisescens* Warren, 1894 and *E. obliqua* Prout, 1915 (Jiang et al., 2014; Li et al., 2019). Others have been model species for famous ecological studies, such as industrial melanism and adaptive colour change in the larvae of peppered moths, *Biston betularia* Linnaeus, 1758 (Eacock et al., 2019), and also as bioindicators (Intachat and Holloway, 2000).

Within Boarmiini, numerous temperate species have lost flight ability (Wahlberg et al., 2010; Müller et al., 2019). This flightlessness is restricted to females, which can be apterous or brachypterous, possessing rudimental dysfunctional wings (Sattler, 1991). Almost all these species fly in late autumn or early spring (the so-called winter moth phenomenon, Hunter 1995, Tammaru et al. 2001), with the young larvae developing on freshly flushed leaves of host trees (Snäll et al., 2007).

Four previous phylogenetic studies have either focused on Boarmiini specifically (Wahlberg et al., 2010; Jiang et al., 2017) or included them in a broader phylogenetic context along with a large number of taxa from across the Geometridae (Murillo-Ramos et al., 2019; Brehm et al., 2019). All these studies recovered short branches for deep internodes, poor branch support, and polyphyletic groupings; in other words, while the monophyly of the tribe itself was uncontroversial, its internal structure has remained problematic. The repeated recovery of poorly resolved deeper relationships and short internal branches suggests that early diversification of Boarmiini happened quickly. Concerning the age of the clade, Wahlberg et al. (2010) suggested that boarmiines started to diversify during the Oligocene ca. 34 Mya. Apart from these few studies, little is known about the origin and biogeographical patterns within Boarmiini, and the factors behind the diversification of this tribe remain unstudied.

In contrast to the usual latitudinal trend of a strong increase in species richness towards the tropics (Pianka, 1966; Brown, 2014), the boarmiines appear to be comparably diverse in temperate forests (Jiang et al., 2017; Müller et al., 2019). However, this generalization must be treated with some caution as taxonomic information may be biased towards the well-studied Palaearctic fauna compared to the tropics (see e. g. Veijalainen et al., 2012). These observations inspire three main questions: I) How has historical biogeography shaped the current distribution of Boarmiini? II) Has Palaearctic diversity resulted from the early appearance of the group at high latitudes or instead from recent colonization and diversification? III) How has flightlessness evolved throughout the evolutionary history of Boarmiini?

To answer these questions, our study aims to resolve the major evolutionary relationships of Boarmiini with an expanded taxon dataset, combining those analysed by Wahlberg et al. (2010), Jiang et al. (2017) and the recent phylogenetic study of geometrid moths by Murillo-Ramos et al. (2019). To better understand the evolutionary history of the group, we inferred a phylogenetic hypothesis with a dataset of eight concatenated genes, using a maximum likelihood (ML) approach. The resulting topology was used to I) elucidate the major evolutionary relationships of Boarmiini and their taxonomic implications, II) estimate the divergence times of the sampled lineages under a Bayesian approach, III) analyse the lineage diversification of Boarmiini using a Bayesian analysis of macroevolutionary mixtures, and finally IV) reconstruct their most probable origin and the biogeographical patterns using the Dispersal–Extinction–Cladogenesis (DEC) model as implemented in BioGeoBEARS.

2. Material and methods

2.1. Data and sampling fraction

Our dataset was primarily retrieved from the recent study published by Murillo-Ramos et al. (2019), which focused on resolving the phylogenetic relationships of the major lineages of geometrid moths, and from previous studies on Boarmiini by Wahlberg et al. (2010) and Jiang et al. (2017). Genomic DNA from additional samples was extracted and purified using a NucleoSpin® Tissue Kit (MACHEREY-NAGEL), following the manufacturer's protocol. DNA amplification and sequencing were carried out following protocols proposed by Wahlberg & Wheat (2008). One mitochondrial (*cytochrome oxidase subunit I,* COI) and seven protein-coding nuclear gene regions (*carbamoylphosphate synthetase* (CAD), *ribosomal protein S5* (RpS5), *wingless* (wgl), *cytosolic malate dehydrogenase* (MDH), *glyceraldehyde-3-phosphate dehydrogenase* (GAPDH), *elongation factor 1 alpha* (EF-1 alpha) and *isocitrate dehydrogenase* (IDH) were sequenced and used for phylogenetic analyses. Multiple sequence alignments were carried out in MAFFT as implemented in Geneious v.11.0.2 (Biomatters, http://www.geneious.com/) for each gene based on a reference sequence of Geometridae downloaded from the database VoSeq (Peña and Malm, 2012). Our final dataset included 346 species, of which 285 belonged to Boarmiini and 61 served as outgroups. We included at least one representative of nearly 50% of the recognized genera in Boarmiini. Aligned sequences were curated and managed in VoSeq (Peña and Malm, 2012). The final dataset had a concatenated length of 6413 bp including gaps. Missing data made up 39.7% of the final data matrix.

2.2. Phylogenetic inference

We ran maximum likelihood analyses with a dataset partitioned by codon position using IQ-TREE V1.6.10 (Nguyen et al., 2015). Best-fitting substitution models were selected by ModelFinder, and the partition finding algorithm (Kalyaanamoorthy et al., 2017) was run on the data partitioned by genes (MFP + MERGE option). The phylogenetic analyses were carried out with the *-spp* (edge proportional) option. Support for nodes was evaluated with 1000 ultrafast bootstrap (UFBoot2) approximations (Hoang et al., 2018) and the SH-like approximate likelihood ratio test (Guindon et al., 2010). SH-Like values $\geq$ 80 and UFBoot2 values $\geq$ 95 indicate well-supported clades. To reduce the risk of overestimating branch support in the UFBoot2 test, we implemented the *-bnni* option, which optimizes each bootstrap tree using a hill-climbing nearest-neighbour-interchange (NNI) search. Trees were visualized and edited in FigTree v1.4.3 (Rambaut, 2012) and iTOL (Letunic and Bork, 2016).

