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A global blueberry phylogeny: Evolution, diversification, and biogeography of Vaccinieae (Ericaceae)

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ABSTRACT

Vaccinieae is a morphologically diverse and species-rich (~1430 species) tribe in Ericaceae. Although the majority of diversity is tropical, Vaccinieae are best known for temperate crops (i.e., blueberries, cranberries, and lingonberries) in *Vaccinium*. *Vaccinium* itself (~500 species) has been previously suggested as highly polyphyletic and taxonomic boundaries among many of the other genera in the tribe remain uncertain. We assessed the evolutionary history of Vaccinieae with phylogenomic analyses based on a target-enrichment dataset containing 256 low-copy nuclear loci and 210 species representing 30 of the 35 genera in the tribe and 25 of the 29 sections of *Vaccinium*. We conducted time-calibrated biogeographic analyses and diversification analyses to explore the area of origin and global dispersal history of the tribe. The analysis recovered a temperate North American origin for Vaccinieae approximately 30 million years ago. Tropical diversity of Vaccinieae was inferred to result from multiple, independent movements into the tropics from north-temperate ancestors. Diversification rate increases corresponded to radiation into the Andes and SE Asia. The pseudo-10-locular ovary evolved once in the tribe from the five-locular state, coinciding with the diversification of a major clade that includes most Asian *Vaccinium* and the group from which commercial blueberries are derived (*V.* sect. *Cyanococcus*). A reconstruction from available chromosome counts suggests that a major polyploid event predated the evolution of nearly half the diversity of Vaccinieae. The extent of polyphyly in *Vaccinium* documented here supports the need for a generic reclassification of the tribe.

1. Introduction

Vaccinieae (Ericaceae) is a large tribe of ~35 genera and ~1430 species, consisting of terrestrial or epiphytic shrubs to small trees (Argent, 2019, Stevens et al., 2004, Vander Kloet et al., 2004). Like other ericaceous groups, plants of Vaccinieae prefer acidic soils and in the tropics are predominantly montane (Kron et al., 2002b, Luteyn, 2002). Putative synapomorphies for Vaccinieae include an inferior ovary and

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the presence of anther tubules (Stevens et al., 2004). The group is perhaps best known for temperate crops of the genus *Vaccinium*, including blueberries (*V.* sect. *Cyanococcus*), cranberries (*V.* sect. *Oxycoccus*), and lingonberries (*V.* sect. *Vitis-idaea*).

The tribe is globally distributed with species diversity highest in the American and eastern Asian tropics, but also with a substantial north-temperate component and a few species distributed among Africa, Madagascar, and northern Australia. Thirty genera of Vaccinieae occur in the Neotropics, 28 of which are endemic, and comprise ~700 species (Luteyn, 2002; Fig. 1, Supplementary Table S1, Supplementary Text S1). Most of the Neotropical genera are endemic to the Andean Cordillera. In the Andes, a tendency toward epiphytism coincident with mountain uplift and hummingbird pollination has likely driven adaptive radiation (Luteyn, 2002, Pedraza-Peñalosa et al., 2015, Salinas, 2015). Paleotropical Vaccinieae (including subtropics and the Himalayas) comprise six genera and ~657 species (Argent, 2019, Stevens et al., 2004). North-temperate Vaccinieae comprise species of *Vaccinium* and *Gaylussacia*. Ten of the 61 species of *Gaylussacia* occur in eastern North America with the rest in South America, mainly southeastern Brazil (Sorrie et al., 2009, Ramão, 2010). Fourteen of the 29 sections of *Vaccinium* as currently circumscribed (Vander Kloet and Dickinson, 2009, Argent 2019; Supplementary Table S1) include north-temperate taxa, amounting to ~60 north-temperate species.

Despite the prevalence of Vaccinieae globally, our understanding of its phylogeny is still woefully incomplete. Molecular phylogenetic studies of the tribe have thus far been based on Sanger-based DNA sequence data from two to four genic regions with low sequence variation and taxon sample sizes. Sampling is particularly sparse from the tropics, where most species are endemic. The first and most comprehensive molecular phylogenetic study of the tribe was that of Kron et al. (2002b), who used plastid *matK* and nuclear ITS DNA sequence data with 93 species. Although clade support was generally weak for the major clades, their analysis recovered three Neotropical clades: a "Meso-American/Caribbean Clade," a more extensive "Andean Clade" comprising species mainly from Andean South America but also including some Central American species, and a separate northern South American clade of *Notopora*, *Orthaea*, and *Vaccinium crenatum*. Among the eastern Asian species, the analysis yielded a Southeast Asian "East Malesian Clade" of *Dimorphanthera* and *Paphia*. These genera were early hypothesized to be more closely related to members of Neotropical Vaccinieae than to other Asian members of the tribe (Stevens, 1974, 1985, 2004) and this was supported by their analysis. Another eastern Asian group, comprising *Agapetes* and parts of *Vaccinium* with no clear morphological delimitation between them, has been proposed as an ancestral group from which the rest of the tribe evolved (Sleumer, 1941). Kron et al. (2002b) found this group to form a clade distinct from the rest of Asian Vaccinieae. Among the other findings of Kron et al. (2002b) were the following: (1) two polytypic sections of *Vaccinium* (*V.* sects. *Myrtillus* and *Oxycoccus*) were monophyletic, whereas *V.* sect. *Hemimyrtillus* was recovered as two separate clades; (2) a "Bracteata-Oarianthe" Clade of some tropical Asian species of *Vaccinium* was recovered corresponding to *V.* sects. *Bracteata* and *Oarianthe* sensu Sleumer (1941, 1966–1967) or the corresponding segregate sections of Vander Kloet and Dickinson (2009); and the Asian genus *Costera* was unresolved.

The only other large-scale phylogenetic studies within the tribe have

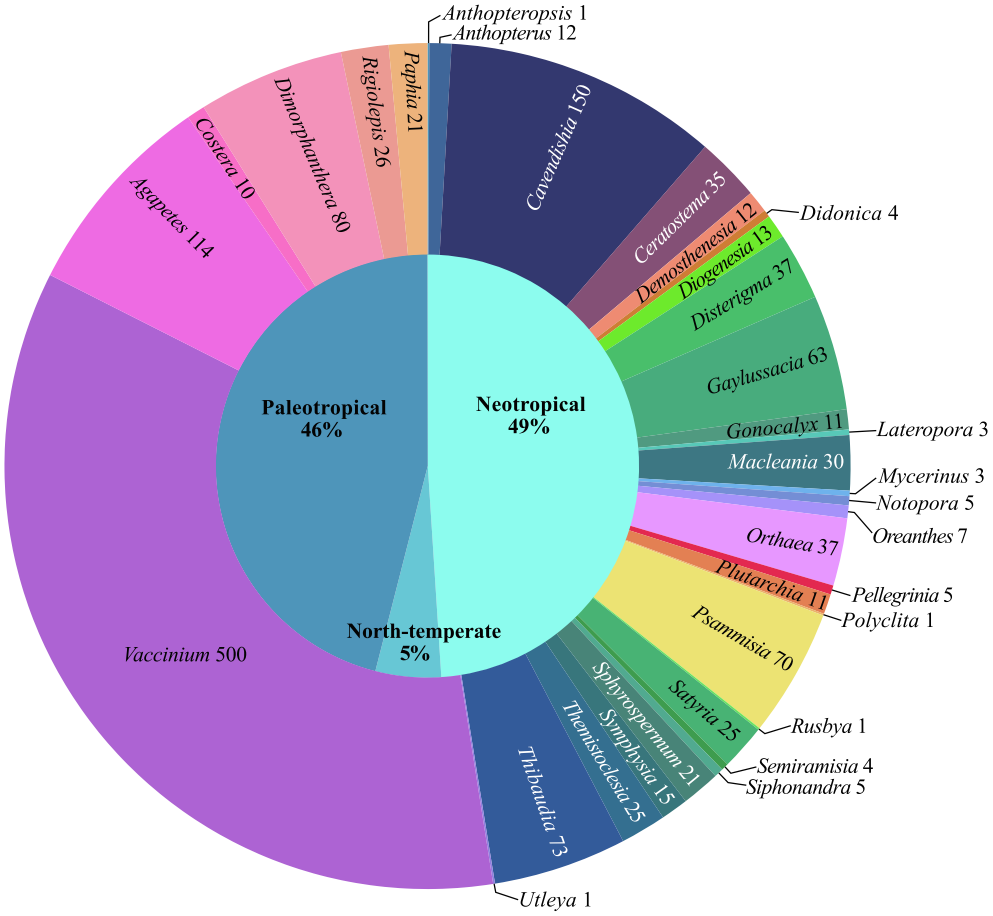

Fig. 1. Species diversity in Vaccinieae by genus and region. See Supplementary Table S1 for details.

focused on the "Andean Clade." Powell and Kron (2003) conducted the first analysis of this clade using plastid *matK*, *ndhF*, *rps4*, and nuclear ITS sequences with 55 species. They found that most of the genera in the clade are not monophyletic and that morphological characters traditionally used to delimit genera in the clade need reevaluation. In their study, seven major clades with strong support were recovered. Pedraza-Peñalosa et al. (2015), also focusing on the Andean Clade, incorporated the data of Powell and Kron (2003) but nearly doubled the number of terminals while reducing the gene sampling to three (*matK*, *ndhF*, and ITS) because *rsp4* was insufficiently variable. They found the same non-monophyly as did Powell and Kron (2003) for most of the Andean genera. They also found strong support for a "Heterandrous and articulate pedicel" clade and a "Homandrous and continuous pedicel clade," although the pedicel character was found to be homoplasious in the tree. Other clades with strong support were a *Satyria* s.s. clade, a *Cavendishia* clade (with also one species of *Thibaudia*), and a *Psammisia* + *Macleania Ceratostema* clade (plus one species of *Thibaudia*).

Here we provide the first phylogenomic analysis of the tribe, with expanded gene and species sampling over previous phylogenetic analyses. We used 256 low-copy nuclear genes with 261 terminals sampled from throughout the genera of the tribe and the sections of *Vaccinium*. Using the resulting topologies as a framework, we explore the evolutionary history of the Vaccinieae, addressing the following questions: (1) What are the major clades of Vaccinieae? (2) Where and when did major dispersal and diversification events take place? (3) How strongly does ovary structure, a character thought to be important in infratribal classification, reflect monophyly? (4) How has fruit color evolved in the tribe? We also offer a general assessment of the degree to which phylogenetic results accord with the current number and circumscription of the genera in the tribe and the sections of *Vaccinium*.

2. Materials and methods

2.1. Taxon sampling

To provide a broad perspective on the evolution of Vaccinieae and assess the extent of polyphyly of *Vaccinium*, we sampled 30 of the 35 genera in the tribe, and 25 of the 29 sections within *Vaccinium* as currently recognized (Vander Kloet and Dickinson, 2009 as modified by Argent, 2019; Supplementary Tables S1, S2). Our sampling includes at least two representatives for small non-monotypic genera sampled and many more for larger groups, including the sections of the large and taxonomically complex genus *Vaccinium*.

