The Origin and Phylogenetic Relationships of the Californian Chaparral ‘Paleoendemic’ Pickeringia (Leguminosae)

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The Origin and Phylogenetic Relationships of the Californian Chaparral ‘Paleoendemic’ *Pickeringia* (Leguminosae)

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Abstract—*Pickeringia*, a monotypic genus of the Leguminosae endemic to the xerophytic sclerophyllous chaparral vegetation of the California Floristic Province, has been considered a “relict” of legume diversity in the North American flora and an example of the classic “paleoendemics” in the flora of California. Evidence is presented for the phylogenetic relationships of this genus, inferred from nucleotide sequence variation in the internal transcribed spacers of nuclear ribosomal DNA and the plastid *matK* gene. Phylogenies derived from maximum parsimony and Bayesian analyses both strongly support a close relationship of *Pickeringia* to the temperate to subtropical, deciduous genera *Cladrastis* and *Styphnolobium* of tribe Sophoreae consistent with morphological and cytogenetic evidence rather than to members of tribe Thermopsideae where the genus has been treated taxonomically. *Cladrastis* is resolved as paraphyletic while *Styphnolobium* is strongly supported as a monophyletic group. These results, plus an estimated age of ~31 million years for the genus, further substantiate the hypothesis that *Pickeringia* is geographically isolated in the flora of western North America, an old and phylogenetically distinct lineage of an early diverging group of papilionoid legumes that were much more widely distributed throughout temperate North America and Asia during the Tertiary but whose modern relatives are restricted to southern North America, Central America, and eastern Asia. These findings have implications not only for the evolutionary history of *Pickeringia* but also for the age and development of chaparral vegetation in the California flora.

Keywords—*Cladrastis*, geographic disjunction, Mediterranean-type climate, *Styphnolobium*, Sophoreae, Thermopsideae.

A predominantly broad-leaved sclerophyllous type of vegetation termed “chaparral,” consisting mostly of low-stature, often evergreen, shrubs and small trees, is a conspicuous vegetation type of southwestern North America (Keeley 2000). This vegetation type, and associated ecosystem, is often defined by a unique climate with typically warm to hot, dry summers and cool, wet winters (“Mediterranean-type” climate), and is referred to by different names in the five regions of the world where it occurs, including California, coastal central Chile, the Mediterranean basin, south-western Australia, and the Cape region of South Africa (Cody and Mooney 1978). The similarities in ecology and physiognomy of these Mediterranean-type floras have been considered classic examples of ecological and evolutionary convergence (Cody and Mooney 1978).

In North America, chaparral vegetation now ranges from northern California (U. S. A.) to northern Baja California (Mexico), thence discontinuously to Arizona and into Nuevo León and Tamaulipas of eastern Mexico (Axelrod 1989). A remarkably similar type of sclerophyllous vegetation (“Tehuacán mexical”) has developed in south-central Mexico under a “non-Mediterranean” wet-summer tropical climate (Valiente-Banuet et al. 1998). The timing of the origin and development of chaparral in western North America, whether in response to topographic, climatic, or edaphic changes that have taken place since the beginning of the Tertiary, has been the subject of much study and debate (e.g. Axelrod 1989; Keeley 2000; Keeley et al. 2012). Both paleoclimatic data (e.g. Flower and Kennett 1994) and fossil evidence (Axelrod 1992; Axelrod and Schorn 1994) indicate the Mediterranean-type climate began forming by the mid-Miocene (~15 Ma) in western North America, with a shift from an earlier summer-wet to the modern summer-dry climate and continued through the late Miocene. However, there is no evidence that the vegetation itself originated in direct response to the onset of the Mediterranea