2.3. BEAST divergence-time analyses

We estimated divergence times using BEAST2.5.2 (Bouckaert et al., 2014, 2019). Due to the size of our dataset, and to guarantee MCMC convergence, the analyses were constrained to the fixed tree topology recovered from IQ-TREE. The data were partitioned by gene; the different models implemented on each partition are listed in Table 1. We ran the analyses using a relaxed molecular clock.

A Boarmiini caterpillar fossil, *Eogeometer vadens* (Fischer, Michalski, & Hausmann, 2019) from Baltic amber, was recently described by Fischer et al. (2019). This fossil suggests a minimum age of boarmiines ca. 44 Mya (Fischer et al., 2019). However, the age of the Baltic amber is still controversial, with estimations ranging from 44-47 Mya (Ritzkowski, 1997) to 34–48 Mya (Seyfullah et al., 2018). To be conservative, we thus used the Lutetian, Middle Eocene age as our calibration point, which ranges from 41 to 47 Mya, according to the latest International Chronostratigraphic Chart (Cohen et al., 2013). The calibration point was set under a uniform distribution with a minimum of 41 Mya and a maximum of 90 Mya. The maximum bound corresponded to the age of stem Geometroidea according to the results of Wahlberg et al. (2013). We had no other fossil constraint available; therefore, we used the same prior settings for both the root (all taxa) node and the crown (only Boarmiini) node. The birth–death model was used on the tree, and we ran 140 million generations in two independent runs, sampling after every 7000 generations.

All the analyses were run to achieve effective sample sizes (ESS) greater than 200 for all parameters once burn-in was discarded. TRACER v1.7.1 (Rambaut et al., 2018) was used to examine overall likelihood and parameter estimates . The first 20% of sampled trees were discarded as burn-in from the results of each run. The remaining trees were combined with LogCombiner v2.5.2., and the maximum clade credibility (MCC) tree with divergence time means and 95% highest probability densities (HPDs) was generated with TreeAnnotator v2.5.2. These packages are available in the latest version of BEAST2 (Bouckaert et al., 2014, 2019). Outgroups were removed from the MCMC tree and the resulting tree was used for all subsequent analyses.

2.4. Analysis of historical biogeography

We inferred the ancestral range of boarmiines using the Dispersal–Extinction–Cladogenesis (DEC) model as implemented in BioGeoBEARS (Matzke, 2013). Biogeographical areas were defined based on the current distribution of extant taxa, using the database of Scoble and Hausmann (2007); this includes the biogeographical areas of type species as given in Scoble (1999), Boarmiini literature published after 2007 (mainly relying on the Zoological Record), georeferenced records (GBIF 2019), and personal communications from authors (field trips). Six realms were defined as follows: (A) Nearctic, (B) Neotropic, (C) Palaearctic, (D) Afrotropic, (E) Indo-Malay, (F) Australasia (Olson et al., 2001).

We tested a model with constraints on the areas allowed, dispersal multipliers and time-stratification (Matzke, 2013). The species were coded as (1) if present in the biogeographical realm, otherwise (0). Areas were coded (1) as allowed, otherwise (0). Dispersal multipliers between realms were set as follows: (0.6) as the medium probability to disperse, (0.3) as hard and (0.1) as very hard to reach the realm. Time-stratifications were defined as follows: TS1– between 60 Mya and 40 Mya, which roughly corresponds to the approximately estimated age of Boarmiini . This period matches with the Eocene warming event and the expansion of the boreotropical forest over Asia and North America (Sanmartín et al., 2001). Presumably, North America was still connected to Europe, while Europe and Asia were separated by the Obik Sea (Smith et al., 1994). TS2– between 40 Mya and 20 Mya, corresponds with a drastic change in climatic conditions (cooler and drier) in the Northern Hemisphere and *trans*-Beringian isolation (Sanmartín et al., 2001). Europe and Asia became contiguous by the Oligocene (ca. 30 Mya) with the disappearance of the Obik Sea; the Arabian plate began separating from Africa (Bosworth et al., 2005; Portik and Papenfuss, 2015); North and South America could have been temporarily connected by the GAARlandia bridge through the Greater Antilles (Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2006). TS3– between 20 Mya and the present day, 0 Mya, with a coniferous forest belt connecting northern Asia with North America across Beringia. During this period, a land bridge connecting North Africa, the Arabian Peninsula and Eurasia was established (Bosworth et al., 2005), North and South America were connected by the Panama isthmus (O'Dea et al., 2016), and important geological rearrangements in South America also occurred (Thode et al., 2019).

Table 1
Evolutionary models implemented in BEAST2 analysis.

Gene partition	Model	Data type
COI	GTR + F + I + G4	Mitochondrial
Wingless	GTR + F + I + G4	Nuclear
EF1a	SYM + I + G4	Nuclear
RpS5, GAPDH	SYM + I + G4	Nuclear
IDH	SYM + I + G4	Nuclear
MDH	SYM + I + G4	Nuclear
CAD	GTR + F + I + G4	Nuclear

2.5. Diversification analysis

To explore potential shifts in diversification rates of Boarmiini we used BAMM (Bayesian Analysis of Macroevolutionary Mixtures). This program models dynamics of speciation and extinction using reversible-jump Markov Chain Monte Carlo (Rabosky et al., 2013). Instead of using a global sampling fraction, sampling probabilities were specified by genus. Information on species numbers by genus was taken from the database of Scoble and Hausmann (2007), followed by an extensive search of all literature published after 2007. We are aware that in Boarmiini there are many undescribed species and the taxonomic status of some groups is doubtful; therefore, only valid described species were considered for the sampling fraction analyses. The data included a sampling fraction of 11%. MCMC convergence, the best shift configuration and rates-through-time plots were obtained with the BAMMtools R package (Rabosky et al., 2014). We ran 100 million generations. Run convergence was assessed using the Coda package in R (Plummer et al., 2006).