The taxonomy of Asian *Vaccinium* has remained uncertain. Sectional boundaries have been loosely defined, treatments have not provided comprehensive lists of taxa included, and many sections are based on poorly defined characters. Stevens et al. (2004) considered *Agapetes* to contain ~400 species and *Vaccinium* 140 species, reflecting their view that many of the Paleotropical members of *Vaccinium* might better be placed in *Agapetes*. This contrasts with the sectional delimitations of Sleumer (1941, 1966–1967) and Vander Kloet and Dickinson (2009) for Paleotropical *Vaccinium*. Insofar as Stevens et al. (2004) considered their view as tentative, we have chosen to follow the most recent treatment (Vander Kloet and Dickinson, 2009) for species diversity estimates of *Vaccinium* and *Agapetes*, as modified by Argent (2019; Supplementary Table S1). We were unable to precisely account for Vander Kloet and Dickinson's (2009) estimates of sectional species diversity within Paleotropical *Vaccinium*, largely because they did not list species under sectional taxon concepts. Therefore, to estimate species diversity in some cases, we referred to previous treatments that specifically assigned species to sections.

Neotropical genera not sampled are *Anthopteropsis* (one species), *Anthopterus* (12 species), *Pellegrinia* (four species), and *Rusbya* (one species; Supplementary Table S1). We were also unable to sample Paleotropical *Rigiolepis* (26 species). Argent (2019) recognized *Rigiolepis* as a genus, whereas Vander Kloet and Dickinson (2009) recognized it as *Vaccinium* sect. *Rigiolepis*. Unsampled sections of *Vaccinium* were all East Asian: *Barandanum* (two species), *Ciliata* (2–10 species), *Epigynium* (11–100 species), and *Neojunghuhnia* (13 species). Whether we included members of *V.* sect. *Galeopetalum* (2–10 species) is uncertain because Vander Kloet and Dickinson (2005) transferred many of its species to *V.* sect. *Calcicolus* but did not mention which species and how many remain in *V.* sect. *Galeopetalum* other than the type, which was not included in our study. We were also unable to distinguish sectional placement of species sampled between *V.* sects. *Nesococcus* and *Euepigynium*: the distinguishing character "ripe ovary exposed at fruiting" for sect. *Nesococcus* (Vander Kloet and Dickinson, 2009) was unclear to us when examining herbarium specimens for this character. Regardless of missing taxa and other uncertainties, we have assembled the largest taxon sampling to date for phylogenetic analysis of Vaccinieae.

Species for the outgroup were chosen from other tribes in subfamily Vaccinioideae and included several genera with excellently preserved fossil fruits and seeds to facilitate divergence-time analysis: Oxydendreae (*Oxydendrum arboreum*), Lyonieae (*Agarista*: nine species; *Craibiodendron*: three species; *Lyonia ovalifolia*), Andromedeae (*Andromeda polifolia*; *Zenobia pulverulenta*), and Gaultherieae (*Chamaedaphne calyculata*; *Eubotrys recurva*; *Leucothoë*: three species; *and Gaultheria*: four species). Two members of subfamily Styphelioideae (*Dracophyllum paludosum* and *Styphelia balansae*), considered the sister group of Vaccinioideae (Stevens et al., 2004), were included to root the tree.

DNA sequence data were derived from three sources. The DNA of most samples was extracted from herbarium specimens with the SLIMS method, a system connecting sampling and wet lab methodology (Folk et al., 2021). Specimens were sampled from the following herbaria (acronyms as in Thiers, updated continuously): FLAS, K, MICH, MO, and NY. Some DNAs (those from P.W.F.) were from silica gel-dried leaf material. The DNA of these samples was extracted with DNeasy®. We quantified DNA amounts of these samples using a Qubit 2.0 fluorometer (Invitrogen, Carlsbad, California, USA) with the Qubit dsDNA Broad Range Assay Kit as per manufacturer recommendations. Finally, some sequence data were generated from the Plant and Fungal Trees of Life project (PAFTOL) and downloaded from GenBank.

The dataset comprised 261 terminals, 233 of which were Vaccinieae and 28 of which comprised the outgroup (Supplementary Table S2). There were 24 species represented by two samples each, and so the total number of species represented in the dataset was 210 for Vaccinieae and 27 for the outgroup, a total of 237 species in the analysis. Duplicate species samples are indicated by one of the two duplicates having a "2" appended to the species name. There were 103 terminals and 86 species of *Vaccinium* represented. Our dataset comprises fairly even sampling across the tribe, with most major clades and groups (genera and sections of *Vaccinium*) represented.

2.2. Sequencing and data processing

Library preparation and target capture were performed at Rapid Genomics (Gainesville, FL, USA) with the Angiosperms353 v1 target capture kit (Johnson et al., 2019) to obtain 353 putatively single-copy nuclear loci from each sample. DNA sequencing was conducted on Illumina sequencing machines (Illumina, San Diego, California, USA) predominantly with 2x150-base pair (bp) chemistry, or occasionally 2x250-bp. Raw sequence data were filtered and adapters removed with Cutadapt v2.6 (Martin, 2011) and FastQC v0.11.9 (Andrews, 2010), with a phred quality score cutoff of 20 (-q 20). Reads were assembled with HybPiper v1.3.1 (Johnson et al., 2016) under default settings. In addition to the standard Angiosperms353 targets, we included available Ericales sequences in the target reference file using the mega353 approach (McLay et al., 2021). Resulting supercontig sequences (introns and exons) were used for subsequent analyses. Putative paralogs were flagged with the *paralog_investigator.py* script in HybPiper. All flagged loci were removed from the dataset, leaving 256 loci for subsequent

analyses.

Individual gene alignments (256 loci; 371 initial samples) and a concatenated gene alignment were constructed with MAFFT v7.245 (Katoh and Standley, 2013). To reduce potential issues with missing data and poorly aligned regions, we removed columns from the individual gene alignments containing >50 % missing data and samples containing >90 % missing data in the concatenated datasets. These quality filtering steps resulted in the final dataset of 261 samples (Supplementary Table S2). Alignments are available from the Dryad Digital Repository:https://doi.org/10.5061/dryad.ksn02v7cr.

2.3. Phylogenetic analysis

A locus-partitioned phylogenetic maximum-likelihood (ML) analysis of the concatenated alignment was performed with IQ-TREE v1.6.9 (Nguyen et al., 2015). The best-fit partitioning scheme was chosen with the PartitionFinder algorithm (*-m TESTMERGE*; Lanfear et al., 2012) implemented in IQ-TREE. A relaxed clustering algorithm was used to only consider the top 10 % of partitioning schemes (*-rcluster* 10; Lanfear et al., 2017). To assess topological support and concordance, 1000 ultrafast bootstrap replicates were performed, and gene concordance factors (gCF) and site concordance factors (sCF) were estimated (Minh et al., 2020). Results for all trees were visualized in FigTree v1.4.4 (Rambaut, 2009).

Individual gene trees were inferred with IQ-TREE. ModelFinder Plus was used to first select the best model for each locus, and the ultrafast bootstrap approximation UFBoot2 (Hoang et al., 2018) was implemented to assess topological support with 1000 replicates, in which sites within loci were resampled. We generated a coalescent-based species tree with ASTRAL-III v5.7.3 (Zhang et al., 2018) using the 256 individual gene trees (after removing putatively paralogous loci). Local posterior probabilities were estimated to provide clade support. In addition to gCF and sCF estimates in IQ-TREE, discordance in our dataset was assessed with PhyParts (Smith et al., 2015), with both the ML and ASTRAL-III topologies as input.

2.4. Divergence time analysis

We used the phylogenetic penalized likelihood method implemented with treePL (Smith and O'Meara, 2012; Supplementary Text S2) on the concatenated topology to estimate divergence times. Analyses were run with the thorough setting and the opt, optad, and optcvad values inferred from standard priming. Smoothing values were inferred from the cross-validation (cv) analysis. Ranges of dates associated with the 95 % highest posterior density (HPD) intervals were estimated for each node, with 1000 bootstrap pseudoreplicates generated from the ML analysis. Replicates were annotated on a maximum clade credibility tree targeting mean node heights with TreeAnnotator v1.8, an application within the program BEAST (Drummond and Rambaut, 2007).

We consider there to be no fossils known to be reliably identifiable as Vaccinieae. We therefore used three fossils from other tribes of subfamily Vaccinioideae as calibration points for divergence time analysis: *Eubotrys* sp. Nutt. (Gaultherieae), *Lyonia danica* Friis (Lyonieae), and *Zenobia fasterholtensis* Friis (Andromedeae), all carbonaceous fossil fruits with seeds from the middle Miocene of western Denmark (Friis,1985). For reasons outlined in Friis (1985), all three fossils are considered to represent close relatives of their extant congeners. Placement of the *Eubotrys* fossil is supported by the combination of (1) a consistent capsular fruit morphology; (2) a spherical-cuneiform seed shape with a straight or slightly curved ventral margin; (3) a prominent, pointed, and regularly shaped hilum; and (4) a reticulate seed testa. With congeners, the *Lyonia* fossil shares (1) the presence of thickened sutures that can break off on the capsule, leaving an indented portion visible on the capsular wall (other genera of Ericaceae can have similar sutures but are not as thickened and do not break off); and (2) similarly shaped seeds with a testa of elongated cells. The capsule of the *Zenobia* fossil is similar to those of other genera in Vaccinioideae, but the combination of the capsule morphology and strongly trapezoidal seeds with pitted testa is unique in the subfamily. Based on these observations, we placed the *Eubotrys* fossil at the crown node of *Eubotrys* and *Chamaedaphne*, the *Lyonia* fossil at the crown node of the clade *Lyonia* + *Craibiodendron* + *Agarista*, and the *Zenobia* fossil at the crown node of *Zenobia* + *Andromeda*. These three fossils have been determined to be of middle Miocene age, i.e., 15.97–11.62 mya (Cohen et al., 2013). Following recommendations by Parham et al. (2012) for fossil calibrations in divergence time analysis, we assigned a minimum age of 11.62 mya to each of the fossils. We considered the inclusion of additional fossils placed in Vaccinieae (e.g., *Juddicarpon* Smith and Manchester; Smith and Manchester, 2019; *Leucothoë nevadensis* Axelrod; Axelrod, 1995) but decided against their use because of uncertainties regarding their identification (Smith and Manchester, 2019, Lu et al., 2019).

We used a fossil-calibrated chronogram of Ericaceae from Lu et al. (2019) to implement a secondary calibration of 30 mya as a maximum age constraint for the stem node of *Chamaedaphne* + *Eubotrys* (but see also results from Rose et al., 2018). In Lu et al. (2019), the stem node of the more inclusive clade (*Chamaedaphne* + *Eubotrys* + *Leucothoë*) was dated to 30 mya, whereas the stem node of *Chamaedaphne* + *Eubotrys* was dated to 27 mya. Therefore, we reasoned that the stem of the *Chamaedaphne* + *Eubotrys* clade should not be older than 30 mya, and we used this age to calibrate the stem node of *Chamaedaphne* + *Eubotrys*.

