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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 Californian 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 Mediterranean-type climate in this region. Rather, there is increasing evidence supporting the contention that most woody chaparral taxa evolved prior to the origin of the Mediterranean-type climate (as early as the Eocene). The onset of this climate served to increase the expanse of landscape subject to periodic drought and other causal factors such as fire that led to the widespread distribution of sclerophyllous shrub vegetation in this and other regions (Keeley et al. 2012). The lack of a fossil flora of any age that includes only chaparral taxa raises the possibility that the rise of the chaparral as a regional vegetation is a comparatively recent event, one that gradually adapted to this particular climatic regime (Axelrod 1989), likely in conjunction with the spatial and temporal sorting of existing lineages across a heterogeneous landscape (Ackerly 2004).

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

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Fig. 1. *Pickeringia montana* Nutt. A. Flower, showing broad banner petal with reflexed sides. B. Branch of shrub, note spinescent branches and palmately 1–3 foliate leaves. C. Developing, few-seeded pods. D. Typical chaparral vegetation with *Pickeringia* in foreground (U. S. A.: California, Otay Mountain, San Diego Co., 18 May 2012). Scale bar = 1 cm. [Photos taken by J. L. Wojciechowski]

(Munz 1959; MFW, personal observations) but typically reproduces vegetatively by resprouting from root crowns and underground stems in response to fire (Raven and Axelrod 1978).

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 Genisteae (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

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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 comprise selected taxa from caesalpinioid, mimosoid, and papilionoid legumes as appropriate based upon earlier studies (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 Duley 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 and pseudogenes (Bailey et al. 2003) PCR products were amplified using annealing temperatures of both 50°C and 55°C and sequenced directly in both the forward and reverse directions, often with two sets of primers (Wojciechowski et al. 1999; Lavin et al. 2003), at the Molecular Phylogenetics Laboratory, University of California, Berkeley, and the High-Throughput Genomics Unit at the University of Washington, Seattle. Reads were assembled and edited with Sequencher version 4 (Gene Codes, Ann Arbor, Michigan), and the resulting sequences revealed no evidence of divergent 5.8S gene sequences or paralogous copies of the entire nrDNA ITS region (Bailey et al. 2003). The plastid *matK* gene was selectively sampled from additional species of *Cladrastis*, *Sophora*, and *Styphnolobium* compared to Wojciechowski et al. (2004). The PCR and sequencing protocols for the *matK* gene were described previously (Wojciechowski et al. 2004).

The nrDNA ITS sequences were initially aligned using 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 13% missing data (0.7% of included characters) whereas the *matK* data set consisted of 64 terminal taxa by 1,617 total aligned characters (1,521 included for analyses) and contained 1% missing data.

Phylogenetic Analyses—Maximum parsimony analyses were conducted in PAUP* version 4.0b10 (Swofford 2002) utilizing heuristic search strategies that maximized the detection of global tree optima and clade stability (e.g. retention of multiple trees, SIMPLE, CLOSEST, and RANDOM addition sequences with tree-bisection-reconnection branch swapping, steepest descent). Relative support for each clade was estimated with non-parametric bootstrap analysis (Felsenstein 1985) implemented in PAUP*, using identical heuristic searches of 1,000 replicate samples. All characters were unweighted and unordered; positions containing insertions/deletions (indels) were excluded prior to all phylogenetic analyses. Nucleotide substitution models for the nrDNA ITS (GTR + I + Γ) and plastid *matK* gene (TVM + Γ) 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 × 10^6 generations which utilized uniform (default) priors, with the exception of the rate parameters (ratepr=variable), and included an estimation of branch length(s), 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 "burnin" (typically 50% of samples) and the 200–500 remaining trees were used to construct a majority rule consensus tree with clade credibility values (posterior probabilities).

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 × 10^6 generations were initiated and sampled every 5,000 generations, with 100 non-autocorrelated Bayesian trees at stationarity (post burnin) saved from each of both runs.

