EVOLUTION OF LEAF FUSION IN HONEYSUCKLE (*PERICLYMENUM*, *LONICERA*)

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Editor: Stefanie Ickert-Bond

Premise of research. Fused or connate leaves are a well-known phenomenon observed across a limited number of angiosperm clades, and no study has attempted to examine this form of fusion from an evolutionary, morphometric, or functional perspective. We examined leaf fusion in honeysuckles, specifically the *Periclymenum* clade (~22 species) of *Lonicera* (Caprifoliaceae, Dipsacales), which exhibits variation in leaf shape, degree of fusion, and the position of fused leaves. As fused leaves co-occurred with reproductive structures, evolutionary correlations between leaf fusion and inflorescence architecture were also examined.

Methodology. Variation of leaf fusion was assessed using elliptical Fourier analysis, and multiple individuals of 19 of the 22 species of *Periclymenum* were sampled. As fused leaves occurred only on reproductive shoots, a suite of inflorescence characters were also studied. A phylogeny for *Periclymenum* was reconstructed using published sequence data, and this tree was used for ancestral character state reconstructions and correlation analyses.

Pivotal results. Leaves directly subtending inflorescences of *Periclymenum* were free or fused but were rarely partially fused. Fused leaves were ancestral to *Periclymenum* and were lost in parallel. Leaf fusion was not correlated with inflorescence architecture features, yet inflorescence architecture has become more complex among *Periclymenum* species.

Conclusions. While free leaves are the ancestral condition in the Dipsacales, fused leaves have been gained at least three times and lost at least twice. Given the proximity of fused leaves to reproductive structures, particularly in *Lonicera*, fused leaves may play a role in protection or in the discovery of flowers and fruits by pollinators and seed dispersers, respectively.

Keywords: Caprifoliaceae, Dipsacales, inflorescence architecture, morphometrics, fused leaves, phylogeny.

Dryad data: https://doi.org/10.5061/dryad.9p8cz8wd1.

Introduction

The evolutionary origins of leaf shape variation among angiosperms remain an enigma within the botanical community. Great variation in leaf form has long captured the attention of biologists, thus becoming a widely studied component of plant biology (Dickinson 1986; Kores et al. 1993; Young et al. 1995; Premoli 1996; Jensen et al. 2002; Plotze et al. 2005; Viscosi et al. 2009; Klingenberg et al. 2012; Silva et al. 2012; Schmerler et al. 2012; Chitwood and Otoni 2017; Spriggs et al. 2018). Historically, leaf shape has played a prominent role in species identification, and with recent improvements in image analysis, software such as Leafsnap (Kumar et al. 2012) makes use of this most notable feature to bring plant identification to the general public. Leaf shape differences have been correlated to changes in climate (Royer et al. 2005, 2008; Santiago and Kim 2009; Schmerler et al. 2012; Edwards et al. 2016; Spriggs et al. 2018) and insect interactions (Rausher 1978; Brown et al. 1991). Yet no universal function has been favored to explain changes in leaf form, though thermoregulatory capacity, hydraulic efficiency, mechanical limitations, herbivory avoidance, and light interception optimization have been prominently featured in such discussions (Nicotra et al. 2011; Chitwood and Sinha 2016).

Although plants may be recognizable because of a particular leaf shape, leaf form within an individual plant is not necessarily uniform. Leaves within a plant that differ due to heterophylly, for instance, might be the result of microhabitat differences due to light availability, whereby leaves in the sun tend to be smaller and lighter in color compared with those in the shade (Yano and Terashima 2001; Tsukaya 2005; McIntyre and Strauss 2014). Different juvenile and adult leaf forms, or heteroblasty, have been observed in a number of plants, including jackfruit (*Artocarpus heterophyllus*;

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Manuscript received February 2020; revised manuscript received February 2021; electronically published August 17, 2021.

  https://doi.org/10.1086/715638

Jarrett 1959) and the tropical vine *Monstera* (Andrade and Mayo 1998). Additionally, seasonal heteroblasty can cause differences in leaf lamina shape and margin serration based on the timing of leaf formation in a single season (Spriggs et al. 2018).

Among the myriad ways that leaf form can differ, the effects of fusion among leaves can produce yet another distinct leaf morphology. One example is perfoliate leaves, which occur when the base of a single leaf at a node surrounds the stem (e.g., *Uvularia perfoliata*). In some species, opposite leaves can become perfoliate-connate (hereafter, fused leaves): fusion of a pair of opposite leaves across the stem results in the formation of a single continuous structure in which the petioles are no longer present. Fused leaves are an uncommon morphological feature but are present in clades such as *Buddleja* (Scrophulariaceae; Chen et al. 2010), *Eupatorium* (Asteraceae; Johnson 1974), *Hypericum* (Hypericaceae; Nürk and Blattner 2010), *Liabellum* (Asteraceae; Robinson 1983), *Lonicera* (Caprifoliaceae; Rehder 1903), *Rumfordia* (Asteraceae; Sanders 1977), *Pedicularis* (Orobanchaceae; Yang et al. 1998), and *Triosteum* (Caprifoliaceae; Ferguson 1966). Despite the fact that fused leaves have been described in a number of different plant groups, the evolutionary origins of fused leaves and the function of this specific form of fusion are unknown. Further, while leaf shape has been studied using morphometrics (Young et al. 1995; Silva et al. 2012) and elliptical Fourier analysis (EFA; Schmerler et al. 2012; Chitwood and Otoni 2017), these methods have not been conducted or investigated in a phylogenetic framework to quantify the variation of fused leaves within and among species. Species of honeysuckles (*Lonicera*, Caprifoliaceae, Dipsacales) exhibit varying degrees of leaf fusion within and among species, providing an excellent system in which to study the evolutionary origins and shifts of leaf forms.

Lonicera comprises approximately 160 species that are largely distributed in the Northern Hemisphere, with a center of species diversity in China. Species in this clade are generally recognized as vines, small trees, or shrubs with opposite leaves and mostly bilaterally symmetric flowers with tubular corollas that vary in length among species (Rehder 1903; Hara 1983; Yang et al. 2011). *Lonicera* species are divided between two well-supported clades, *Chamaecerasus* and *Periclymenum* (Theis et al. 2008), which coincide with the original subgenera described by Rehder (1903). *Chamaecerasus* (~140 species) species produce flowers in pairs from axillary branches, while *Periclymenum* (~22 species) species are largely vines that produce terminal inflorescences with flowers occurring in pairs of three-flowered sessile cymes (Rehder 1903; Perino 1978; Hara 1983; Yang et al. 2011). While fused structures occur throughout *Lonicera*, bract and ovary fusion is largely restricted to *Chamaecerasus*, while leaf fusion is restricted to *Periclymenum*.

