

Niche evolution in a northern temperate tree lineage: biogeographic legacies in cork oaks (*Quercus* sect. *Cerris*)

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- **Background and Aims** Cork oaks (*Quercus* sect. *Cerris*) comprise 15 extant species in Eurasia. Despite being a small clade, they display a range of leaf morphologies comparable to the largest sections (>100 spp.) in *Quercus*. Their fossil record extends back to the Eocene. Here, we explore how cork oaks achieved their modern ranges and how legacy effects may explain niche evolution in modern species of section *Cerris* and its sister section *Ilex*, the holly oaks.
- **Methods** We inferred a dated phylogeny for cork and holly oaks using a reduced-representation next-generation sequencing method, restriction-site associated DNA sequencing (RAD-seq) and used *D*-statistics to investigate gene flow hypotheses. We estimated divergence times using a fossilized birth-death (FBD) model calibrated with 47 fossils. We used Köppen profiles, selected bioclimatic parameters, and forest biomes occupied by modern species to infer ancestral climatic and biotic niches.
- **Key Results** East Asian and Western Eurasian cork oaks diverged initially in the Eocene. Subsequently, four Western Eurasian lineages (subsections) differentiated during the Oligocene and Miocene. Evolution of leaf size, form, and texture partly correlates with multiple transitions from ancestral humid temperate climates to Mediterranean, arid, and continental climates. Distantly related but ecologically similar species converged on similar leaf traits in the process.
- **Conclusions** Originating in temperate (frost-free) biomes, Eocene to Oligocene ranges of the primarily deciduous cork oaks were restricted to higher latitudes (Siberia to north of Paratethys). Members of the evergreen holly oaks (sect. *Ilex*) also originated in temperate biomes but migrated south- and south-westwards into then-(sub)tropical southern China and south-eastern Tibet during the Eocene, then westwards along existing pre-Himalayan mountain ranges. Divergent biogeographic histories and deep-time phylogenetic legacies—in cold and drought tolerance, nutrient storage, and fire resistance—thus account for the modern species mosaic of Western Eurasian oak communities, which comprise oaks belonging to four sections.

Key words: *Quercus*, next-generation sequencing, fossilized birth-death model, fossil, niche evolution, biogeography, leaf life span.

INTRODUCTION

The genus *Quercus* L. (oak trees) is one of the most economically and ecologically important woody angiosperm genera in the northern hemisphere. Oaks comprise about 425 species and occur in a wide range of habitats from dry woodlands to swamp forests and from lowlands to elevations up to 4,500 m a.s.l. (Camus, 1936–1954; Denk *et al.*, 2017a). They are a dominant component of the northern temperate forests (Martinetto *et al.*, 2020). Traditionally, the taxonomy of this genus has been based on key morphological characters, and different classification schemes have been proposed over the centuries (e.g. Ørsted, 1871; Trelease, 1924; Schwarz, 1936; Camus, 1936–1954; Menitsky, 1984; Nixon, 1993; for differences in these schemes see Denk and Grimm, 2010 and Denk *et al.*, 2017a). In recent years, a number of morphological (Solomon, 1983a, b; Denk and Grimm, 2009; Denk and Tekleva, 2014) and molecular studies (Manos *et al.*, 2001, 2008; Oh and Manos, 2008; Denk and Grimm, 2010; Hubert *et al.*, 2014; Hipp *et al.*, 2014, 2018, 2020; Cavender-Bares *et al.*, 2015; Simeone *et al.*, 2016, 2018; McVay *et al.*, 2017a, b; Pham *et al.*, 2017; Vitelli *et al.*, 2017; Deng *et al.*, 2018; Ortego *et al.*, 2018; Cavender-Bares 2019; Crowl *et al.*, 2019; Jiang *et al.*, 2019) have provided a robust phylogenetic framework along with a revised subgeneric and sectional classification. Together, these studies provide a framework to place the extensive fossil record of the genus in a phylogenetic context (e.g. Bouchal *et al.*, 2014; Grímsson *et al.*, 2015, 2016).

Leaf phenology and climate niche have evolved in concert across woody angiosperms (Woodward *et al.*, 2004; Hawkins *et al.*, 2014; Zanne *et al.*, 2014; Edwards *et al.*, 2017; Hipp *et al.*, 2018). A broad phylogenetic comparative study has shown that leaf phenology may evolve as a response to a change in environment (“climate first”) or arise first and predispose lineages to freezing tolerance (“trait first”), with the “climate first” pathway more frequent, particularly in deciduous woody plant lineages (Zanne *et al.*, 2014). Understanding the detailed history of these patterns of evolution requires dissection of individual clades. In *Viburnum*, for example, deciduousness evolved *in situ* as populations were subjected to gradual cooling (Edwards *et al.*, 2017). In the American (“New World”) oak clade (*Quercus* subgenus *Quercus*), one of two major clades within *Quercus*, more than 20 independent shifts from deciduous to evergreen leaf phenology in Mexican white and red oaks (*Quercus* sections *Quercus* and *Lobatae*) are associated with climatic and edaphic shifts, and the evergreen habit is inferred to have evolved in response to decreases in temperature seasonality and decreases in both winter and summer temperature extremes (Hipp *et al.*, 2018). In contrast, in the Eurasian (“Old World”) oak clade (subgenus *Cerris*), leaf phenology is stable within sections. Both the deciduous cork oaks (sect. *Cerris*) and the

evergreen holly oaks (sect. *Ilex*) show considerable distributional overlap with each other and subgenus *Quercus*. Section *Cerris* is moreover the only oak section to reach its highest species richness and absolute phylogenetic diversity in Western Eurasia.

Here we investigate these two closely related sections of the Eurasian (“Old World”) oak clade. We test the trait first and climate first pathways and provide detailed insights into two sister lineages of oaks. We utilized a reduced-representation next-generation sequencing method, restriction-site associated DNA sequencing (RAD-seq; Ree and Hipp, 2015), to infer a fully resolved species phylogeny of the Eurasian cork oaks, including 25 ingroup specimens representing 14 of the 15 species (all except for the narrow-endemic *Q. euboica*). We used 47 fossil-taxa to date the phylogeny using a fossilized birth-death (FBD) approach and to reconstruct the biogeographic history of the cork oaks. Based on habitats, climatic preferences, and leaf morphologies of modern and fossil cork oaks, we investigated the history of climatic niche evolution and the correlation of niche shifts with leaf evolution. Further, we compared the biogeographic histories of sections *Cerris* and *Ilex* to explain modern ranges and niche occupancy of these sections across Eurasia. Finally, we discuss our results against the background of palaeogeographic and tectonic changes in Eurasia during the past 40 million years and diversification patterns established from previous studies of the nuclear and plastid genomes.

MATERIAL AND METHODS

Sampling

Samples from 62 individuals included in Hipp et al. (2020) were re-analysed for this study. Sampling details, vouchers, NCBI short-read archive (SRA) project and accession numbers are provided in Supplementary data Table 1. Twenty-five samples covered all species of section *Cerris* except for *Q. euboica* (Papaioannou) K.I.Chr., for which we were unable to obtain fresh material with sufficient DNA yield. To represent the sister section *Ilex*, we included all its Western Eurasian species: four Mediterranean species (five if *Q. calliprinos* Webb is considered a separate species) plus the western Himalayan-Hindukush *Q. baloot* Griff. (Clade VI in Jiang et al., 2019; see also Simeone et al., 2016, 2018). Additional East Asian *Ilex* species were selected to represent the major lineages within this section: five species including *Q. floribunda* Lindl. ex A.Camus for the Himalayan clade carrying *Ilex*-specific plastomes (cf. Yan et al., 2019; Hipp et al., 2020; Clade IV+V in Jiang et al., 2019); and three species representing the East Asian clade: the (central) Chinese *Q. baronii* Skan, morphologically similar to *Cerris* oaks but with a unique plastome; *Q. dolicholepis* A.Camus, a montane central Chinese species; and *Q. phillyreoides* A.Gray, a widespread north-eastern Asian subtropical to temperate species. The latter two have *Cerris*-similar plastid signatures (Simeone et al.,

2016; Clade II in Jiang *et al.*, 2019). Five species of section *Cyclobalanopsis* (Oerst.) Benth. & Hook.f. represented the third lineage within subgenus *Cerris*, resolved as early diverged sister lineage of sections *Cerris + Ilex* (Hipp *et al.*, 2020). As a further outgroup, we included 15 samples covering Western Eurasian members of subgenus *Quercus* (sects *Quercus* and *Ponticae* Stef.), one eastern North American red oak (*Q. coccinea* Münchh., sect. *Lobatae* Loudon), and the western North American relict genus *Notholithocarpus* Manos, Cannon and S.H. Oh, the most probable closest living relative of oaks (Hipp *et al.*, 2020; Zhou *et al.*, 2022).

RAD-seq data generation and clustering

Next-generation sequencing libraries were prepared at Floragenex Inc. (Portland, OR, USA) following the methods of Baird *et al.* (2008) with *Pst*I, barcoded by individual, and sequenced in 150-bp single-end reactions on an Illumina HiSeq 2000, 2500, or 4000 at the University of Oregon Genomic Facility; past analyses (Hipp *et al.*, 2014, 2018, 2020) demonstrate that phylogenetic results in this sample set are not obviously influenced by variation in sequencing platform. FASTQ files were demultiplexed and filtered to remove sequences with more than 5 bases of quality score < 20 and assembled into loci for phylogenetic analysis using IPYRAD 0.7.24 (Eaton, 2014) at 85% sequence similarity. Consensus sequences for each individual for each locus were then clustered across individuals, initially retaining loci present in at least four individuals and possessing a maximum of 20 SNPs and eight indels across individuals. Data were imported into R using the RADAM1 package (Hipp *et al.*, 2014) to filter loci for analysis to three datasets: (i) a minimum of 15 individuals per locus (m15), (ii) 20 individuals per locus (m20), and (iii) 25 individuals per locus (m25). Loci were concatenated into a single data partition for maximum likelihood and Bayesian phylogenetic analyses, and locus identities were preserved for *D*-statistic analyses of possible introgression (see below).