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*Pickeringia montana* Nutt., an evergreen, spinescent, xerophytic shrub (Fig. 1) distributed in the chaparral and mixed evergreen-woodland forest vegetation of California and northern Baja California, is the only genus of the family Leguminosae (subfamily Papilionoideae) geographically restricted (endemic) to the California Floristic Province (Raven and Axelrod 1978). The “chaparral pea,” *P. montana* (Torrey and Gray 1840), is named for Dr. Charles Pickering of the Wilkes Exploring Expedition, which visited California in 1841 (McKelvey 1955). *Pickeringia montana* var. *montana* is a common inhabitant of the dry, rocky, mountain slopes of the Coast Ranges of northern and central California from Mendocino County south to Monterey County, but occasional to rare in similar habitats from Monterey County south to San Diego County of southern California and northern Baja California (Rudd 1968), and highly localized in the chaparral communities of the west slope of the Sierra Nevada foothills of Butte and Nevada Counties, in eastern central California. *Pickeringia montana* var. *tomentosa* (Abrams) I.M. Johnst. (Johnston 1923), typically densely pubescent, is restricted to the San Bernardino Mountains of San Bernardino County, and the mountains of eastern San Diego County to the northernmost Sierra Juárez of Baja California, Mexico (Wiggins 1980). The amount of pubescence is highly variable and the two varieties intergrade, especially in southern California and northern Baja California (Rudd 1968). *Pickeringia* seldom produces fruits and seedlings...
Pickeringia was first placed in tribe Thermopsideae by Yakovlev (1972) and has been retained there (Turner 1981; Lock 2005). This tribe of approximately 50 species of perennial herbs and shrubs in six genera is distributed across temperate regions of North America and Eurasia. Like the other members of Thermopsideae, Pickeringia possesses morphological characters that have linked it to both the tribes Genistae (Adans.) Benth. (gynoecial characters) and Sophoreae Spreng. (free stamens). Such similarities led earlier authors to originally place Pickeringia in the primarily tropical tribe Sophoreae (Torrey and Gray 1840). Later, cytogenetic evidence also suggested “affinities” to members of Sophoreae (Goldblatt 1981). Of the six genera that are currently treated in Thermopsideae (Lock 2005), only Pickeringia, Thermopsis R.Br., and Baptisia Vent. are native to North America, and of these, only Pickeringia and Baptisia are endemic there. Neither Baptisia nor Thermopsis is known from Mexico (Rudd 1968). The remaining genera, Ammopiptanthus Cheng, Anagyris L., and Piptanthus Sweet, are limited in distribution to areas in southern Europe and northern Africa with Mediterranean-type climates, or central and southern Asia, whereas Thermopsis is widely distributed in montane and steppe regions across temperate Asia as well as North America (Lock 2005; Wang et al. 2006).

Unlike other genera treated in Thermopsideae, Pickeringia possesses a diploid chromosome number of 2n = 28 (compared to 2n = 18, 20) and does not accumulate alkaloids of the “lupine type” which are characteristic of this tribe. These differences led Turner (1981) to suggest a “very old isolated position” for this taxon, a “relict” in the North American flora. Earlier, Raven and Axelrod (1978) suggested an old age for the genus, probably pre-Miocene. Indeed, Pickeringia has been considered one of the “interesting relics” in North America (Polhill 1981a), whose distribution is linked to the expansion of the Sophora group (along with Cladrastis Raf. and Sophora L.) from the Sino-Himalayan region of Asia, and one of the classic “paleoendemics” considered abundant in the flora of California, such as Sequoia sempervirens (D. Don) Endl. and Simmondsia chinensis (Link) C. K. Schneid. (Stebbins and Major 1965).

A previous family-level, molecular phylogenetic study based analyses of the plastid matK gene from 330 legume taxa (Wojciechowski et al. 2004) surprisingly placed Pickeringia phylogenetically in the “Cladrastis clade,” along with Cladrastis and Styphnolobium Schott, an early branching group of papilionoids, rather than closely related to members of Thermopsideae, which are nested in the more derived “Genistoid clade” (Crisp et al. 2000; Wojciechowski et al. 2004). Herein I present a comparative analysis of nucleotide sequence variation in the nuclear rDNA (ITS1, ITS2 and intervening 5.8S gene; nrDNA ITS) and plastid matK gene to further resolve the phylogenetic relationships of Pickeringia vis-à-vis Cladrastis and Styphnolobium, two genera of the Sophora group (i.e. Sophoreae s. s., sensu Polhill 1981b), both of which presently exhibit an eastern North America-eastern Asia disjunct geographic distribution, and are well represented in the Eocene fossil record from North America (e.g. Crepet and Herendeen 1992; Herendeen 1992). Furthermore, a rate and age analysis is undertaken in this study...
to provide credible age estimates for *Pickeringia* and its sister groups.