Species of *Periclymenum* are generally characterized by the presence of fused leaves, which occur on reproductive shoots. For some individuals, only the first set of leaves subtending inflorescences is fused (fig. 1*B*), while other individuals have multiple sets of fused leaves subtending the inflorescence (fig. 1*C*). The extent to which leaves can fuse also varies depending on the position of the leaves relative to the inflorescence. In many cases, the degree of fusion among a set of leaves decreases among leaves that are positioned farther from the inflorescence (fig. 1C; Perino 1978). Despite leaf fusion being a common feature of this clade, three species (*Lonicera periclymenum*, *L. griffithii*, and *L. subspicata*; fig. 1*A*) lack fused leaves (Rehder 1903). Variation in *Periclymenum* allows for the study of fusion in an evolutionary context and may ultimately provide perspectives on the possible functions of leaf fusion both within this clade and in other plant groups with fused leaves.

The observation that fused leaves occur on reproductive shoots may suggest that leaf fusion facilitates pollination or seed dispersal in *Periclymenum* species, perhaps by contributing to visual signaling. Many *Periclymenum* species are pollinated by hawk moths, hummingbirds, or bees (Brown and Kodric-Brown 1979; Ottosen 1986; Jordano 1990; Guitian et al. 1993; Díaz-Valenzuela and Ortiz-Pulido 2011; Lázaro et al. 2015), and most have red fruits that are largely dispersed by birds (Ingold and Craycraft 1983; Drummond 2005; Bartuszevige and Gorchov 2006; McCusker et al. 2010). The identification of connections between leaf fusion and plant-animal interactions may provide insights into the potential ecological functions of fused leaves. This study has three objectives: (1) to describe the variation of leaf fusion in *Periclymenum* species, (2) to examine how fusion has changed throughout evolutionary history, and (3) to characterize and evaluate the evolution of reproductive morphology within the *Periclymenum* clade to determine whether these features correlate with leaf fusion and to elucidate the possible functions of fused leaves.

Material and Methods

Species Sampling

We sampled 19 of 22 species in the *Periclymenum* clade of *Lonicera* as described by Rehder (1903) and as previously published in Smith and Donoghue (2010). Publications on *Lonicera* often used the subgeneric names *Caprifolium* and *Lonicera* following Ferguson (1966). Here, we followed the subgeneric names used in the first global treatment of honeysuckles by Rehder (1903), where *Periclymenum* = *Caprifolium* and *Chamaecerasus* = *Lonicera*, to avoid confusion of the two clades referred to as *Lonicera*. We followed the classifications of Rehder (1903) and Hara (1983) with the following exceptions: *Lonicera carnosifolia* was recognized as a synonym of *L. subaequalis* (Yang et al. 2011), and *L. glaucescens* was recognized as a variety of *L. dioica* (Clements et al. 1912). We recognized *L. prolifera* (Kirchner) Rehder and considered *L. sullivantii* Gray to be a synonym of *L. prolifera* (Rehder 1910). Also with respect to *L. prolifera*, the taxonomy of Rehder (1903, 1910) is followed over that of Rafinesque (1836). Rafinesque applied the name *L. reticulata* to describe a species of *Lonicera* in the north-central area of the United States that in 1903 Rehder considered a potential synonym of *L. sullivantii*. In 1910, Rehder omitted this name as a synonym of *L. sullivantii* (now *L. prolifera*) because it was doubtful that it was a *Lonicera*. However, *L. reticulata* Raf. has since been widely applied instead of *L. prolifera* to recognize this species in the United States (see discussion in Perino 1978). This is problematic, as *L. reticulata* was described by Champion in China in 1858 and is still recognized as a valid species (Yang et al. 2011). Moving forward, we recommend recognizing *L. prolifera* (Kirchner) Rehder from North America and *L. reticulata* Champion from China to reduce confusion between names.

Morphological data were collected for *L. yunnanensis*, though molecular sequences were unavailable for this species. *Lonicera*