ML tree inference and bootstrapping

Initial phylogenetic tree inference and bootstrap analyses were performed under maximum likelihood with RAxML v.8 (Stamatakis, 2014). Analysis was conducted using the general time-reversible model with rate variation (GTR+ Γ ; Rodriguez *et al.*, 1990), and 200 fast nonparametric bootstraps to estimate branch support. To assess the possible role of introgressive hybridization in the clade, we used Patterson's *D*-statistic test (Durand *et al.*, 2011) as implemented in IPYRAD (Eaton and Overcast, 2020). Set-up details and full results are provided in Supplementary Data 1. Two

primary hypotheses were tested: the hybrid origins of *Q. afares* (Mir *et al.*, 2006) and of *Q. crenata* (Schwarz, 1936–1939; Pignatti, 1982). In addition, we performed follow-up tests for admixture between *Q. cerris* and *Q. afares*; among subsections *Aegilops*, *Suber*, and *Libani*; and between *Q. ilex* and *Q. suber*, representing increasingly large phylogenetic distances. Supplementary files, data matrices, and analysis scripts are archived at <https://github.com/andrew-hipp/cerris-fbd> (v1.0-1; <https://doi.org/10.5281/zenodo.7547523>).

Fossils

We compiled a set of 47 fossils as age distribution priors for the fossilized birth-death model (see following section) and mapped the spatio-temporal distribution of oaks with focus on section *Cerris*. Of these fossil occurrences, 24 localities are dated by radiometric dating and/or by vertebrate fossils, for two localities ages are constrained using palaeomagnetic data, and the remaining localities are dated by lithostratigraphic correlation or dinocyst stratigraphy (Supplementary data Table 2). Four fossil-taxa are represented by fruit/cup remains, seven by pollen, and 36 by leaves. Pollen-taxa were assigned to sections based on synapomorphies shared with particular lineages (Denk and Grimm, 2009; Denk *et al.*, 2017), while fruit and leaf fossils were chosen based on (sub)section-diagnostic traits. The full list of selected fossil-taxa with their taxonomic assignments, information on the plant organ, the branch to which they are assigned, geographic origin, ages, constraints and relevant references (if not occurring in the main text) are provided in the electronic supplement (Supplementary data Table 2). See Supplementary Data 1 and 2 for notes on stratigraphic units and mapping of fossils mapped onto palaeoglobes (Scotese, 2013a–e; early Eocene to Last Glacial Maximum).

Fossilized Birth-Death dating analyses

For fossilized birth-death (FBD) analyses, the RAD-seq matrix was reduced to 29 tips, a single tip per species within both sects. *Cerris* and *Ilex*, with the exception of *Q. cerris*, for which two individuals were kept that did not group together in any analyses and might represent pseudo-cryptic or cryptic species. Loci were retained if they were present in at least 10 individuals. A NEXUS file was exported using the RADAM1 package, including 47 additional lines of undetermined positions (coded as “?”), one per fossil included in the FBD analyses. FBD analyses were conducted in BEAST2 (Bouckaert *et al.*, 2014). Markov chain Monte Carlo (MCMC) runs of 50 million generations each were run from ten independent random starting points on each of three random draws from the

uniform distribution of the fossil age ranges. Analyses were conducted using a nucleotide substitution model that allows for rate variation and invariant sites ($\Gamma + I$), with the shape parameter (α) and proportion of invariant positions estimated, and four gamma categories. The relaxed log normal clock was used, with the clock rate estimated. Analysis details are in the Supplemental Methods (Supplemental Data 1). Scripts and RAD-seq data matrices are archived in the code repository for this paper (release v1.0-1: <https://github.com/andrew-hipp/cerris-fbd>; <https://doi.org/10.5281/zenodo.7547523>).

Köppen-Geiger climate types, WorldClim climate data, and major forest biomes

We used grid-weighted 'Köppen signatures' (Denk *et al.*, 2013; Bouchal *et al.*, 2018; Grímsson *et al.*, 2018), henceforth 'Köppen profiles', to summarize the climate niches occupied by species of *Cerris* and to investigate climate niche evolution within and among subsections of *Cerris* (Table 1; Supplementary Data 3). A Köppen profile reflects the proportional coverage of the various Köppen-Geiger climate zones (cf. Kottek *et al.*, 2006; Peel *et al.*, 2007) by a modern species based on gridded distribution data. To simplify interpretation, Köppen profiles are summarized into five climatic niches (see *Maximum likelihood reconstructions of major climate niches and main biomes*); additional details on interpretation and coding are in the supplementary methods (Supplementary Data 1).

Modern species distributions were connected to fossil distributions by using georeferenced occurrence data for each species, downloaded from the GBIF database (www.gbif.org; Supplementary Data 3). Each data set was checked for natural distribution outliers (e.g. specimens from botanical gardens). Published chorological data were used to detect these outliers (e.g. Browicz and Zieliński, 1982; Fang *et al.*, 2009; San-Miguel-Ayánz *et al.*, 2016; Caudullo *et al.*, 2017). The cleaned georeferenced occurrence data were then plotted onto 5 arc minutes Köppen-Geiger grid (1986–2010 data; Rubel *et al.*, 2017) to establish Köppen profiles for all species of section *Cerris*; and on major terrestrial biome maps (Olson *et al.*, 2001; Supplementary Data 3) to assess species' forest biome preferences.

Characterisation of modern leaf types

Leaf morphologies of modern section *Cerris* species were characterized using leaf texture, lamina size, tooth type, and other traits (Table 1; Supplementary Data 1). The overall morphological differentiation patterns were visualized using a neighbour-net (Bryant and Moulton, 2004), a planar (meta-)phylogenetic network (cf. Denk and Grimm, 2009). Twelve traits were scored as a categorical

character matrix (11 binary, one ternary character; matrix *LeafMorphs* in Supplementary Data 1: Data File S4-1) and used to infer simple (Hamming) pairwise distances and to reconstruct character evolution on the dated topology under the *Mk1* model in MESQUITE v 2.75 (Maddison and Maddison, 2011; Supplementary Data 1).

Maximum likelihood reconstructions of major climate niches and main biomes

Based on the quantitative assessment of biome and climate zone preferences of the modern-day species, we binned extant and fossil species into five basic categories, accounting either for biome or climate zone preferences (Table 1; Supplementary Data 3). Our generalisation and categorisation make use of the terminology and concepts introduced by Schroeder (1998; cf. Denk *et al.*, 2013) and allow (i) direct comparison of biome and climate zones preferences, which are commonly correlated but not synonymous, and (ii) relation of quantitative modern-day categorisation qualitatively to our fossil-taxon set. Towards that end, we first defined the putative covered biomes for each fossil-taxon of section *Cerris* (columns *Biome/Major Köppen climate type* in Supplementary data Table 2). Assignment of fossils to climates is described in the Supplementary Methods (see also Supplementary data Table 2; Supplementary Data 1: Data File S1-1). Explicit connection of biomes to Köppen profiles is explained in the Supplemental Methods (Supplementary Data 1). In brief, the biomes and general climate preferences reconstructed are:

0–Moist-Subtropical: Associated exclusively with the Tropical and Subtropical Moist Broadleaf Forests biome. In case of modern-day *Cerris* oaks, species are associated almost exclusively with summer-moist climates with hot summers. The only modern species with an accordingly characteristic climate niche is the East Asian *Q. chenii*, firmly restricted to the *Cfa* climate of central-eastern China.

1–Meridio-Nemoral: Associated with the ecotone between Tropical and Subtropical Moist Broadleaf Forests and Temperate Broadleaf and Mixed Forests biomes.

2–Nemoral: Either restricted to Temperate Broadleaf and Mixed Forests or extending into both Tropical and Subtropical Moist Broadleaf Forests and Temperate Coniferous Forests biomes.

3–Meridional: Generalists tolerating summer-drought, otherwise similar to the Nemoral category.

4–Full-Mediterranean: Summer-drought tolerant specialists restricted to summer-hot and winter-mild biomes and climates.

Ancestral states of the unordered five-state categorical climate character were reconstructed under the *Mk1* model in MESQUITE v 2.75 (Maddison and Maddison, 2011). We used two different input trees: (i) the original dated tree for standard top-down reconstruction of ancestral states, i.e. using only the information scored for the modern-day species; and (ii) the dated tree with nodes and tips added to account for states of fossil-taxa. Fossil-taxa that could be associated with a distinct branch (lineage) were treated as sister lineages and used to break down the according branch. We used the oldest possible age of the fossil-taxon as age of the putative MRCA, and the youngest possible age to define the MRCA-added-tip distance. The Mesquite-NEXUS file is included in the Github repository / Zenodo submission (Supplementary Data 1: Data File S1-1).

RESULTS

Phylogenetic inference

The RAD-seq locus dataset maintaining loci with a minimum of 15 individuals (m15 dataset; Fig. 1) yielded 5300 loci, totalling 464,762 aligned nucleotide positions and 64.1% missing data (N's). The m20 dataset yielded 3145 loci, 277,006 aligned nucleotide positions, and 58.2% missing data. The m25 dataset yielded 1132 loci, 100,841 aligned nucleotide positions, and 46.4% missing data. All datasets yielded the same maximum likelihood (ML) topology for the section *Cerris* subtree (Fig. 1, Supplementary data Figs 1 and 2) with two exceptions. The m25 dataset placed one of the *Q. libani* samples sister to *Q. castaneifolia* + *Q. cerris* with weak support (BP = 30%; the second-best supported alternative, BP = 17%, grouped it with the other *Q. libani* and *Q. trojana*, in agreement with the m20 and m15 ML trees), and placed *Q. variabilis* and *Q. chenii* sister to each other (BP = 78%; no alternative with BP \geq 15%). The m15 and m20 datasets recovered the same topologies, and the m15 provided the strongest mean bootstrap support. Consequently, we report on the m15 dataset topology here (Fig. 1) and used that topology for our FBD constraints. The FBD dataset included 5,075 loci and 444,591 aligned nucleotide positions; 52.2% missing data for the extant species (those with RAD-seq data).