3. Results

3.1. The phylogenetic relationships of Boarmiini

In line with Wahlberg et al. (2010), Jiang et al. (2017) and Murillo-Ramos et al. (2019), our IQTREE results support the monophyly of Boarmiini (SH-like = 99.9, UFBoot2 = 98). The phylogenetic positions of many taxa do not agree with their current taxonomic treatment (Fig. 1). We recovered some deep nodes as poorly supported and with short internal branches. Unsurprisingly, some species-rich genera like *Aphilopota* Warren, 1899; *Cleora* Curtis, 1825; *Colocleora* Prout, 1938; *Ectropis* Hübner, 1825; *Geolyces* Walker, 1860; *Hypomecis* Hübner, 1821; *Melanolophia* Hulst, 1897; *Ophthalmitis* Guenée, 1857 and *Physocleora* Warren 1897 were recovered as para- and/or polyphyletic (supplementary data 1, Fig. 1). Nevertheless, most of the traditionally recognized large genera within Boarmiini were found to form uncontroversial monophyletic units after minor rearrangements. Our analyses also show very well-supported clades, for instance *Erannis* Hübner, 1825 + *Biston* Leach, 1815, *Eubordeta* Rothschild, 1904 + *Orthofidonia* Packard, 1876 + *Arichanna* Moore, 1867, *Alcis* Curtis 1826 + *Selidosema* Hübner, 1823 + *Peribatodes* Wehrli 1943, *Hypagyrtis* Hübner 1818. + *Hyposidra* Guenée, 1857 + *Jankowskia* Oberthür, 1884. Proposed taxonomic changes are summarized in Table 2 and discussed in detail in the Discussion.

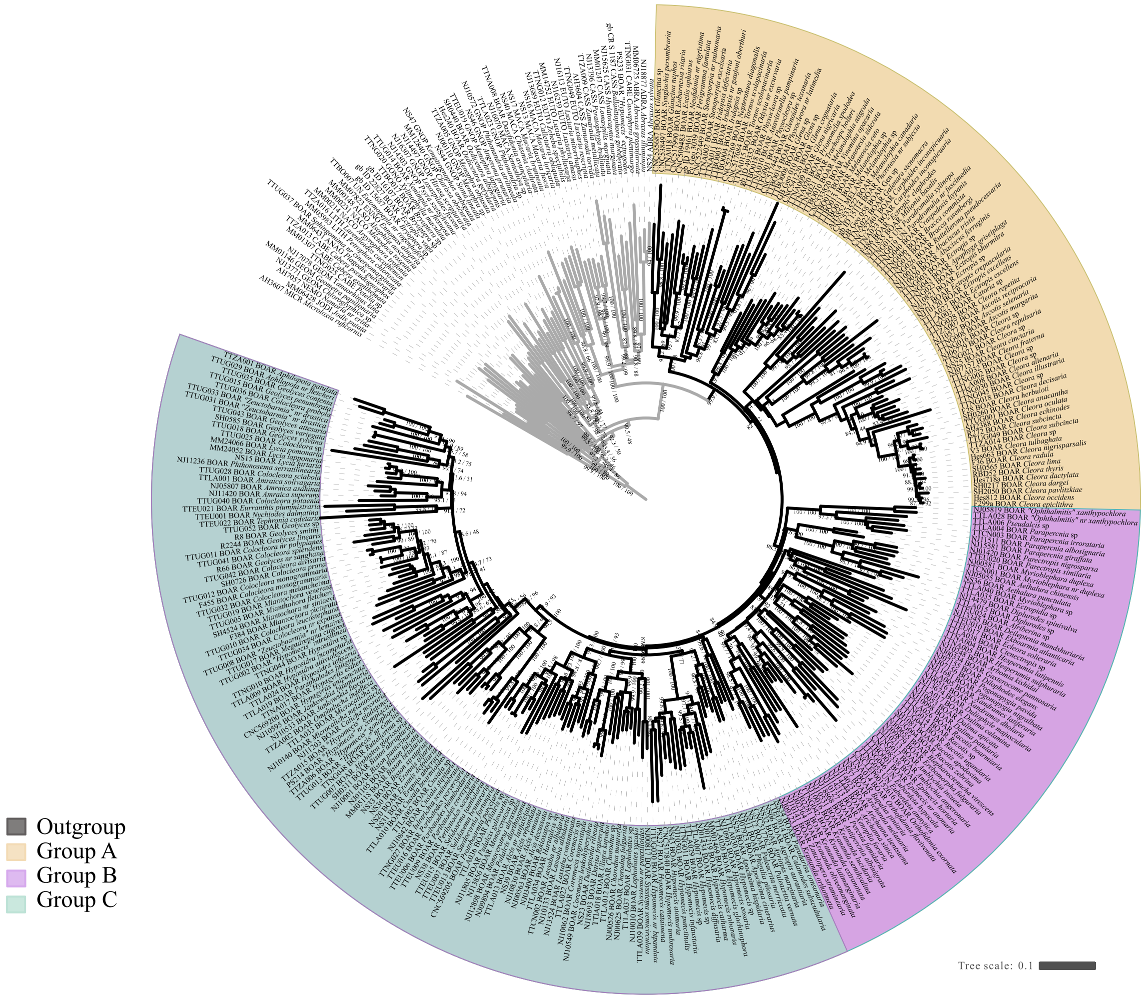

Fig. 1. Phylogenetic relationships of Boarmiini based on a dataset of 346 taxa, with up to eight genetic markers under a maximum likelihood approach. A linear of the tree version is in supplementary data 1.

Table 2

Summary of proposed taxonomic changes in Boarmiini.