**Materials and Methods**

**Taxon Sampling**—Eleven accessions of *Pickeringia montana* from diverse locations in California representing the geographic range of this taxon were sampled for DNA sequence variation. Representatives of the genera *Cladrastis*, *Sophora*, *Styphnolobium*, and *Thermopsis* were sampled from recent collections or herbarium specimens from ASU, DAV, E, MEXU, MO, MONT, SD, UC, and US. Sampling of all other taxa has been described in Wojciechowski et al. (2004) or Queiroz et al. (2010), or their sequences were obtained from GenBank. The outgroups used for this study comprised selected taxa from *Albizia*, *Callicarpa*, *Catalpa*, *Chloris*, *Clethra*, *Diplopogon*, *Diplotis*, *Erythrina*, *Ficus*, *Hermaphodium*, *Hippocastanum*, *Imperata*, *Inga*, *Juniperus*, *Lonicera*, *Malus*, *Melia*, *Mimosa*, *Morus*, *Nelumbo*, *Olea*, *Ochna*, *Osmunda*, *Pachystachys*, *Paletia*, *Plattania*, *Polylepis*, *Psychotria*, *Quercus*, *Rhus*, *Sophora*, *Swietenia*, *Tamarindus*, *Tetraria*, *Theobroma*, *Viburnum*, *Viburnum*, *Vitis*, *Wisteria*, *Xanthoceras*, and *Xylopia*. All newly obtained sequences have been deposited in GenBank, and the final data sets have been deposited in TreeBASE (study number 12561). Details of voucher specimens specifically sampled for this study and GenBank accession numbers for all sequences used are presented in Appendix 1. Nomenclature of sampled *Cladrastis* species follows that of Dudley and Vincent (2003).

**DNA Sequence Data and Analysis**—Total genomic DNA was isolated from leaf tissue of herbarium specimens using DNeasy plant mini kits (Qiagen, Valencia, California) and sequenced for the nrDNA ITS/5.8S region (Baldwin et al. 1995), according to methods described in Wojciechowski et al. (1999) with only slight modification. Because nrDNA ITS sequences may be compromised by the presence of paralogs (Wojciechowski et al. 1999), only sequences sampled from additional taxa as described here (Appendix 1) were included in the analyses presented here. The nrDNA ITS data set was selected for further analyses because of the high level of resolution provided by this region (Pennington et al. 2001; Wojciechowski et al. 2004). All newly obtained sequences have been deposited in GenBank, and the final data sets have been deposited in TreeBASE (study number 12561). Details of voucher specimens specifically sampled for this study and GenBank accession numbers for all sequences used are presented in Appendix 1. Nomenclature of sampled *Cladrastis* species follows that of Dudley and Vincent (2003).

The nrDNA ITS sequences were initially aligned using the program MUSCLE version 3.8 (Edgar 2004) and edited manually with Se-Al version 4.2 (Rambaut 2002). Representative sequences of the *matK* gene derived from the data set of Wojciechowski et al. (2004) were supplemented with sequences sampled from additional taxa as described here (Appendix 1); the alignment of this data set was based on the Wojciechowski et al. (2004) data set. The nrDNA ITS data set consisted of 37 terminal taxa by 833 total aligned characters (629 included for analyses) and contained two plastid *matK* gene (TVM + I + G) data sets were selected in accordance with the Akaike information criterion implemented in Modeltest version 3.7 (Posada and Crandall 1998). Bayesian analyses of both data sets were performed using MrBayes version 3.1.2 (Ronquist and Huelsenbeck 2003), with two separate Metropolis-coupled Markov-chain Monte Carlo (MCMC) runs (four chains each) of 2–5 × 10⁶ generations which utilized uniform (default) priors, with the exception of the rate parameters (rigidly unlinked), and included an estimation of branch lengths, substitution parameters and topology, with sampling every 5,000 generations. Stationarity of the Bayesian MCMC runs was based on the following criteria: (1) convergence to a stable value of the log-likelihood score in separate runs, (2) a value less than 0.01 for the average standard deviation of split frequencies between two runs, and (3) a value approaching 1.0 for the potential scale reduction factor for each parameter in the model. Trees sampled prior to stationarity were excluded by “burn-in” (typically 50% of samples) and the 200–500 remaining trees were used to construct a majority rule consensus tree with credible values (posterior probabilities) greater than 0.95. (Table 1 is provided online as an appendix to this paper with supplementary data and tables with more information on each analysis.)