The RAD-seq maximum-likelihood phylogeny using the complete tip set (Fig. 1) indicates an initial divergence between the East Asian (subsect. *Campylolepides* A.Camus) and the Western Eurasian species of section *Cerris* (Fig. 2). Within the Western Eurasian clade, the earlier 5S-IGS-identified species groups (Cluster 1–4 in Simeone *et al.*, 2018) comprise four unambiguously supported clades, two corresponding to subsections (*Suber*, *Aegilops*), and two unnamed (within

what we are calling the *Cerris* core clade) (Table 2). Subsection *Suber* (Spach) Maleev comprises the Western Mediterranean Cork Oak, *Q. suber*, and the southern French-Italian-Croatian *Q. crenata*, commonly considered a hybrid between *Q. cerris* × *Q. suber*. Diverging next is subsection *Aegilops* (Reichenb.) Menitsky, including *Q. macrolepis*, which ranges from south-eastern Italy to southern Turkey, and *Q. ithaburensis* occurring further east and south to Israel (Jalas and Suominen, 1988; Browicz and Zieliński, 1982). The third species, *Q. brantii*, ranges from south-eastern Turkey and north-western Syria to the Persian Gulf. The most recently diverged section *Cerris* core clade collects members of subsections *Libani* (new) and *Cerris* (Dumort.) Guerke. The former includes the North African and East Mediterranean-Near East species *Q. afares*, *Q. trojana* and *Q. libani*; subsection *Cerris* includes the narrow endemics *Q. castaneifolia* (Hyrcanian forest region of Azerbaijan and northern Iran) and *Q. look* (northern Israel to Syria), and the widespread, genetically and morphologically heterogeneous Western Eurasian *Q. cerris*. The *D*-statistic tests demonstrate inter-locus phylogenetic discordance in the relative placement of subsections *Aegilops*, *Suber*, and *Libani*, but none affect the conclusions presented here. There is no evidence of species-level introgression involving *Q. afares*, *Q. canariensis*, *Q. suber*, or *Q. ilex* (Supplemental Data 1). According to Simeone *et al.* (2018), *Q. euboica*, not included in this study, is a distinct species with subsection *Libani* morphology but genetically closer to subsection *Cerris* as defined here. It would thus be part of the section *Cerris* core clade.

Dating and historical biogeography

For each of three random draws from the uniform age distribution for all fossils, six to nine of the ten independent MCMC runs converged (Supplementary data Table 4). Burn-in was assessed by visual inspection of model likelihoods and estimated age distributions of the constrained nodes, and independent post-burnin MCMC runs were pooled for each random draw of ages. As confidence intervals overlap strongly for all node ages across all three random draws from the fossil age distributions (Supplementary data Table 5), we report only the first of the three age draws in the main text of this paper, but provide results of all three in the supplement. The FBD dating with 47 fossils (Fig. 3; Supplementary data Fig. 3) indicates a pre-Oligocene (late Eocene) divergence between the Western Eurasian and East Asian lineages of *Cerris* (36.7 [40.6–35.0] Ma). Crown-group radiation, i.e. divergences leading to the modern-day species, started ~11 Ma earlier in the Western Eurasian clade (latest Oligocene, 24.3 [28.6–20.8] Ma) than in their East Asian sister lineage, subsection *Campylolepides* (mid-Miocene, 13.1 [17.7–6.2] Ma). The Oligocene and Eocene north-eastern Asian *Cerris* fossils hence form the stem group of the section. The lineages leading to the

modern widespread *Q. acutissima* and *Q. variabilis* diverged in the Middle Miocene to Pleistocene, with high uncertainty (6.8 [13.3–0.1] Ma).

Among Western Eurasian *Cerris*, the western Mediterranean subsection *Suber* diverged from the remaining Western Eurasian *Cerris* in the late Oligocene to Early Miocene (24.3 [28.6–20.8] Ma). The split follows the expansion of section *Cerris* from north-eastern Asia into Central Asia as seen in the fossil record (Fig. 3). The second modern lineage, subsection *Aegilops*, diverged from the *Cerris* core clade (subsects *Libani*, *Cerris*) about 4 Ma later (19.9 [22.7–16.9] Ma), prior to the Mid-Miocene Climatic Optimum. Crown-group radiation in the *Cerris* core clade, the split into subsections *Libani* and *Cerris*, coincided with crown-group radiation in the East Asian subsection *Campylolepides* and starting speciation in subsection *Aegilops* (all mid-Miocene, within ± 1 Ma). Most of the modern species lineages diverged in the Late Miocene (Tortonian, 10 Ma) until earliest Pliocene (Zanclean, 5 Ma). The most recent speciation events were the Pleistocene split between the disjunct eastern Mediterranean *Q. macrolepis* and its eastern sister species, *Q. brantii* of Southeast Anatolia to Zagros Mts (2.4 [0.1, 4.7] Ma) and the Italian to Turkish *Q. trojana* and the Near East *Q. libani* (1.8 [0.1, 10.8] Ma).

Modern distributions, climate niches and major biome types of Cerris oaks

Quercus section *Cerris* is the only oak section to reach its highest species richness and absolute phylogenetic diversity in Western Eurasia (12 spp., vs. 3 spp. in East Asia; Table 1). Each clade shows a broadly cohesive geographic distribution of parapatric to allopatric species (Fig. 2) that replace each other along a climatic cline (details in Supplementary Data 3).

The East Asian subsection *Campylolepides* covers a region from eastern Nepal to Japan and Laos. Its species can be categorized as Moist-Subtropical, Meridio-Nemoral or Nemoral. They thrive predominantly in warm, fully humid or winter-dry climates, occasionally extending into arid and cool climates. Their habitats are characterized by synchronous temperature and precipitation yearly minima (December–January). Only one species, the Nemoral *Q. variabilis* tolerates substantial frost during winter.

The Meridional to Full-Mediterranean subsection *Suber* of the Western Eurasian clade covers a region from Croatia and northern Italy south- and westwards to Tunisia, Algeria and Morocco, and to France, Spain and Portugal, specializing in Mediterranean climates but ranging into temperate climates. Here, *Q. suber*, the section's most west-extending species, occurs predominantly in distinctly Mediterranean climates (hot summers with pronounced drought),

whereas its eastern sister species, *Q. crenata*, thrives in sub-Mediterranean to fully humid climates (rare droughts). Both species form part of the Mediterranean Forests, Woodlands and Scrub and Temperate Broadleaf and Mixed Forests biomes

Within subsection *Aegilops*, *Q. macrolepis* has a disjunct distribution from south-eastern Italy to eastern Turkey and occurs in Full-Mediterranean climates (Mediterranean Forests, Woodlands and Scrub biome; Full-Mediterranean) with extensive summer drought and mild winters. In more continental parts of the Balkan Peninsula and central Turkey, it grows within the Temperate Broadleaf and Mixed Forests biome and the Temperate Grasslands, Savannas and Shrublands biome as part of steppe forests (Supplementary Data 3). *Quercus macrolepis* is replaced eastwards by the more continental (cooler winters) *Q. ithaburensis* (Full-Mediterranean) and *Q. brantii* (Mediterranean into cool climates with summer drought, and into arid climates, with pronounced winter-cold). Both species occur in the Mediterranean Forests, Woodlands and Scrub biome; but *Q. brantii* has its main distribution in steppe forests and steppes (Temperate Broadleaf and Mixed Forests, Temperate Grasslands, Savannas and Shrublands; categorized as Meridional) of south-eastern Turkey, Iraq, and Iran.

In the Meridional to Full-Mediterranean subsection *Libani*, *Q. afares* (Mediterranean climate) occurs in the northern parts of Algeria and Tunisia and is replaced to the northeast by *Q. trojana*, which has a disjunct distribution between Italy and Greece-Turkey (mostly Mediterranean climates), and is replaced in eastern Turkey by *Q. libani*, which thrives in Mediterranean but also in cold summer-dry and cold arid climates. *Quercus libani* represents the most frost- and snow-tolerant species in Western Eurasia; matching most-extreme habitats of *Q. variabilis* in north-eastern Asia (equally cold but drier winters). *Quercus afares* thrives in Mediterranean Forests, Woodlands and Scrub and, at higher elevations, in Temperate Conifer Forests with mild winters and summers without an extensive drought period. Regarding their climate niches, *Q. afares* and *Q. libani* are nearly mutually exclusive, with *Q. trojana* being intermediate. Both *Q. libani* and *Q. trojana* form part of the Mediterranean Forests, Woodlands and Scrub biome and further east, *Q. libani* occurs in sympatry with *Q. brantii* (Temperate Broadleaf and Mixed Forests and Temperate Grasslands, Savannas and Shrublands biomes).

The widespread *Q. cerris* is ecologically variable (summer-dry Mediterranean into cool, frost- and snow-prone climates). Its climatic niche covers most of the total niche of section *Cerris*. It is the only species in its section with a main distribution in areas with a fully humid temperate climate with warm summers, and the only (extant) species in the section producing lobed leaves. The Full-Mediterranean *Q. look* is a narrow endemic in the Levant (Middle East: Mount

Hermon, Anti-Lebanon and Lebanon Mts), in a distinct Mediterranean climate setting, most similar to that of *Q. ithaburensis* in subsection *Aegilops*. *Quercus castaneifolia* is another endemic species south of the Caspian Sea separated from the nearest *Q. cerris* population by more than 600 km. Like other species categorized as Full-Mediterranean, it prefers (sub-)Mediterranean climates, which commonly are transitional to fully humid or summer-dry warm and cool climates. Its general niche resembles that of *Q. afares* with mild but drier winters and no extensive summer drought; the precipitation maxima are concentrated in autumn. In contrast to Full-Mediterranean species, *Q. castaneifolia* typically occurs in mesic Temperate Broadleaf and Mixed Forests (i.e. can be categorized as Meridional). *Quercus cerris* (Meridional or Full-Mediterranean) forms part of Mediterranean Forests, Woodlands and Scrub, as well as of deciduous Temperate Broadleaf and Mixed Forests and, at higher elevations, Temperate Conifer Forests.

Maximum likelihood reconstructions of ancestral climate zones and biomes

Using only extant species, the MRCA of Western Eurasian *Cerris* oaks is reconstructed as Full-Mediterranean/Meridional, since most modern species thrive in Mediterranean Forests, Woodlands and Scrub biomes under a Mediterranean climate with hot and dry summers including the oro-Mediterranean belt (perhumid). For the East Asian subsection *Campylolepides* (biome-wise nemoral, climate-wise variable), the result is similarly biased (MRCA biome: nemoral; climate: ambiguous; small signatures in Fig. 4 and Supplementary data Fig. 4).