The program r8s 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 "Diplotropis 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. kentukea* (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* (JQ676964; 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. monteviridis*, and *S. protantherum*) 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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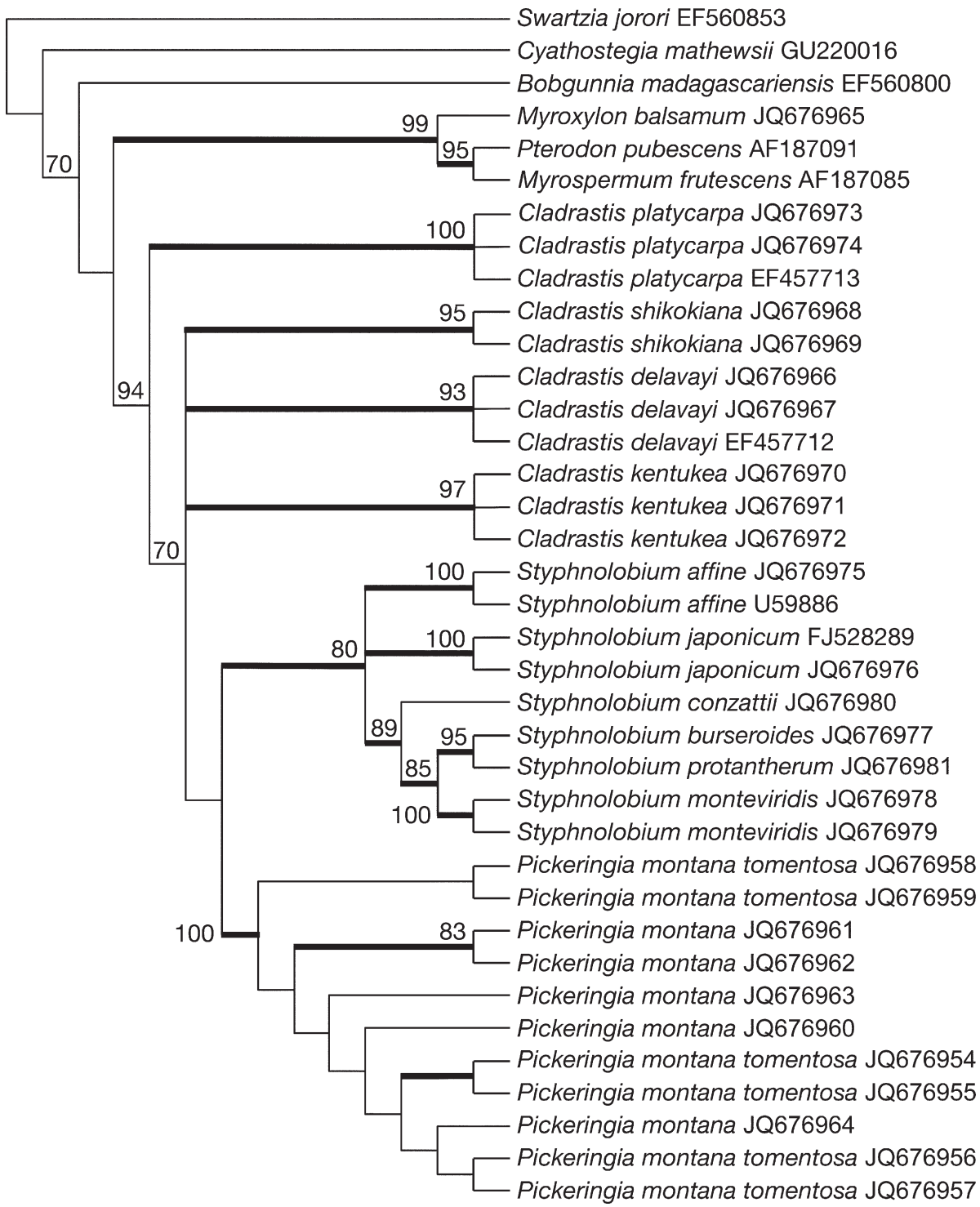

FIG. 2. Phylogenetic relationships of *Pickeringia*, *Cladrastis*, and *Styphnolobium* derived from maximum parsimony analysis of nrDNA ITS sequences. Tree shown is strict consensus of 36 equally most parsimonious trees of 768 steps; 37 terminals, 833 total characters with 629 included, of which 200 (32%) were parsimony informative. GenBank numbers for sequences are indicated. Numbers next to clades represent maximum parsimony bootstrap support values (1,000 replicates) greater than 70%; thickened branches represent clades with Bayesian posterior probabilities greater than 0.95.