**Evolutionary Age and Rates Analysis**—A Bayesian analysis of the *matK* data set was performed, as described above, to generate a set of phylogenetic trees that were then used to estimate ages and rates of nucleotide substitution for *Pickeringia* and related lineages. Two separate MCMC runs of 5 × 10⁶ generations were initiated and sampled every 5000 generations, with 100 non-autocorrelated trees sampled from each run, and the results of the two runs were combined to achieve stationarity (post burnin) saved from each of both runs.

The program CoMBS version 1.71 (Sanderson 2003) was used to estimate ages of clades and rates of nucleotide substitution, as described previously (Lavin et al. 2005). Minimum ages and rates were obtained by constraining the age of the legume crown clade to 59.0 Ma, and setting the “Styphnolobium stem clade” and “Diplopogon stem clade” to minimum ages of 40.0 Ma and 56.0 Ma, respectively (Lavin et al. 2005). The legume crown and latter minimum age constraints derived from the legume macrofossil record have been described in detail elsewhere (Lavin et al. 2005). Consistent with Lavin et al. (2005), the “Styphnolobium stem clade” node is defined here as the most recent common ancestor (MRCA) of *Pickeringia montana* and *Styphnolobium japonicum*. Minimum age estimates were derived via penalized likelihood (PL) rate-smoothing analyses of 200 Bayesian trees sampled from the posterior distribution, with an optimal level of smoothing estimated by a cross-validation procedure (Sanderson 2002) performed prior to the PL analyses.

**Results**

**Nuclear rDNA ITS Analysis**—Maximum parsimony and Bayesian analyses of the nrDNA ITS data set provide strong support for the monophyly of a clade comprising all *Pickeringia* accessions, and a clade comprised of all species of *Styphnolobium* (Fig. 2), nested within the *Cladrastis* clade, the node defined as the MRCA of *Cladrastis platycarpa* and *C. kuntukoa* (Wojciechowski et al. 2004). No definitive sister group to either *Pickeringia* or *Styphnolobium* is resolved or supported by the nrDNA ITS analyses. Within *Pickeringia* there is weak support for the accessions of *P. montana* var. *montana*, from northern and central California (Napa, Nevada, and Solano Counties), nested within the accessions of *P. montana* var. *tomentosa*, from southern California (San Diego County) (Figs. 2, 3), a pattern not easily explained by their known geographic ranges (e.g. Baldwin et al. 2012). The two varieties overlap and intergrade in southern California, as further shown by the one accession of *P. montana* var. *montana* (JQ679664; Fig. 3) sampled for this study from San Diego County.

*Cladrastis* is paraphyletic with four well-supported lineages that are unresolved at the base of the *Cladrastis* clade, and weak support for the east Asian endemic *C. platycarpa* as the sister lineage to the rest of this clade (Figs. 2, 3). Within *Styphnolobium*, the Mexican/Central American endemic species (*S. burseroides*, *S. conzattii*, *S. montevidensis*, and *S. protantheran*) comprise a well-supported subclade that is unresolved with respect to two well-supported subclades containing the east Asian endemic *S. japonicum* and southern U. S. A. endemic *S. affine* (Figs. 2, 3).

**Plastid matK Analysis**—Consistent with results from an earlier *matK* sequence analysis (e.g. Wojciechowski et al. 2004), the *Cladrastis* clade is supported as one of the earlier-branching lineages of papilionoids. Within the *Cladrastis* clade, phylogenetic relationships resolved by parsimony and Bayesian analyses of the *matK* data set were generally

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**Appendix 1**

<table>
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<th>Taxon</th>
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<th>Notes</th>
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**Appendix 2**

