Molecular phylogenetics, phylogenomics, and phylogeography

Phylogenetic systematics, diversification, and biogeography of Cerurinae (Lepidoptera: Notodontidae) and a description of a new genus

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We present the first dated molecular phylogeny of the Cerurinae moths (Notodontidae), based on sequence data for 666 loci generated by anchored hybrid enrichment. Monophyly of Cerurinae is corroborated, which includes the following genera: Pararethona Janse, Pseudorethona Janse, Oreocerura Kiriakoff, stat. rev., Cerurella Kiriakoff, Notocerura Kiriakoff, Hampsonita Kiriakoff, Afrocerura Kiriakoff, Cerurina Kiriakoff, Neoharpyia Daniel, Furcula Lamarck, Neocerura Matsumura, Americerura St Laurent and Goldstein, gen. nov., Cerura Schrank, and Kamalía Koçak & Kemal. The type species of the Neotropical genus Tecmessa Burmeister, T. annulipes (Berg), which had been incorrectly assigned to Cerurinae, is recovered in Heterocampinae; and Americerura gen. nov. is proposed to receive 17 unambiguously cerurine species transferred from Tecmessa. Divergence time estimates recover a crown age of Notodontidae roughly coincident with the K-Pg boundary, and a late-Oligocene crown age for Cerurinae. An African origin is inferred for Cerurinae, followed by colonization of the Palearctic, the Americas, Indomalaya, and Australasia during the Miocene. At least three independent colonizations of the Americas are inferred, one in the mid-Miocene associated with ancestral Americerura gen. nov. and two in the Pliocene and Pleistocene within Furcula. We hypothesize that the global spread of Cerurinae was enabled by that of its primary caterpillar foodplants in the Salicaceae. State-dependent diversification analyses suggest that cerurines diversified most rapidly in temperate climates.

Key words: Africa, Salicaceae, temperate, tropical

Introduction

The Prominent Moths (Lepidoptera: Notodontidae) are one of the most diverse families of large moths and are found on every continent except Antarctica in habitats ranging from Arctic tundra to deserts and tropical rainforests (Miller 1991, Kitching and Rawlins 1998, Schintlmeister 2008). The family includes over 4,000 recognized species and more names are being proposed each year (Schintlmeister 2013, Becker 2014). Notodontid caterpillars eat a wide range of woody and herbaceous plants, with well-documented radiations associated with willows and poplars (Salicaceae), walnuts (Juglandaceae), passion vines (Passifloraceae), Inga Willd. (Fabaceae), and grasses (Poaceae) (Schintlmeister 2008, Miller 2009, Miller et al. 2018). Caterpillars of some species are regarded as agricultural pests, and others as human food sources (Gschloessl et al. 2018, Mabossy-Mobouna et al. 2022).

Notodontid caterpillars have complex ornaments, varied colors, and otherwise highly irregular structures and forms. They also have complex behaviors and life history strategies, including spectacular displays of crypsis and aposematism, as well as solitary and gregarious startle displays and silken tent building behaviors (Miller et al. 2018). Most have modified anal prolegs, which may be nonfunctional or exceptionally hypertrophied to form...
extendable whip-like projections called stemapods, which are perhaps best exemplified by the Cerurinae (Fig. 1). Considering their diversity, widespread distribution, and fascinating life histories, Notodontidae have been the focus of much research since the dawn of lepidopterology. In the past four decades, a particular focus has been understanding their evolutionary history and phylogenetic placement within the Noctuoidea, the most diverse Lepidoptera superfamily.

Notodontidae have long been recognized as belonging to Noctuoidea on the basis of morphology (Packard 1895, Forbes 1923), and recent phylogenetic efforts have robustly supported this placement (Zahiri et al. 2011, Kawahara and Breinholt 2014, Timmermans et al. 2014, Heikkilä et al. 2015, Regier et al. 2017, Kawahara et al. 2019). Notodontid classification has largely followed Miller's (1991, 1992) phylogenetic analysis of adult, pupal, and larval morphological characters, and recent molecular efforts have either had insufficient taxon sampling (Regier et al. 2017) or deficient molecular coverage (Kobayashi and Nonaka 2016) to resolve relationships within the group. No single notodontid classification assigns all genera to established subfamilies. Ongoing phylogenomic efforts, including the present study, use more expansive genome-wide molecular sampling to address key issues in the higher classification of this family.

A particular impediment to Notodontidae research, apart from the lack of a robust higher classification, is the lack of studies with worldwide coverage. Most monographs are regionally focused, albeit comprehensive in their respective geographic areas (Schintlmeister 2008, 2019, 2020, 2022; Miller et al. 2018, 2021). The only subfamily to be reviewed and fully revised on a global scale is the New World endemic Dioptinae (Miller 2008, 2009). The subfamily Nystaleinae has been reviewed (Weller 1992). Neither of these subfamilies are endemic to the Americas, and this precludes their utility for understanding global biogeographic questions, for example. Since many currently recognized subfamilies occur globally (Miller et al. 2018), their systematics are highly provisional. Fortunately, however, the described global diversity of taxa has been cataloged (Schintlmeister 2013, Becker 2014).

Thus far, no study has attempted to infer a molecular phylogeny of an entire subfamily or any other major higher-level clade in the Notodontidae. Because of high notodontid species richness and the lack of a family-wide monograph or well-supported phylogeny, it is difficult to work towards a sound understanding of the biogeography, evolution, or diversity of Notodontidae. While no study has yet tackled the global biogeography of the Notodontidae, Schintlmeister (1989, 2008) studied the biogeography of Notodontidae in the Old World, principally the Palearctic fauna, using the zoogeological categories paradigm of de Lattin (1967). So far, contemporary statistical frameworks using comparative phylogenetics have not been used to study notodontid biogeography.

To understand global patterns of Notodontidae biogeography, we focus on the Cerurinae, a charismatic group of notodontids, best known for their photogenic caterpillars, which have whip-like ‘tails’ (modified anal prolegs) and false thoracic ‘faces’ used to startle predators (Fig. 1). Caterpillars of at least one species are even capable of spraying formic acid from their thorax as a defense mechanism (Poulton 1887). Adult cerurines are also intriguing, with their densely scaled bodies earning them the European common names ‘puss moths’ (Cerura spp.) and ‘kittens’ (Furcula spp.). The subfamily Cerurinae (96 species and 51 subspecies) is globally distributed and is perhaps the most taxonomically stable group among Notodontidae at the species level. The Eurasian genera, including the

Fig. 1. Examples of Cerurinae larvae from nine of the 14 genera: A, Pseudorethona albicans (photo H. Staude); B, Notocerura spiritalis (photo S. Woodhall); C, Hampsonia esmeralda (photo H. Staude); D, Cerurina marshalli (photo L. Mulvaney); E, Furcula furcula (photo W. Bacher); F, Neocerura liturata (photo R. Tawade); G, Americerura scitiscripta (photo R. St Laurent); H, Cerura vinula (photo L. Jonaitis); I, Kamalia australis (photo C. & T. Deane).
most diverse Old World genera Tyncula Lamarck, 1816 and Cerura Schrank, 1802 were treated in Schintlmeister (2008). The most diverse tropical Asian genus, Kamiiaa Koak and Kemaal, 2006, was treated in Schintlmeister (2002, 2008, 2020). The majority of African taxa were reviewed in Schintlmeister and Witt (2015). Finally, the North American fauna was fully reviewed by Miller et al. (2018, 2021). Only Neotropical taxa have yet to be revised, although they have been cataloged (Schintlmeister 2013, Becker 2014). Although Cerurinae are relatively well understood, no single taxonomic effort has treated all species together or conclusively presents evidence that all genera currently placed in Cerurinae belong to this subfamily.

One possible reason for the lack of a uniform taxonomic treatment of Cerurinae may be the fact that taxonomy of the group has traditionally been based on adult morphology, with larval morphology—which contains the single most defining suite of characters for the subfamily—largely absent from taxonomic treatments. Despite this, the original description of Ceruridae (≡Cerurinae) by Butler (1881) was based on caterpillars, which Butler stated ‘...are broad in front, with a distinct angle or hump at the fourth segment, fourteen legs and a forked pair of projecting tails, from which, when annoyed, bright-colored filaments are exerted.’ Since the time of Butler, the treatment of Cerurinae as a family group taxon has differed. Members of Cerurinae have either been included in their own subfamily (Schintlmeister 2008, Becker 2014, Regier et al. 2017, Miller et al. 2018) or recognized as a closely related group of genera that belonged within a more broadly conceptualized Notodontinae: Dicranurini, a concept that includes many non-cerurine genera (Miller 1991, Kobayashi and Nonaka 2016). Some authors have treated this tribal name as a subfamily, Dicranurini (Schintlmeister 2008, 2020, Schintlmeister and Witt 2015).

Recent phylogenetic efforts that either support the status of Cerurinae as a valid subfamily (Regier et al. 2017) or as nested within Notodontinae (Kobayashi and Nonaka 2016) differ greatly in the amount of genetic data used. Regier et al.’s (2017) analysis was more inclusive, using 5–19 genes, whereas Kobayashi and Nonaka (2016) only used one (short) ribosomal gene and one mitochondrial gene. Most recently however, the concept of Cerurinae as a distinct lineage within the Notodontidae has gained traction, mainly following the subfamily arrangement of Schintlmeister (2008, 2013) and a subfamily diagnosis and treatment later given in Miller et al. (2018). Despite these works, monophyly of Cerurinae has not been adequately tested in a phylogenetic context.

Life histories of Cerurinae have received a fair amount of attention in the literature, with caterpillar food plant information documented for all but one genus. Nearly all Cerurinae feed on Salicaceae, and studying these moths presents an opportunity to examine the evolution and biogeography of a globally distributed lepidopteran clade with conserved food plant associations. The relationship of Cerurinae with Salicaceae is noteworthy because these plants are toxified by these compounds (Feistel et al. 2018). Ehrlich and Raven (1964) introduced coevolutionary theory based on Lepidoptera and their food plants, and fostered the idea that food plant specialization and shifts have frequently acted as mediators of the diversification of Lepidoptera (Powell et al. 1998). Less attention, however, has been given to the impact of monophagy and oligophagy on diversification. Salicaceae are believed to have undergone a number of radiations and, importantly, to have spread globally since the Paleocene and Eocene, thereby forming a pathway for the global dispersal of lepidopterans that specialize on these plants, such as Cerurina (de Mestier et al. 2022, Wang et al. 2022). As with Salicaceae, cerurines display a distributional pattern of species richness that does not conform to a common pattern predicted by the Latitudinal Diversity Gradient (LDG) (Fischer 1960, Pianka 1966), in that the majority of named species are found in the Northern Hemisphere in temperate climates (Miller et al. 2018). Because of the close relationship of Cerurinae with Salicaceae, the highlighted chemical defenses of these plants, and their global distribution that contradicts the LDG, we consider Cerurinae relevant in the continued effort to understand the elements governing the distribution of biodiversity on the planet and how Lepidoptera became one of the most successful radiations of herbivores.