Explanation	Taxonomic change
Boarmia ugandaria Swinhoe, 1904 from Uganda is transferred from *Chorodna* (Walker, 1860) (Scoble & Hausmann 2007) to *Racotis* Moore, 1887 as *Racotis ugandaria* (Swinhoe, 1904).	comb. n.
Ophthalmitis Fletcher, 1979 is considered a junior subjective synonym of *Parapercnia* Wehrli, 1939.	syn. n.
Ematurga Lederer, 1853 is considered a junior subjective synonym of *Hypomecis* Hübner, 1821.	syn. n.
Zeuctoboarmia Prout, 1915 is considered a junior subjective synonym of *Hypomecis* Hübner, 1821.	syn. n.
Ectropis elaphrodes Fletcher, 1958 from Uganda is excluded from *Ectropis* Hübner, 1825 (Scoble 1999), but genus combination awaits further studies. It is classified as "*Ectropis*" *elaphrodes* (Fletcher, 1958).	Genus combination *incertae sedis*
Hypomecis intrusilinea Prout, 1915 from Uganda is excluded from *Hypomecis* Hübner, 1821, but genus combination awaits further studies. It is classified as "*Hypomecis*" *intrusilinea* Prout, 1915.	Genus combination *incertae sedis*
Hypomecis gonophora Prout, 1916 from South Africa is excluded from *Hypomecis* Hübner, 1821, but genus combination awaits further studies. It is classified as "*Hypomecis*" *gonophora* Prout, 1916.	Genus combination *incertae sedis*
Hypomecis gladstonei Prout, 1922 from South Africa is excluded from *Hypomecis* Hübner, 1821, but genus combination awaits further studies. It is classified as "*Hypomecis*" *gladstonei* Prout, 1922.	Genus combination *incertae sedis*

3.2. *Timing of divergence*

According to our estimates of divergence times, Ennominae, the subfamily to which Boarmiini belong, began to diversify in the late Cretaceous ca. 69 Mya (95% credibility intervals 56–86). Boarmiines diverged ca. 52 Mya (43–65) and began to diversify in the Eocene into four major radiations ca. 49–48 Mya (41–60) (Fig. 2 and Additional file 1). Divergence time estimates for all clades are presented in Additional file 1.

The most species-rich genera of Boarmiini – *Cleora* and *Hypomecis* Hübner, 1821 – started to diversify 26 Mya (20–33), and *Alcis* Curtis, 1826 started to diversify 13 Mya (8–17) (Fig. 2 and Additional file 1).

Within Boarmiini, flightlessness has appeared at least four times independently. The putatively oldest clade with flightless females is *Phigalia* Duponchel, 1829 + *Apocheima* Hübner, 1825 + *Paleacrita* Ryley, 1876, which diverged from its winged sister group about 37 Mya (29–46). The clade began diversifying about 25 Mya (17–35). Another lineage, *Agriopis* Hübner, 1825, separated from its sister group 30 Mya