2.5. Ancestral area analysis

Biogeographic analysis was performed on the chronogram based on the tree from the concatenated analysis. We inferred ancestral ranges with BioGeoBEARS v1.1.2 (Matzke, 2013) using the chronogram generated from the divergence time analysis, except with 18 duplicated sister-species samples excluded. To score geographic distributions of sampled species, we used the maps in Plants of the World Online (https://powo.science.kew.org) as an initial estimate and refined the distributions with the use of taxonomic treatments (e.g., Sleumer, 1941, 1966–1967, Stevens, 1969, 2004, Vander Kloet and Dickinson, 2009; Supplementary Table S3, Supplementary Text S1) and our own expertise of the taxa. Geographic areas were delimited as follows: North America (United States, Canada, and Greenland), Middle America (Mexico through Panama and the Caribbean islands), South America, Africa (including Madagascar), Northern Eurasia (north of 30°N latitude), Central Eurasia (continental Eurasia between 30°N latitude and the southern islands of East Asia including Taiwan), and South Insular Asia (all islands of Southeast Asia east to New Guinea). Australia and islands of the South Pacific, including Hawaii, were not represented by any taxa in this analysis. We did not constrain the potential maximum number of areas occupied, although no taxon in our dataset had a range of more than three areas. Analyses were run under the three biogeographical models available in BioGeoBEARS (DEC, BAYAREALIKE and DIVALIKE) and their respective versions with the jump parameter (+J), which allows for any given taxon to have a geographic state that differs from its immediate ancestor (Matzke, 2013). We recognize the potential problems with the jump parameter (Ree and Sanmartín, 2018). This parameter is nonetheless appropriate for our dataset because the vast majority of the species samples occupy a single biogeographic area (Matzke, 2022).

2.6. Diversification rates

To provide insight into the diversification of Vaccinieae through time, we used Bayesian Analysis of Macroevolutionary Mixtures (BAMM v2.5.0; Rabosky et al., 2014). Duplicate taxa were removed from the chronogram, resulting in an input tree with 209 terminals. To account for incomplete sampling, we estimated a sampling fraction for each of the major clades recovered in our phylogeny (Supplementary Table S4). The analysis was run for 100 million generations with sampling every

10,000 generations. After removing the first 10 % of samples as burn-in, we assessed convergence with effective sample size (ESS) estimates using Coda (Plummer et al., 2006).

2.7. Evolution of polyploidy

To assess the evolution of ploidy in Vaccinieae, we performed a survey of chromosomal counts for the species of the tribe using the Chromosome Counts Database (Rice and Mayrose, 2023), and the data from Hummer et al. (2015) and Redpath et al. (2022; Supplementary Table S5, Supplementary Text S1). We placed species for which there are chromosome counts and which were sampled in our phylogenetic analysis in clades of the ML concatenated analysis (Fig. 2). Species of *Vaccinium* that we did not sample in our phylogenomic analysis, but for which do have counts, were placed into clades either by correspondence to genus or to section of *Vaccinium*. In several instances, the sectional placement of *Vaccinium* species ascribed to samples is uncertain; we indicated these as such and did not attempt clade placement for them.

2.8. Evolution of ovary structure and fruit color

We inferred the evolutionary history of ovary structure and fruit color with the R packages GEIGER (Harmon et al., 2008) and APE (Paradis et al., 2004) based on the concatenated tree obtained from the

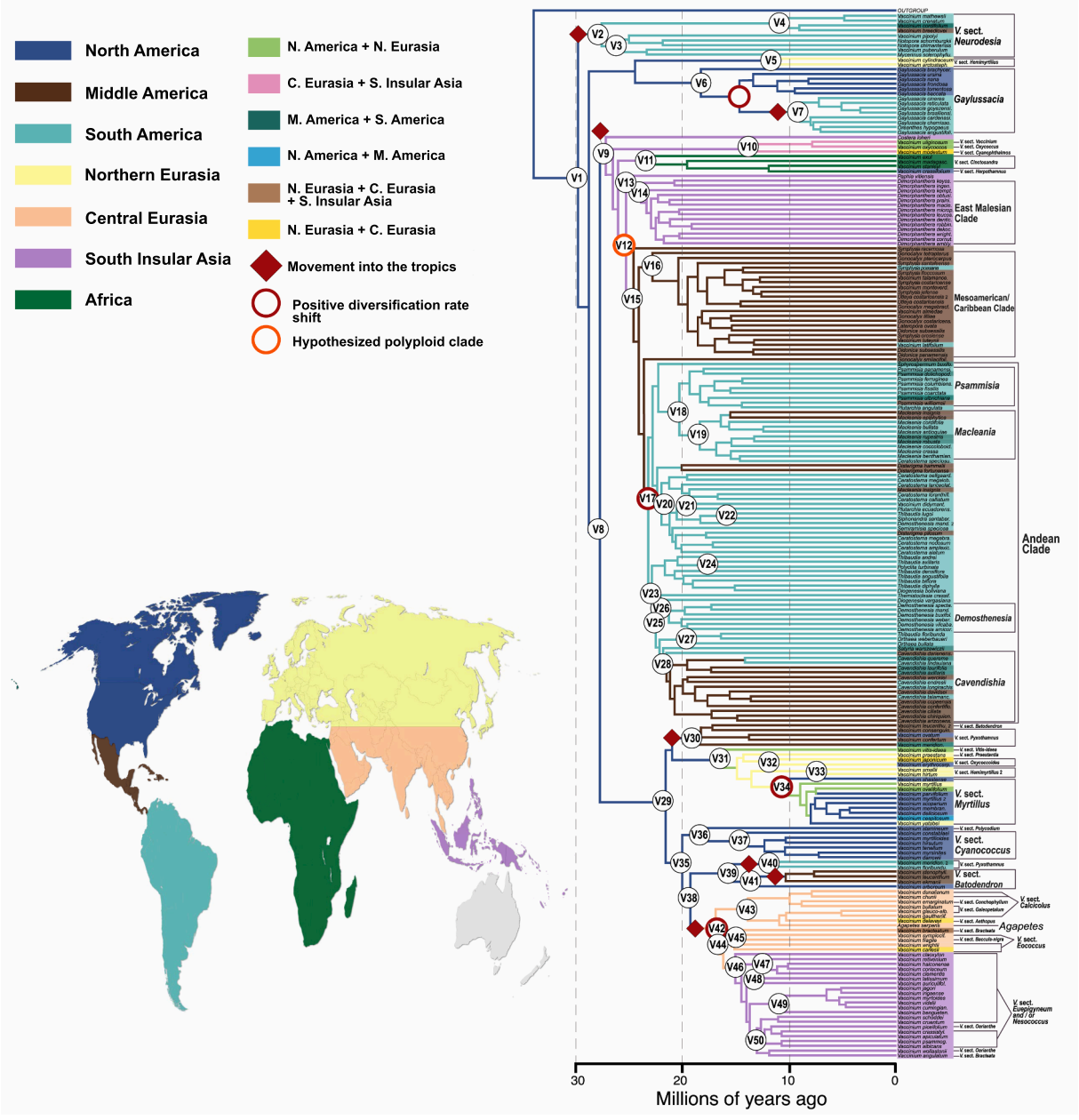

Fig. 2. Chronogram and ancestral area reconstruction of Vaccinieae. The analysis is based on the concatenated dataset. See Supplementary Fig. S4 for full topology including the outgroup, and fossil calibration points. Numbers preceded by a "V" refer to clade designations referenced in text. Names to the right of the species names are informal clade names, often corresponding to genera or sections of *Vaccinium*. Monophyletic species with more than one sample are represented by a single terminal. Colored branches indicate the results of ancestral area reconstruction. Pie diagrams depicting probabilities of geographic range reconstruction for each node can be found in Supplementary Fig. S5. Branches are colored according to the most probable ancestral area state as inferred from node reconstructions. Red diamonds indicate inferred instances of dispersal from temperate regions into the tropics. Support values for relationships can be found in Supplementary Fig. S1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

IQ-TREE analysis. We scored locule morphology and fruit color for Vaccinieae and members of the outgroup based on literature sources, personal observations, and, in rare cases, online sources (Supplementary Table S3, Supplementary Text S1). Each sample was scored for ovary locule structure as one of three discrete categories having either (1) a 4-locular (rare) or 5-locular ovary, (2) a 10-locular ovary, or (3) a pseudo-10-locular (i.e., 5-locular but with each locule containing an incomplete partition extending from the outer locule wall toward the center of the ovary; includes species with pseudo-8-locular ovaries). We could not find information on this character for nine of the samples, and these were excluded from the analysis. We scored fruit color as one of six discrete categories, i.e., (1) brown (generally dry capsules), (2) red, (3) violet (includes blue and black, as in Lu et al. (2019)), (4) white (including translucent), (5) green, or (6) orange (Supplementary Table S3, Supplementary Text S1). We could not find fruit color information on 35 tips in our analysis, and these were excluded from the analysis. *Sphyrospermum xanthocarpum* Pedraza has dark yellow fruits (Luteyn and Pedraza-Peñalosa, 2013) but this species was not sampled in our analysis. The multistate discrete morphological datasets and topology were analyzed under three different classes of models: equal transition rates (ER), with transitions between combinations of states with unique rates that are equal forward and backward (SYM), and transitions between states with rates unique in all directions (ARD).

3. Results

3.1. Phylogenetic analysis based on the concatenated alignment

Bootstrap support in the ML analysis with IQ-TREE based on the concatenated sequence alignment was high throughout the topology, with exceptions at mainly shallower nodes (Fig. 2, Supplementary Fig. S1). As expected on the basis of previous studies, Vaccinieae formed a clade (Clade V1; all clade designations beginning with "V" herein correspond to the crown clades indicated in Fig. 2). Of the genera and sections of *Vaccinium* that are non-monotypic, or that are represented by more than one sample, only a few form clades: *Cavendishia* (V28), *Dimorphanthera* (V14), *V.* sect. *Oxycoccoides* (within V31), *V.* sect. *Myrtillus* (V34), and *V.* sect. *Cyanococcus* (V37). We found *Vaccinium* to be highly non-monophyletic, with members scattered throughout Vaccinieae in clades with other genera.

Four species of the South American endemic *Vaccinium* sect. *Neurodesia* (*V. crenatum*, *V. mathewsii*, *V. pipolyi*, and *V. puberulum*) form a clade with species of *Mycerinus*, *Notopora,* and two Middle American species of *Vaccinium* unplaced to section within the genus (V2); Clade V2 is sister to the rest of the tribe. *Vaccinium crenatum* and *V. mathewsii* form a clade with two unplaced species of *Vaccinium* (V4) and this clade is sister to a clade of the Guayana Highland endemics *V. pipolyi*, *V. puberulum* plus the species of *Mycerinus* and *Notopora* (V3). *Vaccinium arctostaphylos* and *V. cylindraceum*, Madrean members of *V.* sect. *Hemimyrtillus*, form a clade (V5) that is sister to the *Gaylussacia* Clade (V6), which also includes our sample of *Oreanthes*. Clade V6 shows geographic signal, with a South American clade (Clade V7) nested within the North American species sampled. The clade formed by Clades V5 and V6 is sister to the clade comprising the rest of the tribe (V8). Clade V8 is divided into two large clades (V9 and V29).

Clade V9 comprises the following as successive sisters to the remaining members: *Costera loheri*; [*Vaccinium modestum* + *V. oxycoccos* + *V. uliginosum*], representatives of *V.* sects. *Cyanophthalmos* (monotypic), *Oxycoccus* (bitypic), and *Vaccinium* (monotypic; V10); the samples of *V.* sect. *Cinctosandra* (Africa) + *V. crassifolium* of bitypic *V.* sect. *Herpothamnus* (Southeastern U.S.; V11); an "East Malesian Clade" (term from Kron et al., 2002b; V13) comprising *Paphia* as sister to *Dimorphanthera* (V14); the Central American species *Symphysia racemosa*; a "Meso-American/Caribbean Clade" (term from Kron et al., 2002b but also including *S. racemosa* in that work; V16; the Middle American species *Gonocalyx smilacifolius* (Lesser Antilles); and an "Andean Clade" (term as in Kron et al., 2002b, albeit with a number of Middle American species included; V17). *Vaccinium crassifolium* is sister to *V. stanleyi*, one of the African species. The Meso-American/Caribbean Clade (V16) comprises predominantly Middle American species, including many species of *Vaccinium* unplaced to section, the predominantly Middle American genus *Gonocalyx*, and the endemic Middle American genera *Didonica*, *Lateropora*, *Symphysia* (sensu Vander Kloet et al., 2004), and *Utleya*. The subclades of this clade do not correspond uniquely to any non-monotypic genus, and five nodes have low BS support (see Supplementary Fig. S1 for bootstrap values).