In contrast, ML reconstructions incorporating fossil-taxa suggest late (Early to Middle Miocene) biome and climate niche shifts in East Asian members of sect. *Cerris* from Moist-Subtropical to (Meridio-)Nemoral. A shift from warm fully humid (Subtropical) to winter-dry monsoon climates (Meridio-Nemoral) is reconstructed for the Late Miocene (11.6–5.33 Ma; Supplementary data Fig. 4). In Western Eurasia, probable climate shifts from fully humid climates to climates with temperature and/or precipitation seasonality are inferred for the Middle Miocene (16.0–11.6 Ma) for the *Cerris* core group (sections *Cerris* and *Libani*). This is in accordance with high resolution palynological data from East Mediterranean strata, which suggest a transition from equable warm-humid temperate climates to more seasonal (precipitation) and cooler climates (Bouchal *et al.*, 2018). Shifts to fully Mediterranean climates are reconstructed with high confidence for the Pleistocene (2.58–0.012 Ma). No shifts are reconstructed with high confidence for Mediterranean Forests, Woodlands and Scrub biome before the Pliocene when fossil assemblages containing the fossil-taxa are considered. The strong effect of including fossils in ancestral state reconstructions is illustrated in subsection *Suber*, where the fossil(s) cause a shift in inferred biome

and climate from summer-wet to summer-dry conditions during the latest Miocene. Without information from the fossil record, no biome shift is reconstructed, while already by the Oligocene a preference for summer-dry climates (Meridional; Full-Mediterranean) is reconstructed within the Western Eurasian clade of section *Cerris*.

Leaf evolution and climatic niches in section Cerris

Section *Cerris* exhibits high leaf variability in response to temperature (mean temperature of the coolest month, MTCM; Figure 5). A potentially ancestral leaf type with narrow elliptic lamina, triangular teeth or reduced teeth with long bristle-like extensions is present in all members of the East Asian subsection *Campylolepides* (Fig. 5A–C) thriving in summer-wet climates across a wide temperature range (Supplementary Data 3). This leaf type is also found amongst the earliest known leaf fossils of the section (*Q. gracilis* [Pavlyutkin] Pavlyutkin; Supplementary data Table 2) and has been retained in the Western Eurasian subsection *Libani*, part of the *Cerris* core clade (Fig. 5 L). Within *Campylolepides*, a correlation between leaf size and petiole length and cold tolerance is seen in the increase in both from *Q. chenii* to *Q. variabilis* and *Q. acutissima* (Fig. 5A to C; Supplementary Data 3).

A second leaf type is represented by the fossil-species *Q. kraskinensis* Pavlyutkin, which co-occurs with the fossil-species *Q. gracilis* in the early Oligocene site of Kraskino (Supplementary data Table 2). This leaf morphotype is potentially symplesiomorphic in section *Cerris*, as it shares features with Western Eurasian species that are absent from the modern East Asian oaks (Supplementary Data 1: Fig. S1-6): teeth are usually strongly developed, with mucronate to cuspidate apexes, and convex to sigmoid basal and apical sides. Early diverging species in all Western Eurasian clades, irrespective of their diverse niche preferences, possess such leaves (subsect. *Suber*: *Q. crenata*, Fig. 5D; subsect. *Aegilops*: *Q. brantii*, Fig. 5G; subsect. *Libani*: *Q. afares*, *Q. trojana*, Fig. 5J, K; subsect. *Cerris*: *Q. castaneifolia*, Fig. 5N; and in *Q. euboica*, *Cerris* core clade, Fig. 5M).

Subsection *Suber* exhibits a leaf morphological gradient from a *crenata* type to a *suber* type, expressed by a reduction in leaf size and tooth area and a change from (semi)deciduous to (semi)evergreen, more leathery leaves. This gradient is associated with a climatic gradient from mesic (Nemoral; *Q. crenata*) to (Full-)Mediterranean conditions (*Q. suber*; Supplementary Data 1, 3). Small ovate leaves with reduced cuspidate teeth lacking soft bristle-like extensions are only found in the semi-evergreen western Mediterranean *Q. suber* (Fig. 5E) and superficially resemble evergreen

leaves of *Q. ilex* in section *Ilex*. Subsection *Libani* (Fig. 5J–L) exhibits a similar decreasing gradient in leaf size and tooth area associated with a decreasing gradient in cold tolerance and aridity, from *Q. afares* to *Q. trojana* to *Q. libani*. In contrast to the diversity found in subsections *Suber* and *Libani*, all species in subsection *Aegilops*—the only subsection in which all members are adapted to pronounced summer-drought as well as winter-cold climates (Supplementary Data 3)—have medium-sized leaves though range from weakly developed to complex, coarse teeth with subsidiary teeth (Fig. 5H, I).

Finally, in subsection *Cerris*, the greatest tooth area and largest leaf size are seen in *Q. cerris*, the most Nemoral species in Western Eurasia, and *Q. look*, a Full-Mediterranean species occupying a climate niche that overlaps with both subsections *Aegilops* and *Libani*. Lobed leaves displaying an enormous variability are exclusively found in the widespread *Q. cerris* (Fig. 5O), which also exhibits a broad climatic niche, surpassed in the section only by the East Asian *Q. variabilis*. The remarkable leaf polymorphism of *Q. cerris* includes leaf types seen in *Q. castaneifolia* and *Q. look* (Fig. 5N, P; cf. fig. 7 in Denk *et al.*, 2021a). The ecological-climatic and leaf-morphological variation of *Q. cerris* parallels the lack of genetic coherence in our RAD-seq data set, with some *Q. cerris* sharing the genotype of *Q. castaneifolia*, while others are genetically highly similar to *Q. look* (hence, represented by two tips in the subset used for dating). This might indicate ongoing speciation in subsection *Cerris*.

DISCUSSION

Evolutionary and biogeographic history of section Cerris

Section *Cerris* appears to have originated and diversified morphologically in northern East Asia by the early Oligocene. The oldest fossils of section *Cerris* are dispersed pollen grains from early Eocene (Ypresian, 56.0–47.8 Ma) strata of the Russian Far East (Shkotovskii Basin; Naryshkina and Evstigneeva, 2020; Pavlyutkin *et al.*, 2020). By the early Oligocene, section *Cerris* was present with at least two distinct fossil-species based on leaves in the Russian Far East Kraskino Flora (34–30 Ma; Pavlyutkin *et al.*, 2014; Pavlyutkin, 2015). Importantly, these oldest East Asian fossil records predate the earliest known fossils of *Cerris* in Western Eurasia (dispersed pollen from Germany, Altmittweida; earliest Miocene, 23–20.5 Ma; Kmenta, 2011; Standke *et al.*, 2010) by more than 10 million years, and unambiguous leaf records of section *Cerris* are not known in Western Eurasia before the Miocene (e.g. Mai, 1995; Knobloch and Kvaček, 1976). Foliage described as '*Q. gracilis*' (Pavlyutkin) Pavlyutkin (nom. illegit.) is very similar to modern leaves of East Asian members of section *Cerris* (Fig. 5). Another species described from the Kraskino Flora, *Q. kraskinensis* Pavlyutkin

(Pavlyutkin, 2015) is strikingly similar to a number of modern Western Eurasian *Cerris* oaks, in particular to *Q. crenata*, the root-proximal species in the second-diverging subsection *Suber*, and to a lesser degree to *Q. trojana* and *Q. cerris*, members of *Cerris* core clade (this study; Supplementary Data 1: Plate S1-1). Thus, this leaf morphology is characterized by shared features, ancestral (possibly symplesiomorphic) within section *Cerris*. *Quercus kraskinensis* might represent a precursor or early member of what would become the Western Eurasian clade of *Cerris* (Fig. 3). The East Asian Paleogene record thus demonstrates that most of the range of *Cerris* leaf morphological diversity evolved at the dawn of the section, with the “*kraskinensis-crenata*” leaf type originating in East Asia and surviving in Western Eurasia (Supplementary Data 1).

The northern East Asian origin of section *Cerris* (cf. Fig. 3) is also supported by evidence from previous molecular studies. First, all modern *Cerris* share the same, section-unique plastid lineage, indicative of a single point of origin and quick dispersal, with the East Asian subsection *Campylolepides* showing the overall highest plastid divergence (Simeone *et al.*, 2018; Zhang *et al.*, 2020; Li *et al.*, 2022). Second, the *Cerris* plastomes are part of a haplotype lineage shared with a group of section *Ilex* species thriving in modern-day Japan and the mountains of northern and central China (East Asian clade in Figs 1, 3; Simeone *et al.*, 2016: *Q. engleriana* Seemen, *Q. phillyreoides*, *Q. spinosa* David; Zhou *et al.*, 2022: *Q. dolicholepis*, *Q. engleriana*, *Q. spinosa*, *Q. pseudosetulosa* Q.S.Li & T.Y.Tu), i.e. geo-historically close to the oldest *Cerris* fossils of the Russian Far East (Fig. 6). Most of these species belong to Jiang *et al.*'s (2019) early diverging “clade II” (prior to mid-Eocene, $\geq \sim 40$ Ma, in Jiang *et al.*, 2019; median divergence stem age of 49 Ma, this study, Fig. 3). In combination, the fossil and molecular data thus work together to provide a robust picture of the East Asian origins for the iconic European section *Cerris*.

The fossil record of *Cerris* then leads westward along a northern route, via northern and Central Asia, chiefly following the then-high-latitude ($\geq 60^\circ\text{N}$; Scotese *et al.*, 2014) ‘warm’ climate zone and avoiding the shrinking boreotropics (sensu Wolfe, 1975; paratropical floras sensu Mai 1995). Fossil-taxa comparable to section *Cerris* have been reported from Oligocene and Early Miocene central and eastern Kazakhstan and Russia under various names (*Q. pseudocastanea*, *Q. furuhjelmii*, *Q. pseudorobur*, *Q. sp.* etc.; e.g. Kryshstofovich *et al.*, 1956; Yakubovskaya, 1957; Kornilova, 1960; Rajushkina, 1979; Takhtajan, 1982). From late Oligocene strata of south-western Siberia, Denk *et al.* (2021b) reported dispersed pollen and leaves [*Q. cf. kubinyii* (Kováts in Ettingsh.) W.Berger] unambiguously belonging to sect. *Cerris*. The large potential area and relatively smooth palaeo-topography (Scotese, 2014) would fit with the overall low plastid differentiation observed in the section, as topographic variation is broadly associated with phylogenetic diversity and speciation

in woody plants (Verboom *et al.*, 2015; Feng *et al.*, 2016; Jin *et al.*, 2021) and oaks in particular (Hipp *et al.*, 2018). Furthermore, our FBD dating places the initial radiation of *Cerris* c. 10 Ma after that of its sister lineage section *Ilex* (Fig. 3), which took a southern route via the ‘Himalayan corridor’ (Simeone *et al.*, 2016; Jiang *et al.*, 2019).