The primary aims of the present study are (i) to provide the first phylogenetic hypothesis for Cerurinae, (ii) establish its composition, (iii) test its monophyly and that of its component genera, and (iv) infer a dated biogeographic hypothesis to account for the group’s distribution. We also explore the impacts of latitude on the diversification of Cerurinae and the potential role of Salicaceae in permitting the global spread of cerurines. Finally, we consolidate the long taxonomic history of cerurines in a checklist.

Material and Methods
Taxon Sampling and Terminology
Sequences in this study were published/publicly available (Wellcome Sanger Institute 2022) or generated de novo from specimens in the following collections: American Museum of Natural History, New York, NY, USA (AMNH); African Natural History Research Trust, Leominster, UK (ANHRT); Carnegie Museum of Natural History, Pittsburgh, PA, USA (CMNH); collection of Hermann Staude, South Africa (HS); McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL, USA (MGCL); National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM).

Identifications were made using the literature (Schintlmeister 2002, 2008, 2016, 2020; Schintlmeister and Witt 2015; Miller et al. 2018) and expertly curated collections in MGCL and USNM. Morphological terminology follows Miller (1991) and Miller et al. (2018). Cerurinae taxonomy follows Becker (2014), Miller et al. (2018), Schintlmeister (2013), and Schintlmeister and Witt (2015), as well as some taxonomic changes made in the present study. For outgroups we broadly follow the aforementioned references and some changes proposed by Kobayashi and Nonaka (2016). The identifications of caterpillars of Tecmesa annulipes (Berg, 1878) and T. elegans Schaus, 1901, which we figure for the first time, with color photos are based on inflated caterpillars and images curated in the Natural History Museum, London, U.K. (NHMUK), which were examined by the first author.

Sampled taxa include all 14 Cerurinae genera and 53 of the species/subspecies that we recognize based on a combination of taxonomic sources (including some unnamed taxa) (Table S1). To root the tree and determine the placement of Cerurinae, all other Notodontidae subfamilies sensu Miller et al. (2018), except Scranciniinae, are sequenced, using type genera whenever possible. Complete taxon samplings of the ingroup and outgroups are listed in Table S2.

In addition to some taxonomic changes that we make in the Results below, our treatments of Cerurina Kiriakoff, 1963 and the subspecies of Cerura erminea (Esper, 1783) differ from those of Mulvaney (2021) and Schintlmeister (2008) respectively. We treat Cerurina as monotypic with two subspecies C. marshalli marshalli (Hampson, 1910) and C. marshalli argentata (Gaede, 1934) based
on ongoing research (Mulvaney et al., unpubl. data). The East Palearctic/Indomalayan Cerura menciana Moore, 1877 is treated as a valid species with subspecies C. e. formosana (Matsumura, 1929) and C. e. birmanica (Bryk, 1949). In recent literature C. menciana is confusingly treated as either a subspecies of C. erminea (Schintlmeister 2008) or as a valid species (Dai et al., 2015), but based on morphology and biogeography, we consider these distinct species. The Asian taxa formosana and birmanica are therefore treated as subspecies of C. menciana based on morphological similarities if the name menciana is given specific status, as in the present paper.

Molecular Data
This study includes phylogenomic data derived from (i) newly generated anchored hybrid enrichment (AHE; Lemmon et al. 2012) sequences using the Lep1 probe set (up to 855 highly conserved genomic loci) described in Breinholt et al. (2018) and (ii) publicly available transcriptomes and genomes of Cerurinae, Notodontidae outgroups, and non-Notodontidae outgroups. For our dating analyses we include outgroups from Kawahara et al. (2019) since this was also the source of secondary calibrations (see Divergence time estimation below).

Newly generated AHE data were compiled in the same manner as numerous recent Lepidoptera studies (St Laurent et al., 2018, 2020; Homziak et al. 2019). While various methods of DNA extraction have been used for previous AHE studies, we extracted DNA from all samples for the present article by soaking abdomens (with one to three legs for some samples) in a 1:50 solution of proteinase K and lysis buffer for ~18 h. An adapted OmniPrep DNA extraction protocol (G-Biosciences, St. Louis, MO) was used as described in Hamilton et al. (2019). Library preparation and sequencing were conducted by Rapid Genomics (Gainesville, FL, USA). The bioinformatic pipeline for AHE locus-trimming, assembly, and ortholog selection follows Breinholt et al. (2018). In summary, raw reads were filtered with trimgalore! v.0.4.0 (bioinformatics.babraham.ac.uk), and assembled using a custom iterative baited assembly python script, which employs USEARCH (Edgar 2010) and BridgeR (Chang et al. 2015). Assembled AHE loci were aligned with MAFFT version 7.407 (Katoh and Standley 2013), and consensus sequences were built in FASconCAT-G version 1.02 (Kuck and Longo 2014), which was also used for concatenation. The only modification to this process was that MAFFT alignment also included the ‘--adjuredirectionaccurately’ command to permit alignment of reverse complimented sequences. Transcriptomes were assembled as above to ensure seamless combination with the AHE dataset. The genomes, however, proved too data-rich to assemble to the AHE loci using the IBA process, and therefore the ‘genome_getprobe_BLAST.py’ script from Breinholt et al. (2018) was used to extract the AHE probe regions from the available genome assemblies, downloaded as complete chromosome assemblies from The European Nucleotide Archive (ENA) and made available by the Darwin Tree of Life project (Wellcome Sanger Institute 2022). AHE assembly was carried out on the University of Florida’s HiPerGator High Performance Computing Cluster. FigTree v. 1.4.4 was used for phylogenetic tree visualization (Rambaut and Drummond 2009).

Phylogenetics
We base our results on a maximum likelihood (ML) phylogeny inferred in IQ-TREE version 2.1.2, but see below for alternative tree inference analyses that we also performed (Nguyen et al., Minh et al. 2020). Using our concatenated dataset of 666 AHE loci, we performed 100 independent IQ-TREE analyses. In all analyses, 1,000 Ultrafast Bootstrap (UFBoot) and 1,000 Shimodaira-Hasegawa approximate likelihood ratio test (SH-aLRT) replicates were calculated for support values (Minh et al., 2013, Hoang et al. 2018a) and the command ‘-m TESTNEWMERGEONLY’ which employs ModelFinder to identify the best partitioning scheme and model of nucleotide evolution of our 1,998 a priori (666 loci, each split into codon position) locus partitions (Kalyaanamooorthy et al. 2017). The a priori partitions were consolidated into 128 by ModelFinder. All partitioning schemes and selected best fit models of nucleotide evolution are available on Dryad along with raw sequencing reads (St Laurent et al. 2023). The best tree of the 100 independent runs was selected according to likelihood value. A ‘robustly supported’ clade, as per IQ-TREE documentation, is defined as having UFBoot ≥ 95 and SH-aLRT ≥ 80; a clade is considered ‘moderately supported’ with UFBoot ≥ 95 or SH-aLRT ≥ 80.

To test the robustness of our dataset with other tree inference methods, we performed a multiparts coalescent (MSC) analysis with ASTRAL v. 5.7.8 (Zhang et al. 2017). Individual gene trees were inferred with IQ-TREE (unpartitioned) as above and ASTRAL was used to infer a consensus tree considering the multispecies coalescent. Branch support is expressed as posterior probability ASTRAL support values (ASV), with values >0.95 considered to be evidence of robust support. Finally, we employed MPBoot, a fast parsimony method, on our concatenated supermatrix of 666 loci, with 1,000 MPBoot bootstrap replicates (Hoang et al. 2018b).

All post-assembly analyses, except ASTRAL and MPBoot, which were performed locally on a MacBook Pro (macOS Catalina), were carried out on the Smithsonian Institution High Performance Computing Cluster, Smithsonian Institution (https://doi.org/10.25572/SIHPC) or the University of Florida’s HiPerGator High Performance Computing Cluster. FigTree v. 1.4.4 was used for phylogenetic tree visualization (Rambaut and Drummond 2009).