Cavendishia is the only non-monotypic genus of the Andean Clade sampled in our study that forms a clade (V28). The other non-monotypic genera of the Andean Clade form clades that also include at least one species of a different genus. The species of *Demosthenesia* form a clade (V26) but one of the two samples of *D. mandonii* groups outside this clade. The species of *Ceratostema* resolve in two clades (V19 and V20), each also including species of various other genera. Species of *Psammisia* form a clade with one species of *Plutarchia* (within V18). *Sphyrospermum buxifolium* is sister to a clade mostly comprising species of *Macleania* and *Psammisia* but which also includes species of other genera. Another species of *Macleania* groups in another clade (V20) that includes species of *Ceratostema, Disterigma*, and one species each of *Demosthenesia, Plutarchia*, *Semiramisia, Siphonandra*, *Thibaudia*, and *Vaccinium.* Clade V23 includes a clade encompassing much of our sampling of *Thibaudia* but also with one species each of *Diogenesia* and *Polyclita*, and another (V25) that includes Central and South American species of various genera. Clade V27 comprises species of *Orthaea* and *Thibaudia*. One species of *Vaccinium*, *V. didymanthum*, unplaced as to section, resolved in the Andean Clade (V21).

Clade V9 is sister to another that comprises the remaining samples of the Vaccinieae (V29). Clade V29 includes our sample of *Agapetes* (in V43) and the vast majority of *Vaccinium* species in our study, only some of which form clades that correspond to currently recognized sections. Clade V30 comprises *Vaccinium* species of *V.* sects. *Batodendron* and *Pyxothamnus*, albeit with low support (BS = 56 and 65). This clade is sister to a clade (V31) that comprises, as successive sister clades, monotypic *V.* sect. *Vitis-idaea*, [*V. praestans* of monotypic *V.* sect. *Praestantia* + bitypic *V.* sect. *Oxycoccoides*], northeastern Asian members of *V.* sect. *Hemimyrtillus* (V33), and *Vaccinium* sect. *Myrtillus* (V34). The bulk of Clade V31 comprises north-temperate species. The remaining species of the tribe form a large clade comprising a mixture of North American, Middle American, and most Asian *Vaccinium* in our analysis. Clade V36 is a North American clade comprising *V. stamineum* (of monotypic *V.* sect. *Polycodium*) and a clade of *V.* sect. *Cyanococcus* (V37). Clade V36 is sister to Clade V38, comprising a clade of more species of *V.* sects. *Batodendron* and *Pyxothamnus* (V39) that is sister to a clade of our sample of *Agapetes* plus the bulk of Asian *Vaccinium* in our analysis (V42).

Clade V42 comprises subclades that generally correspond only weakly to sections. Clade V43 comprises two subclades of *Vaccinium* species in *V.* sects. *Aethopus*, *Calcicolus*, *Conchophyllum*, and *Galeopetalum* and includes our sole sample of *Agapetes*. This clade is sister to Clade V44, which comprises species from various Asian sections of *Vaccinium*: *V.* sects. *Baccula-nigra, Bracteata*, *Eococcus, Euepigyneum*, *Nesococcus*, and *Oarianthe*. Within V44, Clade V49 comprises species endemic to the Philippines except for *V. myrtoides*, which also occurs in the Moluccas and Sulawesi. Species that we consider included in either of the poorly differentiated sections *V.* sect. *Euepigyneum* or *V.* sect. *Nesococcus* resolve in various clades within Clade V46.

3.2. Species-tree phylogenetic analysis

The species tree from the ASTRAL-III analysis (Supplementary Fig. S2) recovered clades generally similar to those from the concatenated dataset but with lower overall support. Key differences include the following, also depicted in Supplementary Fig. S3.

The placement of species of various genera within the Mesoamerican/Caribbean and Andean clades differs between the species tree and the ML-concatenated tree. For example, in the Mesoamerican/Caribbean Clade, two samples of *Utleya costaricensis* of monotypic *Utleya* form a clade in the species tree (PP = 1.00) but are separated in the concatenated topology, with one sample resolving in a clade with species of *Symphysia* and *Vaccinium* (BS = 86) and the other resolving in a clade with *Gonocalyx megabracteolatus* (BS = 100); the latter clade is sister to a clade that includes *Symphysia* + *Vaccinium* + the other sample of *Utleya costaricensis*.

In the concatenated tree, *Vaccinium* sect. *Neurodesia/Notopora/Mycerinus* forms the first-diverging clade within the tribe, with *Gaylussacia/Oreanthes* + *V.* sect. *Hemimyrtillus* (in part) as the next-diverging clade. In the species tree, *V.* sect. *Hemimyrtillus* (in part) forms the first-diverging clade followed by *Gaylussacia/Oreanthes* as the next-diverging clade, with *V.* sect. *Neurodesia/Notopora/Mycerinus* grouping farther up in the tree.

In the concatenated tree, *Costera loheri* resolves as sister to the clade comprising *Vaccinium* sects. *Vaccinium/Oxycoccus/Cyanophthalmos*, the African clade, the East Malesian Clade, the Mesoamerican/Caribbean Clade, and the Andean Clade (BS = 100). In the species tree, it resolves as sister to the clade that consists of only *V.* sects. *Vaccinium/Oxycoccus/Cyanophthalmos* (PP = 0.39). In the concatenated tree, Clade V2 (*V.* sects. *Neurodesia/Notopora/Mycerinus*) resolves as sister to the rest of Vaccinieae, whereas in the species tree it resolves as sister to the clade comprising the African Clade, *V.* sect. *Cinctosandra*), *V.* sects. *Vaccinium/Oxycoccus/Cyanophthalmos*, the East Malesian Clade, the Mesoamerican/Caribbean Clade, and the Andean Clade (PP = 0.82).

Two samples each of *Vaccinium meridionale* and *V. leucanthum* are split in the concatenated tree between Clades V30 (mostly species of *V.* sect. *Pyxothamnus*) and V39 (mostly species of *V.* sect. *Batodendron*); BS support within V39 is high at all nodes but low in Clade V30. In the species tree, the sample of *V. meridionale* is placed in the *V.* sect. *Pyxothamnus* clade, whereas in the concatenated tree (V30) it is placed as sister to a clade (PP = 0.06) that includes the other sample of *V. meridionale* and species of *V.* sect. *Batodendron* (V39). Both samples of *V. leucanthum* are placed in the *V.* sect. *Batodendron* clade (V39 in the concatenated tree; PP = 1.0 at the ancestral node of each sample) in the species tree, whereas in the concatenated tree one sample of *V. leucanthum* is placed in the *V.* sect. *Pyxothamnus* clade (V30). In the species tree, *V. consanguineum* is placed as sister to the clade formed by *V.* sects. *Myrtillus/Hemimyrtillus 2/Vitis-idaea/Praestantia/Oxycoccoides* and the clade comprising *V. confertum* + *V. ovatum*. In the concatenated tree, *V. consanguineum* was found to be nested in *V.* sect. *Pyxothamnus*, sister to *V. leucanthum*.

3.3. Analyses of divergence times, ancestral areas, and diversification

The chronogram from the divergence time analysis (Fig. 2, Supplementary Fig. S4) yielded a date of 29.5 mya for crown-node Vaccinieae (95 % HPD 21.5, 35.6). Estimated ages at the three fossil-calibrated nodes were older than their respective age calibrations by ~4–25 million years. Other notable dates are addressed in the Discussion.

Standard log-likelihood and AIC statistical comparisons indicate that the best-fitting model for the ancestral area analysis was DEC+J (Supplementary Text S3). Results indicate that the ancestral area of Vaccinieae with the highest probability was North America (Fig. 2, Supplementary Fig. S5). Additionally, most of the deeper nodes in the topology infer North American ancestry as well (e.g., Clades V8, V29, V35, and V38). Seven major dispersals into the tropics from temperate North America were inferred (red diamonds, Fig. 2): (1) to South America from node V1 to node V2; (2) to South America within *Gaylussacia/Oreanthes* (V7); (3) to South Insular Asia from node V8 to node V9 (and subsequent dispersal within this clade from South Insular Asia to Middle America, and then from Middle America to South America); (4) to Central Eurasia from node V38 to node V42, and then from Central Eurasia to South Insular Asia from node V44 to V46; (5) to Middle America from nodes V29 to V30, giving rise to members of *V.* sects. *Batodendron* and *Pyxothamnus*; (6) to South America from node V39 to node V40, giving rise to other members of *V.* sect. *Pyxothamnus*; and (7) to Middle America within Clade V41 (and then to South America along the branch to *V. stenophyllum*). The African clade dispersed from South Insular Asia. Several dispersals were inferred between North America and Eurasia (V5, V10, within V31).

Clades generally clustered according to geographic region. Clade V2 comprises mainly South American species, with a subclade consisting exclusively of endemics to the Guayana Highland region. South American species of *Gaylussacia* + *Oreanthes* form a clade (V7) that is nested within North American *Gaylussacia*. Clade V10 is north-temperate/Himalayan/northern polar, and African species cluster together (V11). *Dimorphanthera* groups with *Paphia*, both of which are South Insular Asian (V13). Clade V16 comprises mostly Middle American species. The Andean Clade (V17) comprises mainly South American species, albeit with several movements within that clade into Middle America, especially involving *Cavendishia* (V28). Clades V30 and V39 comprise mostly Middle American and South American *Vaccinium*. *Vaccinium* sect. *Myrtillus* (V34) is mainly north-temperate circumboreal with presumed dispersal to several Pacific island groups, and *V.* sect. *Cyanococcus* is temperate-North American (V37). Clade V42 comprises Asian *Vaccinium* and *Agapetes* and is divided by region, with Clades V43 and V45 primarily Central Eurasian and V46 South Insular Asian. Clade V49 comprises Philippine endemics except for the more widespread *V. myrtoides*. Notable exceptions to the trend of clustering by region include the various occurrences of South American species in Clade V16 and Middle American species in V17, North American *V. crassifolium* in the otherwise African Clade (V10), and the North American *V. ovatum* and *V. arboreum* resolving with Middle American and South American species in Clades V30 and V39, respectively.

The backbone branching of Vaccinieae experienced an elevated rate of diversification (Myr^{-1}) (0.55) ~30 mya, decreasing to 0.31 ~24 mya, 0.31 ~20 mya, and decreasing again to 0.02 near most tips except for the following (Fig. 3). Notable upward shifts in diversification rate were recovered in four clades across Vaccinieae: the Andean Clade (V17), Central Eurasian and South Insular Asian *Vaccinium/Agapetes* (V42), *V.* sect. *Myrtillus* (V34), and within *Gaylussacia* (one node above the crown node V6). In the Andean Clade, the highest diversification rate, 1.2, reflects branching near the crown of the clade, aligning with 23–17 mya, and slows to 0.31 ~17 mya and finally to 0.21–0.13 within 14–0 mya, during which time there is little additional branching. For the Central Eurasian and South Insular Asian *Vaccinium/Agapetes* clade, diversification rate is highest at 0.55 at branching near the crown between 17–14 mya, slows to 0.31 ~10–5 mya, then to its lowest point, 0.2, between 5–0 mya. Branching between the stem and crown nodes of *V.* sect. *Myrtillus* coincides with a rate shift from 0.08 to 0.40 ~17 mya, which decreases gradually to 0.28 near the tips of the topology. Similarly, the branch above crown-node *Gaylussacia* ~16 mya coincides with a rate shift from 0.13 to 0.40, which decreases gradually to 0.25 near the tips of the topology.