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 the sister group 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 Thermopsideae, and *Styphnolobium* is not closely related to Sophoreae s. s.,

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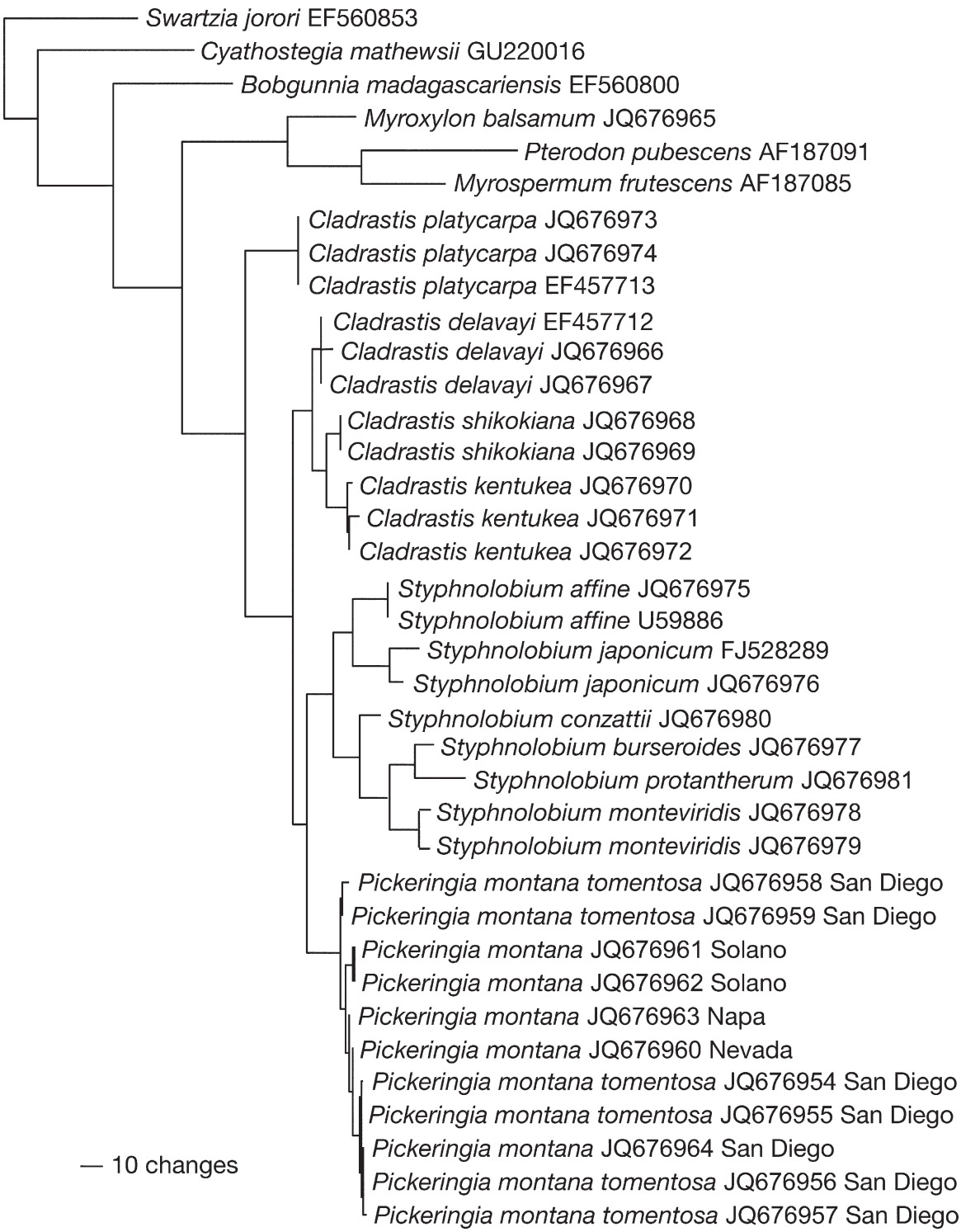

FIG. 3. One of the equally most parsimonious trees (36 at 768 steps) derived from maximum parsimony analysis of nrDNA ITS sequences: CI = 0.6107, RI = 0.7242. Collection localities (California counties) of the *Pickeringia* accessions are indicated.