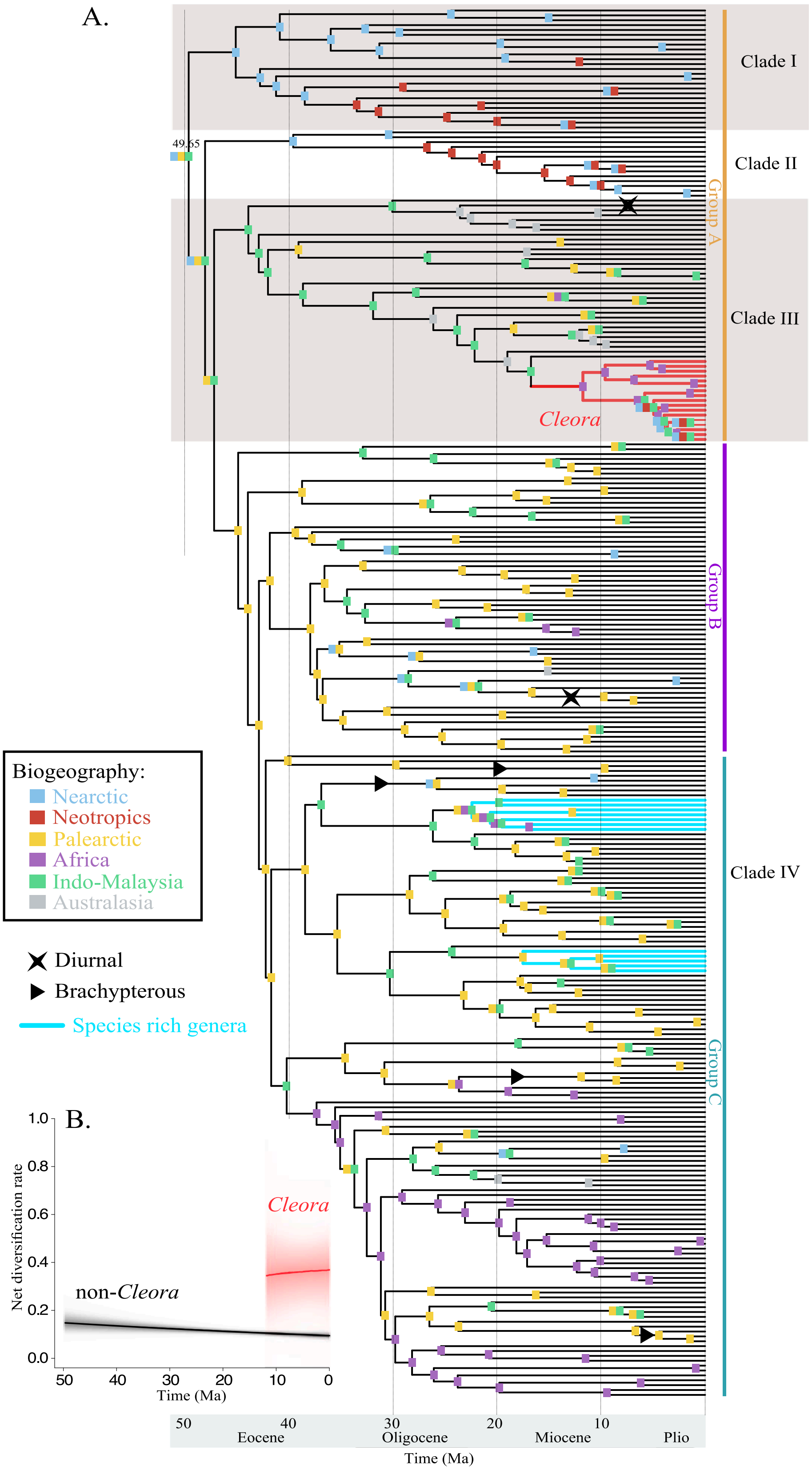

Fig. 2. A–Time-calibrated phylogeny and biogeography of Boarmiini moths. Coloured squares on nodes indicate the most likely biogeographical area from BioGeoBEARS estimations. Triangles indicate diurnal lineages. Red *Cleora*, highlight one of the richest clades within Boarmiini, which showed a high diversification rate. Blue lines indicate species-rich genera. The timescale spans the evolutionary history of the group. B–Estimated net diversification rate from BAMM analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(19–40) and the two sampled *Agriopis* species diverged from each other ca. 9 Mya (4–15). The most recent ancestor of *Erannis* and its winged relatives lived about 30 Mya (23–39) and the three sampled *Erannis* species began to diverge ca. 8 Mya (4–12). Finally, the genus *Lycia* Hübner, 1825 appears to be the youngest clade in which some species have wingless females. *Lycia* separated from its sister group about 7 Mya (4–9), with the three sampled *Lycia* species starting to diverge from each other ca. 4 Mya (0.68–2) (Fig. 2 and Additional file 1).

3.3. Main biogeographical events and diversification patterns

Our analysis suggested a Holarctic origin of Boarmiini covering the Nearctic, Palaearctic and Indo-Malay realms during the Eocene ca. 49 Mya. Based on the results using BioGeoBEARS (Matzke, 2013), it is unclear from which biogeographic region the most recent common ancestor of the Boarmiini derived. Three separate dispersal events may have occurred from the Nearctic to the Neotropics during the late Eocene, the early Oligocene and the middle of the Miocene (between 35 and 14 Mya) in clades I and II (Fig. 2, and Additional file 2).

Other independent dispersal events may have occurred from Indo-Malaysia to the Palaearctic, Australasia and Africa, during a period ranging from the Eocene, ca 40 Mya, to the Pliocene, ca. 5 Mya, in clade III. Finally, the last major events occurred in the middle of Eocene, ca 40 Mya, where many dispersals from the Palaearctic to Indo-Malaysia may have occurred, followed by another independent dispersal event from Indo-Malaysia to Africa in clade IV (Fig. 2, and Additional file 2).

Based on our BAMM (Rabosky et al., 2013) analysis, the net diversification rate for all Boarmiini has been relatively constant through time (Additional file 3), except for one significant shift in diversification rates along the stem of the African *Cleora* in the middle of Miocene, ca. 12 Mya. This shift happens concordantly with the colonization of Africa by *Cleora* from the Indo-Malay region (Fig. 2, clade III).

4. Discussion

4.1. Towards understanding the evolutionary relationships of boarmiines

Based on our analyses of a new comprehensive dataset for Boarmiini, we highlight some of the advances made to disentangle the phylogenetic relationships within the tribe.

Wahlberg et al. (2010) and Jiang et al. (2017) suggested that Boarmiini *s. str.* are monophyletic. Conversely, in the large-scale studies of Murillo-Ramos et al. (2019) and Brehm et al. (2019) Boarmiini were recovered as polyphyletic, and consequently, some taxa would need to be reclassified in different tribes to make the group monophyletic. Our results reveal Boarmiini (in a slightly revised sense) as a clearly monophyletic taxon. The revised delimitation suggests that some genera (*Cleorodes* Warren 1894, *Menophra* Moore 1887, *Bryoptera* Guenée 1858, *Dasyfidonia* Guenée 1857, *Eutomopepla* Warren 1894), which are traditionally considered to belong to Boarmiini, have to be excluded from the tribe (see e.g. Viidalepp et al. 2007; Brehm et al. 2019 for discussion of some of these cases). The former misclassification of these genera is probably a result of previously unrecognized convergent evolution in the morphology of large forest geometrids; a “*Boarmia*-like appearance”, which appears to have evolved repeatedly.

In this study, relationships between many of the basal branches of the tribe were resolved with reasonable certainty. In the New World, for example, we find that most boarmiines belong to a few well-defined clades not represented elsewhere. In turn, the boarmiines of the European fauna include species from more than a dozen distantly related clades, typically represented by just a few species. Most of those clades have their centres of diversity in the Oriental region. Nevertheless, the sequence of many of the initial branching events within the tribe still remains obscure, probably resulting from a rapid initial diversification of the tribe (Wahlberg et al. 2010).

Traditionally, many ‘non-*Boarmia*-looking’ genera (i.e. not being slender-bodied moths with tree-bark-like wing patterns, e.g. *Biston*, *Erannis*, *Lycia*) have been treated in the separate tribe Bistonini. The validity of the latter tribe has been questioned by Holloway (1994), and we consider that the present study provides proof in favour of merging Bistonini with Boarmiini. Curiously, also, the genera *Bupalus* and *Ematurga* have sometimes been treated as belonging to separate tribes (Bupalini and Ematurgini, respectively, e.g. Viidalepp, 1996); we find no grounds for this, and this example demonstrates that caution is needed to not misinterpret relatively recent, ecologically driven adaptations (to diurnal activity of adults in this case). Also, at a more general level, given that relationships among major clades within the tribe are characterized by short branches, there is currently no basis for a taxonomic subdivision of the tribe Boarmiini, even if this might be seen as practical given the richness of the global fauna.

In addition to the taxonomic changes proposed by Murillo-Ramos et al. (2019) and Brehm et al. (2019), we discuss some uncertainties in the classification and we propose taxonomic rearrangements to the current classification of boarmiines. Given our still incomplete taxon sampling and wide geographic range of some taxa, the interpretation of some of the results is to be taken with caution.