3.4. Evolution of polyploidy

From our survey of ploidy in Vaccinieae ($x = 12$), we compiled data for 120 species of Vaccinieae, including 94 species of *Vaccinium*. The majority of the species for which there are counts are of relatively well studied north-temperate/northern polar species such as *V.* sect. *Cyanococcus* (V37). Thirteen of the 35 genera in Vaccinieae have been assessed for ploidy level. Most counts of species in genera other than *Vaccinium* are few (<five species per genus).

We found polyploidy in *Agapetes*, *Cavendishia*, *Dimorphanthera*, *Diogenesia*, *Disterigma*, *Gaylussacia*, *Gonocalyx*, *Macleania*, *Paphia*, *Satyria*, *Sphyrospermum*, *Symphysia*, and *Vaccinium* sects. *Cyanococcus*, *Hemimyrtillus*, *Myrtillus*, *Oarianthe*, *Oxycoccus*, *Pyxothamnus*, and *Vaccinium*.

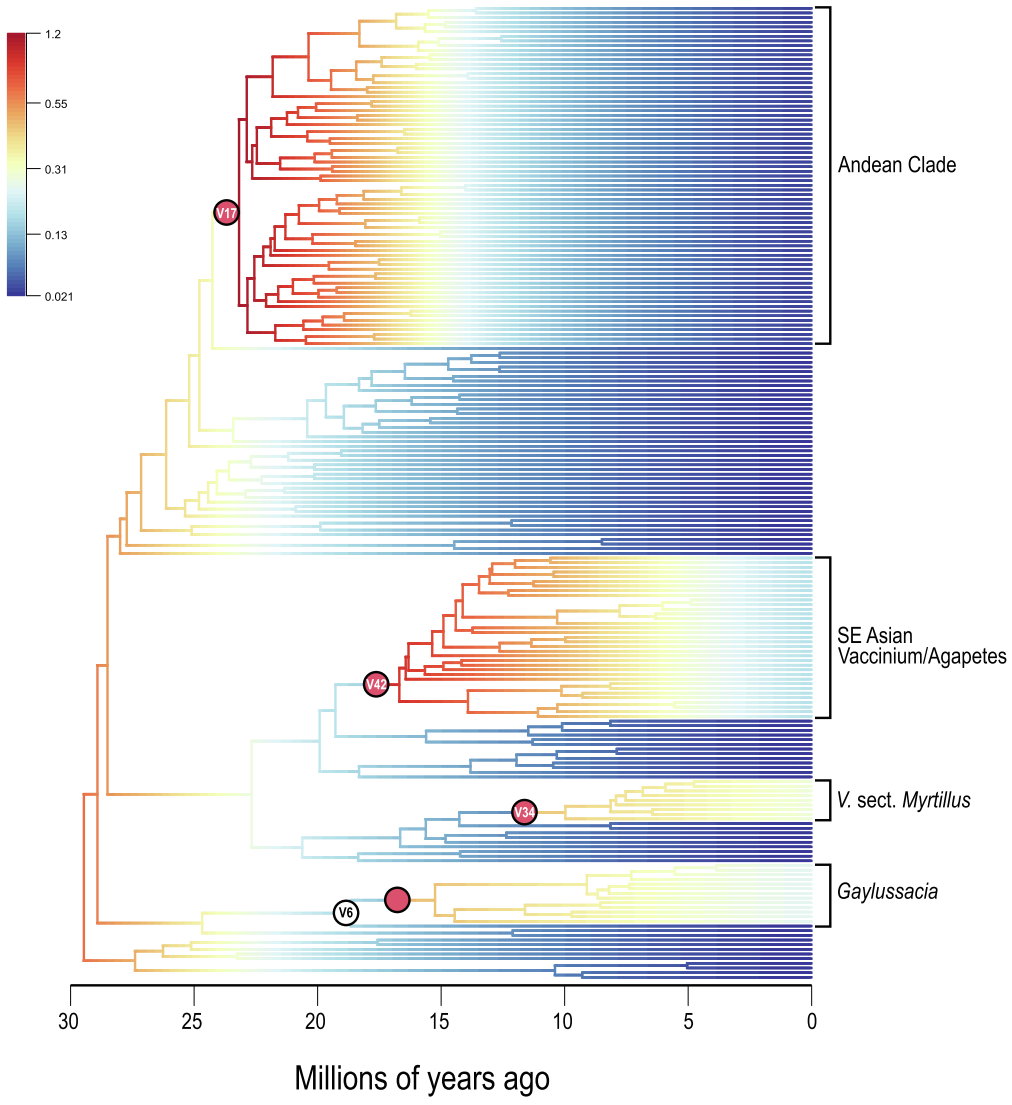

Fig. 3. Diversification rates of Vaccinieae. Red circles indicate significant upward shifts in diversification rates, and colors indicate diversification rate. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Among *Cavendishia*, *Dimorphanthera*, *Diogenesia*, *Disterigma*, *Gonocalyx*, *Macleania*, *Paphia*, *Sphyrospermum*, and *Symphysia*, all of which are included in Clade V9 (>1000 species) and include the East Malesian Clade, Mesoamerican/Caribbean Clade, and Andean Clade, only polyploids were found. The highest levels of ploidy in the tribe occurred in Neotropical members of this clade: 13*x* in *Disterigma*, 8*x* in *Macleania*, and 8*x* and 11*x* in *Sphyrospermum*.

The rest of the polyploids in the survey were scattered in taxa that also included diploids: *Agapetes*, *Gaylussacia* and *Vaccinium* sects. *Cyanococcus*, *Hemimyrtillus*, *Myrtillus*, *Oarianthe*, *Oxycoccus*, *Pyxothamnus*, and *Vaccinium*. Except for one tetraploid sample each of *Agapetes* (*A. flava*; Himalaya), *V.* sect. *Oarianthe* (*V. densifolium*; New Guinea), and *V.* sect. *Pyxothamnus* (*V. meridionale*), these polyploids fall in north-temperate/northern polar clades of the tribe.

3.5. Evolution of ovary structure and fruit color

Log-likelihood ratio and chi-square tests in GEIGER yielded the ER model as best fit to the ovary character dataset, and the ARD model as best fit for the fruit color dataset (Supplementary Text S4). The analysis over the corresponding topology inferred a single shift from the 4- or 5-locular condition to the pseudo-10-locular condition along the branch between nodes V29 and V35 of Fig. 2 and resulting in the pseudo-10-locular condition characterizing *Vaccinium* sects. *Cyanococcus*, *Polypodium*, and parts of *Pyxothamnus* and *Batodendron*, as well as *Agapetes* and the large Asian *Vaccinium* clade (V42; Fig. 4). A single shift from the 4- or 5-locular condition to the 10-locular condition occurred along the branch subtending node V6, the crown node of *Gaylussacia*.

Fruit color reconstruction yielded 75 % probability for red and 25 % for blue at crown-node Vaccinieae (V1 in Fig. 2; Fig. 4). We infer shifts from red to blue in various parts of the tree including *Gaylussacia* (V6), the clade including African *Vaccinium* and *V. crassifolium* (V11), the Mesoamerican/Caribbean (V16) and Andean (V17) clades, part of *V.* sect. *Myrtillus* (V34), and Clade V35. One shift from red to white and one from white to green occurred in the Andean Clade. A shift from white to either red or blue occurred in one clade of *Macleania*.

4. Discussion

Although species relationships varied slightly between the concatenated and species-tree topologies, the overall topologies (genus-level and broader relationships) were consistent. We therefore focus our

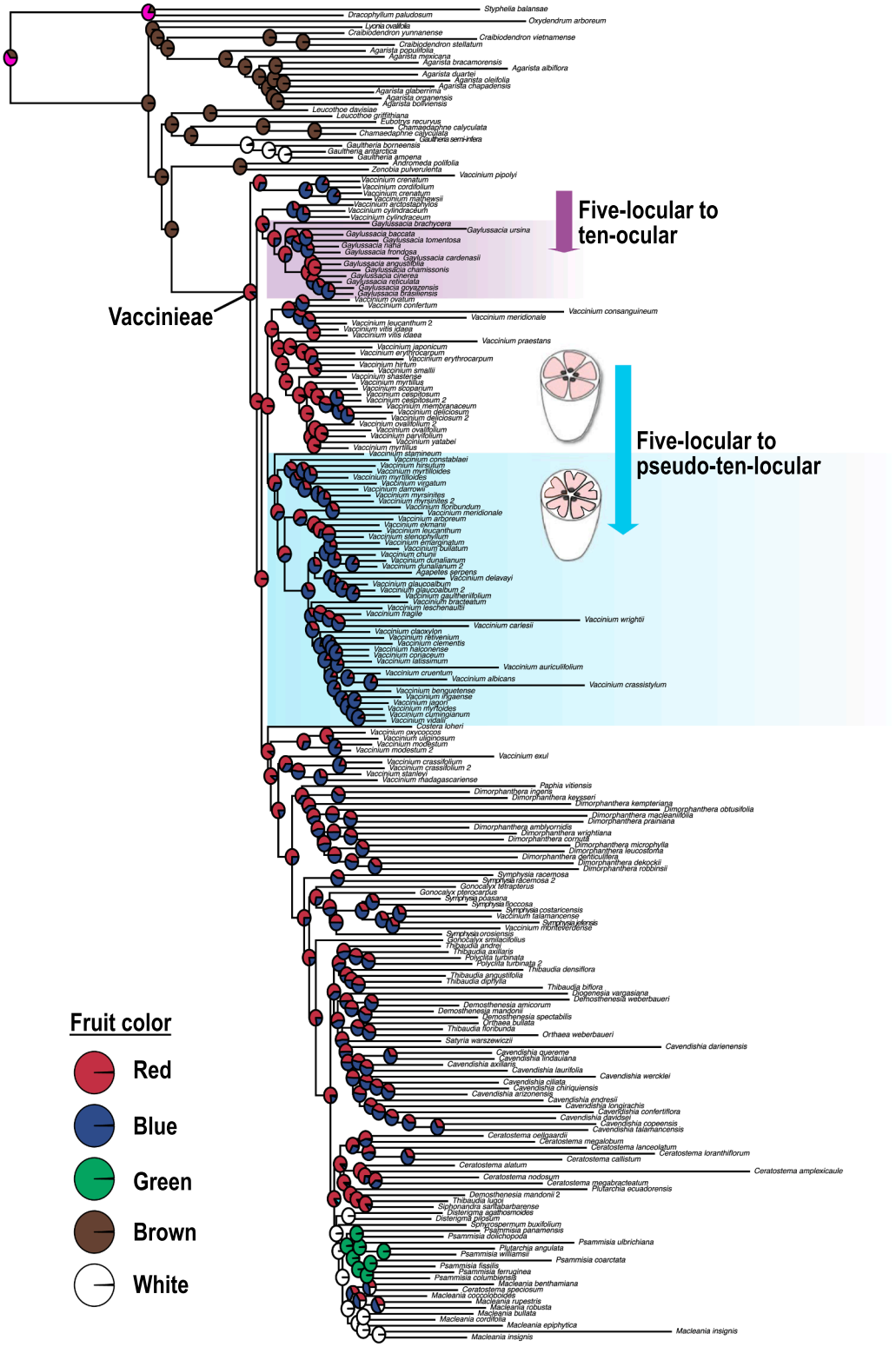

Fig. 4. Ancestral state reconstruction of ovary morphology and fruit color. The analysis was conducted over the best maximum-likelihood tree based on the concatenated dataset (Supplementary Fig. S1). Pie diagrams at nodes depict probabilities of fruit color states for each ancestor. The transition from 5-locular to pseudo-10-locular ovaries corresponds to the branch between nodes V29 and V35 in Fig. 2, and the transition to 10-locular ovaries corresponds to the branch subtending node V6 in Fig. 2.

presentation and discussion of downstream analyses (biogeography, divergence time, and diversification) on the results from the concatenated topology.