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 Cladrastis 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

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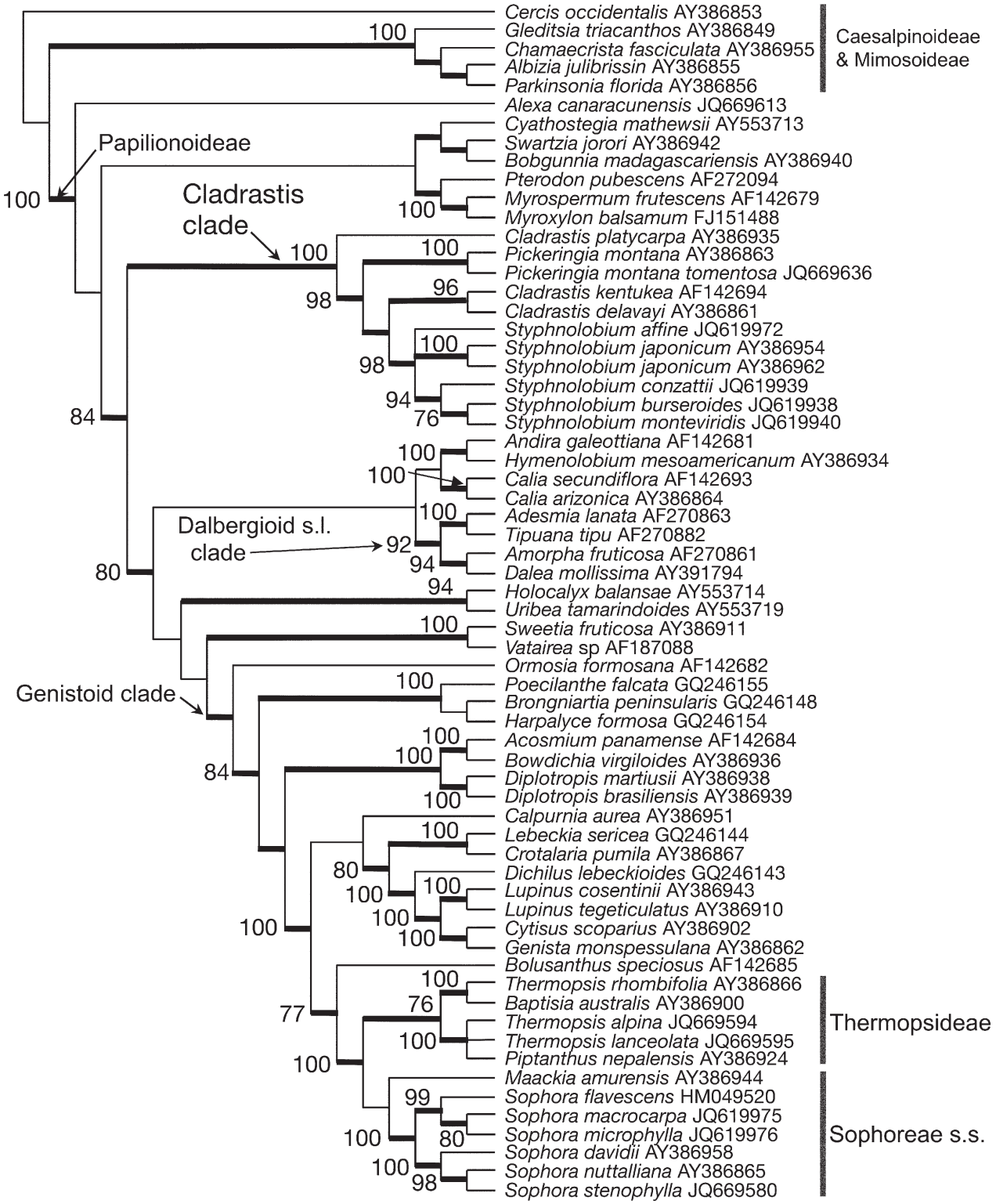