Two large Neotropic radiations extend into the Nearctic but are not represented in the Old World – one comprising *Physocleora* Warren, 1897, *Glena* Hulst, 1896 and *Iridopsis* Warren, 1894; and the other consisting of *Prionomelia* Warren, 1895, *Melanolophia* Hulst, 1896 and *Carphoides* McDunnough, 1920 (Brehm et al., 2019). Within these Neotropic radiations, our results suggest that the species-rich genera *Physocleora* and *Melanolophia* are paraphyletic (Fig. 1, group A). *Physocleora* is a genus with 45 described species, but their taxonomy has been noted as quite confusing by previous morphological studies (Pitkin, 2002). The genus *Physocleora* is most likely more diverse than currently acknowledged, with many species still waiting to be described, especially in the Neotropic realm. Our results recovered *Physocleora* intermixed with *Glenoides* McDunnough, 1920 and *Glena* Hulst, 1896, but, with limited taxon sampling, a taxonomic treatment is not yet feasible. *Melanolophia,* with its 105 described species, was suggested by Pitkin (2002) to be monophyletic based on wing pattern and genital morphology. However, our results do not support this view as *Melanolophia* came out intermixed with the genera *Vinemina* McDunnough, 1920, *Melanotesia* Rindge, 1964, *Melanoscia* Warren, 1904, *Pherotesia* Schaus, 1901, *Galenara* and *Carphoides* McDunnough, 1920; these genera have been treated as the tribe Melanolophiini (Rindge, 1990) but were later considered to be a subgroup of Boarmiini (Pitkin, 2002). Merging of these genera into a single larger genus may be desirable. Nevertheless, we suggest that more extensive and detailed studies of morphological characters are needed to clarify the position and status of these genera.

Support for the monophyly of *Ectropis* and *Cleora* – two major Old World-based genera – requires some minor adjustments (Fig. 1, group A). With respect to *Ectropis*, our current data set (29% of known species sampled) suggests that the genus becomes monophyletic by simply excluding the African species *Ectropis elaphrodes* Fletcher, 1958 (Table 2). *Cleora* is a diverse genus distributed in the Old World tropics, with a few species reaching the Palaearctic and Nearctic regions (Holloway, 1994). However, what we know about the taxonomy of this genus is based on morphological studies from more than 50 years ago (Fletcher (1967). Our analysis, based on 7% of known *Cleora* species*,* revealed *C. repetita* Butler, 1882 as sister of *Ascotis* Hübner, 1825 (although with a weak support) and this lineage is sister to *Cleora* s. str. Our results would support the monophyly of *Cleora* if *C. repetita* were to be excluded from the genus or, taking a less conservative approach, if we synonymized *Ascotis* with *Cleora.* More data (including additional species) are required to better understand the evolutionary relationships of these closely related genera, and thus we do not propose any formal taxonomic change in this case.

The species of the genera *Ophthalmitis* Fletcher, 1979 and *Parapercnia* Wehrli, 1939 were intermixed (Fig. 1, group B). *Parapercnia* is a Palaearctic genus that currently comprises two species (Scoble and Hausmann, 2007). This genus was previously considered a subgenus of *Percnia* Guenée, 1858 but was subsequently validated at the genus level by Inoue (1992). *Parapercnia giraffata* Guenée, 1857 is the type species of the genus, which in our analysis falls nested within *Ophthalmitis*. Morphological and molecular analyses by Jiang et al. (2017) suggested a close relationship between *Ophthalmitis* and *Parapercnia* but no synonymization was proposed. We increased the taxon sampling compared to Jiang et al. (2017), and therefore, we propose synonymizing

Ophthalmitis **syn. nov.** with *Parapercnia.*

Chorodna ugandaria [Swinhoe, 1904] is nested within *Racotis* Moore, 1887 (Fig. 1, group B) with strong support (SH-Like, UFBoot2 = 100). *Chorodna* is a morphologically heterogeneous group of species occurring mainly in the Indo-Malay realm, with the type species *Chorodna erebusaria* Walker, 1860 being described from India. Therefore, it is not surprising that *Chorodna* comprises misplaced taxa, including *C. ugandaria*, which is the only African species classified in *Chorodna*. We hereby transfer *C. ugandaria* from *Chorodna* to *Racotis*, resulting in the combination *Racotis ugandaria* (Swinhoe, 1904) **comb.n.**

Unsurprisingly (see Murillo-Ramos et al. 2019), the genera *Zeuctoboarmia* Prout, 1915 and *Ematurga* Lederer, 1853 were recovered as nested within *Hypomecis*. Jiang et al. (2017) reached the same conclusion and pointed at the similarity of male genitalia between *Ematurga* and *Hypomecis*. Wahlberg et al. (2010) recovered *Ematurga* as a sister to *Hypomecis* based on more limited taxon sampling. Our results support the synonymization of these genera and we include *Ematurga* **syn. nov.** and *Zeuctoboarmia* **syn. nov.** as part of *Hypomecis*. *Hypomecis intrusilinea* Prout, 1915, *H. gonophora* Prout, 1916 and *H. gladstonei* Prout, 1922 were found to be unrelated to the rest of *Hypomecis,* and thus we propose to exclude them from the genus *Hypomecis* to *incertae sedis* within Boarmiini.

We also recovered *Iulotrichia semiumbrata* Warren, 1896 as sister to *Cusiala* Moore, 1887*,* which appears to be a strongly supported clade of morphologically similar taxa as was already noted by Holloway (1994). Merging the two genera might be desirable, but because we did not include the type species of *Iulotrichia* in our analyses, we do not propose any taxonomic change until more data become available.

Although the African genera *Colocleora* and *Geolyces* Warren, 1894 have not been considered related before, our results recovered them intermixed in two well-defined lineages (Fig. 1, group C). *Colocleora* is a species-rich genus with 69 described species, while *Geolyces* comprises 18 species. Although our findings support a close relationship between *Colocleora* and *Geolyces*, this group requires more study and a more extensive sampling effort before any taxonomic changes can be proposed.