4.1. Classification

We recovered a strongly supported tribe Vaccinieae, in line with expectations based on morphology and prior phylogenetic work (Kron et al., 2002a,b, Stevens et al., 2004). We found evidence for the non-monophyly of most of the genera ($n = 14$) in the tribe for which we sampled multiple species. *Vaccinium* itself is non-monophyletic, with seven other genera recovered as sisters to clades that include *Vaccinium*, generally concordant with previous phylogenetic results based on two to four genic regions (Kron et al., 2002b, Powell and Kron, 2003, Pedraza-Peñalosa et al., 2015). The non-monophyly of *Vaccinium* likely can be partly explained by placement of its species into newly formed or resurrected genera of the tribe, but without full consideration of other species left in the genus as a result. For example, *Symphysia* has been resurrected by Vander Kloet et al. (2004) to accommodate some Middle American species with green flowers despite the fact that many other Middle American species, such as *V. breedlovei*, have remained in a residual *Vaccinium*, without clear sectional placement; another example is the Peruvian species *V. didymanthum*, which has remained unplaced in any section. The more general problem is that *Vaccinium* itself is not defined on any clear morphological set of characters. For example, traditionally *Agapetes* and *Vaccinium* are separated by long versus short corolla lengths. It has long been understood that there is much overlap in this character and that it is not reliable by itself for the placement of species in either genus (Sleumer, 1941, Stevens, 2004). Yet, reliable characters have not been found to separate them, although several anatomical characters may be informative to some degree in this regard (Stevens, 1969). Many non-monotypic sections of *Vaccinium* were revealed to be non-monophyletic as well. Our analyses recovered monophyly for *V.* sects. *Cynaococcus* and *Myrtillus* but non-monophyly for *V.* sects. *Batodendron*, *Hemimyrtillus*, *Neurodesia*, *Pyxothamnus*, and various Asian sections resolving in Clade V42 of Fig. 2 (*Bracteata*, *Calcicolus*, *Eococcus*, *Euepigyneum*, *Galeopetalum*, *Nesococcus*, and *Oarianthe*).

The vast majority of non-monophyly across the tribe involves tropical genera. This is fundamentally a problem caused by the insufficient study of these lineages, leading to poor taxonomic concepts. For example, the heat map resulting from a search for *Vaccinium* on the Global Biodiversity Information Facility (gbif.org) returns a disproportionately large number of north-temperate accessions relative to known species diversity in the genus.

Most genera of the Mesoamerican/Caribbean and Andean clades of Vaccinieae were found to be non-monophyletic (sometimes rampantly so) in our study. Similar results have been obtained in previous studies based on plastid and nuclear ITS Sanger sequence data and largely different species samples (Kron et al., 2002b, Powell and Kron, 2003, Pedraza-Peñalosa et al., 2015). The strongly different species sampling among the studies thus far conducted on these clades, combined with low support in many clades in the Sanger sequence-based works, limits the conclusions that can be drawn regarding classification. Nonetheless, a notable area of concordance among the studies is the close relationship between *Cavendishia* and *Satyria* (the "Heterandrous and articulate pedicel" clade in Pedraza-Peñalosa et al., 2015), albeit in our study only a single sample of *Satyria* was included. Another clear area of concordance across all studies is the recovery of a Mesoamerican/Caribbean clade ("Mesoamerican" in Pedraza-Peñalosa et al., 2015) as sister to the Andean Clade. Although all studies have disparate species sampling, they are consistent in their unique placement of the samples of *Gonocalyx*, *Symphysia*, and *Utleya* in the Mesoamerican/Caribbean clade. Various species of other genera appear in this clade across studies, suggesting that geography is a stronger predictor phylogeny than generic classification. In extrapolating this finding to the non-monophyly of most of the other genera in the Andean Clade, it is clear that much more systematic research is needed on this complex group of plants.

4.2. Historical biogeography and diversification rates

We infer a North American origin for Vaccinieae. These results support the hypothesis of Kron et al. (2002b) and Kron and Luteyn (2005) that Vaccinieae radiated into the tropics from north-temperate origins and refute the opposing hypothesis of Sleumer (1941) that the group originated in the Asian tropics. We find four separate north-temperate/northern polar clades of *Vaccinium* (Clades V5, V10, V31, and V36), supporting previous findings that Vaccinieae of these northern regions do not form a single clade (Kron et al., 2002b, Kron and Luteyn, 2005).

Two clades corresponding to *Gaylussacia/Oreanthes* and *Vaccinium* sect. *Myrtillus* experienced an upward shift in diversification rate, likely the result of long-distance dispersal and radiation into tropical regions (Brazil in *Gaylussacia*, and Hawaii in *V.* sect. *Myrtillus*). In *Gaylussacia*, this rate shift coincides with the evolution of the 10-locular ovary from the 5-locular state, apparently a unique shift within Vaccinieae.

The following discussion focuses primarily on terrestrial dispersal corridors for Vaccinieae lineages in light of our ancestral range reconstruction results, although *trans*-oceanic long-distance dispersal is apparent in this group as well. The species of the tribe bear fleshy fruits that attract frugivorous birds indiscriminately. Some fruits have seeds that survive digestion and/or have sticky mucilage that adheres to birds externally (J.L.L., unpubl. results). Some birds with wide geographic ranges must have served as dispersal vectors for Vaccinieae. This is apparent from the presence of *Vaccinium* species endemic to Hawaii, which appear to have dispersed from temperate circumboreal regions (A.L.B. et al., unpubl. results). Conversely, short-distance flying birds (and perhaps other animals, such as spectacled bears in the Andes) apparently served as dispersal vectors for many tropical members of Vaccinieae, as we observe that many tropical groups inhabit relatively narrow geographic ranges.

The geographic range of Vaccinieae largely corresponds to an *amphi*-Pacific tropical pattern of distribution (Raven and Axelrod, 1974). The largest portions of its diversity occur in the tropical regions of the Americas and East Asia, albeit in our results one clade includes species of tropical Africa as well. Although several hypotheses have been raised to explain this type of distribution, our results align with a scenario beginning with Northern Hemisphere expansion in the early Cenozoic (65–35 mya), followed by southward migrations (Tiffney and Manchester, 2001). During progressive global cooling and drying beginning roughly in the Oligocene ~38 mya, many plant lineages adapted to tropical-like conditions in the Northern Hemisphere moved southward to tropical America and tropical East Asia, with only a few lineages colonizing or persisting in Africa because of aridification (Tiffney and Manchester, 2001). Our divergence time and biogeographical analyses indicate several southward movements occurring between ~30–15 mya, which align well with the southward-migration hypothesis. Kron and Luteyn (2005) also suggested that the Vaccinieae (along with other members of Ericaceae) are "Laurasian" (versus Gondwanan) in origin.

The same type of tropical montane habitat that supports so much of the species diversity of Vaccinieae also occurs in Africa. The small representation of Vaccinieae occurring in Africa today (~seven species) supports this hypothesis as well, although the species diversity in Madagascar appears to be substantially underestimated (P.W.F., unpubl. results). Under this scenario, the African species, which diverged relatively early in the history of Vaccinieae (~27–25 mya), could merely be what has remained after most lineages that colonized Africa became extinct during the drying period (Tiffney and Manchester, 2001).

An alternative hypothesis of widespread tropical origins followed by vicariance would predict predominantly northward movements (Tiffney and Manchester, 2001), of which we observe few. These were recovered

in localized regions and relatively recently dispersed (e.g., in Clade V28). The three fossils we used were outside of Vaccinieae (see Section 2.4), all of which dated to the middle Miocene. It is unfortunate that there are no reliably identified fossils of Vaccinieae to further test these hypotheses.

Analysis of the concatenated dataset resulted in a phylogeny with a high proportion of long terminal branches compared to internal branches (Fig. 2). To investigate this and test for data artifacts that may have caused this pattern, we ran numerous analyses exploring missing data, model misspecification, and assembly errors. None changed the ratio of terminal:internal branch lengths (results not shown). Because we failed to find a data-related reason for this result, we suggest these long terminal branch lengths likely result from sampling degraded tissue from herbarium specimens or sampling relatively few taxa across this enormous clade. Results of divergence time estimates, however, should be taken as hypotheses and verified in future studies.

4.2.1. Neotropical historical biogeography

Dates of the uplift of the Andes have been debated, from rapid pulses of uplift suggested during the Miocene to a gradual uplift since the Eocene, with a major burst in the last 20 million years (Gregory-Wodzicki, 2000, Garzione et al., 2008, Pérez-Escobar et al., 2022). These events were thought to have played major roles in the diversification of various plant groups (Antonelli et al., 2009, Pérez-Escobar et al., 2022). Our estimated age of node V17, 23.2 mya (95 % HPD 17.0, 27.1) and coinciding with a dispersal from Mesoamerica to South America along its subtending branch, aligns well with the tectonic activity ~20 mya and also shows an increase in diversification rate. Our age for this node is similar to ages recovered for other high-elevation Andean groups (Leubert and Weigend, 2014). Our results also support the hypothesis of Luteyn (2002), who, based on the high diversity of ericaceous groups thriving in the montane regions of Central and South America, suggested that Neotropical Ericaceae had already been adapted to temperate environments at the time of the Andean uplift.

Our results showing increased diversification in the Andean Clade also support the hypothesis of Luteyn (2002) of adaptive radiation in Andean Vaccinieae. Luteyn (2002) considered Andean diversification to be driven by a combination of life-form plasticity, colonization abilities, adaptation to epiphytic habits, and coevolution with hummingbirds as pollinators. The exaptation of cold tolerance in Andean Vaccinieae was thought to allow species to easily fill open niche space at higher elevations than in their putative temperate ancestral home. Another possible exaptation resulting in diversification in Andean Vaccinieae is the specialized mycorrhizal association in the group (and most members of Ericaceae). Like many orchid groups, this may have opened niche space as epiphytes in montane forests (Cairney and Ashford, 2002, Martos et al., 2012). A phylogenetic study of mycorrhizal associates of Vaccinioideae suggests comigration from North America to the Neotropics (Setaro and Kron, 2011). These ideas on the drivers of diversification in Andean Vaccinieae can now be further tested in the context of our results.