After the earliest appearance of *Cerris* in Western Eurasia in Early Miocene deposits of Germany, dispersed pollen grains of section *Cerris* are also known from slightly younger Burdigalian strata of Turkey and Greece (Denk *et al.*, 2017b). Given the complex tectonic situation and the availability of different \pm temperate niches during the Early and Middle Miocene, it is conceivable that *Cerris* evolved several lineages within its first 10 Ma (subsects *Suber*, *Aegilops*, *Cerris* core clade; Fig. 3). One outcome of a rapid diversification may be partial reproductive compatibility between these lineages, as evidenced by admixture among subsections (Supplementary Data 1). A rapid origin and spread with gene flow between lineages is also supported by the low plastid differentiation, decoupled from main intra-sectional lineages (subsections) and species. *Cerris* oaks then became relatively widespread (*Q. kubinyii*) in Western Eurasia during the Middle Miocene, ranging from Denmark to Anatolia (Kováts, 1856; Christensen, 1976; Knobloch, 1986; Güner *et al.*, 2017; Denk and Bouchal, 2021). These leaf remains resemble modern species of section *Cerris* that possess ancestral leaf types (Fig. 5, leaf types “0” and “1”). Section *Cerris* thus appears to have colonized and diversified in Europe and the Mediterranean from the Early through the mid-Miocene, providing the ancestry for the modern-day species and subsections. Our combination of phylogenomic data with a rich set of fossils suggests that main lineages in Western Eurasia may have been established before their modern morphologies (Figs 3, 5; Supplementary Data 1).

The *Cerris* history becomes all the more interesting in light of its parallels with the section *Ilex* history. Fossil pollen of both *Quercus* sections *Cerris* and *Ilex* in early Eocene strata of the Russian Far East (Naryshkina and Evstigneeva, 2020) indicate that both lineages might have originated in high-latitude warm temperate biomes (cf. Scotese *et al.* 2014). But whereas section *Cerris* had a first radiation in Northeast Asia and subsequently migrated to Western Eurasia north of the progressively enlarging Qinghai-Tibet Plateau, its sister clade, the evergreen section *Ilex*, initially migrated southwards and south-westwards into tropical China and south-eastern Tibet (Hoffman, 2010; Linnemann *et al.*, 2017; Su *et al.*, 2019), thence westwards into Europe and the Mediterranean along the proto-Himalayas south of the Qinghai-Tibet Plateau (Jiang *et al.*, 2019). Section *Cerris* makes it into southern China only in Late Miocene strata of western Yunnan (Xia *et al.*, 2009; Xu *et al.*, 2012). The co-occurrence of the sections in East Asia is further supported by shared plastids of northern East Asian species of section *Ilex* (mostly Jiang *et al.* 2019, clade II) with section *Cerris*

(Simeone et al. 2016; Yan et al. 2019; Zhou et al. 2022). Moreover, the *Cerris-Ilex* shared plastome lineages differ substantially from plastome lineages shared between section *Ilex* and the East Asian section *Cyclobalanopsis* (Yang et al., 2018), further pointing to the divergent history of these sections in southeast Asia. Thus, molecular data corroborate that Western Eurasian *Cerris* came into contact with *Ilex* only after the East Asian Eocene and Oligocene members of *Cerris* had begun to move westwards. Plastid phylogeography hence fits with a scenario of largely isolated early evolutionary histories of *Cerris* (Northern Asia) and *Ilex* (Himalayan Corridor).

Ecological and climatic niche evolution

Our reconstructions of biome and climatic niche suggest persistence of the Tropical and Subtropical Moist Broadleaf Forests biome during the Oligocene, consistent with fossil records (e.g. Kvaček, 2010; Pavlyutkin et al., 2014). By contrast, reconstructions that ignore the fossils (Fig. 4) suggest shifts into the Mediterranean Forests, Woodlands and Scrub biome that are at odds with the Western Eurasian fossil record, where this biome is not recorded before the Plio-Pleistocene (Suc, 1984; Velitzelos et al., 2014). The early Eocene (Ypresian, 56–47.87 Ma) split between sections *Cerris* and *Ilex* must have coincided with the origins of deciduousness in *Cerris*, whereas *Ilex* retained the original evergreen leaf habit of subgenus *Cerris* (which is also characteristic of section *Cyclobalanopsis*, sister to the *Cerris* + *Ilex* clade). The subsequent biogeographic histories of the two lineages reflect this change. Members of section *Cerris* moved westwards as a northern lineage, part of a more or less temperate forest biome dominated by deciduous tree species during the Oligocene (Kryshtofovich et al., 1956; Popova et al., 2013; Willis and McElwain, 2002; Pavlyutkin et al., 2014; Scotese et al., 2014; Averyanova et al., 2021; Denk et al., 2021b). Extensive lowlands in large parts of Siberia and northern Kazakhstan provided nutrient rich substrates dominated by deciduous woody plants (“warm temperate biome” in Willis and McElwain, 2002; “warm [temperate]” climate zone in Scotese et al., 2014). To the south of this ± temperate forest belt, a drier region was occupied by the “subtropical summerwet biome” (coined wooded savannah to semi-desert; Willis and McElwain, 2002) corresponding to an arid climate zone with frosts according to Scotese et al., (2014). Here, sect. *Cerris* oaks would have had an advantage due to the earlier origins of deciduous leaf phenology.

This trait diversity likely also shaped the ecological diversification of section *Cerris* and the high community-level diversity of Mediterranean oaks. In Western Eurasia, *Cerris* oaks colonized a wide range of habitats, reflected in their Miocene distribution from southern Scandinavia to southern Turkey, a range of almost 20 degrees latitude (Fig. 6). Three key morphological features of

Cerris oaks may have provided advantages during subsequent shifts into their modern Mediterranean habitats: deciduous or semi-deciduous leaves, large acorns protected by sturdy cups, and corky stems. By contrast, the evergreen oaks of section *Ilex* that spread southwards and south-westwards during the Eocene from the temperate to the subtropical summer-wet biome differentiated geographically (Jiang et al., 2019) but remained evergreen. The resulting climatic niche partitioning in the Western Eurasian subsections of *Cerris* oaks (Supplementary Data 3) and between sections *Ilex* and *Cerris* may have enabled the coexistence of several summer- and wintergreen oak lineages: up to 13 species of both deciduous and evergreen oaks from three sections—*Quercus*, *Cerris* and *Ilex*—presently co-occur in southern Turkey, for example (Hedge and Yaltirik, 1982; Blumler, 2015).

Ecological lability of section *Cerris* manifests as well in both niche convergence and trait convergence. *Quercus suber*, for example, is the only European tree species that is able to re-sprout after fire damage (Pausas, 1997; Houston Durrant et al., 2016). It is also highly flexible in the timing and duration of leaf abscission and can rapidly replace old leaves with new shoots (Escudero and del Arco, 1987), characteristics typical of all members of section *Cerris*. Yet a number of *Q. suber* adaptations are more reminiscent of evergreen species of section *Ilex*: its ability to switch between annual and biennial fruit maturation in response to climate, semi ring-porous wood anatomy that reduces the risk of embolism in droughty springs, and sandy lowland habitat (Elena-Rosello, 1993; Sousa, 2009). By contrast, *Quercus crenata*, the sister species of *Q. suber*, retains many putatively ancestral traits of section *Cerris*—corky bark, leaf texture, leaf abscission, leaf shape, ring-porosity, partly humid temperate climate niche—and is morphologically similar to some of the oldest known fossil-species of *Cerris* (e.g., *Q. kraskinensis*), perhaps due to niche conservatism and repeated phases of introgression (Table 3). *Quercus cerris*, the most temperate of the *Cerris* oaks, provides an even more pronounced example of convergence between sections. It is the only oak in all of subgenus *Cerris* with complex lobed leaves, reminiscent of the lobed white oaks of *Quercus* sect. *Quercus* (subgenus *Quercus*). Lower hydraulic resistance in deeply lobed leaves may provide a mechanism for improving water balance under dry atmospheric conditions (Siso, 2001) and also enable leaves to pack more efficiently into buds (Edwards et al., 2016; Givnish and Kriebel, 2017; Zohner et al., 2019). Lobedness is thus a convergent trait that may contribute to the ability of *Q. cerris* to grow sympatrically with (co-)dominant lobed white oaks such as *Q. robur* L., *Q. petraea*, *Q. frainetto* Ten. and *Q. vulcanica* Boiss. ex Kotschy and account for its long history of cultivation in the British Islands (Loudon, 1838). Section *Cerris* thus contributes to our growing understanding of the importance of both divergence within sections and convergence between them in shaping oak diversity and patterns of coexistence (cf. Cavender-Bares et al., 2004, 2015, 2018).

CONCLUSIONS

Two different migration routes resulted in distinct diversity patterns in the sister sections *Cerris* and *Ilex*. The deciduous section *Cerris* is most ecologically and taxonomically diverse in Western Eurasia (12 of 15 species), while the evergreen section *Ilex* is most diverse in East and Southeast Asia into the Himalayas (21 of ca. 25 species). Globally, evergreen broadleaf species occur in relatively humid (~1,500–3,000 mm mean annual precipitation, MAP) and warm (mean temperature of the coldest month, MTCM > 0°C) climates, whereas winter deciduous broadleaf species typically occur in relatively less humid (MAP ~700–1,500 mm) and cooler climates (MTCM < 0°C; Woodward *et al.*, 2004). Nevertheless, both evergreen sclerophyllous and deciduous oak species are at present highly diverse in summer-dry Mediterranean areas. Extensive research in modern Mediterranean ecosystems suggests that neither evergreen nor deciduous species grow optimally there (Escudero *et al.*, 2017).