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**Appendix 3**

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</table>
consistent with those obtained from the nrDNA ITS analysis (Fig. 4) but more strongly supported. Both *Pickeringia* and *Styphnolobium* were again strongly supported as monophyletic groups nested within a paraphyletic *Cladrastis*, with each group sister to a different lineage of *Cladrastis*. *Cladrastis* platycarpa is strongly supported as sister to the rest of the Cladrastis clade whereas *C. delavayi* from central and western China is strongly supported as sister to *C. kentukea*, the only North American species of the genus, endemic to the central southern U. S. A. (Duley and Vincent 2003). These analyses also unequivocally demonstrate that *Pickeringia* is not closely related to any of the other genera in Thermopsidaceae, and *Styphnolobium* is not closely related to Sophoreae s. s.,
respectively (Fig. 4), as proposed by their traditional taxonomic classifications (Polhill 1981b; Turner 1981; Lock 2005; Pennington et al. 2005).

**Evolutionary Rates Analysis**—The optimal rate-smoothing value selected by cross validation analysis of trees derived from Bayesian analysis of the matK data set was $10^{1.5}$ ($S = 32$). In this analysis the PL estimated age for the Cladastis clade crown node is 41.3 Ma (Table 1), which is less than that estimated previously (47.4 Ma) based on analyses of the larger, family-level 335-taxon matK data set (Lavin et al. 2005). The PL estimated age of 30.6 Ma for the Pickeringia stem node is considerably older than that estimated for the Pickeringia crown node of 10.4 Ma (Table 1). The estimated age of the Styphnolobium crown node (18.2 Ma; Table 1) is slightly older than the estimated divergence time of the North American *S. affine* from the...
Asian *S. japonicum* (17.9 Ma; Table 1). The substitution rate estimated for the *Pickeringia* stem clade, approximately $2.9 \times 10^{-10}$ substitutions per site per year, as well as for the *Styphnolobium* stem clade ($2.8 \times 10^{-10}$ substitutions per site per year; Table 1), is about half the rate estimated for the Cladrastis clade stem node of $5.5 \times 10^{-10}$ substitutions per site per year (Table 1). Substitution rates for these largely woody lineages are on the order of 5 times less than those
estimated for primarily herbaraceous legume groups (cf. Lavin et al. 2005).

**Discussion**

The results of analyses of both nrDNA ITS and matK sequences presented here provide unequivocal molecular evidence that strongly supports *Pickeringia* as phylogenetically nested within a clade that includes two genera of Sophoreae s. s., *Cladrastis*, and *Styphnolobium* (Figs. 2, 4), each of whose modern day relatives exhibit a disjunct eastern North America-eastern Asia distributional pattern. These three genera comprise the Cladrastis clade, one of the earliest-branching lineages in the diversification of papilionoid legumes (~58 Ma; Lavin et al. 2005). Furthermore, these genera are well separated from other North American or Eurasian members of Sophoreae s. s. and Thermopsideae that have traditionally been considered among their closest relatives, a result that is also strongly supported by more exhaustive sampling from related papilionoid groups (Cardoso et al. 2012). The absence of lupine-type or quinolizidine alkaloids in *Cladrastis* and *Styphnolobium* (Kite and Pennington 2003), and *Pickeringia* (Turner 1981), further supports the phylogenetic position of these taxa as separate from Sophoreae s. s. and Thermopsideae, which are nested in the Genistoid clade (Fig. 4), respectively.

*Cladrastis* is a deciduous, predominantly woody genus of five species endemic to temperate eastern Asia (China and Japan), and one, *Cladrastis kentukea* (yellowwood), endemic to the woodlands of the south-central and southeastern U. S. A. (Polhill 1981b; Duley and Vincent 2003). Based on results presented here, the genus is clearly paraphyletic, forming at least two distinct lineages within the Cladrastis clade (Figs. 2, 4). Although taxonomically treated in the same group (Sophoreae s. s.) as *Maackia* Rupr. & Maxim. and *Sophora* (Sophoreae s. s.; Polhill 1981b), the results presented here indicate *Cladrastis* is not closely related to either *Maackia* or *Sophora*.