Within *Vaccinium*, our sampled species of *V.* sect. *Neurodesia* were found to group with species of *Notopora, Mycerinus*, and *Vaccinium* (V2). All these species are endemic to the Guayana Highland region, specifically the Pantepui area. Our analysis dates this clade to ~27.4 mya, an age predating but near that of the Andean uplift (Gregory-Wodzicki, 2000, Garzione et al., 2008, Pérez-Escobar et al., 2022) and before the emergence of most of Vaccinieae. The Pantepui area, with its many isolated tabletop mountains, harbors many endemic species (and genera) of plants that tend to represent early-diverging lineages of many plant families (Berry and Riina, 2005). Our early date for the divergence of this portion of Vaccinieae accords with this trend. Species of *Thibaudia* and *Orthaea* (Vaccinieae) endemic to this area (not sampled) share the presence of anther disintegration tissue with species of *V.* sects. *Neurodesia*, *Notopora*, and *Mycerinus* (Luteyn, 1987; J.L.L., unpubl. results). This character is thought to be ancestral in the tribe, thus providing putative morphological support for the early evolution of the group.

Gaylussacia, with 14 of 69 species sampled, is disjunct between South America (mainly Brazil) and Eastern North America. It is distinguished from other members of Vaccinieae in having a 10-locular ovary, as distinct from a 5-locular or pseudo-10-locular ovary. Camp (1941) proposed a Brazilian origin for the group based on a center-of-diversity concept, but our results instead yield movement into the tropics from temperate North America. Diversification analysis reveals a rate increase at the crown node above the first split in *Gaylussacia*, above *G. brachycera* of eastern North America. Although this increase encompasses the nine other North American species of *Gaylussacia*, the vast majority of species in the genus occur in the Cerrado and Atlantic Rain Forest regions of Brazil, both major biodiversity hotspots that harbor some of the most diverse habitats in the world (Myers et al., 2000). We suggest that speciation in *Gaylussacia* was driven by the dissected topography in the Cerrado (Colli et al., 2020) and benefited from the historical forest refugia and relative stability of the Atlantic Rain Forest (Carnaval and Moritz, 2008).

Movement is inferred from Middle America to South America at the beginning of the Miocene (V15–V17), then back to Middle America by node V28 and then again to South America in *Cavendishia* in the early to middle Miocene, well before the final rise and continuity of the Isthmus of Panama ~3 mya (O'Dea et al., 2016). Current consensus generally points to ages that predate the continuity of the Isthmus of Panama for the Great American Biotic Interchange between Central and South America (15–10 mya), with which our recovered ages for these events align more closely (Bacon et al., 2015, Erkens, 2015, Montes et al., 2015, Dick and Pennington, 2019). The findings of Kron and Luteyn (2005) based on the phylogenetic results of Kron et al. (2002a) of a widespread origin of the Andean Clade in the mountains of the Andes, Central America, and the Antilles is not supported by our data. Their conclusions may have been affected by low species and gene sampling relative to those in our study. Conversely, their results that support some taxa currently found in Central America (*Cavendishia*, *Satyria*) as recent "back-dispersals" to Central America from the Andes are supported by our data. In our study, the *Cavendishia* Clade (V28) was found to have evolved ~21.7 mya (95 % HPD 16.0, 25.6), within which were inferred several such back-dispersals to South America.

4.2.2. Paleotropical and north-temperate historical biogeography

Dispersals inferred along the branches between nodes V8 and V9 at ~28.0 mya (95 % HPD 20.1, 32.9) mya, and between nodes V38 and V42 at ~16.7 mya (95 % HPD 13.0, 22.2), highlight biogeographic connections between North America, Central Asia, and South Insular Asia, which mirror well-studied histories of many angiosperms with East Asia-North America disjunctions (Wen, 1999). One such movement that gave rise to all Central Eurasian and South Insular Asian *Vaccinium* and *Agapetes* from temperate North American ancestors (V42) is also associated with an upward shift in diversification rate. Although several hypotheses exist for North American and East Asian disjunctions and historical connections among these regions, the Bering Land Bridge is thought to have played the most vital role in floristic movements between the two regions from the Cretaceous until the Pliocene, especially for temperate deciduous plants in the Miocene (23–5.3 mya; Sanmartín et al., 2001, Wen et al., 2010). We consider this scenario applicable to both Asian clades.

Movement through the North Atlantic Land Bridge has traditionally been considered a less favorable hypothesis for the migration between the Americas and Eurasia <30 mya, when conditions were generally unfavorable for most plants in the area. From 30 mya onward, plants instead have been presumed to have used the Beringian route (McKenna, 1983, Donoghue and Smith, 2004). Dispersal in Vaccinieae from North America to Central Asia ~28.9–28.0 mya (between nodes V8 and V9) may be a candidate for this history. However, there is growing paleontological evidence for plant migration through the North Atlantic Land Bridge well into the late Miocene, possibly through discontinuous land

masses via short-distance dispersal across water barriers (Tiffney, 2008, Denk et al., 2010).

According to our ancestral range reconstruction, several dispersals occurred between North America and northern Eurasia in the Miocene. In Clade V31, a dispersal from North America to northern Eurasia occurred between ~16.7–15.6 mya, followed by at least five dispersals between these areas, with some of the species ultimately circumboreal (e.g., *Vaccinium vitis-idaea*). Similarly, we find dispersals between these landmasses at V5 and within V10, again in the Miocene. These dispersals generally occurred at shallower nodes than the dispersals involving North America and the Paleotropics, consistent with the predictions of Northern Hemisphere historical biogeography (Tiffney, 1985, Wen, 1999, Tiffney and Manchester, 2001, Wen et al., 2010).

One surprising outcome of the phylogenetic analysis is the placement of *Vaccinium crassifolium* of *V.* sect. *Herpothamnus* with the African species of Vaccinieae in Clade V11. After dispersal from South Insular Asia to Africa inferred ~25.0 mya, dispersal from Africa to North America occurred between ~19.9–8.7 mya (Fig. 2). The explanation for the latter disjunction must lie in either widespread extinction from a formerly widespread ancestor or long-distance dispersal because the Americas were well separated from Africa by that time (Raven and Axelrod, 1974). We favor long-distance dispersal in this case because the dispersal is too recent to be consistent with the timing of land connections between North America and Africa (Davis et al., 2002).

We observe South Insular Asian *Vaccinium* aligning with regions delineated by Wallace's Line (Raes and Van Welzen, 2009, Van Welzen et al., 2011, Crayn et al., 2015; Fig. 5). During lower sea levels at the last glacial maximum, the Sunda and Sahul shelves were contiguous, each closest to mainland Southeast Asia and Australasia, respectively, and each having different climatic regimes resulting in high local endemism (Hall, 1997, 1998, Van Welzen et al., 2005, Raes and Van Welzen, 2009). Sunda and Sahul still harbor high proportions of endemics today but also share clades that arose primarily after land-bridging events of the middle to late Miocene. This history is reflected in our main topology, albeit based on a small sample size.

Clade V46 comprises species endemic to South Insular Asia and are derived from Southeast Asian mainland groups (Figs. 2, 5). Between 10–5 mya, tectonic activity ushered the convergence of the Sunda and Sahul shelves, which, combined with post-glaciation changes in sea level, resulted in the emergence of multiple islands, including most of the Philippines, and cumulatively referred to as Wallacea (Hall, 1997, 1998, Van Welzen et al. 2005, Raes and Van Welzen, 2009). Wallacea bridged the gap between Sahul and Sunda, which collectively experienced climate change that facilitated rainforest expansion and species exchange (Crayn et al., 2015).

Within Clade 46 we recovered two clades comprising a mix of species from Sunda and Wallacea (V47 and V48), a clade of species endemic to Wallacea (V49) and a clade of species endemic to New Guinea (V50). Although we did not conduct a formal biogeographic analysis because of our paucity of samples, we propose a biogeographic scenario based on our data consistent with the historical biogeography of the region (Fig. 5). In this scenario, dispersal occurs first from Sunda to Sahul, when these two areas were in proximity to each other prior to 10 mya. Then at ~10 mya, our data suggest that three dispersals from Wallacea occurred, two from Sunda and one from Sahul. The dispersals to Wallacea would have occurred within the time that Wallacea became subaerial and dispersal corridors opened between 10–5 mya. Disjuncts between Sunda and Sahul that arose before the time of the bridging are assumed to have done so via short-distance dispersal (Crayn et al., 2015). More land may have been above water at earlier ages allowing for such earlier dispersal (Michaux, 2010). This could have facilitated the observed dispersal from Sunda to Sahul prior to the bridging events in our results and perhaps also for *Vaccinium auriculifolium* closer to the time of formation of Wallacea. Expanded sampling of Southeast Asian *Vaccinium* beyond our study can provide the means for a definitive test of the preliminary pattern proposed here.

Paphia, a genus endemic to the far eastern islands of Sahul, is geographically separated from *Dimorphanthera*, which occurs mainly in New Guinea with some diversity in the Philippines. The close relationship between these two genera (Clade V13), also found by Kron et al. (2002b), supports the theory of ancient land connection producing historical biological continuity in the area. Our limited sampling of *Dimorphanthera* (we only sampled species from New Guinea, Sahul) prevents an assessment of its migration into Wallacea after the bridging events (10–5 mya). The generally much earlier ages of clade divergence in our topology (Clades V13, V14) among these genera probably reflect lineages that originated in Sunda and Sahul before the bridging.

4.3. Evolution of polyploidy

The paucity of chromosome counts for species of Vaccinieae prevents a robust assessment of ploidal evolution in the tribe. Nonetheless, some patterns of chromosome evolution are suggested by the available data in the context of our phylogenetic results. Polyploidy appears to be distinctly clustered within specific clades of the tribe. In the large Clade V9 of mostly tropical genera, only polyploids have been found, suggesting a polyploidization event along the stem of this clade. Polyploidy may be one factor in the positive diversification shift observed in Clade 16 linked to movement into South America, although polyploidy was presumably already present in the Mesoamerican/Caribbean species outside of this clade. In the East Malesian Clade of *Dimorphanthera* and *Paphia* only polyploids are known (tetraploids and hexaploids), but most other tropical Asian Vaccinieae are known only as diploids. The rest of the polyploids in the tribe group predominantly in north-temperate clades, consistent with overall global polyploid patterns (Rice et al., 2019). These clades are scattered throughout the tree and always include diploids as well. Polyploidy among these clades must thus have evolved multiple times from the diploid condition. Because the number of species with ploidy information is still low in Vaccinieae, the phylogenetic patterns derived from the data can only be considered

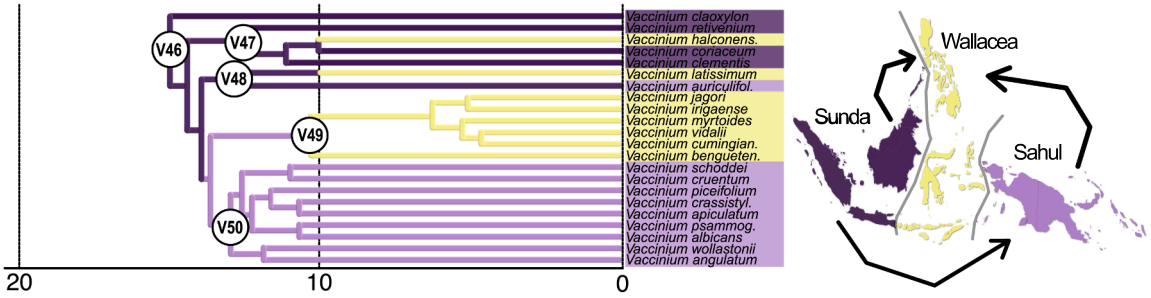

Fig. 5. A biogeographical hypothesis of South Insular Asian *Vaccinium*. The topology depicts the phylogenetic relationships based on Fig. 2. Ancestral areas on the topology are indicated by the colors of the areas on the map. Arrows on the map portray likely routes of dispersal based on the tree topology, divergence time estimates, and geologic history.

preliminary and need testing on many more species whose ploidy levels are unknown.