Our time-calibrated phylogenetic reconstruction using 47 fossils suggests that suboptimal adaptation to current Mediterranean climate may be a deep time evolutionary legacy in both the evergreen section *Ilex* and the deciduous section *Cerris*, resulting from their differential early range expansions from Northeast Asia. Section *Cerris* shifted to deciduous leaves in frost-free environments, which would have preadapted the lineage to the dry and cold climates it encountered in its westward expansion (*trait first* pattern). Section *Ilex* retained its evergreen leaf phenology and did not shift to deciduous leaves when colonizing winter-cold and -dry habitats in the Himalayas and warm, summer-dry environments in the Mediterranean region. Western Eurasia thus became a meeting ground for old relatives of divergent sources: the northeast Asian *Cerris*, the southeast Asian *Ilex*, and, ultimately, the eastern North American white oaks of section *Quercus*, who joined them between 10 and 20 million years ago (Denk *et al.* 2010; Denk and Grimm 2010; Hipp *et al.* 2018, 2020). These legacies explain why species of all three sections co-occur in contemporary Mediterranean climates of Western Eurasia and how their distributions follow environmental and climatic gradients within the wider Mediterranean region.

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Table 1 Currently recognized members of *Quercus* section *Cerris* and information about geographical distribution, representative Köppen-Geiger climate and biome types, and some morphological characteristics.

Distribution data from GBIF (<https://www.gbif.org/>), Fang *et al.*, 2009.

^a ≥ 10% of occurrences (unique grid cells); dominating occurrences in bold. See Supplementary Data 3 for complete occurrence data. ^b Hot dry summers plus very cold winters; (A) = < 3%; ^c transitional to fully humid Cf climate.

Biome abbreviations: TBMF, Temperate Broadleaf & Mixed Forests; TSMBF, Tropical & Subtropical Moist Broadleaf Forests; MFWS, Mediterranean Forests, Woodlands & Scrub.

Data on vertical distribution and quantitative morphological traits are from: le Hardy de Beaulieu & Lamant, 2010; Hedge & Yaltirik, 1982; Hegi, 1981; Hélaridot, 1987 onwards; Huang *et al.*, 1999; Kotschy, 1862; Menitsky, 2005; Mucina, 2000; Stephan *et al.*, 2018.

Species	Region	Köppen-Geiger climate types	Representative climate types ^a	Environmental stress
(Kottek <i>et al.</i> , 2006, Peel <i>et al.</i> , 2007)				
<i>Q. acutissima</i>	E Asia	(A), Cw, Cf, Dw, Df, (BSk)	Cfa , Cwa	Humid=no stress [Snow, Continentality]
<i>Q. chenii</i>	E Asia	Cf	Cfa	Humid=no stress
<i>Q. variabilis</i>	E Asia	Cw, Cf, Dw, Df, BSk	Cfa , Cwa, Cwb	Humid=no stress [Snow, Continentality]
<i>Q. crenata</i>	W Eurasia	Cf, Cs	Csa , Csb, Cfb	Drought [Humid=no stress]
<i>Q. suber</i>	W Eurasia	Cf, Cs, (BSk)	Csa , Csb	Drought, Fire
<i>Q. brantii</i>	W Eurasia	Cs, Ds, BSk	Csa , Dsa	Drought [Snow, Continentality] ^b
<i>Q. ithaburensis</i>	W Eurasia	Cs, (BSk), (BWk)	Csa , Csb	Drought [Continentality] ^b
<i>Q. macrolepis</i> [incl. <i>Q. vellonea</i>]	W Eurasia	(Cf), Cs	Csa , Csb	Drought
<i>Q. afares</i>	W Eurasia	Cs	Csa , Csb	Drought
<i>Q. libani</i>	W Eurasia	Cs, Ds, (BSk)	Csa , Csb, Dsa, Dsb	Drought [Snow, Continentality] ^b
<i>Q. trojana</i>	W Eurasia	(Cf), Cs, (Ds)	Csa , Csb	Drought [Snow]
<i>Q. euboica</i>	W Eurasia	Cs	Csa	Drought
<i>Q. castaneifolia</i>	W Eurasia	Cs, Ds ^c	Csa^c	Humid=no stress ^c [Snow]
<i>Q. look</i>	W Eurasia	Cs	Csa	Drought
<i>Q. cerris</i>	W Eurasia	Cf, Cs, Df, (Ds)	Cfb , Csa , Csb	Humid=no stress, Drought [Snow]

Major biogeographic region	Terrestrial biome	Altitude	Cup diameter	Leaf size	Leaf type
(Olson <i>et al.</i> 2001)	(Olson <i>et al.</i> , 2001)	(m a.s.l.)	(cm, incl. bracts)	(length, cm)	(cf. Fig. 5)
Palaearctic, Indo-Malay	TBMF, TSMBF	100–2200	1.2–4.2	8-19	0
Palaearctic, Indo-Malay	TBMF, TSMBF	<600	0.8–1.7	7-12	0
Palaearctic, Indo-Malay	TBMF, TSMBF	<3000	1.5–4	8-15(-20)	0
Palaearctic	TBMF	<1000	2.5	4-9	1
Palaearctic	MFWS	<800	2–2.5	3-7	2
Palaearctic	MFWS	350–1700	1.5–4	6-10(-13)	1
Palaearctic	MFWS	50–500	3–5	4-9	1
Palaearctic	MFWS	50-1700	2.5–6.5	5-9	3
Palaearctic	MFWS	900–1900	1.8–3.5	7-14	1
Palaearctic	MFWS	700–2000	2–3.5	7-12	0
Palaearctic	TBMF, MFWS	300–1800	2.2–3	3-8(-10)	1
Palaearctic	MFWS	100–500	Not known	5-9(-11)	1
Palaearctic	TBMF	<2400	1.5–2	10-20	1
Palaearctic	MFWS	1000–2000	2–3.3	5-7.5	3
Palaearctic	TBMF, MFWS	<1900	2.5–3.5	5.5-14(-20)	4

Table 2 Subsectional classification of *Quercus* sect. *Cerris* in the present study and comparisons to previous classification schemes.

Species	This study	Ørsted (1871)	Schwarz (1936)	Camus (1936–1954)	Menitsky (1984)
	Subsection	Section	Section	Subsection	Subsection
<i>Q. acutissima</i> Carruth.	<i>Campylolepides</i> A.Camus	[not considered]	<i>Erythrobalanopsis</i>	<i>Campylolepides</i>	<i>Aegilops</i>
<i>Q. chenii</i> Nakai	<i>Campylolepides</i> A.Camus	[described later]	[not covered]	<i>Campylolepides</i>	<i>Aegilops</i>
<i>Q. variabilis</i> Blume	<i>Campylolepides</i> A.Camus	<i>Mucronatae</i>	[not covered]	<i>Campylolepides</i>	<i>Aegilops</i>
<i>Q. crenata</i> Lam.	<i>Suber</i> (Spach) Maleev	[described later]	<i>Aegilops</i>	[not recognised]	[not covered]
<i>Q. suber</i> L.	<i>Suber</i> (Spach) Maleev	<i>Suber</i>	<i>Suber</i>	<i>Suber</i>	<i>Suber</i>
<i>Q. brantii</i> Lindl.	<i>Aegilops</i> (Reichenb.) Menitsky	<i>Mucronatae</i>	<i>Aegilops</i>	<i>Macrolepides</i>	<i>Aegilops</i>
<i>Q. ithaburensis</i> Decne.	<i>Aegilops</i> (Reichenb.) Menitsky	<i>Dentatae</i>	<i>Aegilops</i>	<i>Macrolepides</i>	<i>Aegilops</i>
<i>Q. macrolepis</i> Kotschy [incl. <i>Q. vallonaea</i> Kotschy]	<i>Aegilops</i> (Reichenb.) Menitsky	<i>Eucerris</i>	<i>Aegilops</i>	<i>Macrolepides</i>	<i>Aegilops</i>
<i>Q. afares</i> Pomel	<i>Libani</i> subsect. nov.	[described later]	<i>Eucerris</i>	<i>Macrolepides</i>	<i>Cerris</i>
<i>Q. libani</i> Olivier	<i>Libani</i> subsect. nov.	<i>Mucronatae</i>	<i>Erythrobalanopsis</i>	<i>Macrolepides</i>	<i>Aegilops</i>
<i>Q. trojana</i> Webb	<i>Libani</i> subsect. nov.	<i>Mucronatae</i>	<i>Erythrobalanopsis</i>	<i>Macrolepides</i>	<i>Aegilops</i>
<i>Q. euboica</i> (Papioann.) K.I.Chr. ^a	<i>Cerris</i> (Dumort.) Guerke vel <i>Libani</i>	[described later]	[described later]	[not recognised]	[not covered]
<i>Q. castaneifolia</i> C.A.Mey.	<i>Cerris</i> (Dumort.) Guerke	<i>Serratæ</i>	<i>Eucerris</i>	<i>Macrolepides</i>	<i>Cerris</i>
<i>Q. look</i> Kotschy	<i>Cerris</i> (Dumort.) Guerke	<i>Mucronatae</i>	[not covered]	<i>Macrolepides</i>	<i>Aegilops</i>
<i>Q. cerris</i> L.	<i>Cerris</i> (Dumort.) Guerke	<i>Eucerris</i>	<i>Eucerris</i>	<i>Eucerris</i>	<i>Cerris</i>

^a*Quercus euboica* was recently recognized as a distinct species (Simeone *et al.*, 2018)

Remarks to newly recognized (emended) subsectional classification:

Subsection *Campylolepides* Camus, 1934, included the East Asian members of sect. *Cerris* but also *Quercus acutissima* subsp. *roxburghii* (Endl.) A.Camus.

Subsection *Suber* (Spach) Maleev, 1935. Published in Bot. Zhur. 20, 2: 162.

Subsection *Aegilops* (Reichenb.) Menitsky, 1971, is the valid name. Subsection *Macrolepides* in Camus 1936–38 is an invalid name as the same name was used by Camus in 1934 for a group of white oaks. Published in Fl. Iranica [Rechinger] 77: 12.

Subsection *Libani*. Typus: *Quercus libani* Oliv. 1801. Leaves thin or thick, glabrous or tomentose, lamina narrow elliptic, narrow ovate or oblong; tips of teeth pointed short to long bristles; cupule hemispherical and barrel-shaped, cupule scales broad, rhombic or broadly triangular, adpressed.

Subsection *Cerris* (Dumort.) Guerke, 1897. Published in Richter, Pl. Eur. 2: 69.