In addition, these results provide the first molecular phylogenetic evidence for the monophyly of *Styphnolobium* (Sousa and Rudd 1993), represented here by the species *S. affine*, *S. burseroides*, *S. convolutii*, *S. montevidensis*, and *S. protantherum* of sect. *Oreobis*, and *S. japonicum* of sect. *Styphnolobium*. *Styphnolobium*, recognized as a segregate from *Sophora* L. (as *Sophora* sect. *Styphnolobium* (Schott) Yakovlev) on the basis of fruit and vegetative morphology, and chromosome number, is a genus of nine species of herbaceous perennials and deciduous trees (Palomino et al. 1993; Sousa and Rudd 1993). Of these, only *S. japonicum*, the widely cultivated “Japanese pagoda tree,” is endemic to western and central China (naturalized in Japan), while the remaining eight species of the genus are distributed in the southern U. S. A. (*S. affine*), southern Mexico and Central America, with one species reaching Colombia (Sousa and Delgado 1993; Sousa and Rudd 1993). Results of the age estimation analyses suggest the Asian (e.g. *S. japonicum*) and American (e.g. *S. affine*) lineages of this genus had diverged by the early Miocene (17.9 Ma; Table 1). With the exception of *S. japonicum*, all species of *Styphnolobium* are narrowly restricted endemics that inhabit regions with warm to hot, arid and/or seasonally dry climates. *Styphnolobium japonicum* is typically found in more mesic to semi-arid temperate habitats. The possession of more “primitive” features, compared to *S. japonicum*, led Sousa and Delgado (1993) to suggest that the Mexican/Central American species should be considered “paleoendemics” in the flora of those regions.

Both *Cladrastis* and *Styphnolobium* have been frequently described from the Tertiary (Eocene to Miocene) floras of central, southern, and western North America (e.g. Axelrod 1956; MacGinitie 1962; Becker 1969; Raven and Axelrod 1978; Herendeen 1992; and references therein), but neither is found in the modern floras of California or western North America (Wiggins 1980; Baldwin et al. 2012). Present day populations of *C. kentukea* (e.g. Oklahoma to North Carolina) and *Styphnolobium* (e.g. southern U. S. A. and southern Mexico) are separated from *Pickeringia* (in southern California) by a distance of at least 1,500 km.

The fossil record of the Leguminosae is abundant and diverse, and shows that several genera of woody papilionoids related to *Pickeringia* such as *Cladrastis* and *Sophora* s. l. (i.e. including *Styphnolobium*), and others such as *Robinia* L., were much more widespread throughout temperate North America during the Tertiary than they are at present, with their more restricted and modern disjunct distributions likely the result of regional extirpations, perhaps due to climatic changes (Herendeen et al. 1992). For example, fossil leaves and fruits of *Cladrastis* species are known from a large number of North American sites, most notably the Early Eocene Claiiborne Formation of Kentucky and Tennessee in the southeastern U. S. A. (Herendeen 1992), the Oligocene of Oregon (Brown 1937; Meyer and Manchester 1997), and the Early Oligocene of south-central Mexico (Calvillo-Canadell and Cevallos-Ferriz 2005), and are similar to fruits of extant Asian species (Herendeen 1992). It is worth noting that two of the *Cladrastis* groups recovered in this analysis are documented by fossil taxa. Similarly, fossil leaves and fruits resembling *S. japonicum* (taxon described in *Sophora* subgenus *Styphnolobium*) are also known from the same Claiiborne Formation localities (Herendeen 1992). The
remarkable diversity of Sophoreae taxa among fossil papilionoid legumes dating from the early Tertiary is further illustrated by the zygomorphic (pea-like) floral morphology of the extinct taxon Barnebyanthus buchananensis from the Claiborne Formation, features of which are shared with representatives of several extant Sophoreae genera that co-occur at this locality, including Cladrastis, Diplotropis Benth., Ormosia Jacks., and Sophora (Crepet and Herendeen 1992). The presence of Barnebyanthus is particularly significant because this taxon represents the earliest, unequivocal evidence of papilionoid legumes, and of taxa characteristic of Sophoreae in particular, in the fossil record (Crepet and Herendeen 1992).