4.4. Evolution of ovary structure

Sleumer (1941) hypothesized that the pseudo-10-locular ovary is the plesiomorphic state in Vaccinieae, considering groups that have this trait (*Agapetes* and many species of Southeast Asian *Vaccinium*) to be the "least derived" members of the tribe. Conversely, Stevens (1972) proposed that pseudo-10-locular ovaries were derived in the tribe from the 5-locular condition, on the observation that the latter is the most common state in Ericaceae. Our findings support the hypothesis of Stevens in this respect. Stevens (1972) also suggested that pseudo-10-locular ovaries evolved multiple times within Vaccinieae, apparently based on the supposition that the temperate sections of *Vaccinium* with pseudo-10-locular ovaries were not closely related to the Southeast Asian groups with this character state. Our finding of a single shift from a 5-locular ovary to a pseudo-10-locular ovary refutes the hypothesis of multiple origins and provides a morphological synapomorphy for Clade V35.

The pseudo-10-locular ovary may have been assumed to have evolved multiple times throughout *Vaccinium* partly because *V.* sects. *Batodendron* and *Pyxothamnus*, as traditionally delimited, are mixtures of species with both 5-locular and pseudo-10-locular ovaries (Vander Kloet and Dickinson, 2009). The placement of some species in one or the other of these sections is inconsistent with our topology because all of the species sampled with pseudo-10-locular ovaries group together, regardless of sectional placement. This prompts the need for a careful examination of all species in these sections as to ovary type and suggests that a reclassification of the species in these sections is warranted.

Although not sampled in our study, the west South Insular Asian genus *Rigiolepis* is expected to be placed in the large Asian clade (V41), as recovered in Kron et al. (2002b). Our data recovering a single clade of South Insular Asian species suggests that it would be expected to group there. Argent (2019) considered the ovary in this genus to be 10-locular, like *Gaylussacia*, but observations indicate that it is instead pseudo-10-locular (P.W.F. and M.N. Tamayo, unpubl. results), consistent with its phylogenetic placement in Kron et al. (2002b) and our results of a single origin of the pseudo-10-locular condition in the tribe. It is also possible that *Rigiolepis* is polymorphic for ovary type (10-locular and pseudo-10-locular) and the genus is not monophyletic, in which case the 10-locular ovary might have evolved in at least one other clade of Vaccinieae besides *Gaylussacia*, but this needs to be tested.

4.5. Evolution of fruit color

Our character-state reconstruction of fruit color yielded red for the crown node of Vaccinieae followed by repeated evolution of violet fruits (including blue and black, as in Lu et al., 2019). Although we did not conduct a detailed analysis of color linked to specific ecological traits, an overall trend of red fruit in north-temperate regions evolving to violet in tropical regions (Central American, Andean, and Asian *Vaccinium* clades; Fig. 4) seems apparent from our data. About 75 % of our sampling had violet fruit color, which reflects the high proportion of Vaccinieae that are tropical. Vaccinieae in the tropics typically inhabit high-elevation and light-intensive habitats.

The red, blue, violet, and black surface colors of the fruits of Vaccinieae are imparted by various classes of anthocyanins, with occasional glaucous bloom also affecting fruit appearance (Luby et al., 1991). Fruit color depends on several factors, including anthocyanin chemical structure, cell pH, and most importantly, concentration of anthocyanin, with high values imparting a purplish black appearance (Schaefer, 2011). High concentrations of anthocyanins are thought to accumulate via adaptation to defense against strong light intensity or pathogens, especially fungi; there is little evidence that anthocyanins in fruit developed to communicate with animals (Schaefer et al., 2007, Schaefer, 2011).

Gaultherieae is the other large tribe of subfamily Vaccinioideae and the only other tribe in Vaccinioideae besides Vaccinieae with fleshy fruits. In a study of fruit color across the global distribution of tribe Gaultherieae over a phylogenetic framework, Lu et al. (2019) found a significant association between violet fruit color at lower latitudes versus red and white at higher latitudes in both the Northern and Southern hemispheres. They also found that red fruit color was significantly associated with low elevations and was found to be the ancestral state of the Gaultherieae, with violet evolving multiple times within the clade. These patterns seem to parallel the findings here in Vaccinieae, suggesting consistent patterns for fruit color evolution across the subfamily. Lu et al. (2019) suggested that the violet colors of Gaultherieae fruits may better protect seeds against the intense ultraviolet radiation of the tropics because of higher delphinidin levels in these fruits. However, stronger protection against ultraviolet radiation in the violet to black fruits could be imparted merely through higher anthocyanin levels in general, as Schaefer (2011) implies. Lu et al. (2019) also found that violet coloration was related to increased diversification rates, as found in a previous study (Spriggs et al., 2015) and suggested in our data. We hypothesize that the first members of Vaccinieae thrived in high-latitude, shaded understories before dispersing southward to the tropics, where they diversified into high-elevation niches characterized by abundant light exposure and perhaps increased pathogen activity that selected for the blue fruit color that is so persistent today. This can be initially tested by conducting a similar detailed study of the Vaccinieae as in Lu et al. (2019) for the Gaultherieae.

4.6. Phylogenetic discordance

Phylogenetic discordance was observed between the concatenated and species-tree analyses, particularly within the Mesoamerican/Caribbean and Andean clades. These results could indicate hybridization, allopolyploidy, and/or incomplete lineage sorting associated with recent speciation. Much more in-depth systematic work is required in this still poorly understood clade before firm conclusions about its classification and evolution can be drawn.

Discordance was observed at the first-diverging branch of the tribe, with the South American Clade V2 (*Mycerinus*, *Notopora*, and *Vaccinium* species) as either first-diverging in the tribe (concatenated) or placed as sister to the African Clade + East Malesian Clade + Mesoamerican/Caribbean Clade + Andean Clade (species tree). We slightly favor the concatenated reconstruction of V2 as sister to the rest of Vaccinieae because the unique biogeographic characteristics of the Guayana Highland region tend to harbor early-diverging lineages of many plant families (see Section 4.2.1), albeit its placement in the species tree is still early diverging relative to the rest of the Neotropical species of the tribe.

Further discordance occurred near the base of the Vaccinieae, with *Vaccinium* sect. *Hemimyrtillus* (in part) grouping as sister to *Gaylussacia*/*Oreanthes* (concatenated) or as the second-diverging branch in the tribe (species tree). There are no clear putative synapomorphies to support the sister-group relationship of these clades, and their respective species are divergent in any number of characters, e.g., ovary 5-locular in *V.* sect. *Hemimyrtillus* (versus 10-locular in *Gaylussacia*). However, their putatively close relationship in the species-tree analysis, relatively early-divergent position in both analyses, and the other part of *V.* sect. *Hemimyrtillus* grouping in a far-distant part of the phylogeny should prompt further morphological and molecular investigations into these groups.

Based on morphological similarities, several South and Central American species of *Vaccinium* (*V. consanguineum*, *V. floribundum*, *V. leucanthum*, and *V. meridionale*) have been hypothesized to form a continuously hybridizing complex (J.L.L., unpubl. results). Phylogenetic discordance between *V. meridionale* of *V.* sect. *Pyxothamnus* and *V. leucanthum* of *V.* sect. *Batodendron* may indicate hybridization between these species, although their ranges do not overlap. Vander Kloet and Dickinson (2009) stated that the ovaries of the species of *V.* sect.

Pyxothamnus are mostly 4- or 5-locular, and occasionally pseudo-10-locular, apparently the only section of *Vaccinium* variable for this character other than in *V. cereum* of the Marquesas Islands in the Pacific. *Vaccinium cereum* is considered to constitute, at least in part, a hybrid complex between 5-locular *V.* sect. *Myrtillus* and a pseudo-10-locular ancestor from Asia because it displays nuclear/plastid phylogenetic discordance (Powell and Kron, 2002). Our data suggest that a similar hybrid scenario among one or more species of *V.* sects. *Batodendron* and *Pyxothamnus* may be occurring.

5. Conclusions

This study provides insights into the evolution of the large, ecologically and economically important angiosperm clade Vaccinieae (Ericaceae). A temperate North American origin is inferred for the tribe followed by numerous independent movements into tropical and north-temperate Eurasian regions. Movements into the South American Andes and Central and South Insular Asia were followed by significant increases in diversification rates, likely accounting for the high species diversity in these areas.

The finding of rampant non-monophyly across the tribe has important implications for our understanding of its subdivisional classification. It challenges conventional taxon limits and highlights the need for extensive future research, particularly for taxa in tropical regions. We aim to highlight in more detail the degree to which clades are misaligned with taxonomic boundaries and comment on various reclassification strategies in a follow-up publication (A.L.B. et al., unpubl. results). At the extremes, options for a ranked reclassification range from narrowing *Vaccinium* to the single species *V. uliginosum* (the type of the genus) and raising the sections of *Vaccinium* to genus level, to expanding *Vaccinium* to encompass the entirety of Vaccinieae and lowering the rank of genera to sections within *Vaccinium*. We consider infratribal reclassification premature and await more taxonomic and phylogenetic study of the many problematic generic and sectional boundaries needing resolution, especially those of tropical regions. We especially advocate for detailed systematic studies of localized regions of the Vaccinieae phylogenetic tree that includes the search for morphological characters that can help to support clades recovered here and to elucidate clade membership in the absence of molecular data. In this regard, two areas of active research from members of our team are the focus on Hawaiian *Vaccinium* and *V.* sect. *Cyanococcus*. In each case, it is clear that current estimates dramatically underestimate true species diversity (Crowl et al., 2022, Fritsch et al., 2022, Weakley et al., 2024; P.W.F. et al., unpubl. results). This also appears to apply to South Insular Asian *Vaccinium* (Tamayo et al., 2023 and M.N. Tamayo, unpubl. results) and the Andes (Luteyn, 2002; J.L.L., unpubl. results).

CRediT authorship contribution statement

Anna L. Becker: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Andrew A. Crowl:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Visualization, Writing – original draft. **James L. Luteyn:** Writing – review & editing, Investigation, Resources. **Andre S. Chanderbali:** Resources, Data curation, Funding acquisition, Methodology, Project administration. **Walter S. Judd:** Conceptualization. **Paul S. Manos:** Funding acquisition, Supervision. **Douglas E. Soltis:** Resources, Funding acquisition, Project administration. **Stephen A. Smith:** Resources, Funding acquisition, Project administration. **Deise J.P. Goncalves:** Resources, Data curation. **Christopher W. Dick:** Resources, Funding acquisition, Project administration, Writing – review & editing. **William N. Weaver:** Resources, Data curation. **Pamela S. Soltis:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Resources. **Nico Cellinese:** Writing – review & editing, Supervision, Project administration, Investigation. **Peter W. Fritsch:** Writing – review & editing, Writing – original draft, Validation, Resources, Investigation, Data curation, Conceptualization, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data, novel scripts, and output files that support the findings of this study are openly available in supplementary materials attached here. Raw sequence reads are available from NCBI PRNA839108, PRJEB49299, and PRJEB51566. Sequence alignments are available on Dryad https://doi.org/10.5061/dryad.ksn02v7cr.

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Appendix A. Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.ympev.2024.108202.

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