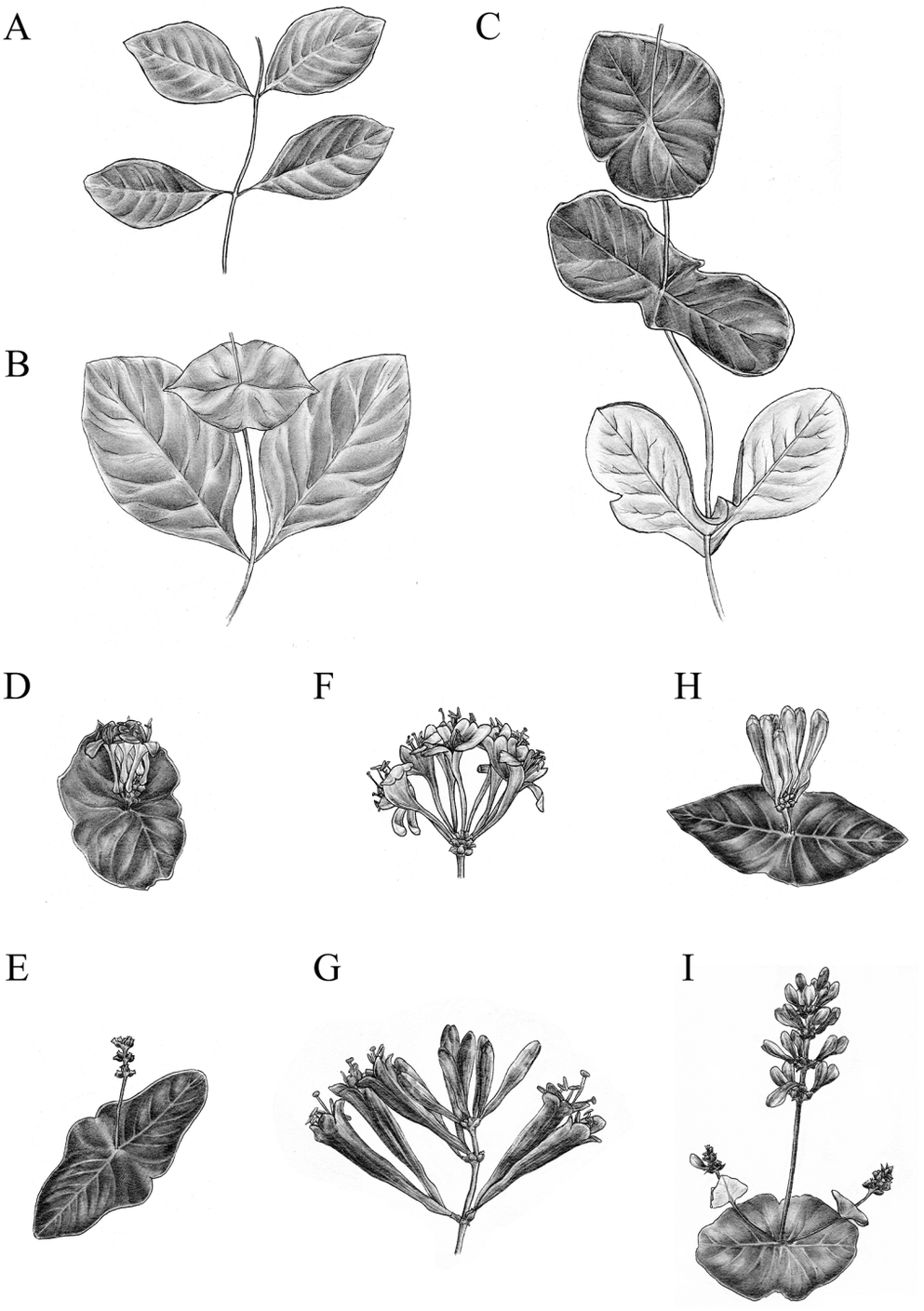

Fig. 1 Leaf and inflorescence architecture variation in the *Periclymenum* clade of *Lonicera*. For each trait, the species illustrated and voucher material referenced are provided, followed by the magnification in parentheses. *A*–*C*, Leaf fusion. *A*, No fusion, *Lonicera dioica*, J.E. Parsons s.n. (NY), iNaturalist 8168368 (×0.37). *B*, Single fused leaf, *L. hirsuta*, C.O. Grassl 5788 (NY), iNaturalist 15061735 (×0.4). *C*, Multiple fused leaves, *L. prolifera*, D.B. Ward & A.R. Bechtel 17531 (NY), iNaturalist 6309481, 14724654 (×0.39). *D*, *E*, Peduncle. *D*, Absent, *L. dioica*, C.D. Richards 4715 (NY), iNaturalist 13726671, 13456274 (×0.51). *E*, Present, *L. caprifolium*, O.R. Willis s.n. (NY), iNaturalist 14730194 (×0.35). *F*, *G*, Verticel clustering. *F*, Present, *L. flava*, W.C. Coker s.n. (NY), iNaturalist 12066275, 12066255, 5121980 (×0.49). *G*, Absent, *L. sempervirens*, D. Gully 15 (NY), iNaturalist 11787878, 12805306, 15992951 (×0.64). *H*, *I*, Lateral shoots. *H*, Absent, *L. ciliosa*, A.J. Cronquist 6650 (NY), iNaturalist 12331824 (×0.45). *I*, Present, *L. hispidula*, J.M. Coulter 8489 (NY), iNaturalist 13628377, 14307899 (×0.57). Illustrations by L. Zhang.

morrowii (*Chamaecerasus*) was included as an outgroup (Smith and Donoghue 2010).

Leaf Morphometrics

Digitized herbarium specimens were used to sample leaf shapes (app. A). The first pair of leaves subtending an inflorescence was selected on the basis of minimal leaf damage, folding, and visual obstructions, such as flowers or adhesion strips applied in specimen mounting. All image editing was performed using GIMP 2.8.22 (GIMP Team 2018). The set of leaves was isolated from the herbarium specimen image using the free selection tool. The fuzzy select tool was applied to the leaf before the selection was inverted and the remainder of the image was deleted to eliminate background noise. Leaf pairs were then rotated such that the primary leaf vein was parallel to the horizontal axis. All leaf pair images were binarized using the threshold tool with the range minimum set to 255. Images containing holes within the leaf laminae were manually filled in to prevent errors during image input for analyses. Because of the limited number of optimal specimens for analysis, several leaf samples that were partially obstructed by additional morphological features were collected. We manually resolved regions of the leaf outline that were obscured by best approximating the leaf margin, which is entire in *Lonicera*. Images were saved as JPEG files.

Images of pairs of leaves were collected from 140 individuals across 19 species, representing 4–10 replicates per species (no more than one pair of leaves per specimen analyzed). Most species sampled were represented by eight replicates. *Lonicera arizonica* ($n = 4$) and *L. stabiana* ($n = 4$) were undersampled because there was a limited number of digitized herbarium specimens. No leaves of *L. pilosa* were of a high enough quality to be sampled, though we were able to score leaf and inflorescence characters for this species (see below).

All morphometric analyses were conducted in RStudio version 5.3.2 (RStudio Team 2015) with R version 3.5.2 (R Core Team 2019) using the Momocs package (Bonhomme et al. 2014). First, all binarized JPEG images of *Periclymenum* species were imported. Next, outlines of the leaf images were extracted and aligned based on the longest horizontal axis across the outline. Aligned outlines were then used to perform EFA. The results of the EFA were analyzed using principal component analysis (PCA) to visualize the morphospace of leaf fusion in *Lonicera* using the ggplot package (Wickham 2016). We generated the morphospace by plotting principal components.

Leaf and Inflorescence Characters

We examined a total of 1075 digitized herbarium specimens (app. B) to score the morphological characters of all *Periclymenum* species. Specimens from Harvard University Herbaria were examined and photographed in person. Characters scored in this study were observed only in flowering shoots. A total of four characters were scored; these were (1) leaf fusion, (2) peduncles, (3) verticel clustering, and (4) inflorescence lateral shoots (fig. 1). Character states were assigned based on the condition exhibited by the majority of the specimens examined. The characters and character states were as follows.

Leaf fusion. Leaf fusion was scored as free (0) or fused (1; fig. 1*A*–1*C*). Leaf fusion was observed only on reproductive branches on the pair of leaves directly subtending an inflorescence or infructescence. Plants with free leaves had only pairs of opposite leaves with discernible leaf bases and petioles (fig. 1*A*). Fused leaves were scored when the first pair of leaves subtending an inflorescence was partially or fully fused (fig. 1*B*, 1*C*). Additionally, we documented whether stems had a single pair or multiple pairs of fused leaves subtending an inflorescence. In the case of a single set of fused leaves, only the set of leaves subtending the inflorescence was fused, and all other pairs of leaves on the stem were free (fig. 1*B*). Multiple fused leaves were noted when there was partial or full fusion of two or more pairs of leaves subtending reproductive structures (fig. 1*C*).

Peduncles. Peduncles were scored as absent (0) or present (1; fig. 1*D*, 1*E*). We determined the absence or presence of a peduncle by examining the junction of the base of the inflorescence and the pair of leaves (whether free or fused) subtending it. Absence of peduncles occurred when the inflorescence was sessile and sitting on the set of leaves directly subtending it (fig. 1*D*). When present, a peduncle separating the inflorescence and a set of subtending leaves was visible (fig. 1*E*). Peduncles separating whorls of flowers were not considered in scoring this trait.

Verticel clustering. Verticel clustering was scored as absent (0) or present (1; fig. 1*F*, 1*G*). We scored verticel clustering by examining the distance between verticels (here, whorls of six flowers) along an inflorescence axis. Plants lacking verticel clustering had elongated peduncles separating floral whorls along the inflorescence axis (fig. 1*G*). Plants with verticel clustering lacked or had short pedicels between floral whorls, giving the appearance of a single large cluster of flowers or fruits (fig. 1*F*).

Inflorescence lateral shoots. Inflorescence lateral shoots were scored as absent (0) or present (1; fig. 1*H*, 1*I*). Lateral shoots were observed as the production of additional reproductive branches originating from the base of the peduncle on a terminal inflorescence. The absence of lateral shoots was scored for species with a single inflorescence stalk, regardless of the number of verticels that occurred along that stalk (fig. 1*H*). The presence of lateral shoots was scored when axillary branches were observed arising from the peduncle, typically with a total of three branches within the inflorescence (fig. 1*I*). An individual with lateral shoots could have enlarged and/or fused bracts subtending the inflorescences.