That Pickeringia is nested within a clade containing Cladrastis and Styrpholobium, both of which have North American macrofossil records that date to the early Eocene, has important implications for the origin and age of this lineage. Although there is no known fossil record for Pickeringia, its antiquity in the flora in western North America is strongly suggested by estimates for the stem group age of the genus (30.6 Ma; Table 1). This long period of divergence from its sister group(s), Cladrastis and Styrpholobium, is consistent with an Early Oligocene origin of this genus. Additional lines of evidence argue for an Oligocene origin of Pickeringia. First, the fossil record indicates that by the early Miocene (~20 Ma) evergreen, sclerophyllous taxa had already become abundant and widespread across southwestern North America from the Rocky Mountains to California (e.g. Wolfe and Schorn 1989), accompanying the climatic trends toward cooler and drier conditions globally since the Eocene. The late Miocene to early Pliocene was also a time of widespread mountain building in western North America, particularly of the Sierra Nevada (Graham 1999), which led to additional geographic and climatic boundaries. Second, there is increasing comparative and fossil evidence that many of the relevant morphological and physiological traits characteristic of chaparral taxa such as Pickeringia pre-date the onset of the modern Mediterranean-type climate and vegetation (Axelrod 1975, 1989; Ackerly 2004), i.e. the evergreen, sclerophyllous leaf type is not recently derived in Mediterranean-type floras. Furthermore, Ackerly (2004) concluded that this leaf type represents the ancestral state in most Californian chaparral lineages with such leaves that he examined.

The notion that Pickeringia is a relic in the flora of California was first suggested by Stebbins and Major (1965) who proposed that a large proportion of the endemics in California were either relatively old taxa, isolated by the extinction of their close relatives (“paleoendemics”), or very recently evolved species (“neoendemics”). These authors further defined paleoendemics as systematically isolated taxa (often monotypic at section level or higher) that are “ancient,” show little variability, and are often ecological specialists whose presence in the flora is now relictual (i.e. belonging to groups that were once larger and more widespread). Stebbins and Major (1965; Table 2) considered paleoendemics to be abundant in California, and included examples such as Sequoia sempervirens (redwood), Calocedrus decurrens (Torr.) Florin (incense cedar), Coleogyne ramosissima Torr. (blackbush), and Simmondsia chinesis (jojoba), in addition to Pickeringia. Based on these criteria and results presented here (phylogenetic relationships, estimated ages) a convincing argument for Pickeringia’s designation as a paleoendemic can also be made.

Assuming a relatively old age (~31 Ma) for Pickeringia, what is known about its biogeographical origin and evolutionary history in the flora of western North America? The lack of any known fossil record for this taxon precludes estimates of where Pickeringia originated and whether it has been more or less widely distributed in the past. However, it appears likely that Pickeringia and sister lineages (Cladrastis and Styrpholobium) were derived from subtropical/tropical, probably semi-arid or seasonally dry adapted, sophorean ancestors early in the Eocene (Polhill 1981a). If true, this suggests that the modern distribution of most species of Cladrastis, and at least one species of Styrpholobium (S. japonicum), represents subsequent, and probably relatively recent, diversifications into cooler, more mesic temperate regions of east Asia and North America. It is noteworthy that the Californian flora shows strong geographic patterning, with the highest percentages of taxa derived from subtropical groups found in the Coast Ranges and Sierra Nevada foothills, corresponding to the present day distribution of chaparral (Ackerly 2009). Thus, it is plausible that Pickeringia was present in the regional flora by the early Miocene along with other subtropical-derived lineages, persisting in this niche and migrating in response to climatic shifts in precipitation or temperature during the late Miocene and Pliocene (‘synclimatic’ migration; Ackerly 2009).

The relationships and estimated old age for Pickeringia provide additional insights that contribute to our understanding of the evolution and assembly of chaparral vegetation in California, as well as in other floras shaped by Mediterranean-type climates. In California, chaparral dominates the dry slopes and ridges of the Sierra Nevada foothills and Coast Ranges, forming a nearly continuous cover of closely spaced shrubs and subshrubs, which because of complex patterns of topographic, climatic, and edaphic variation, results in a mosaic pattern in which patches of grassland, oak woodland, or coniferous forest are interspersed (Keeley 2000). Chaparral is shrub-dominant, with other growth forms such as herbs (e.g. grasses, annuals) generally lacking, except after fire. Indeed, there is widespread theoretical and empirical evidence of the influence of fire on Mediterranean-type floras such as chaparral, serving as an essential factor determining species diversity and community dynamics through time (Keeley 2000; Keeley et al. 2012).