FIG. 4. Phylogenetic relationships of *Pickeringia*, *Cladrastis*, and *Styphnolobium* based on maximum parsimony analyses of plastid *matK* gene sequences. Tree shown is strict consensus of two equally most parsimonious trees of 1,775 steps: 64 terminals, 1,617 total characters with 1,521 included, of which 505 (33%) were parsimony informative. GenBank numbers for sequences are indicated. Numbers next to clades represent maximum parsimony bootstrap support values (1,000 replicates) greater than 70%; thickened branches represent clades with Bayesian posterior probabilities greater than 0.95. Clades of interest identified.

Asian *S. japonicum* (17.9 Ma; Table 1). The substitution rate estimated for the *Pickeringia* stem clade, approximately 2.9×10^{-10} substitutions per site per year, as well as for the *Styphnolobium* stem clade (2.8×10^{-10} substitutions per site per year; Table 1), is about half the rate estimated for the Cladrastis clade stem node of 5.5×10^{-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

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TABLE 1. Penalized likelihood age and rate estimates for the *Pickeringia*, *Cladrastis*, and *Styphnolobium* crown and stem nodes derived from r8s analyses of *matK* sequences. Ages are reported in millions of years (Ma) and rates are reported as number of substitutions per site per million years (sub/s/Ma), with standard deviations (std. dev.). Node (*) is defined as the MRCA of *Cladrastis kentukea* and *Styphnolobium affine* (Fig. 4).

Clade	Mean age (Ma)	Std. dev. (age)	Mean rate (sub/s/Ma)	Std. dev. (rate)
Pickeringia crown node	10.4	4.6	0.000241	0.000060
Pickeringia stem node	30.6	4.7	0.000294	0.000041
Cladrastis clade (crown node)	41.3	5.1	0.000351	0.000033
Cladrastis clade (stem node)	57.1	0.2	0.000553	0.000044
Styphnolobium crown node	18.2	4.8	0.000324	0.000063
Styphnolobium stem node (of genus*)	26.9	5.3	0.000285	0.000050
Styphnolobium japonicum stem node	17.9	4.9	N. D.	N. D.

estimated for primarily herbaceous 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. conzattii*, *S. monteviridis*, and *S. protantherum* of sect. *Orebios*, 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 Claiborne 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 Claiborne Formation localities (Herendeen 1992). The

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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 *Styphnolobium*, 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 *Styphnolobium*, 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 relict 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 often are 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 chinensis* (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 *Styphnolobium*) 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 *Styphnolobium* (*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 contributes 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 Nevadan 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 geofloras that existed in the early Tertiary, with California forming an "ecotone" 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 geofloras, 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

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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 (Keeley 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; Keeley 2000). Some are represented by a few lineages often barely distinguishable from modern species, while others, such as *Arctostaphylos* and *Ceanothus*, 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; Keeley 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 *Ceanothus* (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 predates 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. sclerophylly, sunken stomata) are instead adaptations that evolved before this climate developed in California and western North America (Burge et al. 2011).

Like *Adenostoma* and *Ceanothus*, *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 (sclerophylly), 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 dominance during the assembly and expansion of chaparral as a regional vegetation.

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Appendix 1. Taxonomic information and GenBank accession numbers, reported as [1]nrDNA ITS and [2]*matK*, for all sequences included in this study. For taxa sampled specifically for this study voucher specimen information is followed by GenBank accession number(s). Images of ASU voucher specimens sampled specifically for this study are available on SEINet [swbiodiversity.org/seinet/index.php] by searching for collector last name and number.