Divergence Time Estimation
Due to difficulties in inferring divergence times with large genomic datasets, we performed ML analyses that could accommodate large datasets of hundreds of loci at once. For more traditional, computationally intensive Bayesian dating approaches, we subsampled our dataset, reducing the number of loci used in downstream analyses (Jarvis et al. 2014, Misol et al. 2014, Prum et al. 2015, Smith et al. 2018, Kawahara et al. 2019, St Laurent et al. 2021). Regardless of the analysis employed, we used nine secondary calibrations derived from Kawahara et al. (2019), the most comprehensively fossil-calibrated chronogram of Lepidoptera. Dates were assigned to the following nodes: (i) The most recent common ancestor (MRCA) of the pyraloid Galleria (Fabricius) + Macrolepiotera, (ii) crown of Mimmalonoidea, (iii) Mimmalonoidea + remaining Macrolepiotera, (iv) crown of Drepanoidea, (v) crown of Bombycoidea + Lasiocampioidea, (vi) crown of Geometroidea, (vii) an internal Noctuoidea node (MRCA of noctuid Helicoverpa Hardwick + noldi Manduca Hampson), (viii) the Notodontidae root, and (ix) an internal Notodontidae node (MRCA of Phoeis Hübner + Nototilus Schaus). The uniform prior dates, based on the 95% confidence intervals in Kawahara et al. (2019) are shown in Table S3.
Our maximum likelihood dating approach used the program TreePL (Smith and O'Meara 2012). TreePL provides a single tree with single dates for each node as output, and therefore does not permit the calculation of confidence intervals at the nodes. To infer a range of dates for all nodes, we used a custom set of Python scripts that enabled us to independently run TreePL many times, permitting a summary of all analyses in the form of a maximum clade credibility (MCC) tree with date intervals at all nodes. This method was recently used by St Laurent et al. (2021) and in summary, uses RAxML (Stamatakis 2006) to generate 100 bootstrap replicates from a supermatrix (which in this case is our 666-locus dataset, partitioned as above), and then uses these bootstrap replicates to infer branch lengths on a user-supplied tree that lacked branch lengths. The user-supplied tree was our best-of-100 (highest likelihood) 666-locus (128 partitions) IQ-TREE output. The 100 resulting RAxML trees, which by design are identical in topology, with only branch lengths allowed to vary, were then input into 100 independent TreePL analyses. The custom Python scripts allowed parameters to be optimized using the ‘prime’ command of TreePL and we performed a randomly sampled cross-validation analysis to determine the best smoothing parameter for downstream TreePL analyses. The cross-validation step was run three times, allowing the smoothing parameter to vary to check for consistency across each run. All analyses were run using the ‘thorough’ command of TreePL. The 100 resultant trees dated by TreePL were summarized with TreeAnnotator v. 1.10.4 in the BEAST v. 1.10.4 package (Drummond et al. 2012, Suchard et al. 2018), in an MCC tree with divergence time intervals at each node. These intervals are not confidence intervals calculated over a posterior distribution, but instead are the range of dates recovered for each node across 100 independent TreePL analyses. Our Bayesian approach used the methodology recently employed by St Laurent et al. (2021), which uses SortaDate (Smith et al. 2018) to select AHE loci best suited for divergence time estimation according to the following criteria: (i) clock-like evolution; (ii) maximizing tree length; and (iii) least topological conflict with a pre-defined species-tree. As in St Laurent et al. (2021), we prioritized the parameters 3-1-2 in that order since we used a constrained tree topology and the previous study found little impact when changing the order of parameter priority if up to 75 loci were selected. The best species tree according to likelihood among 100 independent IQ-TREE runs based on the full, 666-locus AHE dataset, partitioned as described above, was used as the constraint tree for testing criterion 3. Upon identifying the 75 loci for divergence time estimation, we ran ModelFinder in IQ-TREE as above to identify the best consoliated partitioning scheme and models of nucleotide evolution from the 75 a priori locus partitions, resulting in 15 new partitions. However, for this step we restricted models to those available in BEAST (Drummond et al. 2012, Suchard et al. 2018) since that program would be used for dating. We then carried out 100 independent IQ-TREE runs, as above, on a concatenated supermatrix of the 75 loci partitioned in the 15 partitions to ensure that the topology of the subset of data did not conflict with the full 666-locus dataset. The resulting topology was effectively identical to our 666-locus dataset (Fig. S2).  SortaDate then tests each locus independently for criteria 1 and 2 using gene trees, which we inferred using an unpartitioned alignment in IQ-TREE, and criterion 3 against the full data species tree, to check for topological conflict. The ‘pxrr’ command in Phyx (Brown et al. 2017) was used to root all gene trees to the Pyraloidea outgroup. Twenty-four loci that were not represented in the Pyraloidea outgroup were excluded.

For the Bayesian analysis with BEAST, using our 75-locus dataset, we performed six sets of molecular clock/tree prior combinations: (i) one molecular clock, Yule; (ii) one molecular clock, Birth-death; (iii) three molecular clocks (one per codon position), Yule; (iv) three molecular clocks, Birth-death; (v) 15 molecular clocks (one per partition), Yule; and (vi) 15 molecular clocks, Birth-death. Path sampling and steppingstone marginal likelihood estimations (MLE) were calculated for all analyses and Bayes factors (Table S4) were used to identify the best clock/tree prior pair for use in downstream analyses. For each of these combinations, three separate runs of 200 million generations each were performed to confirm each run ran to convergence, with all 600 million runs per analysis combined with LogCombiner and TreeAnnotator (to generate the MCC tree). We confirmed all effective sample size (ESS) values were above 200 for all parameters across all analyses in Tracer v. 1.7.0 (Rambaut et al. 2018). Only one statistic, ‘(tmrca(Mimallonoidea))’, was found to be below 200 in some analyses, but this particular lineage presents difficulty in dating analyses because of the extremely long branch subtending the Mimallonoidea (St Laurent et al. 2021). Although both the BEAST MCC and TreePL trees resulted in similar divergence time estimates (see Results), for simplicity, we use the best BEAST MCC tree for all downstream analyses and related discussion.

Biogeography
We inferred the geographic origin for the Cerurinae using ancestral range reconstruction and calibrated the direction and relative timing of colonization. Considering the presence of two distantly related cerurine genera in the Americas, we hypothesize at least two invasions of the Americas from the Old World and sought to test this with our biogeographic reconstructions. Specimen distribution data were gathered by the first author from the Cornell University Insect Collection, Ithaca (CUIC), the MGCIL, the NHMUK, and the USNM. Additional data were provided from the ANHRT, Collection Pe. Jesus S. Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil (DZUP); the collection of Tim McCabe, Albany, New York, USA (TM), and the Vitor Becker Collection, Camaçá, Brazil (VOB). Literature resources, particularly those that included distribution maps (Schintlmeister 2002, 2008, 2020; Schintlmeister and Witt 2015; Miller et al. 2018), were consulted, as well as the current maps on iNaturalist.org with Cerurinae sightings continuously curated by the first author (iNaturalist 2022).

Since Cerurinae are found on all continents except Antarctica, we partitioned the globe into seven biogeographic regions, following Kawahara et al. (2022) who investigated the biogeography of butterflies, which have a global distribution similar to that of Notodontidae. The regions are shown in Fig. 3, and include Nearctic (R), Neotropical (N), East Palearctic (E), West Palearctic (W), Africa (A), Indomalaya (I), and Australasia (U). The delimitation of the biogeographic regions in Kawahara et al. (2022) was used here as well, and we coded all cerurine species in our tree according to those regions. However, Neocerura littorata (Walker, 1855) was treated as exclusively Indomalayan since only one record in Schintlmeister (2008) was from the Indomalayan-East Palearctic boundary. This species is not generally considered Palearctic in distribution [based on recent observations from (iNaturalist 2022)]. The compcated taxon F. furcula (Clerck, 1759) is coded as occurring in both the East and West Palearctic. The single representative of F. furcula is from the United Kingdom where the West Palearctic subspecies F. f. furcula is present, but the complex taxonomic history and uncertain validity of some subspecies, which range across the Palearctic results in our treating this taxon as more widespread for biogeographic reconstruction purposes.
For ancestral range reconstruction we used the ML methods implemented in BioGeoBEARS v. 1.1.2, specifically the Dispersal Extinction Cladogenesis (DEC) and Likelihood equivalent of the Dispersal-Vicariance model (DIVALIKE) (Matzke 2013). These analyses were run either unconstrained (no adjacency nor dispersal multiplier matrices) or constrained (with both adjacency and dispersal multiplier matrices) to compare results, though all analyses were stratified across four time periods (0.1, 5.33, 23.03, and 31.38 Ma). The matrices and time slices were adapted from Kawahara et al. (2022) with the oldest time slice reflecting the crown age of Cerurinae. The maximum range size, which is defined as the number of areas any single species is allowed to occupy, was set to two because higher values resulted in an inability to infer ancestral ranges at most nodes.

We also performed time-stratified Bayesian biogeographic analyses in RevBayes (Hohna et al. 2016). We adapted the RevBayes code employed by Thode et al. (2019) which incorporates adjacency matrices into the dispersal rate matrix (as opposed to a distance scaling factor), in some ways resembling our BioGeoBEARS analyses with adjacency matrices. The Markov chain Monte Carlo (MCMC) chain was set to 100,000 and maximum areas set to two as for BioGeoBEARS. A burnin of 25% was set before generating the MCC tree from RevBayes. Our RevBayes inputs are available on Dryad with the specific Rev code from Thode et al. (2019) available at that source.

Food Plants and Latitude
We conducted an ancestral state reconstruction (ASR) of food plants (here the term ‘food plants’ refer to plants fed upon by caterpillars in nature) using SIMMAP in the R v. 3 package phytools with the symmetrical (‘SYM’) model and 10,000 simulations (Bollback 2006, Revell 2011, R Core Team 2020). Food plant data were compiled from various published and online sources and are presented together for the first time (Table S5). SIMMAP incorporates multiple states (in case of polyphagous species) per tip by the user assigning equal prior probabilities to each of the known food plants. The majority of cerurines feed on Salicaceae (Table S5), but a few are polyphagous on Salicaceae and other plants in nature, or feed only on non-Salicaceae plants. Thus, states were assigned for the following plant families for which there are unambiguous Cerurinae feeding records: Salicaceae, Burseraceae, Rosaceae, Betulaceae, Fagaceae, Proteaceae, Malvaceae, Rutaceae, and Combretaceae; prior tip states are found in Table S6. This ASR was intended simply to illustrate the conserved nature of this association across the tree and test the hypothesis that Cerurinae fed on Salicaceae ancestrally.

Because Cerurinae reach their highest species richness in temperate climates (~60% of named cerurine taxa occur in temperate regions), we sought to examine whether environmental variables impacted cerurine diversification rates. We approached this question from the perspective of present day temperate vs. tropical distributions using the Geographic State Speciation and Extinction Model (GeoSSE) with the R packages hisse and diversitree (Goldberg et al. 2011, FitzJohn 2012, Beaulieu and O’Meara 2016, Caetano et al. 2018). Taxa may be considered habitat temperature-limited, occurring in either temperate or tropical regions, or widespread, occurring in both. Taxa were assigned a ‘temperate’ state (i) if they inhabit Nearctic, East or West Palearctic biogeographic regions, and a ‘tropical’ state (ii) if they inhabit the Neotropics, Africa, Indomalaya, or Australasia. Taxa inhabiting both a temperate and tropical biogeographic region were treated as ‘both’ (0). In Southern Hemisphere taxa that could be considered temperate (e.g., that range into southern South Africa) we alternatively coded them as ‘both’ instead of ‘tropical’ to test whether this impacted model selection. We tested five models with GeoSSE: (i) dispersal parameters free to vary, with no range-dependent diversification; (ii) a so-called ‘canonical GeoSSE’ model with a range effect on diversification; (iii) a hidden-state GeoSSE (GeoHiSSE) model that includes one hidden trait and no range-dependent diversification; (iv) a GeoHiSSE model with one hidden trait, and range-dependent diversification; (v) and a Multi-state Speciation and Extinction-like Model (MuSSE) with no hidden trait and no cladogenetic effects, but anagenetic changes allowed. For model 5, anagenetic change refers to changes along the branches rather than during cladogenesis. Habitat-temperature specialization, therefore, is not explicitly linked to speciation events (cladogenesis), but potentially to extirpation of widespread species (Goldberg et al. 2011). The best fit model was determined with Akaike information criterion (AIC), corrected AIC (AICc), and AIC weight. GeoSSE requires a sampling fraction of taxa in the tree from each of three states to correct for incomplete sampling from each region. We determined these fractions to be 33% of temperate cerurines are present in our study, 51% of tropical species are present in our study, and 33% of cerurines that inhabit both types of environments are present in our study. Our GeoSSE code is available on Dryad. Table S1 presents temperate/tropical assignments for all cerurine species and subspecies, including those not in our trees.