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Figure captions

Figure 1 Maximum likelihood tree inferred from RAD-Seq data of *Quercus* section *Cerris* including members of *Quercus* sections *Ilex* and *Cyclobalanopsis* (subg. *Cerris*), *Quercus* subgenus *Quercus*, and *Notholithocarpus* as extended outgroup. Annotated are the number of fossil priors (stars) that can be linked to each clade (cf. Supplementary data Table 2) and their maximum possible age range; separately for main geographic regions where applicable. Tip labels give geographic distribution of species (bold font, abbreviations see upper left) or provenance of the individual sample (normal font, in square brackets).

Figure 2 Distribution of *Quercus* section *Cerris* (main intra-sectional clades: subsections, and their constituent spp.) across Eurasia and main Köppen-Geiger climate types (cf. Table 1, Supplementary Data 3).

Figure 3 First of three chronograms for *Quercus* section *Cerris* and its sister clade section *Ilex* inferred with the FBD approach (pruned to modern-day tip set). The phylogenetic, stratigraphic (time/ time slice) and geographic position of the used fossil data set is indicated (23 and 14 fossil-species; see Supplementary data Table 2). See Supplementary data Table 3 for details across all three runs; median rates and 95% highest posterior density intervals are depicted in Supplementary data Figure 4.

Figure 4 Maximum likelihood mapping of preferred biomes on the chronogram of the first run (Fig. 3); scored as five categories: Moist-Subtropical, Meridio-Nemoral, Nemoral, Meridional, Full-Mediterranean.

Large pie charts give proportional likelihoods for most-recent common ancestors (MRCAs) of modern-day species (at nodes) and (along branches) additional (shadow) MRCAs inferred by using fossil-taxa (stars connected to tree) to break down subsequent branches.

Coloured outlines of stars indicate the provenance of included fossil-taxa and fossil-taxa that could not be clearly assigned to a branch in the dated tree (unconnected stars). Small pie charts above big charts give the results when only modern-day states are considered. Purple dashed lines indicate

potential phases of introgression with the minimal obtained (partitioned) *D*-values indicated (cf. Supplementary data Table 5).

Figure 5 Leaf morphologies in extant subsections of *Quercus* sect. *Cerris*

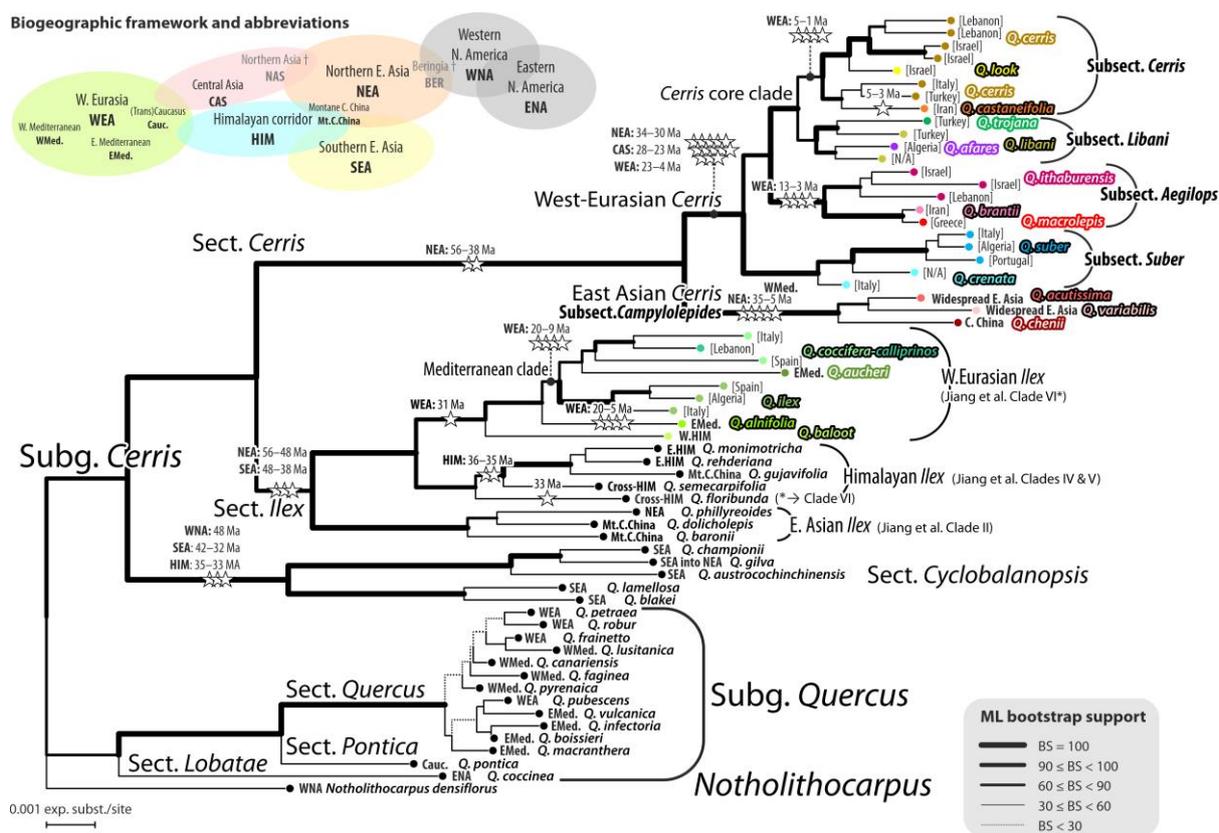
A–C Subsection *Campylolepidis*: **A** *Q. chenii* (P; P06859115), **B** *Q. variabilis* (E; E00294063_5), **C** *Q. acutissima* (E; E00671511_5); **D, E** Subsection *Suber*: **D** *Q. crenata* (P; P06856456), **E** *Q. suber* (S; Denk & Gruber 2005265_02); **F–I** Subsection *Aegilops*: **F** *Q. ithaburensis* (P; P06859855), **G** *Q. brantii* (E, E00404287_6), **H** *Q. macrolepis* (S; Denk & Grimm 2006051), **I** *Q. macrolepis* (P; P06859855); **J–L** Subsection *Libani*: **J** *Q. afares* (S; Denk & Gruber 2005256_02), **K** *Q. trojana* (S; Denk & Grimm 2006365), **L** *Q. libani* (Denk & Grimm 2006203); **M** *Cerris* core clade: *Q. euboica* (S; Denk, Ruhri, Ruhri 20081018_4); **N–P** Subsection *Cerris*: **N** *Q. castaneifolia* (E00404346_6), **O** *Q. cerris* (Denk & Grimm 2006110), **P** *Q. look* (Avishai 25_4).

Thermometers indicate climate (temperature) niche evolution within subsections. For climate data see Supplementary Data 3. Numbers to the left of representative leaves refer to leaf (tooth) types as defined in Supplementary Data 1: Figs S1-7.

Figure 6 Distribution of fossil members of sect. *Cerris* used for the chronogram (Fig. 3).

Map produced with the software QGIS (QGIS 2021).

Figure 1



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Figure 2



Figure 3

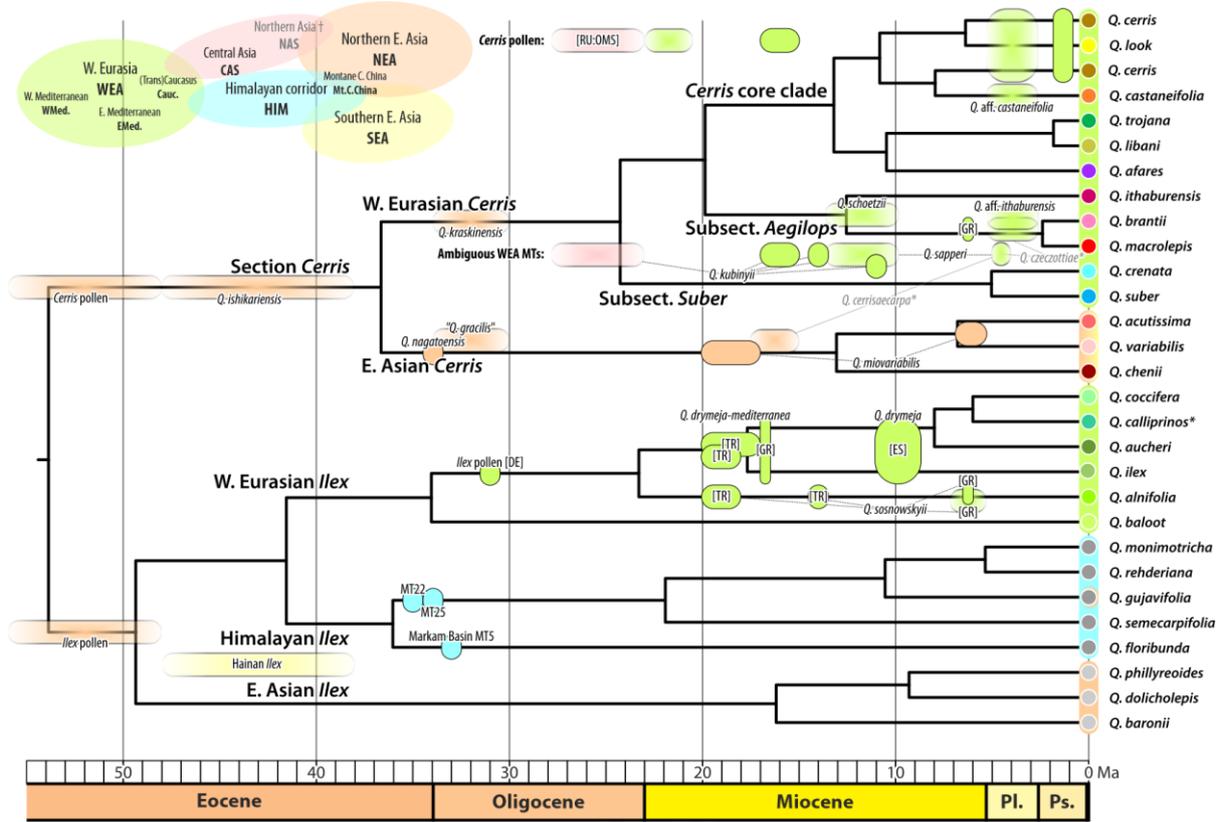
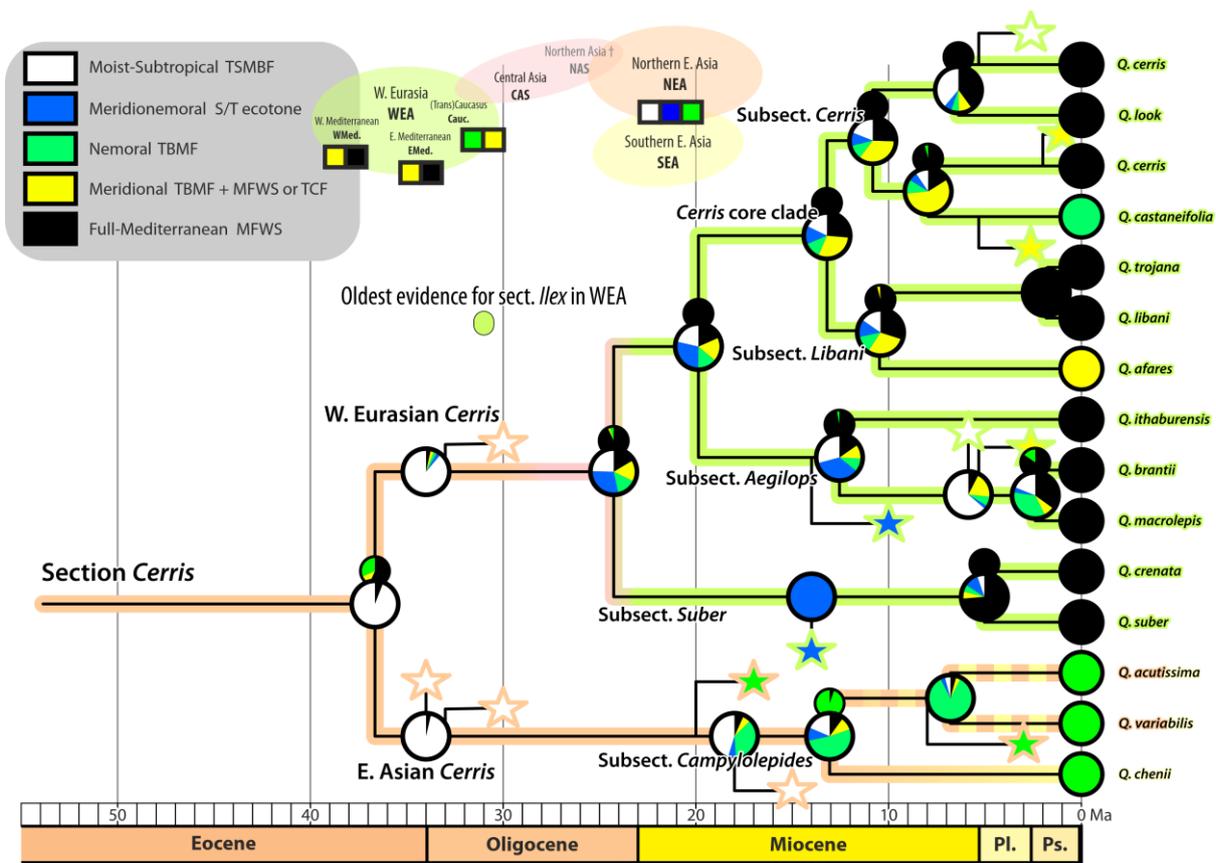