Cladrastis delavayi (Franch.) Prain; [1]EF457712, [2]AY386861; *P. S. Herendeen 1-V-2003-6* (US), U. S. A., Washington, D. C. (cult.), [1]JQ676966; *R. T. Pennington s. n.* (E); [1]JQ676967. ***Cladrastis kentukea*** (Dum. Cours.) Rudd; *M. Lavin s. n.* (BH), [1]JQ676971, [2]AF142694; *W. R. Faircloth 8104* (ASU), U. S. A., North Carolina, [1]JQ676970; *D. Pittillo & S. McCall 5120* (ASU), U. S. A., North Carolina, [1]JQ676972. ***Cladrastis platycarpa*** (Maxim.) Makino; [1]EF457713; *P. S. Herendeen 1-V-2003-11* (US), U. S. A., Washington, D.C. (cult.), [1]JQ676974, [2]AY386935; *R. T. Pennington s. n.* (E), [1]JQ676973. ***Cladrastis shikokiana*** (Makino) Makino; K. Oka 990 (UC), Japan, Honshu, [1]JQ676969; *H. Kato & M. Kuribayashi 940586* (KYO), Japan, [1]JQ676968. ***Pickeringia montana*** var. ***montana*** Nutt.: *M. F. Wojciechowski 853* (ASU), U. S. A., California, Solano Co., 1999, [1]JQ676961;

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M. F. Wojciechowski 883 (ASU), U. S. A., California, Solano Co., 1999, [1]JQ676962, [2]AY386863; *M. F. Wojciechowski 895* (ASU), U. S. A., California, Napa Co., 2000, [1]JQ676963; *M. F. Wojciechowski 896 & K. P. Steele* (ASU), U. S. A., California, Nevada Co., 2000, [1]JQ676960; *J. Lightner 352* (SD), U. S. A., California, San Diego Co., 2005, [1]JQ676964. ***Pickeringia montana*** var. ***tomentosa*** (Abrams) I. Johnston: *M. F. Wojciechowski 907 & C. Burrascano* (ASU), U. S. A., California, San Diego Co., 2000, [1]JQ676954, [2]JQ669636; *C. Christie 155* (ASU); U. S. A., California, San Diego Co., 1997, [1]JQ676957; *A. C. Sanders 26458 & C. Burrascano et al.* (ASU), U. S. A., California, San Diego Co., 2003, [1]JQ676956; *J. Rebman 9280* (SD), U. S. A., California, San Diego Co., 2003, [1]JQ676959; *J. Rebman 8796* (SD), U. S. A., California, San Diego Co., 2003, [1]JQ676955; *J. Snapp-Cook 55* (SD), U. S. A., California, San Diego Co., 2007, [1]JQ676958. ***Styphnolobium affine*** (Torr. et A. Gray) Walp.: [1]U59886; *A. Sandbothe 60* (ASU), Texas, 2004,[1]JQ676975, [2]JQ619972. ***Styphnolobium burseroides*** M. Sousa, Rudd & Medrano: *G. Herrera 4110* (MEXU), Mexico, [1]JQ676977, [2]JQ619938. ***Styphnolobium conzattii*** (Standl.) M. Sousa & Rudd: *R. Torres C. 5231* (MEXU), [1]JQ676980, [2]JQ619939. ***Styphnolobium japonicum*** (L.) Schott: [1]FJ528289; [2]AY386954; *M. F. Wojciechowski 856* (DAV), U. S. A., California, Yolo Co. (cult.), [1]JQ676976, [2]AY386962. ***Styphnolobium monteviridis*** M. Sousa & Rudd: *E. Bello 3* (MO), Costa Rica, 1983, [1]JQ676979; *L. R. Landrum 10506* (ASU), Costa Rica, 2002, [1]JQ676978, [2]JQ619940. ***Styphnolobium protantherum*** M. Sousa & Rudd: *J. A. S. Magallanes 2177* (MO), Mexico, 1980, [1]JQ676981.