Nomenclature
This paper and the nomenclatural act(s) it contains have been registered in ZooBank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. LSID: urn:lsid:zoobank.org:pub:26CDD49C-BB73-415D-8DC4-C1623936B9CB.

Results
Monophyly of Cerurinae
All phylogenetic analyses support monophyly of Cerurinae (notwithstanding the erroneous assignment of some American cerurine taxa to Tecmessa Burmeister, 1878; see below). Although family-wide systemsatics are not addressed pending ongoing sequencing efforts, we provide a basic subfamilial backbone of Notodontidae to determine the monophyly of Cerurinae and to improve the accuracy of divergence time calibration. The summary of the current backbone phylogeny of Notodontidae, including the placement of Cerurinae, based on our ML results is shown in Fig. 4. Figs. S1–4 show Notodontidae relationships from a variety of phylogenetic inference methods.

Based on our phylogenetic results, Cerurinae are not nested within Notodontinae, but are sister to two genera usually associated with Dicranurinae: Shachia Matsumura and Liparopsis Hampson (Schintlmeister 2020). Hartypia Ochsenheimer, another genus often assigned to Dicranurinae, is then sister to ([Liparopsis, Shachia, Cerurinae]). Because we include the type genera (using type species of those genera) of Cerurinae (Cerura) and Notodontinae (Notodonta Ochsenheimer), the separation of the two subfamilies is unequivocal, rejecting the arrangement of Notodontinae with tribe Dicranurini containing cerurine genera, as in Kobayashi and Nonaka (2016). Based on results presented here, Dicranurinae as it is currently understood is polyphyletic. Ongoing phylogenomic research including all subfamilies of Notodontidae and Dicranurinae Reichenbach (type genus of Dicranurinae) indicates that the true concept of Dicranurinae excludes all genera currently assigned to that subfamily except Dicranura due to the placement of that genus sister to nearly all other Notodontidae subfamilies (St Laurent et al.
in prep.). Future work will establish new subfamily or tribal level taxa for the clades including Hartypia, Shachia, and Liparopsis.

The same relationship of Cerurinae to the aforementioned Dicranurinae s.l. genera is also recovered with the parsimony analysis in MPBoot (Fig. S4). And while our ASTRAL analysis recovers a nearly identical topology for the ingroup (the placement of the clade containing Oreocerura Kiriakoff, 1963, stat. rev. + Cerurilla Kiriakoff, 1962 shifts, however) with robust bootstrap support for its monophyly (Fig. S3), the relationship of Cerurinae to Shachia and Liparopsis is much less well-supported (ASV = 0.59 for [Cerurinae, Shachia, Liparopsis]).

An important issue highlighted by our results is that the genus Tecmessa, which was assigned to Cerurinae by Schintlmeister (2013) and retained there by Becker (2014) and Miller et al. (2018), is polyphyletic, with representatives appearing in both Cerurinae and Heterocampinae in all phylogenetic analyses (Figs. S1–4). Importantly, the type species of Tecmessa, T. annulipes (Berg, 1878), does not fall within Cerurinae, but within Heterocampinae, and displays at least one apomorphy (albeit in a reduced form) of that subfamily: a tuft of elongated scales that extend below the head, termed a ‘beard tuft’ by Miller et al. (2018). Therefore, a new genus is proposed below to remedy the issue of polyphyly of Tecmessa and, by extension, Cerurinae.

In summary, the recognized genera of Cerurinae are (in order displayed in Fig. 2): Paratetraphana Janse, 1920 (Figs. 1A, 2A, 5A, 6A, 7A), Pseudotetraphana Janse, 1920 (Figs. 1A, 2B, 5B, 6B, 7B), Oreocerura stat. rev. (Figs. 2D, 5C, 6D, 7D), Cerurilla (Figs. 2C, 5D, 6C, 7C), Notocerura Kiriakoff, 1963 (Figs. 1B, 2E, 5E, 6E, 7E), Hampsponita Kiriakoff, 1963 (Figs. 1C, 2F, 5F, 6F, 7F), Cerurina (Figs. 1D, 2G, 5G, 6G, 7G), Afrocerura Kiriakoff, 1963 (Figs. 2H, 5J, 6J, 7H), Neoharpyia Daniel, 1965 (Figs. 2I, 5G, 6I, 7I), Furcula (Figs. 1E, 2J, 5F, 6H, 7J), Neocerura Matsumura, 1929 (Figs. 1F, 2K, 5K, 6K, 7K), Americerura gen. nov. (Figs. 1G, 2L, 5M, 6N, 7L, 11–14), Kamalila (Figs. 1L, 2M, 5L, 6L, 7M), and Cerura (Figs. 1H, 2N, 5N, 6M, 7N). The monophyly of each of these 14 genera is robustly supported with bootstrap values across all analyses (Fig. 2, Figs. S1–4).

For discussion purposes we refer to the clade containing African genera Notocerura, Hampsponita, Afrocerura, and Cerurina as ‘Clade A’, which is sister to ‘Clade B’; Furcula, Neoharpyia and ‘Clade C’; Neocerura, Americerura gen. nov., Cerurina, and Kamalila. These clades are denoted in Fig. 2.

In general, species-level taxonomy of Cerurinae has been well-studied except for the faunas of the Tropical Americas and parts of Africa. Ongoing taxonomic revisionary efforts, including among African genera, are the focus of other studies (Mulvaney et al. unpubl. data; Schintlmeister pers. comm.). Males of each genus of Cerurinae are shown in Fig. 5 and their terminalia in Figs. 6 and 7.

**Oreocerura and Cerurilla**

Oreocerura stat. rev. (type species Cerura dissodectes Kiriakoff, 1958) is reinstated as a valid genus with the sole species being Oreocerura dissodectes, comb. rev. There is a rather significant (~10 Ma) divergence between Oreocerura and the sister genus Cerurilla (type species Cerurilla natalensis Kiriakoff, 1962) with which it had been synonymized by Schintlmeister and Witt (2015). This divergence is greater than that between most other pairs of sister genera in the Cerurinae. We note that the terminalia of Oreocerura are remarkably morphologically distinct from those of Cerurilla (compare Figs. 6C, D and 7C, D) and from other cerurine genitalia, being one of the most complex genitalia structures in the subfamily. We did not sample Cerurilla whitakeri (Kiriakoff, 1962) the only other named taxon expected to fall within this clade, but, based on its genitalia, this South African endemic appears to be a close relative of *C. natalensis* (Schintlmeister and Witt 2015). Oreocerura is the only cerurine genus for which food plant information is unknown. Cerurilla natalensis, on the other hand, has been recorded from *Homalium rufescens* (Salicaceae) (Kroon 1999).

### Furcula

The data support the need to reassess use of the name Furcula furcula in North America, as recently proposed by Miller et al. (2018). These authors determined that the North American *F. occidentalis* (Lintner, 1878) represents two species. Based on Cytochrome c oxidase subunit I (COI) ‘barcoding’ (Hebert et al. 2003), the western North American populations are more closely related to Paleartic *F. furcula* than to North American *F. occidentalis*. In our analyses we included the following three relevant taxa: nomenclaturally *F. furcula furcula* from the United Kingdom, what was called ‘*E. furcula*’ in Miller et al. (2018) from Colorado, USA, and *F. occidentalis* from New York, USA. The phylogenetic results recover the two North American taxa as sister species with Old World *F. furcula* furcula sister to them, rendering *Furcula furcula* sensu Miller et al. (2018) paraphyletic. Fortunately, two available names for American populations exist: *deorum* Dyar (TL: USA: Colorado, Manitou) and *gigans* McDunnough (TL: Canada: Alberta, Head of Pine Creek, Calgary), both of which were named in 1922, but with *gigans* being named earlier (Dyar 1922a, McDunnough 1922). We therefore revalidate *F. gigans* stat. rev. to be applied to North American populations and synonymize *F. deorum* syn. nov. with *F. gigans*. Although we sampled *F. gigans* from Colorado, nearer to the type locality of *deorum* than to that of *F. gigans* from Alberta, ongoing phylogenomic efforts include a near topotype of *F. gigans* from Alberta, which is recovered as sister to, with weak genetic divergence from, the *F. gigans* from Colorado included in the present study, further supporting this synonymy (St Laurent in prep.). Miller et al. (2018) provided extensive morphological evidence supporting the separation of North American populations of *F. gigans* (as ‘*F. furcula*’) from *F. occidentalis*, but erroneously stated that the caterpillar of ‘*F. furcula*’ from North America was unknown. McDunnough (1922) provided a detailed description of the caterpillars of *F. gigans*, and it closely matches the known caterpillars of *F. furcula* and *F. occidentalis*. Future efforts should continue to examine fine-scale population genetics of *F. furcula*, its numerous Palearctic subspecies, and the American *F. gigans* and *F. occidentalis*, since this is a group with complex taxonomy and biogeography.