A discrete character matrix was assembled in Mesquite version 3.61 (Maddison and Maddison 2018). We determined character states for each species by examining approximately 47 specimens per species on average (app. B) and consulting the literature (Rehder 1940; Perino 1978; Yang et al. 2011; Villarreal-Quintanilla et al. 2016, 2017). Character state assignment was based on the most common state for the species, though some individuals within each species may deviate from the associated character state. Taxa were scored as polymorphic if multiple character states were observed in similar proportions.

An additional character matrix was created to score the presence or absence of fused leaves across the Dipsacales using data gathered from the literature (Torrey 1824; Roxburgh 1832; Hooker 1882; Chapman and Eaton 1884; Small 1913; Piper and Beattie 1914, 1915; Rydberg 1917; Wiegand and Eames 1926; Makins 1937; Jones 1940; Ohwi 1965; Correll 1968; Nash 1976; Scoggan 1979; Das and Giri 1991; Straley 1994; Pojarkova 1999; Donoghue et al. 2001). Any instance of a pair of leaves fused across the stem was scored as present. Data matrices are available on the Dryad Digital Depository (https://doi.org/10.5061/dryad.9p8cz8wd1; Zhang and Clement 2021).

Phylogenetic Reconstruction

Publicly available sequence data were obtained from Genbank (app. A) for 19 *Periclymenum* species and included the nuclear ribosomal internal transcribed spacer (ITS) region, seven plastid regions (*atp*B-*rbc*L, *mat*K, *pet*N-*psb*M, *psb*M-*trn*D, *rbc*L, *rpo*B-*trn*C, and *trn*S-*trn*G), and the low-copy nuclear region *LEAFY* (*LFY*; app. A). Though the majority of the data compiled were published by Smith and Donoghue (2010), this is the first time that this combination of gene regions has been analyzed for *Periclymenum*.

Each gene region was aligned individually using MUSCLE (Edgar 2004) with default parameters. The ITS sequence for *L. caprifolium* (MG220043) was removed because of difficulty aligning this sequence with the rest of the matrix. Aligned gene regions were concatenated with SequenceMatrix (Vaidya et al. 2011). A partitioning scheme and models of evolution for the resulting partitions were determined using PartitionFinder version 1.1 (Lanfear et al. 2012). Phylogenetic analyses were performed using maximum likelihood (ML) and Bayesian inference (BI). A total of five independent ML analyses, each with five iterations, were conducted using GARLI version 2.01 (Zwickl 2006). An ML bootstrap analysis with 500 replicates was also conducted using GARLI version 2.01 (Zwickl 2006). Bayesian analysis was performed using MrBayes version 3.2.6 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). The analysis included two runs, each with 40 million generations sampled every 1000 generations. Convergence between the two runs and an appropriate burn-in was determined using Tracer version 1.5 (Rambaut et al. 2018).

To examine the evolution of fused leaves across the Dipsacales, we used the Dipsacales phylogeny published by Donoghue et al. (2003) and collapsed branches to represent major lineages in the clade. However, as *Triosteum* contained multiple species with fused leaves, we grafted a species tree of *Triosteum* (Gould and Donoghue 2000) onto the Dipsacales phylogeny (Donoghue et al. 2003). All sequence data matrices and trees are available on the Dryad Digital Depository (https://doi.org/10.5061/dryad.9p8cz8wd1; Zhang and Clement 2021).

Ancestral Character State Reconstruction and Character Correlations

An ancestral character state reconstruction using maximum parsimony (MP) and ML was performed for all four characters using the BI maximum clade credibility consensus tree in Mesquite version 3.61 (Maddison and Maddison 2018). The ML ancestral character state reconstruction required that taxa be coded as nonpolymorphic. Polymorphisms were resolved by recoding present and absent states as present. We also conducted an ancestral character state analysis of fused leaves across Dipsacales in Mesquite (Maddison and Maddison 2018) using MP. As the tree used in the analysis was grafted, branch lengths were not a factor in the analysis.

Pagel's test of correlated evolution (Pagel 1994) was implemented using the fitPagel function in the phytools package (Revell 2012) in R (R Core Team 2019) and was used to test possible two-way and one-way evolutionary correlations along the *Periclymenum* ML tree between leaf fusion and the following characters: lateral shoots, peduncles, and verticel clustering. Two-way correlations were also computed for all combinations of the three inflorescence architecture characters. By examining all combinations of inflorescence architecture and leaf fusion correlations, we were able to fully explore how leaves and inflorescences may affect one another in *Periclymenum*. Species exhibiting polymorphisms (e.g., absent and present) were recoded as having the presence of that particular character. Significance was assessed using the likelihood ratio test (LRT) and *P* values.

To test hypotheses of correlated evolution across a distribution of trees, independent contrast: correlation tests were conducted with BayesTraits version 3.0.1 (Pagel et al. 2004; Pagel and Meade 2017) for the same comparisons described above. A stepping stone sampler was used to obtain the marginal likelihood under an independent or dependent model. The sampler was set to use 100 stones, and each stone ran for 10,000 iterations. An LRT was used to compare the likelihood of the correlated versus uncorrelated model for each pair of traits.

Phylomorphospace

To examine the morphospace in an evolutionary context, we generated a phylomorphospace by projecting the ML phylogeny onto the PC plot. The tree was pruned to remove *L. pilosa*, which could not be sampled in the morphometrics study, and *L. morrowii*, which was used to root the tree. Since the original PCA contained multiple individuals per species, PC1 and PC2 scores were averaged for replicates within a species and were replaced by a single point. All phylomorphospace analyses were conducted in RStudio version 5.3.2 (RStudio Team 2015) with R version 3.5.2 (R Core Team 2019) using the phytools (Revell 2012) and ape (Paradis et al. 2019) packages.

Results

Morphological Variation of Shape in Periclymenum *Leaves*

The EFA revealed that *Periclymenum* species were concentrated in two distinct areas of the morphospace, free or fused, with very few species or individuals exhibiting partial fusion, in which the petiole is still distinguishable from the leaf lamina or there is constriction of the leaf lamina near the base of the leaf (fig. 2). PC1 accounted for 92.6% of the variation in leaf shapes observed in this clade, and increasing PC1 scores represented a transition from unfused to fully fused leaves (fig. 2). PC2 accounted for 2.76% of leaf shape variation, and increasing PC2 scores represented a transition from absent to increasingly acute leaf apexes. PC3 scores accounted for 0.7% of leaf shape variation. Increasing PC3 scores represented a decrease in the amount of constriction at the base of the leaves that separate opposite leaves across the stem.