A widely prevailing model of the spatial and temporal development of the chaparral in California envisages a dramatic shift beginning by the mid-Miocene from an earlier summer-rain climate to the modern summer-dry Mediterranean-type climate with concomitant assembly and evolution of chaparral taxa (i.e. adaptation) in ‘islands’ that eventually coalesced into larger patches with consequent displacement of other vegetation (Keeley 2000). The Pleistocene marked the final establishment of a Mediterranean-type climate in California (Axelrod 1981; Keeley 2000). Much of this model is based on Axelrod’s (1975, 1989, and references therein) concept of regional geoflora that existed in the early Tertiary, with California forming an “ectone” between a more mesic-adapted Arcto-Tertiary geoflora and a xeric-adapted Madro-Tertiary geoflora. Climatic shifts that occurred during the Pleistocene resulted in latitudinal and elevational shifts in representative taxa of both geoflora, such that contemporary chaparral communities are the result of the mixing of these plant assemblages (Axelrod 1975; Keeley 2000) and whose modern distribution patterns were subsequently influenced.
by periods of temperature change and severe drought over the past 8,000 yr (Axelrod 1981; Raven and Axelrod 1978). Although an oversimplification, the concept of a geoflora as a cohesive floristic unit was nevertheless helpful in understanding the history and composition of large-scale vegetation patterns.

More than 100 evergreen shrub species occur in Californian chaparral, with species of Adenostoma (Rosaceae), Ceanothus (Rhamnaceae), and Arctostaphylos (Ericaceae) the most prominent and widespread, while species of Cercocarpus and Heteromeles (Rosaceae), Garrya (Garryaceae), Quercus (Fagaceae), Rhus (Anacardiaceae), and Pickeringia are frequent constituents in many communities (Keeyee 2000). As already noted, fossil evidence indicates many of these chaparral genera date to the Miocene (or earlier), but the evolutionary histories of most taxa are poorly known at best (Axelrod 1989; Keely 2000). Some are represented by a few lineages often barely distinguishable from modern species, while others, such as Arctostaphylos and Ceanthus, appear to have undergone rapid speciation only recently (i.e. Pleistocene), perhaps in response to extensive mountain building in western North America and an increase in the incidence of fire (Axelrod 1975, 1977; Raven and Axelrod 1978; Keely et al. 2012). As an example, Adenostoma fasciculatum Hook. & Arn., the most ubiquitous shrub in chaparral, with narrow evergreen leaves, and one of only two species in the genus, is only known from pollen samples from the late Pleistocene (e.g. Heusser 1978), but a fossil-calibrated age analysis of Rosaceae suggests Adenostoma may be as old as ~20 Ma (C. Lipka and M. F. Wojciechowski unpubl. data). A recent study estimated the initial diversification of Ceanthus (divergence of the two subgenera, Ceanothus and Cerastes), with now some 38 of ~53 species endemic to the California Floristic Province, began in the middle Miocene (~13 Ma; Burge et al. 2011), although reliably identifiable fossils for the genus date to the early Pliocene (~6 Ma). This diversification pre-dates the onset of a Mediterranean-type climate in the region, providing further evidence to substantiate the contention that certain morphological characteristics once presumed to represent de novo adaptations in response to this climate (e.g. sclerophyll, sunken stomata) are instead adaptations that evolved before this climate developed in California and western North America (Burge et al. 2011).

Like Adenostoma and Ceanthus, Pickeringia shares certain traits such as similarities in shrub habit and leaf physiognomy that are typical of many contemporary chaparral species. These examples from California, together with earlier observations (Axelrod 1975, 1989; Ackerly 2004) suggest that such similarities, especially in leaf type (sclerophyll), found across the five Mediterranean-type floras did not arise as a result of convergent evolution in response to the onset of the Mediterranean-type climate in those regions of the world. Rather, it is more likely that these vegetative similarities, and presumably other characters (e.g. reproductive traits), have repeatedly been the result of ecological convergence (Ackerly 2009) among persistent lineages from a once more diverse and widespread flora that ultimately came to dominate during the assembly and expansion of chaparral as a regional vegetation.

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