**Tecmessa and Americerura**

Tecmessa contains the type species *Thoea annulipes* Berg, 1878 from Argentina (later moved to *Tecmessa* by Burmeister (1878)) and *Tecmessa elegans* from southeastern Brazil (Berg 1878, Burmeister 1878, Schaus 1901). *Tecmessa annulipes* and *T. elegans* are both similar in patterning to cerurines and have simple genitalia, superficially similar to those of some cerurine genera (e.g., *Cerurina*, see Figs. 8 and 9. Schintlmeister (2013), in his comprehensive checklist of global Notodontidae and Oenosandridae, transferred all American representatives placed in *Cerurina* since the time of Draudt (1932) to *Tecmessa* based on these superficial similarities. This classification was followed by Becker (2014) and Miller et al. (2018). However, the transfer of species from Old World endemic *Cerurina* to *Tecmessa* by Schintlmeister (2013) was erroneous, although these species do not belong in *Cerurina* either. Morphologically, true *Tecmessa* display...
the following characters not shared with Cerurinae: narrowly pectinate (not plumose) antennae and somewhat developed ‘beard tufts’ below the haustellum, the latter of which is a derived condition of Heterocampinae (Miller et al. 2018). We also note the strong similarity of Tecmessa genitalia (see revised genus diagnosis below) to some Heterocampinae genera, such as Coelodasys Packard (Miller et al. 2021). The caterpillar morphology (Fig. 10) and behavior, which are known for both T. annulipes and T. elegans, are also highly distinct from those of Cerurinae. The caterpillars of these two species lack the main larval apomorphies of Cerurinae, namely stemapods and enlarged thoracic segments (Berg 1878, Oleiro et al. 2011, St Laurent pers. obs., Wheeler pers. comm.); and both feed on

**Fig. 2.** Best IQ-TREE result of 100 independent analyses. Absence of bootstrap values means UFBoot ≥ 95 and SH-aLRT ≥ 80. See Fig. S1 for outgroup relationships and full support values. Caterpillar in bottom left is Americerura scitiscripta showing a defense display (photo J. Miller). Adult cerurine moths shown to the right: A, Pararethrina argenteascens (photo D. Fischer); B, Pseudorethrina albicans (photo M. FitzPatrick); C, Cerurella natalensis (photo Q. Grobler); D, Oreocerura dissodectes (photo R. St Laurent, NHMUK); E, Notocerura spiritalis (photo W. Roland); F, Cerurina marshalli (photo L. Mulvaney); H, Afrocerura sp. (photo M. FitzPatrick); I, Neoharpyia verbasci (photo F. Romão); J, Furcula furcula (photo G. Kunz); K, Neocerura liturata (photo S. Lamberts); L, Americerura scitiscripta (photo A. Sourakov); M, Kamalia sp. (photo G. Kunz); N, Cerura vinula (photo A. Hardacre).
Anacardiaceae, not Salicaceae as is typical of Cerurinae (Biezanko et al. 1974, Oleiro et al. 2011). We also note that these two species have gregarious caterpillars, whereas those of Cerurinae are nearly always solitary in all stages, except for the aposematic caterpillars of Cerurina (Mulvaney 2021, St Laurent pers. obs.).

We transfer Tecmessa from Cerurinae to Heterocampinae based on our phylogenetic results (Figs. S1–4) and the characters considered apomorphic for Heterocampinae and Cerurinae by Miller et al. (2018). Two additional taxa, following our examination, are also included in Tecmessa: the monotypic genus Corania Schaus, 1939, syn. nov., assigned to Cerurinae in Becker (2014), is hereby synonymized with Tecmessa: Tecmessa pedrana comb. nov. (TL: Argentina). Tecmessa pica (TL: Chile), which was already transferred to Tecmessa by Becker (2014), is highly similar morphologically to T. pedrana and the genitalia of the two species are nearly identical (compare Fig. 9C and D). Although DNA extraction of these two species failed to provide enough DNA for AHE sequencing, the genitalia provide sufficient evidence for the placement of T. pedrana in Tecmessa and maintenance of Becker’s (2014) assignment of T. pica to Tecmessa. Furthermore, among the series of T. pica, we found specimens intermediate in coloration and patterning between T. pica and T. pedrana, suggesting a close relationship between these two species. So far as is known, true Tecmessa under this concept of the genus are endemic to South America, inhabiting Brazilian Atlantic Forest, grasslands in Brazil and Uruguay, arid regions of Argentina, and Chilean mountain ranges. Habitus and male genitalia of all known true Tecmessa are shown in Figs. 8 and 9, and caterpillars of two species in Fig. 10. The two generic synonyms listed under Tecmessa in Becker (2014), Eucerura Schaus, 1901 and Eunaduna Dognin, 1901, ...
remain synonyms of *Tecmessa* because the type species of both were examined and determined to be *Tecmessa* species. Namely, the type of *Eucerus*, *Drymonia pica* Butler, 1882, is *Tecmessa pica* and the type of *Eunaduna*, *Eunaduna cerurata* Dognin, 1901, is a synonym of *Tecmessa annulipes*.

Three other species transferred to *Tecmessa* by Schintlmeister (2013) belong neither in Cerurinae nor in *Tecmessa*, but to another as yet unnamed heterocampine genus. These species, *T. olindata* (Schaus, 1939), *T. gonema* (Schaus, 1905), and *T. laqueata* (Schaus, 1911) are each very similar to one another but together are divergent in morphology (Figs. 8E, F, 9E) and phylogenetically (Figs. S1–4) from true *Tecmessa*. Only *T. gonema* is included in our analyses, but external and genitalia morphology of these three species are nearly identical. They differ greatly from Cerurinae and from *Tecmessa* s.s. in that they bear cteniophores, a widespread trait in Heterocampinae which is absent in Cerurinae (Miller et al. 2018) and *Tecmessa* s.s. Maintaining our focus on Cerurinae, we do not formally transfer these taxa from *Tecmessa* at this time, but they will require a new genus to maintain monophyly of *Tecmessa* and this is the topic of a future work (St Laurent et al. in review).

Below we describe a new genus to accommodate the cerurine contingent of species formally assigned to *Tecmessa* s.l. and transfer them accordingly. Adult habitus and male genitalia are given for all of the transferred species in Figs. 11–13. Description of *Americerura* gen. nov. ensures that all genera in Cerurinae, and the subfamily itself, are monophyletic. Miller et al. (2018) provide a detailed description of *Tecmessa* consisting of the North American species of *Americerura*, thus we provide a new description here taking into consideration all Neotropical species and excluding the species now established as heterocampines.

**Americerura** St Laurent and Goldstein, gen. nov.


**Type species.**

*Cerura scitiscripta* Walker, 1865: 408, by present designation.

**Etymology.**

The name is a combination of ‘America’ and ‘*Cerura*’ referencing that this is the only American contingent of a principally Old World clade containing *Cerura* and its closest relatives. The name is feminine.

**Diagnosis.**

As is typical of most cerurines, adult *Americerura* are primarily black and white, with the white of the wings deriving from lustrous, reflective scales in most species. Antennae are feathery, bipectinate to the tips in both sexes, with those of males bearing longer pectinations. The male genitalia (Fig. 12) are rather simple, and within Cerurinae, most similar to the related Old World genera *Cerura* and *Kamalia*, on the basis of smoothly upwardly curved rounded valvae, an ellipsoidal vinculum, a short but well-sclerotized blunt uncus, and heavily sclerotized, short, curled fingerlike socii. Typically, *Americerura* valvae are narrower and more widely splayed than in *Cerura*, and the phallus and eighth sternite less robust than in *Kamalia*. The phallus is variable, but usually pointed. The eighth sternite (Fig. 13) nearly always bears a trident plate forming a ‘W’, a similar trait seen in *Kamalia*. Female genitalia are generally simple (Fig. 14), without a heavily sclerotized ostium, prominent antevaginal plate, or a notable differentiation between the vaginal plates. Most species of *Americerura* are also smaller moths, in general, and thus genitalia are smaller overall than those of the large *Cerura* and *Kamalia*.

*Americerura* may be confused with some of the paler *Furcula* species in North America where they are sympatric, but *Furcula* can be easily recognized by the presence of dark, metallic scales on the thorax that give it a characteristic sheen. *Americerura* could also continue to be confused with members of *Tecmessa* s.l. as they have been since Schintlmeister (2013), but the genitalia of *Tecmessa* s.l. are distinct, with narrower valvae, a narrower phallus, and a less modified eighth sternite lacking a W-shaped structure. The antennae provide an immediate clue to their differentiation given that in *Tecmessa* s.l. they are longer and less feathery. *Americerura* also lack the beard-tufts of the head and the cteniophores of some species of *Tecmessa* s.l. as well.

All known last instar *Americerura* caterpillars are green or yellow, with a variably shaped and colored dorsal saddle on the thoracic and abdominal segments, and broad thoracic segments into which the head can partially retract. Usually, the head is edged by red or pink on the prothoracic segment, with false eyespots flanking the head on each anterior corner of the prothorax. All species of *Americerura* have stemapods with eversible internal whips that are yellow, orange, or red (or some combination). *Americerura* caterpillars are only likely to be confused with *Furcula*, and only in Canada, the U.S.A., and Mexico where the genera co-occur. *Furcula* caterpillars generally lack colored prothoracic margins around the head (and are less contrasting if present), have darker stemapods, and are generally much more motiled in overall appearance.

**Description.**

*Adult*. Male: Head: Width more than half that of thorax, frons coloration white, gray, black or bicolored black and white with black...
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ventrally, eyes large, naked, occupying more than 2/3 area of head, eyes usually bordered posteriorly by dark brown or black scales; labial palpus reduced, not extending beyond frons, two-segmented, coloration usually as for frons; haustellum very short, not typically visible, antennal scape scaled in erect tuft of white or gray scales, antennae brown to black with white and/or black scales coating dorsal surface, bipectinate to tip with rami increasing in length from antennal base to roughly half antennal length where rami length abruptly become shorter, remaining short until terminus. Thorax: overall patterning gray or black and white, prothorax often with black margin or fully clothed in black scales, meso thorax and meta thorax with white ground color and black spots; thickly scaled.