Boarmiini remain a taxonomically challenging group. Despite substantial progress in recent studies thanks to increased taxon sampling, the classification of many genera and their phylogenetic relationships are far from being resolved. The para- and polyphyletic character of some genera and the difficulties in their phylogenetic placement reflect the current taxonomic uncertainty in major lineages. In several instances, we were not able to sample the type species, which would make the taxonomic decisions more robust.

4.2. *Divergence patterns of major Boarmiini lineages*

Boarmiines diverged from their extant sister group (Macariini + Abraxini) about 52 Mya (43–65). Our time calibration suggested older ages than those proposed by Wahlberg et al. (2010) and Kawahara et al. (2019) (ca. 34 Mya), and we propose that the diversification of the major groups of Boarmiini happened during the Oligocene. Our estimated divergence times suggest that *Cleora*, *Hypomecis* and *Alcis* started to diversify between 26 Mya and 21.3 Mya. These genera represent the most successful lineages within Boarmiini in terms of species diversity (Scoble and Hausmann, 2007). *Cleora* is diverse throughout Old World tropics and extends into temperate latitudes with a few North American and North Eurasian representatives. *Hypomecis* is a Holarctic genus with some tropical representatives and *Alcis* includes a large number of oriental species (Holloway, 1994). Most of the ecologically studied species in these genera are polyphagous (Holloway, 1994; Müller et al. 2019) which, combined with the high species diversity, do not support the hypothesis of a relationship between host specialisation and diversification of herbivorous insects (Ehrlich and Raven, 1964, Nylin and Janz 2009, Wang et al. 2017). Further ecological aspects may deserve attention: we here propose that the capital breeding strategy (=limited role of adult feeding), characteristic of most boarmiines, may have contributed to allopatric speciation. In particular, the limited mobility characteristic of capital breeding females (Davis et al. 2016, with the flightless females providing the extreme example) may have reinforced distribution barriers. Overall, however, the factors which may explain the successful diversification of these three genera, and Boarmiini in general, currently remain unknown.

As in Wahlberg et al. (2010), we found multiple independent evolutionary events toward flightless (apterous or brachypterous) females (Heppner, 1991; Sattler, 1991). However, the estimated ages of the divergence of the now flightless clades from their winged sisters are now shown to be significantly older. Flightlessness in female Lepidoptera has been found to be mostly associated with extreme environments, such as cold seasons, high altitudes, desert regions and coastal areas (Heppner, 1991), though the selective forces leading to the loss of flight ability are not unequivocally clear (Hunter, 1995; Snäll et al., 2007). Perhaps the most intuitive advantage of female flightlessness in insects is the possibility to reallocate resources from the flight apparatus to egg production (Hackman, 1966; Roff, 1986; Zera and Denno, 1997). Indeed, numerous studies have found flight ability to come at the cost of fecundity (e.g. Zera and Brink 2000, Roff and Gélinas, 2003), and/or other functions (e.g. Zera 2009; reviewed in Guerra 2011). Nevertheless, such effects may well be taxon-specific (Roff, 1995; Guerra, 2011), and Lepidoptera are not prominently represented in studies on the topic. Indeed, there is some recent evidence against the universal validity of a strong trade-off between mobility and fecundity (Tigreros and Davidowitz, 2019), leaving some space for other, perhaps also more ecologically based factors. Specifically, for forest geometrids, Snäll et al. (2007) proposed that reduced detectability for predators constitutes a major advantage of the wingless phenotype, as mortality risk strongly depends on the size of the potential prey in insects (Remmel et al., 2011), and losing wings reduces the visually perceived size of the moth by an order of magnitude. Such an effect should be particularly strong in Boarmiini, as these moths are typically broad-winged, and rest during daytime in a planiform position (Hausmann, 2001). This may explain why female flightlessness has evolved more frequently in Boarmiini than in other geometrid lineages.

Phylogenetic studies like the present one can significantly contribute to the evolutionary-ecological analysis of the female flightlessness phenomenon, both by finding the closest winged relatives of flightless moths and by estimating the ages of these transitions. As a novel contribution, this study revealed *Calamodes* as the closest winged sister group of *Agriopis*, with no convincing sister group recoveries for other Holarctic wingless genera. With the exception of *Lycia*, the timings of the separation of clades with now-wingless females from their sister groups cannot be determined with a precision greater than tens of millions of years, which makes it – given the current level of knowledge – difficult to associate this evolutionary change with the environments that gave rise to it.

4.3. *Biogeographical history and diversification patterns*

Our results suggest a Holarctic origin for boarmiines ca. 52 Mya (43–65), followed by multiple dispersal events across the former Gondwanan continent, as already proposed by Brehm et al. (2019) and Fischer et al. (2019). Our findings are further strengthened by the only fossil record of Boarmiini, *Eogeometer vadens*, which is from Europe and dates back to 44 Mya (Fischer et al., 2019). Most of the diversification events seem to have occurred during the Eocene, a period of intense geological activity and climate change. During that time, the Thulean and Beringia land bridges connected Europe and North America (Sanmartín, 2012). Furthermore, the Arabian and Eurasian plates had already collided, followed by the closure of the Tethys Ocean (Allen and Armstrong, 2008). The large islands in the western Pacific Ocean (Sundaland and Asian islands) were presumably connected, which may have allowed interchanges of early Boarmiini lineages. Similar interchanges via these land bridge connections occurred in several other lepidopteran families (Braby et al., 2005; Braby et al., 2007) and other taxonomic groups such as lizards (Vidal et al., 2008; Pyron, 2014) and birds (McCullough et al., 2019).

According to our ancestral state estimation, three dispersal events from North to South America – one in clade I and two in clade II – seem to be synchronized with the existence of GAARlandia. It has been suggested that this land was a temporary connection between the Greater Antilles and South America around 30–33 Mya (Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2006). The GAARlandia biogeographical pattern has been hypothesized and is supported in lineages such as spiders (Tong et al., 2019), scorpions (Esposito and Prendini, 2019) and butterflies (Wahlberg and Freitas, 2007; Matos-Maravi et al., 2014). Nevertheless, this hypothesis has been critically questioned by some authors who consider it played only a minor role in biotic dispersals (Ali, 2012; Fabre et al., 2014; Nieto-Blazquez et al., 2017).