Two general groups of leaf shapes were identified from the morphospace. The first grouping of species in the morphospace included *Lonicera subspicata* and *L. periclymenum*, which are distinguished by their low PC1 scores, indicating unfused leaves. While these species varied little with regard to the separation of opposite leaf laminae, there was considerable variation in both species regarding the shape of the leaf apex. The second grouping included all other species sampled, which overall had higher PC1 scores, indicating fused leaves, relative to *L. subspicata* and *L. periclymenum*. Although species with fused leaves overlapped

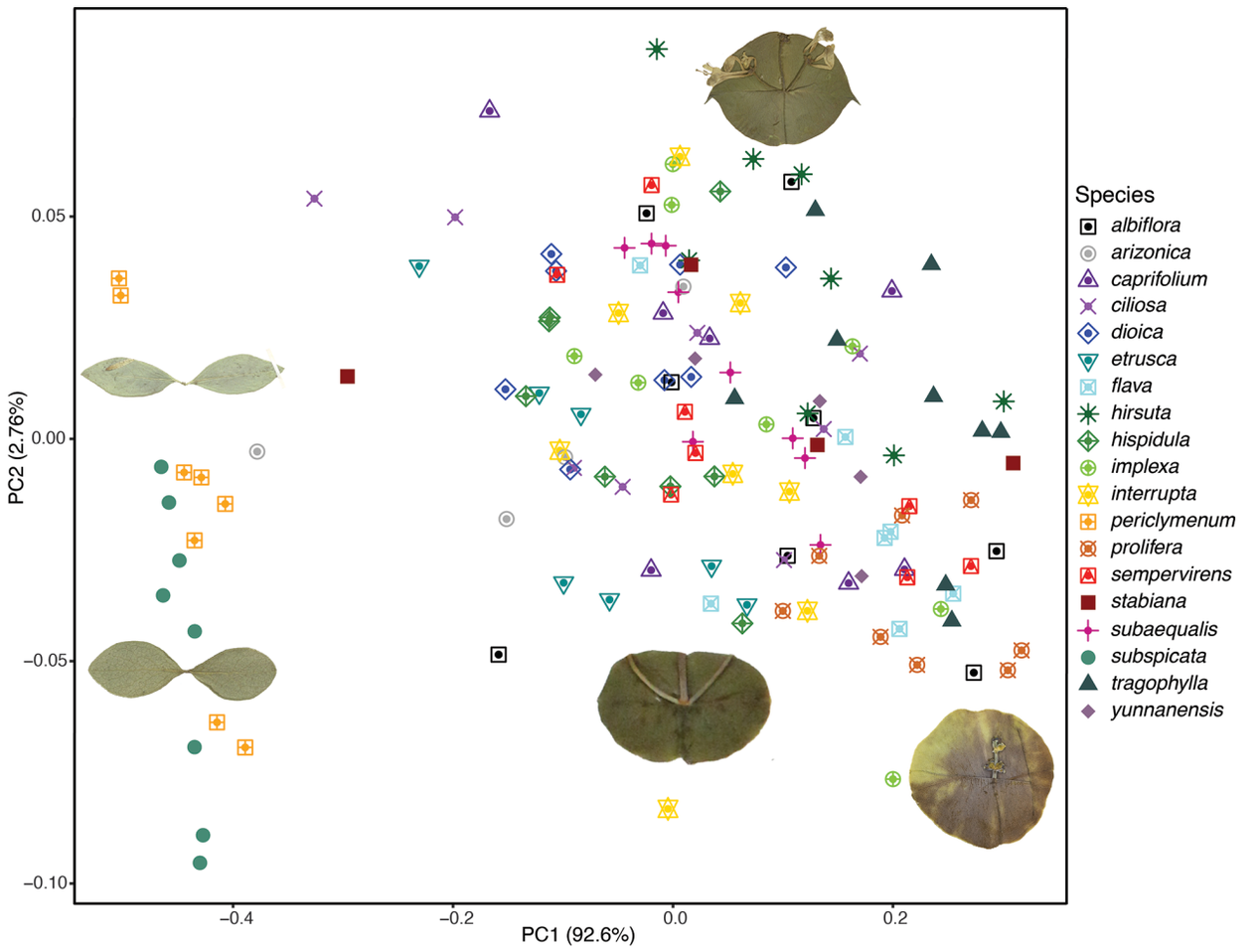

Fig. 2 Morphospace representing the variations in the shapes of paired leaves directly subtending inflorescences in species of *Periclymenum*. The principal component analysis (PCA) was constructed from the results of an elliptical Fourier analysis of 140 individuals representing 19 species of *Periclymenum*, and percent variations explained by each PC are indicated on the axis. Each species is indicated by a different color and symbol, and leaves from five *Periclymenum* species have been placed throughout the figure to indicate the general shape of leaves in that area of the morphospace. *Top left*, *Lonicera periclymenum*. *Top right*, *Lonicera hirsuta*. *Bottom left*, *Lonicera subspicata*. *Bottom middle*, *Lonicera etrusca*. *Bottom right*, *Lonicera prolifera*.

in the morphospace, some species tended to cluster in specific regions. For example, *L. dioica* and *L. prolifera* occupied regions in the morphospace that are distinct from one another (fig. 2). Finally, while some species within the morphospace exhibited limited variation with regard to the amount of fusion (becoming more orbicular with less definition along opposite leaf laminae), we detected variations in leaf apex shape in nearly all species sampled.

Periclymenum *Phylogeny*

The aligned data matrix included nine gene regions with a combined length of 9128 bp. A partitioning scheme allowing for a separate partition for each gene region was selected. Models of sequence evolution were as follows: ITS, TIM+I; *LFY*, GTR+I+G; *atp*B-*rbc*L, *pet*N-*psb*M, and *rpo*B-*trn*C, K81uf+G; *mat*K, *psb*M-*trn*D, and *trn*S-*trn*G, K81uf+I+G; and *rbc*L, K80+I. Trees generated using ML (fig. 3) and BI (fig. 4) had no supported topological conflicts. Seven strongly supported clades (bootstrap support > 70; posterior probability > 0.95) were recovered (fig. 3). Clades corresponded to geography rather than to the existing subsectional classification of the subgenus *Periclymenum*.

Ancestral Character State Reconstruction

Ancestral character state reconstructions performed using MP and ML identified fused leaves as the ancestral state of *Periclymenum* (proportional likelihood [pl] = 0.99; fig. 4*A*). Two independent transitions from fused to free leaves were recovered along the branches leading to *L. periclymenum* (pl = 0.963) and *L. subspicata* (pl = 0.913; fig. 4*A*). Ancestral character state reconstructions of the number of fused leaves recovered transitions from multiple fused leaves to single sets of fused leaves or from multiple fused leaves to no fused leaves. We note, however, that there was much lability in the number of fused leaves along a stem, and we scored six taxa (*L. flava*, *L. hirsuta*, *L. hispidula*, *L. sempervirens*, *L. subaequalis*, and *L.*