Fig. 5. Males of each genus of Cerurinae, type species shown unless otherwise indicated. A, Pararethalia hierax (ANHRT); B, Pseudorethalia albicans (ANHRT); C, Oreocerura dissocinctus primary type (NHMUK); D, Cerurella natalensis (NHMUK); E, Notocerura spiralis (ANHRT); F, Furcula furcula (USNM); G, Hampsonita esmeralda (NHMUK); H, Cerurina marshalli marshalli (NHMUK); I, Neoharpyia pulcherrima, not type species (MGCL); J, Afrocrrura leonensis (ANHRT); K, Neocerura liturata (NHMUK); L, Kamalia cf. priapus, not type species (NHMUK); M, Americerura scitisscripta (MGCL); Cerura vinula (MGCL). Scale bar = 1 cm.
In species with darker (not white) forewings, thorax tends to approximate darker wing ground color. Legs mostly concolorous with thorax, basal segments black and white, tarsi typically black. Tibial spurs thin, short, clothed in fine white scales, in formula 0-2-2. Tarsal claws simple. Forewing length 11–24 mm (measured from edge of thorax to wing tip), wingspan 23–46 mm (measured wing span).
tip to wing tip); subtriangular, outer margin weakly convex, apex not pronounced. Forewing dorsum ground color ranging from gray (A. duomunennia [Dyar, 1912]), gray-brown (A. annulifera [Berg, 1878]), to off-white or lustrous immaculate white (all other species). Antemedia, medial, and submarginal ground color concolorous. Overall forewing pattern variable but always with some combination of wavy or zigzagging lines ranging from extremely reduced or nearly absent (e.g., A. splendens [Jones, 1908], A. candida [Lintner, 1878]) to nearly covering the forewings (some forms of A. scitiscripta). Antemedia proximal to thorax usually a weakly defined transverse black line present, antemedia band usually present, may range from complete and filled with light blue-gray scales to incomplete or replaced by yellow splotches. Wing with variable number of zigzagging black lines medially. Postmedial line usually most well-defined line of wing, typically thickest subapically with a secondary outer submarginal line paralleling postmedial line to varying degrees, both postmedial and submarginal lines sharply crenulate, forming points at vein intersections. Discal spot usually absent but may be weakly defined as black mark, thick markings usually present along costa and anal angle. Most species bearing black markings between veins along wing margin, with wing fringe further invaded by black scales aligned with intervenular marks along wing margin. Forewing venter usually lacking markings but may be variously smudged by darker scales, particularly subapically. Hindwing dorsum generally devoid of markings, although dark discal marks, marks at anal angle, and along margin may be present; hindwing coloration ranging from gray, blackish, to pure white. Hindwing venter as for hindwing dorsum, usually without markings except along costa. Frenulum a single bristle. Wing venation as for other Cerurinae, but forewing bearing a small accessory cell and radial veins arising from its apex. Abdomen: Clotheden in white, gray, or black scales, separation between abdominal segments usually poorly defined but may be delimited by margins of hoary scales; terminal segment often with lighter scales. Eighth sternite (Fig. 13) either with W-shaped sclerotization (lacking the medial prong in A. brattetata [Draudt, 1932]) or with more complex five-pronged structure (A. rarata [Walker, 1865] and A. tehuacana [Draudt, 1932]). Central prong variable in width and length depending on species. Genitalia (Fig. 12) (n = 25) simple in overall structure, with ovoid, weakly connected vinculum ventrally.

Tegumen weakly defined. Uncus simple, bifid, or distally widened, thickly sclerotized, blunt, covered in setae. Socii simple, fingerlike, upcurved and heavily sclerotized, thickness variable, externally ranging from smooth to rugose. Gnathos absent. Valvae simple, rounded to somewhat acutely angled apically. Juxta typically a thin sclerotized strip, partially fused to phallus. Phallus somewhat variable, but typically broadest mesally, downcurved distally, with sharp apex, vesica thin, simple, bag-like without cornutus.

Female. Sexual dimorphism in general not greatly pronounced. Head: As for male but antennae with shorter rami overall, rami longest basally and becoming gradually shorter along antennal length to apex. Thorax: As for male. Forewing length 18–26 mm, wingspan 23–50 mm; subtriangular, outer margin weakly convex, apex not pronounced. Forewing dorsum as for male but wing broader. Hindwing dorsum gray, gray-brown to black, rarely white (e.g., A. rarata). Hindwing venter as for hindwing dorsum, usually without markings. Frenulum with numerous tightly packed bristles. Abdomen: As for male but bulkier, terminal segments with corethrogyne in some species. Eighth sternite simple, lacking the W- or five-pronged structure present in males. Genitalia (Fig. 14) (n = 4) simple; tergite eight a narrow, sclerotized bar. Apophyses anteriores reduced to thick prominences; apophyses posteriores thin, relatively short, not extending well beyond margin of eighth, if at all. Antevaginal plate a simple sclerotized bar; ostium a narrow longitudinal opening or more circular; postvaginal plate either a simple sclerotized region or forming more of a sclerotized pocket. Ductus bursae indistinct; corpus bursae thin, bag-like, lacking signa, smaller or only slightly larger than remaining genitailia complex. Papillae anailes broad, covered in long, fine setae.

Egg. Circular, compressed, coloration variable, including white, brown, pink, or green, usually with reticulate pattern. Laid singly on adaxial leaf surface.

Caterpillar. (Figs. 1G and 2 inset) Head large relative to prothorax, reddish brown to black, head withdrawn deep into prothorax when not feeding and especially during threat displays; body ground color...
yellow to bright apple-green, becoming reddish brown when prepupal; prothorax usually with pink or red coloration along margin with head, forming a hood when head retracted, in all but the final instar, each anterior corner of prothorax with spiked knob, these knobs absent and may be replaced by black eye spots in final instar, one on either corner of triangular prothorax above head; metathorax usually with dorsal single or pair of knob-like protrusions; thoracic and abdominal segments with contrasting dorsal saddle varying in color from brown, white, purple, red, maroon, or green, saddle widest on T1 and A4 where it may become discontinuous or lengthened towards the second pair of prolegs; some species with prominent white subspiracular line (A. scitiscripta and A. candida), spiracles white, black, or orange; body usually speckled laterally; stemapods black, brown, or with coloration of saddle bleeding into them basally, with a yellow, orange, or red eversible component that can be shunted outwards with fluid during threat.
display. A10 bears thick green or black paranal spines (paraprocts) which assist in catapulting fecal pellets far from the body. True legs vary from green to black or are striped green and black. Five to six larval instars.

Pupa.
Obtect, dark red-brown, cremaster absent. Formed inside rigid cocoon spun lengthwise along partially excavated notch in wood, with chewed wood and other material that may have coated the wood (e.g., moss) integrated in or on matrix of silk.

Natural history.
Available host records for Americerura species are in the Salicaceae, as is typical of Cerurinae. Feeding records include the food plant Americerura available host records for species are in the Salicaceae, Natural history. (e.g., moss) integrated in or on matrix of silk. Chewed wood and other material that may have coated the wood (e.g., moss) integrated in or on matrix of silk.

Systematic remarks.
The long branch length between the species pair A. scitiscripta and A. candida and the remaining Americerura species, is similar to the divergence time (over 15 Ma) between the two Old World genera Kamaelia and Cerura. However, given the American taxa are monophyletic, and genitalia morphology is consistent across species, we do not feel the need to introduce yet another genus at this time. Upon examination of all named species assigned to Americerura, we determine that A. argynnis and A. argentina (Dognin, 1911), syn. nov. are synonymous. The male genitalia of the type of A. argentina are within the range of specific variation among other A. argynnis genitalia preparations and are comparable to those of a paralectotype of A. argynnis. Americerura argynnis is a common, widespread species in Brazil and Argentina (St Laurent unpubl. data). Other cases of seemingly closely related Americerura species (e.g., A. dandon [Druce, 1894] and A. grandis [Schaus, 1901]) were named from widely separate type localities with major geographic barriers between populations; we do not consider such species pairs synonyms as we do A. argentina and A. argynnis.

We do not propose additional taxonomic changes within Americerura but hasten to point out that the illustration of A. xicona (Dyar, 1924) in Draudt (1932) is incorrect, and instead, a weakly marked A. cf. rarata is figured (similar to our specimen LEP34078 from MGCL). The type of A. xicona in the USNM is in actuality very similar to A. scitiscripta as pointed out in Miller et al. (2018). The synonym of A. scitiscripta, platea (Schaus, 1890) named from Veracruz, Mexico, may actually be more properly placed as a
synonym of *A. xicona*, named from Distrito Federal, Mexico. But pending sampling that includes toptotypical *A. scitiscripta*, *A. xicona*, and *platea*, we do not make those changes here. Our results show that the taxon *A. candida*, the validity of which was considered uncertain by Miller et al. (2018), is only weakly divergent from *A. scitiscripta* and may not warrant specific status. Further research on these matters, as well as the species-level taxonomy of Neotropical *Americerura*, is needed. The figure of *Tecmessa gonema* (as *Cerura gonema*) in Draudt (1932) is also incorrect, and instead shows a female of *A. rivera* (Schaus, 1901).
For a list of species currently included in *Americerura*, see the summary of taxonomic changes in the following section.

**Summary of Taxonomic Acts**

**Taxonomic acts in Cerurinae:**
*Americerura* St Laurent & Goldstein, gen. nov. (Type species: *Cerura scitiscripta* Walker)
*A. annulifera* (Berg, 1878), comb. nov., (Figs. 11A, 12A, 13A)
*A. argynnis* (Schaus, 1901), comb. nov., (Figs. 11B, C, 12B, C, 13B, C)
*A. argentina* (Dognin, 1911), comb. nov., syn. nov.
*A. bratteata* (Draudt, 1932), comb. nov., (Figs. 11H, 12H, 13H)
*A. candida* (Lintner, 1878), comb. nov., (Figs. 11P, 12O, 13N)
*A. dandon* (Druce, 1894), comb. nov., (Figs. 11I, 12J, 13I)
*A. duonumennia* (Dyar, 1912), comb. nov., (Figs. 11O, 12M, 13P)
*A. grandis* (Schaus, 1901), comb. nov., (Figs. 11J, 12K, 13J)
*A. lancea* (Schaus, 1905), comb. nov., (Figs. 11L, 12L, 13K)
*A. presidio* (Dyar 1922b), comb. nov., (Figs. 11K, 12I, 13M)
*A. purusa* (Schaus, 1928), comb. nov., (Figs. 11F, 12G, 13G)
*A. rarata* (Walker, 1865), comb. nov., (Figs. 11Q, 12Q, 13Q)
*A. rarata* optima (Bryk, 1953), comb. nov.
*A. rivera* (Schaus, 1901), comb. nov., (Figs. 11D, 12D, 13D)
*A. scitiscripta* (Walker, 1865), comb. nov., (Figs. 1G, 2 inset, 2L, 5M, 6N, 7L, 11M, 12N, 13L)
*A. candida* (Lintner, 1878), comb. nov., (Figs. 11P, 12O, 13N)
*A. dandon* (Druce, 1894), comb. nov., (Figs. 11I, 12J, 13I)
*A. grandis* (Schaus, 1901), comb. nov., (Figs. 11J, 12K, 13J)
*A. lancea* (Schaus, 1905), comb. nov., (Figs. 11L, 12L, 13K)
*A. presidio* (Dyar 1922b), comb. nov., (Figs. 11K, 12I, 13M)
*A. purusa* (Schaus, 1928), comb. nov., (Figs. 11F, 12G, 13G)
*A. rarata* (Walker, 1865), comb. nov., (Figs. 11Q, 12Q, 13Q)
*A. rarata* optima (Bryk, 1953), comb. nov.
*A. rivera* (Schaus, 1901), comb. nov., (Figs. 11D, 12D, 13D)
*A. scitiscripta* (Walker, 1865), comb. nov., (Figs. 1G, 2 inset, 2L, 5M, 6N, 7L, 11M, 12N, 13L)
A. splendens (Jones, 1908), comb. nov., (Figs. 11G, 12E, 13E)
A. tehuacana (Draudt, 1932), comb. nov., (Figs. 11R, 12R, 13R)
A. trigonostigma (Dyar, 1925), comb. nov., (Figs. 11E, 12F, 13F)
A. xicona (Dyar, 1924) comb. nov., (Figs. 11N, 12P, 13O)
Furcula gigans (McDunnough, 1922), stat. rev.
F. deorum (Dyar, 1922), syn. nov.
Oreocerura dissodectes (Kiriakoff, 1958), comb. rev.