Figure 4



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Figure 5

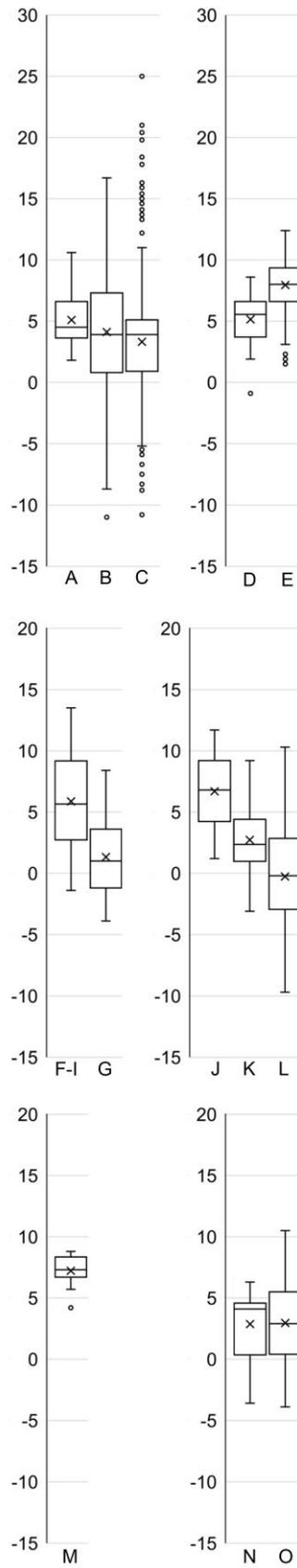
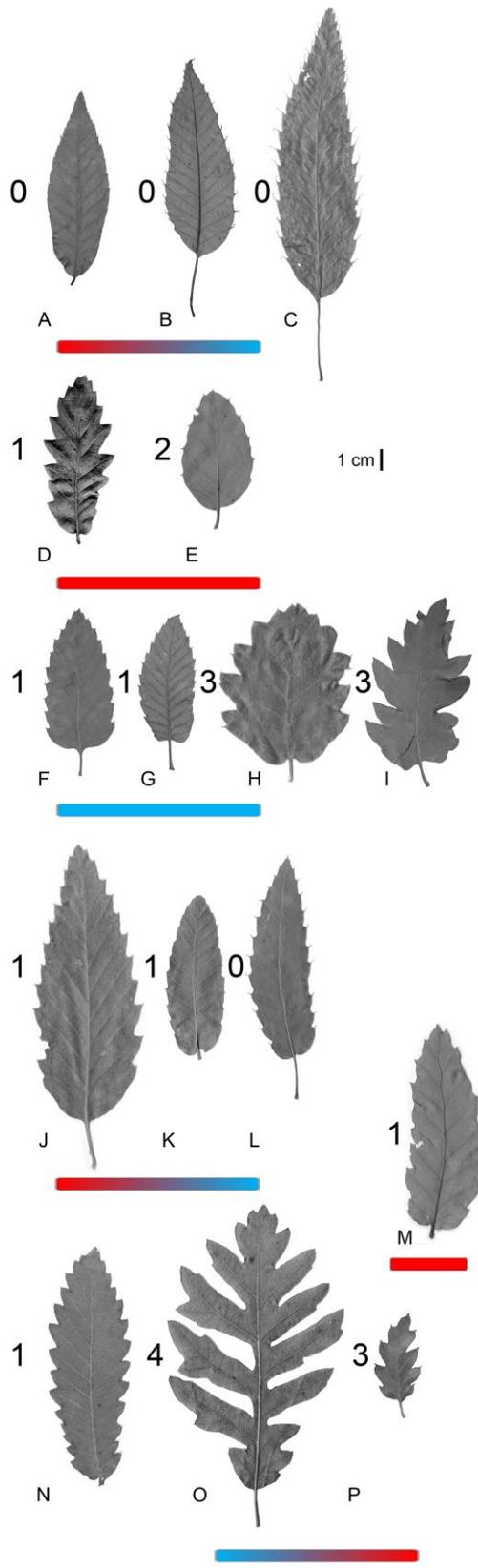
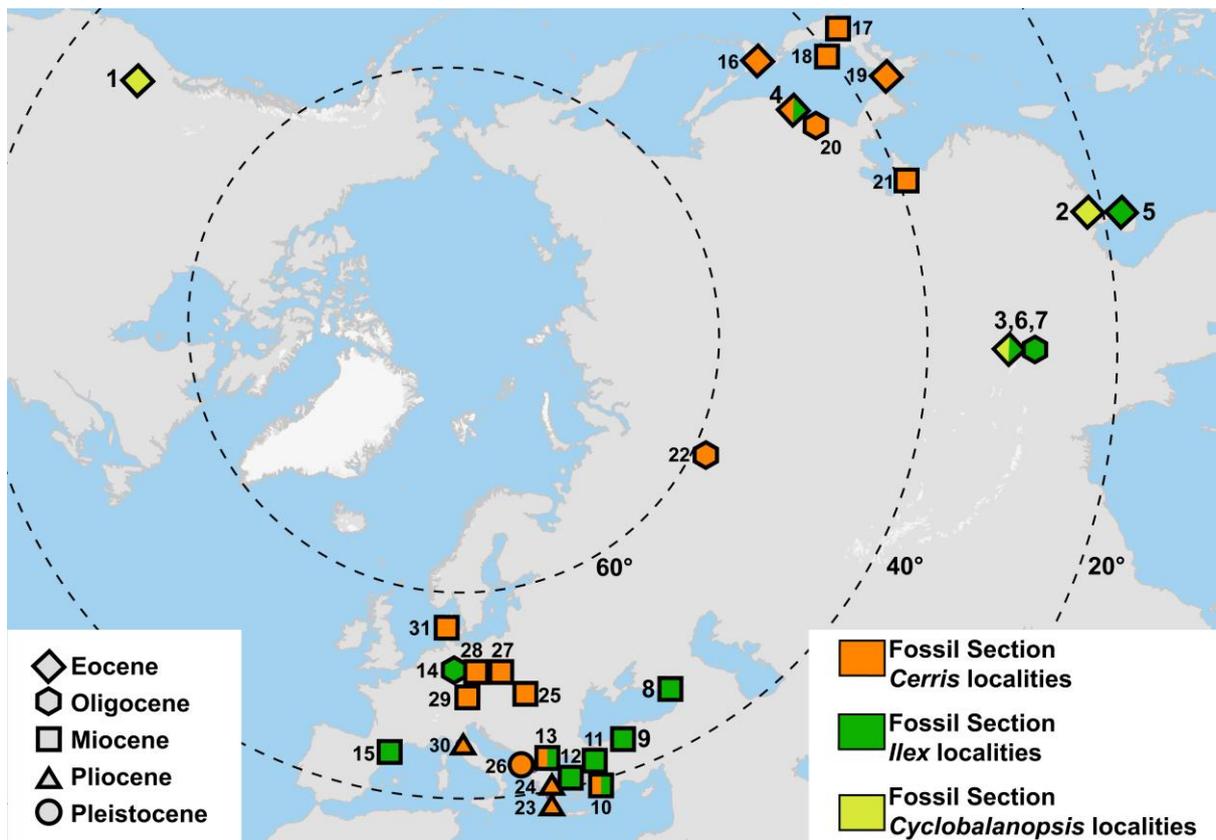


Figure 6



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