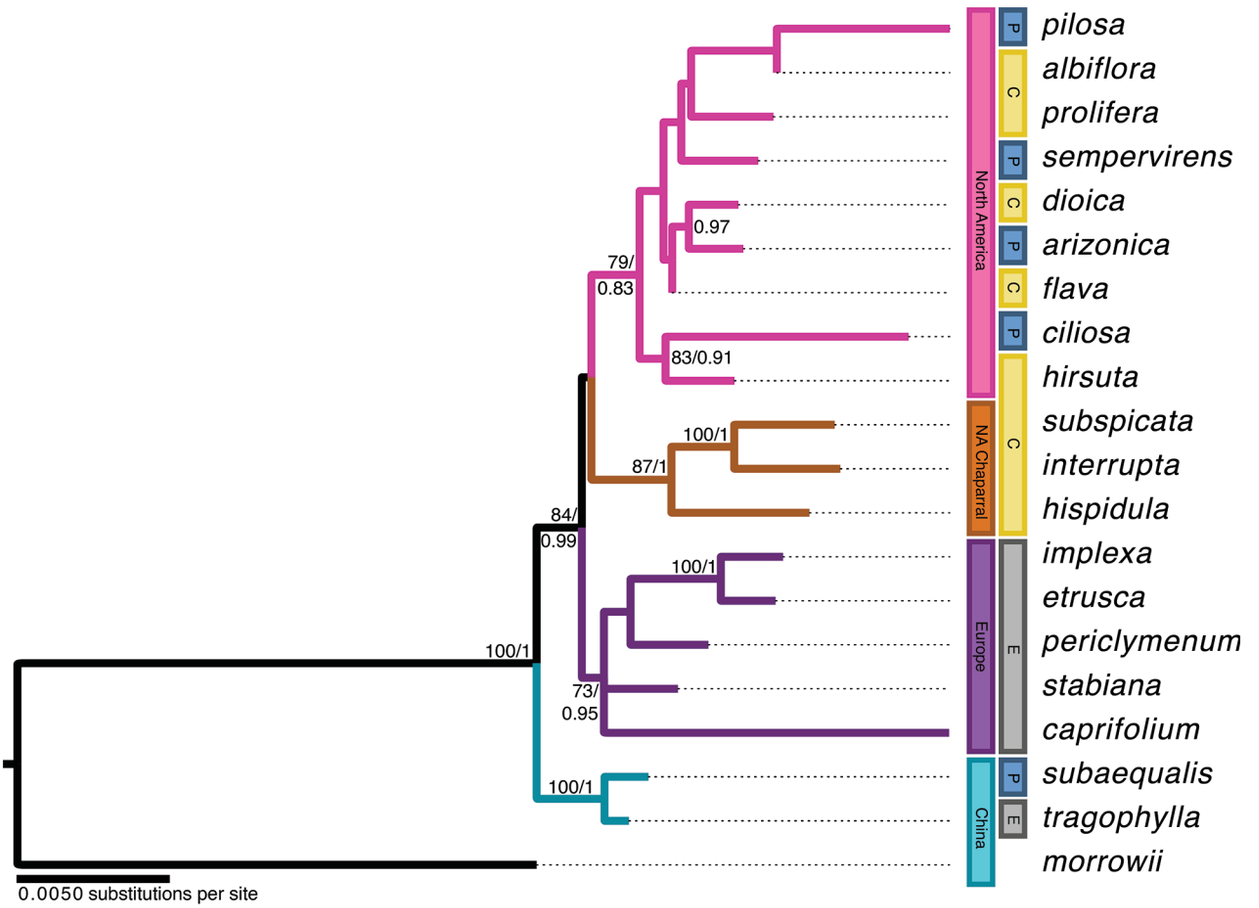

Fig. 3 Results from the maximum likelihood (ML) analysis of 19 *Periclymenum* species constructed using *LFY*, internal transcribed spacer, and seven plastid gene regions. ML bootstrap values greater than 70%, followed by posterior probabilities greater than 0.90, are indicated above or below the branches. Geographic distributions (*left*) and subsectional classifications (*right*) of *Periclymenum* (Rehder 1903) are indicated in the columns to the left of the taxon names. Branch colors correspond to the phylomorphospace (fig. 5). C = *Cyhpeolae*; E = *Eucaprifolia*; NA = North American; P = *Phenianthi*.

tragophylla; fig. 4*A*) as polymorphic. Also, while species scored as having a single set of fused leaves exhibited this condition among the majority of specimens observed, there were typically a small number of individuals observed as having a second set of partially fused leaves.

Absence of lateral shoots was favored as the ancestral state under MP and ML (pl = 0.696). Five independent shifts from absent to present lateral shoots were recovered along branches leading to *L. stabiana*, *L. etrusca* (pl = 0.487), *L. hirsuta* (pl = 0.5), *L. prolifera*, and the clade containing *L. hispidula-L. subspicata* (pl = 0.649). When polymorphisms were rescored as the presence of lateral shoots, no changes occurred in the ancestral character state reconstruction.

For verticel clustering, the presence of clustering was identified as the ancestral state under MP and ML (pl = 0.997). Two losses of verticel clustering occurred along the branch to *L. sempervirens* and the clade containing *L. hispidula-L. subspicata* (pl = 0.903; fig. 4*A*).

For peduncles, the absence of a peduncle was ancestral under MP, with eight shifts from absence to presence (reconstruction not shown). However, the absence or presence of a peduncle was equally likely as the ancestral state under ML (pl = 0.5). Further, many species were observed as polymorphic for this trait. When polymorphisms were resolved as present, the ancestral character state recovered in the MP analysis flipped from absent to present, with at least five shifts to absent. Reconstructing ancestral character states under ML resulted in all nodes being equally likely to have either the presence or absence of peduncles.

Within the Dipsacales, free leaves were ancestral, and fused leaves were gained at least three times (fig. 4*B*). Reconstructing leaf fusion in *Triosteum* resulted in two equally likely possibilities, that leaf fusion was gained three times independently or that leaf fusion was gained once and lost twice (fig. 4*B*).

Evaluating Correlated Evolution

Fused leaves were not correlated with any other character using Pagel's test of correlated evolution (LRT < 2; $P > 0.05$; Pagel 1994) and BayesTraits (log Bayes factor < 2; fig. 4). Since we were unable to confidently assign an ancestral character state