Complete checklist of Tecmessa including taxonomic acts:
Tecmessa Burmeister, 1878
Corania Schaus, 1939, syn. nov.
Eucerura Schaus, 1901
Eunaduna Dognin, 1901
T. annulipes (Berg, 1878), (Figs. 8A, 9A, 10A)
T. elegans (Schaus, 1901), (Figs. 8B, 9B, 10B)
T. pedrana (Schaus, 1939), comb. nov., (Figs. 8D, 9D)
T. pica (Butler, 1882), (Figs. 8C, 9C)
The following species are provisionally maintained in Tecmessa:
T. gonema (Schaus, 1905), (Figs. 8E, 9E)
T. laqueata (Schaus, 1915), (Fig. 8F)
T. olindata (Schaus, 1939)

Divergence Time Estimation
Overall, maximum likelihood (Fig. S5) and Bayesian divergence time estimates were largely congruent for deep nodes. The Birth-death tree prior with three unlinked molecular clocks, one per codon position, was the preferred BEAST analysis (Fig. S6). Tree files showing age ranges, means, and medians for all nodes from each dating analysis are available on Dryad.

Node-dating analyses recovered a range of 64.8–67.8 Ma (TreePL) and 61.2–70.9 Ma (BEAST) for the crown age of Notodontidae. The split of cerurines from the sister lineage comprising Shachia + Liparopsis was estimated at 39.4–42.3 Ma (TreePL) and 34.2–41.5 Ma (BEAST). The crown age of Cerurinae was inferred to be 30.5–33.7 (TreePL) and 28.3–34.7 Ma (BEAST). Here and in the discussion below, we refer to the major clades A, B, and C within Cerurinae, with the topology (A,[B,C]). The recovered crown ages for these are in the Miocene: Clade A: 14.8–16.2 Ma (TreePL), 13.5–18.3 Ma (BEAST); Clade B: 17.2–19.9 Ma (TreePL), 14.9–20.4 Ma (BEAST); Clade C: 18.4–19.8 Ma (TreePL), 16.1–20.0 Ma (BEAST). All Cerurinae genera, except the recently diverged sister genera Afrocerura and Cerurina and the ancient monotypic Pseudorethona, also had their origins in the Miocene.

Biogeography
The Bayesian and ML biogeographic analyses resulted in similar scenarios for Cerurinae over the ~30 My since their origin, especially when constraints on dispersal and adjacency were imposed. For purposes of discussion, we consider the constrained analyses that include both adjacency and dispersal matrices the most realistic approaches since they reflect paleogeography, though they do introduce user-imposed assumptions on historical biogeography. We focus our discussion on the Bayesian, constrained DEC analysis in RevBayes (Fig. 3) and the BioGeoBEARS analyses are found in Figs. S7–10.

We infer that Cerurinae originated in the Afrotropics and remained there exclusively until ~25 Ma when they most likely dispersed to the East Palearctic. The most recent common ancestor of all Cerurinae except the Afrotropical genera (the ancestor of clades B and C) therefore likely inhabited the East Palearctic. Clade B is
found entirely in the Northern Hemisphere and is inferred to have been restricted ancestrally to the East Palearctic, dispersing thence to the Americas in the late Miocene with subsequent back-colonization to the Old World and later a second colonization of New World much more recently in the Pleistocene. Alternatively, considering that we permitted up to two areas per species, we can also report these results in terms of a widespread East Palearctic and Nearctic distributed ancestor of all *Furcula*, that diverged into a New World clade and a mostly Old World Clade, with the ancestor of *F. furcula*, *F. gigans*, and *F. occidentalis* becoming widespread across the East Palearctic and Nearctic, and then subsequent isolation of the North American lineage leading to *F. gigans* and *F. occidentalis*. The remaining Cerurinae (Clade C) had an equally complex biogeographical history, with an ancestral range in the East Palearctic, and subsequent dispersal to Indomalaya (*Neocerura* and Kamalia spp.), the Americas (*Americerura gen. nov.*), and Palearctic (*Cerura*).

**Food Plant Use and Diversification**

Our SIMMAP ASR expectedly recovers Salicaceae as the ancestral host at all nodes in Cerurinae (Fig. S11), including as the ancestral condition of the subfamily. Shifts to non-Salicaceae hosts occurred at three tips: *Hampsonita esmeralda* (to Proteaceae), *Furcula borrealis* (to Rosaceae), and *Furcula bicuspid* (Borkhausen, 1790) (to Betulaceae).

Of the five GeoSSE models tested (Table S7) the best supported based on AIC, AICc, and AIC weight was a MuSSE-like model with

no hidden trait and anagenetic effects. Importantly, turnover rates (temperate, $\tau_0 = 2.40$ vs. tropical, $\tau_1 = 0.55$) are higher in temperate lineages, but because we found anagenetic rather than clado- genetic effects there is not an explicit link between shifting from temperate to tropical or tropical to temperate ranges and speciation. An alternative coding strategy that treats Southern Hemisphere taxa that range into cooler regions as inhabiting both temperate and tropical climates also recovered the MuSSE-like model with no hidden trait and anagenetic effects as the best model.

**Discussion**

**Composition of Cerurinae**

The genera assigned to Cerurinae by previous authors, except *Tecmessa* and *Corania* (here a synonym of *Tecmessa*) (Schintlmeister 2008, Becker 2014, Schintlmeister and Witt 2015, Miller et al. 2018), are monophyletic under a variety of phylogenetic inference methods. To alleviate the polyphyly of *Tecmessa* (Heterocampinae), we propose *Americerura* and transfer 17 species to it from *Tecmessa*. Based on our phylogenomic results, which included all genera of Cerurinae, the generic classification of this subfamily is likely to be stable.

At the notodontid subfamily level, the nearly comprehensive (lacking only Scranciinae and Dicranurinae s.s.) outgroup sampling showed that Cerurinae is monophyletic and not nested within Notodontidae. Its relationship with Dicranurinae is yet unresolved. In the ML analyses, Cerurinae shares a common ancestor with the Dicranurinae s.l. genera *Shachia*, *Liparopsis*, and *Harpyia*. The ASTRAL analysis (Fig. S3) only weakly supports (ASV = 0.59) the sister relationship of Cerurinae with *Shachia*, and does not recover *Liparopsis* and *Shachia* as monophyletic, illustrating the instability of the ((*Shachia*, Liparopsis), Cerurinae) grouping recovered in ML analyses. While caterpillars of both *Shachia* and *Liparopsis* are similar to those of Cerurinae (e.g., by virtue of the presence of stempods), they are physiologically distinct, feeding on FAGaceae and Juglandaceae rather than Salicaceae (Schintlmeister 1989, 2008, 2020; Miller 1991; Funamoto and Sugíra 2017).

The composition of the Dicranurinae will ultimately depend on the placement of its type genus *Dicranura* in a more exhaustively sampled phylogenetic analysis of the family. This will require the reclassification and re-assignment of various ‘Dicranurinae’ to subfamilies better circumscribed by a combination of genomic and morphological data (Laurent et al. unpubl. data). Pending additional sampling, it is conceivable that the concept of Cerurinae could eventually be broadened to include other taxa. Regardless, the monophyly of the genera here considered to compose Cerurinae is well-established on the basis of our analyses and corroborated morphologically; establishing higher taxa is outside the scope of the present work.

**Divergence Time Estimation**

The inferred origin of Notodontidae (61.2–70.9 Ma) straddles the Cretaceous-Paleogene (K-Pg) boundary, an important extinction event that immediately preceded the radiation of other globally distributed clades of Lepidoptera (Espeland et al. 2018, Kawahara et al. 2019). This result is an important advance in our understanding of the age of Notodontidae because the divergence time analysis is the first to include the majority of Notodontidae subfamilies. Previously, the only available sources of divergence times for Notodontidae were those reported in Wahlberg et al. (2013), which recovered a crown age of Notodontidae at ~69 Ma, and Kawahara et al. (2019), which
recovered the most recent common ancestor of *Pheosia* Hübner (Notodontidae) and *Nototilia* Schaus (Nystalinae), an internal node of Notodontidae, to be ~50 Ma. The study by Wahlberg *et al.* (2013) had more comprehensive taxon sampling but still lacked Platychasmataceae, an enigmatic subfamily thought to be sister to all other Notodontidae (Kobayashi and Nonaka 2016). We included one representative of Platychasmataceae, corroborating its placement as sister to all other Notodontidae. Therefore, the inferred crown age of 61.2–70.9 Ma, as found here, can be seen as a reasonable hypothesis for Notodontidae considering these previous studies and our inclusion of the earliest diverging lineage. However, comprehensive family-wide sampling was not the focus of the present study; we caution that these dates are provisional and will be reassessed with more complete sampling. Since Cerurinae were absent from both Wahlberg *et al.* (2013) and Kawahara *et al.* (2019), we present the first estimated crown age for the subfamily in the Oligocene (30.5–33.7 Ma [TreePL] and 28.3–34.7 Ma [BEAST]).

**Biogeography of Cerurinae**

An African origin for Cerurinae makes sense because all extant species of the sequentially sister lineages of Cerurinae until Clades (B+C) are Afrotropical. There is no evidence of secondary dispersal back into Africa south of the Sahara desert from any of the biogeographic analyses. The Mediterranean African Cerura delavoei (Gaschet, 1876) is the only taxon believed to have recolonized Africa, but only north of the Sahara in Morocco, Algeria, Tunisia, and the Canary Islands (Schintlmeister 2008), a region we treat biogeographically as part of the West Palearctic.