Our results also suggest dispersal between the Indo-Malay and Australasian realms at the end of the Oligocene and early Miocene in clade III. Biogeographical studies have suggested that the Indo-Australasian archipelago (Lohman et al. 2011), which has undergone major geographical changes in the past and currently comprises a complex tropical region, has facilitated dispersals between the Asian and Australasian biota since the mid-Oligocene (de Jong, 2001). Our findings are consistent with biogeographical patterns in nymphalid butterflies, for example *Cethosia* Fabricius, 1807 and *Charaxes* Ochsenheimer, 1816 (Müller and Beheregay, 2010; Müller et al., 2010), and for other taxa too, such as mammals (Rowe et al., 2019), for which the Indo-Australasian archipelago has served as a stepping stone for species interchange between these two realms.

The dispersal of boarmiines between Indo-Malaysia and the Palaearctic, as well as the African plate, was also possible during the Eocene (clade IV) and the Miocene (clade III). Perhaps the most striking dispersal event is for the genus *Cleora* in clade III. Range expansion of *Cleora*, from Indo-Malaysia to Africa, occurred ca. 16 Mya, at approximately the same time that a land bridge connecting the Arabian plate and Eurasia probably existed (Portik and Papenfuss, 2015). Clades of skippers, for instance, originated in the Oriental realm with later dispersal towards Africa ca. 20 Mya in the mid-Miocene (Toussaint et al., 2019), which also supports the existence of a connection during this particular period. Other biogeographical analyses in butterflies, for example Miletinae and Nymphalidae, have also shown species interchange between Africa and Asia during the Miocene (Kaliszewska et al., 2015; Sahoo et al., 2018).

Boarmiini are the most species-rich tribe within the Geometridae, and short, deep internal branches indicate that the early diversification occurred relatively fast. Rapid early diversification followed by a decreasing rate of diversification is usually expected in cases of adaptive radiations. However, our results from BAMM analyses do not indicate that the diversification rate decreased towards the present but instead remained relatively constant. Therefore, in this regard, diversification of Boarmiini does not conform with the classical expectations of adaptive radiations.

We found, however, that the African *Cleora* diversified at a higher rate. This shift follows the dispersal event from Indo-Malaysia to Africa in our biogeographical analysis. Perhaps new ecological opportunities associated with this dispersal event triggered this fast speciation within *Cleora*. A recent study (Holm et al., 2019) found that Ugandan *Cleora* show some host-plant specialization, which makes host-plant-related diversification (Ehrlich and Raven, 1964) in a new environment a possibility worth considering. The case of African *Cleora* is hardly unique, however; further research may well reveal similar rapid within-genus radiations elsewhere in the tropics.

A high-latitude origin of Boarmiini covering the modern Palaearctic and Nearctic is supported by our biogeographical and diversification analyses. However, given the prevalent dispersal events from the Indo-Malay to the African, Australasian and Palaearctic realms, we do not discard the idea that Indo-Malaysia has been the main origin of dispersal events, similarly to Chazot et al. (2020) for the butterfly family Nymphalidae. A detailed study including more taxon sampling would be needed to test this hypothesis. Regarding the latitudinal trend, the species richness of boarmiines is not as pronounced towards the tropics as in many other insect taxa. Partly, this may be an artefact resulting from a bias in taxonomic data towards the extensively studied European fauna. However, the shallow latitudinal diversity gradient might also be the consequence of the Holarctic origin of Boarmiini, which allowed lineages to accumulate at high latitudes over a longer period than in the later-colonized tropical regions (Neotropics and Afrotropics in particular; “time-for-speciation hypothesis”) (Stephens and Wiens, 2003). Without specifically testing for this, we did not identify any clear difference in diversification rates across latitudes, which would be another hypothesis that may explain latitudinal differences in species richness (Mittelbach et al., 2007). The large number of missing taxa in our dataset is probably one of the reasons why we did not find a lot of variation in diversification rates across the tree, thereby limiting our ability to assess the relationship between biogeography and diversification. Many species await taxonomic descriptions, which will increase the known species richness at low latitudes. Further evaluation of the global patterns of boarmiine diversity and its origin will be necessary in the future in the light of better-sampled phylogenies.

5. Conclusions

This study is a significant contribution towards understanding the rich diversity of the globally distributed Boarmiini. The results presented here suggest that boarmiines have undergone intercontinental dispersal and successfully diversified. Despite remarkable progress in establishing the evolutionary history of Geometridae and the availability of large phylogenetic datasets, poor information about the ecology and diversity of geometrid moths, mainly in tropical clades, strongly limits our understanding of the historical processes and potential key innovations that underlie the successful diversification of Boarmiines. A particular question that calls for more ecological data is the degree of host plant specialisation which should provide insights with respect to the role of host plant shifts as drivers of insect diversification. Nevertheless, our results form a starting point for future investigations on the peculiar latitudinal diversity gradient of Boarmiini and on potentially key groups (such as the genus *Cleora*) that could explain the initial burst and continued diversification of boarmiine moths overall.

CRediT authorship contribution statement

Leidys Murillo-Ramos: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Nicolas Chazot:** Conceptualization, Methodology, Formal analysis, Writing - review & editing. **Pasi Sihvonen:** Investigation, Resources, Writing - review & editing. **Erki Õunap:** Conceptualization, Investigation, Resources, Data curation, Writing - review & editing. **Nan Jiang:** Investigation, Resources, Writing - review & editing. **Hongxiang Han:** Investigation, Resources. **John T. Clarke:** Investigation, Resources, Writing - review & editing. **Robert B. Davis:** Investigation, Resources, Writing - review & editing. **Toomas Tammaru:** Conceptualization, Resources, Writing - review & editing. **Niklas Wahlberg:** Conceptualization, Resources, Writing - review & editing, Supervision, Funding acquisition.

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Appendix A. Supplementary data

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