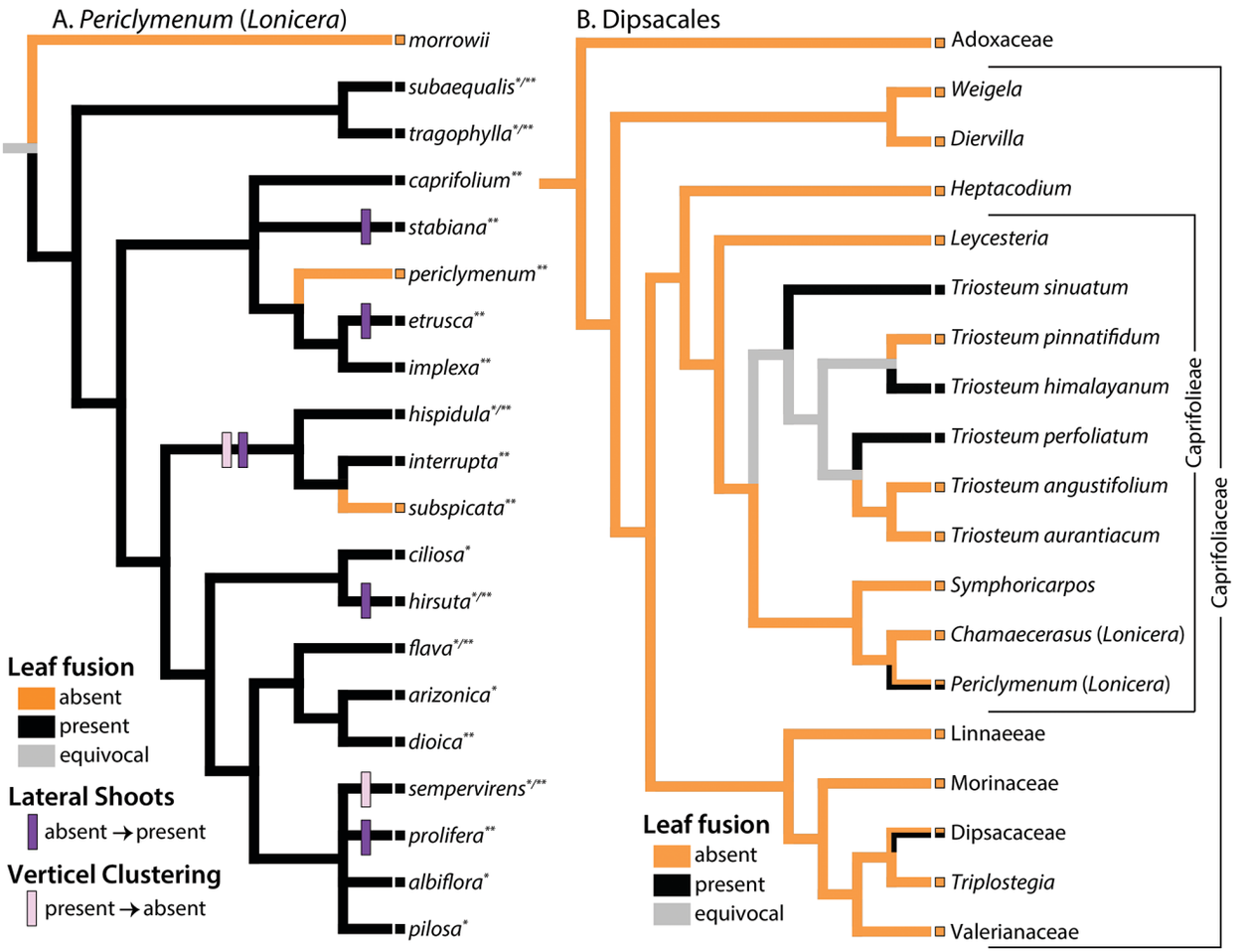

Fig. 4 Ancestral character state reconstructions for *Periclymenum* (*A*) and Dipsacales (*B*). *A*, Ancestral character state reconstruction of leaf fusion under maximum parsimony (MP) using the maximum clade credibility tree resulting from the Bayesian inference analysis of 19 *Periclymenum* species. Colored bars indicate the gain of lateral shoots and the loss of verticel clustering. The number of fused leaves along an observed stem is indicated by asterisks following taxon names (excluding the outgroup): one asterisk indicates a single set of fused leaves, two asterisks indicate multiple sets of fused leaves, and both one and two asterisks indicate that it is polymorphic for single and multiple sets of fused leaves. *B*, Ancestral character state reconstruction of leaf fusion using MP was reconstructed across the Dipsacales phylogeny obtained by grafting the species tree of *Triosteum* (Gould and Donoghue 2000) onto the most recent phylogeny of Dipsacales (Donoghue et al. 2003). Terminal branches with two colors indicate polymorphism in a species or clade, and internal gray branches indicate an equivocal result from the ancestral character state analysis.

for peduncles, this character was excluded from tests of correlated evolution. The evolution of lateral shoots was found to depend on the absence of verticel clustering (LRT = 5.69; P = 0.0581).

Phylomorphospace

The results of the phylomorphospace further emphasize the distinction of taxa having free or fused leaves and the absence of a leaf shape that would conform to partially fused leaves. *Lonicera periclymenum* and *L. subspicata* occurred in a similar region of the morphospace but represent two independently evolving lineages, thus supporting the parallel loss of fused leaves in this clade. The remaining sampled species generally formed a large cluster that retained the ancestral condition of fused leaves for this clade. Fused leaves of *Periclymenum* species have lost distinct leaf bases, but the fusion form can range from oval (e.g., *L. hispidula*) to orbicular (e.g., *L. albiflora*). Two species, *L. hirsuta* and *L. prolifera*, extended from this cluster, representing extreme forms of fused leaf shapes. Fused sets of leaves in *L. prolifera* were nearly spherical, with rounded leaf apexes. On the other extreme, fused leaves of *L. hirsuta* were also nearly spherical but had acuminate leaf apexes.

The North American clade of *Periclymenum* (fig. 3) covered the widest area of the morphospace, while clades distributed through the North American chaparral, Europe, and China occupied more restricted areas within the morphospace. However, both the European and North American chaparral clades had extensions to the region of the morphospace representing free leaves, while no other species of the North American clade exhibited free leaves subtending the inflorescence.

Discussion

While leaf fusion can be treated as a discrete character, analysis of leaf shape as a continuous character through EFA provided insights into the degree of fusion within and among species of *Periclymenum*. Additionally, a range of shapes that represented fusion would have otherwise been masked by scoring discrete character states. For example, *L. etrusca* and *L. prolifera* both occurred in the fused region of the morphospace, but fused leaves of *L. prolifera* consistently formed a rounder structure, compared with those of *L. etrusca* (figs. 2, 5).

To ensure the comparison of homologous structures, our morphometric analysis was restricted to sampling the first set of fused leaves subtending an inflorescence and did not measure additional sets of leaves farther from the apical meristem. However, we observed two patterns of leaf forms along a reproductive shoot—first, multiple sets of fused leaves subtending an inflorescence, and second, a single set of fused leaves directly subtending an inflorescence, followed by pairs of free leaves. In the case of multiple fused leaves, leaves became increasingly fused moving along the growing axis, with the final set of leaves subtending an inflorescence being completely fused. Here we discuss the implications of the evolution of leaf fusion and consider potential functions of fusion in this context.

Evolutionary Relationships within Periclymenum

We presented a comprehensive phylogeny of *Periclymenum* analyzing four additional plastid gene regions, compared with the last phylogenetic study of the group (Smith and Donoghue 2010). With all but three species of the clade sampled, a number of strongly supported clades were recovered within *Periclymenum*, although many relationships within these clades remained unresolved. As in Smith and Donoghue (2010), we did not recover the monophyly of established subsections but instead recovered clades that corresponded to geography rather than to the subsectional classification proposed by Rehder (1903).