Outside of Africa, the biogeography of Cerurinae is more complicated, with several major dispersal events. However, the most likely scenario is that Cerurinae invaded the Palearctic from Africa via the Balkans or Asia Minor, from whence they spread throughout the East and West Palearctic and spawned all subsequent radiations of Cerurinae. Two major lineages evolved in the Palearctic, the first (Clade B) leading to the sister genera Neoharpyia and Furcula, which spread from the Palearctic to the Americas; and the more speciose Clade C which independently colonized the Americas (*Americerura*), Indomalayan and Australasian (*Neocerura* and *Kamalia*), and radiated in situ within the Palearctic (*Cerura*).

The dispersal events that led to the colonization of the Americas by *Americerura* and *Furcula* occurred during the Miocene. *Americerura* are found from Canada to Uruguay and have radiated in the Neotropical realm, whereas *Furcula* are found exclusively in the Northern Hemisphere. The ancestor of *Americerura* arrived in the Americas via North America some 15 Ma, requiring either long distance dispersal from the Old World or shorter dispersal routes in the Bering region. The ancestor of *Furcula*, on the other hand, spread from an exclusively East Palearctic range to a more widespread East Palearctic and Nearerctic range during the Miocene, potentially overlapping the period when *Americerura* is inferred to have arrived in the Nearctic. The ancestor of *Furcula* eventually led to two major lineages in the late Miocene to early Pliocene, one each in the Old World and New World. Within the Old World *Furcula* clade, at the beginning of the Pleistocene, the ancestor of *F. furcula*, *F. giganis*, and *F. occidentalis* likely spread again to a semi-Holarctic distribution (Nearerctic and East Palearctic) and in less than 2 My, split into *F. furcula* in the East and West Palearctic and the ancestor of *F. giganis* and *F. occidentalis* in the Nearctic. These two extant species occur in boreal/subarctic habitats ranging into temperate deciduous forests, and the sister to the clade of these two species, Eurasian *F. furcula*, is found throughout the northern Palearctic. Thus, the biogeography of these high-latitude *Furcula* species was likely impacted by glacial cycles and sporadic Beringian land bridges rather than long distance dispersal (the latter being a more likely scenario in *Americerura*, for example). Previous research suggested possible affinities between American *F. furcula* and Old World *F. furcula* subspecies found in Siberia and the Russian Far East (Miller *et al.* 2018), but further research is needed to contextualize the biogeography of each lineage in this clade because we lack other *F. furcula* subspecies and toptotypical *F. giganis*, which may be more closely related to Old World *F. furcula* than Coloradoan populations (e.g., *deorum*) based on COI barcodes (Miller *et al.* 2018). Ongoing work with nuclear AHE phylogenomics, including both Alberta and Colorado *F. giganis* populations, however, seems to contradict the mitochondrial data (St Laurent unpubl. data).

Concurrent with the invasion of the Americas in Clade C, the predominantly Indomalayan and Australasian genus *Kamalia* and the principally Palearctic genus *Cerura* evolved from an East Palearctic ancestor. While we only sampled one species of the Australasian contingent of *Kamalia* (*K. amoa* [Holloway, 1979] from New Caledonia), it is worth noting that it was found to be sister to the remainder of the genus. This makes determining the ancestral range of *Kamalia*, and thereby the ancestral range of the most recent common ancestor of *Kamalia* and *Cerura*, more complicated because the majority of *Kamalia* species are Indomalayan and not Australasian. To further complicate matters, *K. malaysiana jakli* (Schintlmeister, 2002) occurs on both sides of Wallace’s Line in Bali and Sumbawa, suggesting a second invasion of Australasia by the relatively widespread *K. malaysiana* (Holloway, 1982). *Kamalia* and *Cerura* were considered a single genus until Schintlmeister (2002) split them on morphological grounds. Due to the estimated 15 My divergence and the pronounced morphological differences between them, treating these as separate genera is warranted and conveys historical biogeography and morphological information.

**Cerurinae Food Plants and Global Temperature**

Cerurinae are nearly entirely oligophagous on Salicaceae, a plant family which originated much earlier than Notodontidae in the Mesozoic (Li *et al.*, 2019, de Mestier *et al.*, 2022). Most molecular phylogenies that include Salicaceae do not sample densely across the family, with available research examining specific clades or genera (de Mestier *et al.*, 2022; Wang *et al.*, 2012) or the parent order, Malpighiales, with limited Salicaceae sampling (Xi *et al.*, 2012, Cai *et al.*, 2020). Li *et al.* (2019) however, did examine the timing of divergence based on plastid genomes and sampled 18 genera across Salicaceae. There is also some disagreement as to what constitutes Salicaceae sensu stricto, with the relevant studies differing on the inclusion of Casuarina, which is consistently found to be sister to all or most other Salicaceae (Xi *et al.*, 2012, Li *et al.*, 2019, Cai *et al.*, 2020, de Mestier *et al.*, 2022). However, based on what is known at this point, Salicaceae had a Cretaceous origin, with stem ages reported as 102.08–86.05 Ma in de Mestier *et al.* (2022), ~93 Ma in Li *et al.*, 2019, and 78.7–59.8 Ma in Xi *et al.* (2012). Regardless of whether or not Salicaceae includes Casuarina and some other debated lineages, the crown age of Salicaceae excluding these taxa still antedates the crown of Cerurinae by some 20–30 My (65.1–51.3 Ma in Xi *et al.*, 2012). Based on these ages, the Salicaceae biogeography reconstruction in de Mestier *et al.*, 2022, and our own biogeographic reconstruction of Cerurinae, Salicaceae had already colonized much of the globe by the time Cerurinae arose.

Within Salicaceae, there is not a clear affinity for a single clade or genus of plants. For example, the ‘derived’ Asian cerurine genus *Neocerura* is known to feed on *Casuarina* in the Old World Tropics.
Hemisphere, relatively unrelated but sympatric Cerurinae clades of Cerurinae in Africa (de Mestier et al. 2022) were recently synonymized with Casearia and phylogenetic evidence supports the synonymy (Samarakoon and Alford 2019, de Mestier et al. 2022). Extensive searching for caterpillars on Casearia spp. by the first author has not revealed the presence of any cerurines despite their abundance on nearby Salicaceae genera Xylosma and Banana (St Laurent pers. obs.). Casearia is one of the most ancient lineages of Salicaceae, and originated in the Neotropics ~10 million years before the origin of Cerurinae in Africa (de Mestier et al. 2022). In the Northern Hemisphere, relatively unrelated but sympatric Cerurinae clades (e.g., Cerura and Furcula in the Paleartic; Americerura and Furcula in the Nearctic) feed on Salix and Populus, the two primary, and often only, Salicaceae genera found in temperate regions (Wang et al. 2022). There are also cases of non-Salicaceae feeding by Furcula borealis (on Rosaceae) and F. bicuspis (Betulaceae) in these areas. In the tropics, where Salix and Populus are not major components of forests, cerurines feed on a wide range of other Salicaceae genera from the various accepted Salicaceae subfamilies: Azara, Banana, Casearia (=Laetia), Hasseltia, and Xylosma in the New World tropics and Casearia, Doryalis E.Mey. ex Arn., Homalium Jacq., Flacourtia Comm. ex L'Hé., Scoliopta Schreb., Trimeria Harv., and Idesia Maxim. in the Old World tropics (Kroon 1999, Schintlmeister 2008, 2020, Chandra et al. 2018). The fidelity to Salicaceae is nearly universal among Cerurinae, but utilization of specific food plants appears to be opportunistic with respect to local availability of Salicaceae species rather than a distinct pattern of coevolution. This fact that Salicaceae appear to have anadated Cerurinae supports the scenario that Cerurinae dispersed around the globe opportunistically due to the widespread availability of Salicaceae food sources. Yet another indication of opportunistic feeding on Salicaceae by Cerurinae can be found in South America, where there are reports of several Americerura feeding on introduced, ornamental Salix species (Biezanko et al. 1974). The single native Salix in the region (S. humboldtiana Willd.), is a host of A. annulifera (St Laurent pers. obs.), similar to how A. scitissipra feeds on various Salix and Populus in North America, where other genera of Salicaceae are absent.

As inferred from our GeoSSE analyses, Cerurinae turnover rates are highest in temperate regions with an anagenetic impact of temperature on turnover (Table S7). This suggests that while Cerurinae had a tropical African origin, and clearly are present in most tropical regions, their ability to diversify in temperate regions may explain their relatively high extant diversity in the Northern Hemisphere. However, the observed effect of range (defined as either widespread or restricted to temperate/ tropical climates) on net diversification is anagenetic, and so could be explained by local extirpation of widespread species over time rather than cladogenesis explicitly being the precursor of temperature specialization. The clade containing Americerura (mostly tropical), Cerura (mostly temperate), and Kamala (mostly tropical) exemplify this scenario well, in that they had a widespread ancestor but regional specialization, possibly due to extirpation, leading to three climate-limited genera.

As shown by our food plant ASR (Fig. S11), the ancestral caterpillar feeding condition was unequivocally on Salicaceae, with rare instances of recently divergent feeding behavior. And while there is evidence that temperature has impacted Cerurinae diversification, the nearly uniform extant and ancestral Salicaceae-feeding in this group supports the hypothesis that, conversely, food plant shifts on the scale of plant family did not impact diversification. This latter point is important because food plant shifts and ability to colonize new plants has been a central tenet in attempts to understand Lepidoptera diversification dynamics (Janz et al. 2006, Ebel et al. 2015, Fagua et al. 2017, Sahoo et al. 2017, Strutzenberger et al. 2017, Braga et al. 2018, Kergoat et al. 2018, Bruzese et al. 2019, Toussaint et al. 2019, Allio et al. 2021, St Laurent et al. 2021). We also do not consider food plant shifts within Salicaceae to be a major factor driving cerurine diversity since the larvae of this group tend not to specialize, and essentially feed on any available Salicaceae (see our earlier discussion about tropical Cerurinae feeding preferences). Cerurinae are physiologically adaptable, given the range of latitudes and habitats they occupy and their species richness in the temperate regions. To further understand the mechanisms by which Cerurinae so successfully spread across the planet, future research might investigate the chemical ecology of Salicaceae feeding and how cerurine detoxification of foods may have allowed them to utilize an abundant, but chemically defended group of food plants. Such a pathway may have been paved by an ancient adaptation to feeding on Salicaceae in Africa, deep in the Oligocene, that led a curious group of insects with familiar ‘faces’ and whip-like ‘tails,’ all over the world.

Supplementary Material
Supplementary data are available at Insect Systematics and Diversity online.

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