Acosmium panamense (Benth.) Yakovlev: [2]AF142684. ***Adesmia lanata*** Hook.: [2]AF270863. ***Albizia julibrissin*** Durazzini: [2]AY386855. ***Alexa canaracunensis*** Pittier: *G. P. Lewis & W. Milliken 1683* (K), Brazil, [2]JQ669613. ***Amorpha fruticosa*** L.: [2]AF270861. ***Andira galeottiana*** Standl.: [2]AF142681. **Baptisia australis** R. Br.: [2]AY386900. ***Bobgunnia madagascariensis*** (Desv.) J. H. Kirkbride & Wiersema; [1]EF560800, [2]AY386940. ***Bolusanthus speciosus*** (Bolus) Harms; [2]AF142685. ***Bowdichia virgiloides*** H. B. & K.; [2]AY386936. ***Brongniartia peninsularis*** Rose; [2]GQ246148. ***Calia arizonica*** S. Watson; [2]AY386864. ***Calia secundiflora*** (Ortega) Yakovlev; [2]AF142693. ***Calpurnia aurea*** Baker; [2]AY386951. ***Cercis occidentalis*** Torr.; [2]AY386853. ***Chamaecrista fasciculata*** Rydb.; [2]AY386955. ***Crotalaria pumila*** Ortega; [2]AY386867. ***Cyathostegia mathewsii*** (Benth.) Schery; [2]AY553713. ***Cytisus scoparius*** (L.) Link; [2]AY386902. ***Crotalaria pumila*** Ortega: [2]AY386867. ***Cyathostegia matthewsii*** (Benth.) Schery: [1]GU220016, [2]AY553713. ***Cytisus scoparius*** (L.) Link: [2]AY386902. ***Dalea mollissima*** (Rydb.) Munz; [2]AY391794. ***Dichilus lebeckioides*** DC.; [2]GQ246143. ***Diplotropis brasiliensis*** Benth.; [2]AY386939. ***Diplotropis martiusii*** Benth.; [2]AY386938. ***Genista monspessulana*** (L.) L. A. S. Johnson; [2]AY386862. ***Gleditsia triacanthos*** L.; [2]AY386849. ***Harpalyce formosa*** DC.; [2]GQ246154. ***Holocalyx balansae*** M. Micheli; [2]AY553714. ***Hymenolobium mesoamericanum*** H. C. Lima; [2]AY386934. ***Lebeckia sericea*** Thunb.; [2]GQ246144. ***Lupinus cosentinii*** Guss.; [2]AY386943. ***Lupinus tegeticulatus*** var. ***duranii*** (Eastw.) Barneby; [2]AY386910. ***Maackia amurensis*** Rupr.; [2]AY386944. ***Myrospermum frutescens*** Jacq.; [1]AF187085, [2]AF142679. ***Myroxylon balsamum*** Harms; *E. Martinez 4051* (ASU), [1]JQ676965; [2]FJ151488. ***Ormosia formosana*** Kanchira; [2]AF142682. ***Parkinsonia florida*** S. Watson; [2]AY386856. ***Piptanthus nepalensis*** Sweet; [2]AY386924. ***Poecilanthe falcata*** (Vell.) Heringer; [2]GQ246155. ***Pterodon pubescens*** Benth.; [1]AF187091, [2]AF272094. ***Sophora davidii*** Kom. ex Pavol.; [2]AY386958. ***Sophora flavescens*** Aiton; [2]HM049520. ***Sophora macrocarpa*** Sm.: *L. R. Landrum 5855 & J. Bricker* (ASU), Chile, [2]JQ619975. ***Sophora microphylla*** Aiton: *L. R. Landrum 7622* (ASU) Chile, [2]JQ619976. ***Sophora nuttalliana*** B. L. Turner; [2]AY386865. ***Sophora stenophylla*** A. Gray: *R. K. Gierisch 4997* (ASU), Arizona, [2]JQ669580. ***Swartzia jorori*** Harms; [1]EF560853, [2]AY386942. ***Sweetia fruticosa*** Spreng.; [2]AY386911. ***Thermopsis alpina*** Ledeb.: D. G. Long et al., *Sino-British Qinghai Expedition 497* (E), China, [2]JQ669594. ***Thermopsis lanceolata*** R. Br.; D. G. Long et al., *Sino-British Qinghai Expedition 526* (E), China, [2]JQ669595. ***Thermopsis rhombifolia*** var. ***montana*** (Nutt. ex Torr. & Gray) Isely; [2]AY386866. ***Tipuana tipu*** (Benth.) Kuntze; [2]AF270882. ***Uribea tamarindoides*** Dugand & Romero; [2]AY553719. ***Vatairea*** sp.; [2]AF187088.

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