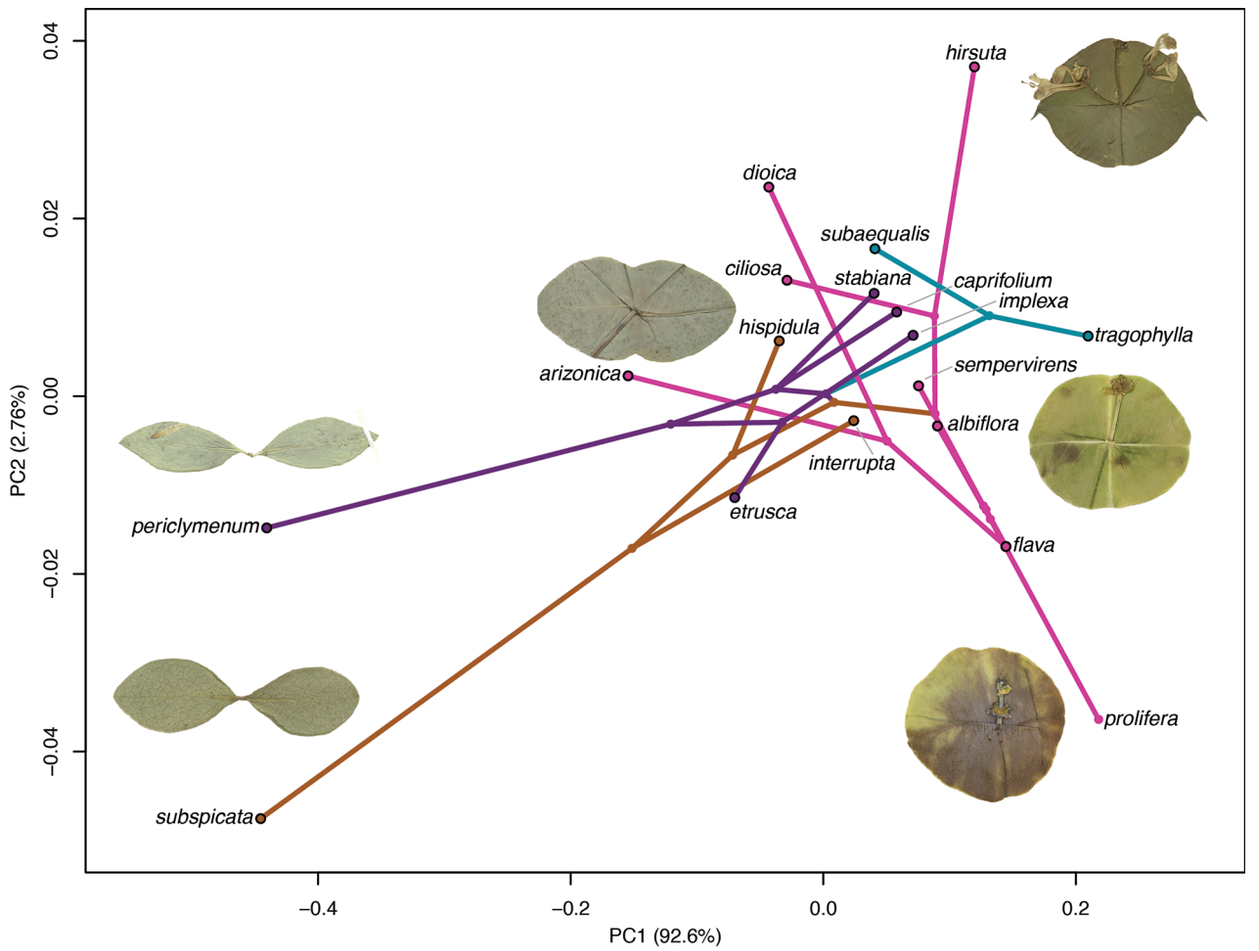

Fig. 5 Phylomorphospace comprising the morphospace (fig. 2) and maximum likelihood phylogeny (fig. 3) pruned to include only taxa sampled in the morphometrics study. Terminal taxa represent species averages in the morphospace and are indicated by circles. Leaf shapes are placed in corresponding regions of the morphospace to indicate the leaf shape in that region. *Middle left*, *Lonicera periclymenum*. *Bottom left*, *Lonicera subspicata*. *Middle*, *Lonicera hispidula*. *Top right*, *Lonicera hirsuta*. *Middle right*, *Lonicera sempervirens*. *Bottom right*, *Lonicera prolifera*. Clades are colored according to their geographic distributions (fig. 3). PC = principal component.

In 1903, Alfred Rehder published the first global monograph of *Lonicera* and recognized four subsections of *Periclymenum*, emphasizing features of the corolla and bracteoles over geography. Section *Cyhpeolae* comprised nine species from North America and one from China, *L. yunnanensis*. Section *Phenianthi* included five North American species and a single species from China, *L. subaequalis*. *Lonicera subaequalis* was newly described in this treatment, and Rehder noted that *L. subaequalis* was not closely allied with any other species of *Lonicera*. Further, Rehder noted that the North American species of *Cyhpeolae* and *Phenianthi* seemed more closely associated with each other than with the remaining two sections, *Eucaprifolia* and *Thoracianthae*. Section *Eucaprifolia* comprised all European *Periclymenum* species and, here again, a single species from China, *L. tragophylla*. Finally, the fourth subsection, *Thoracianthae*, was monotypic and included *L. griffithii*, from Afghanistan.

Instead of recovering the three sampled subsections in our phylogenetic analysis, we recovered a topology similar to previous phylogenetic work (Smith and Donoghue 2010) that included three clades corresponding to geography: (1) a clade containing *L. subaequalis* (*Phenianthi*) and *L. tragophylla* (*Eucaprifolia*), native to China, (2) a clade native to Europe and the Caucasus (largely *Eucaprifolia*), and (3) a clade native to North America, extending from Canada south through Mexico (largely *Cyhpeolae* and *Phenianthi*; fig. 3). The clade of species from China was well supported as sister to all other *Periclymenum* species. We would predict that the third species from China, *L. yunnanensis* (*Cyhpeolae*), would also fall within this clade rather than among the species from North America, where it has been classified on the basis of morphology (Rehder 1903). The European clade largely contained members of *Eucaprifolia*, aligning with Rehder's vision of the *Periclymenum* classification, with the one exception of *L. tragophylla* from China, discussed above. We were unable to sample *L. splendida*, native to Spain and placed in *Eucaprifolia*, but we predict that it would fall within this clade. The European clade is strongly supported and may be sister to a clade of North American species. However, strong support for a monophyletic North American group was lacking. Instead, the North American species fell between two well-supported clades, one clade distributed across North America and a second clade comprising species with distributions that include the chaparral of western North America. These two clades did not correspond to subsections *Cyhpeolae* and *Phenianthi* and instead represented a mixing of the two subsections.

The third and final *Periclymenum* species not sampled in this study was *L. griffithii*, the sole member of subsection *Thoracianthae* collected from the Kuram Valley of Afghanistan (Rehder 1903). Though *L. griffithii* may not be closely associated with any of the *Periclymenum* clades recovered, on the basis of the geographic distribution of *L. griffithii*, a case could be made for assigning it to the clade containing species from either Europe/Caucasus or China. Further, this species has a unique set of attributes that sets it apart from the typical form of *Periclymenum* species, further clouding its evolutionary affinities. Unlike the majority of *Periclymenum* species, *L. griffithii* joins *L. periclymenum* and *L. subspicata* in having distinct leaves rather than fused leaves. Further, as with all *Periclymenum* species, *L. griffithii* has a whorl of six flowers. Here, however, the sets of bracteoles that subtend each of these six flowers fuse together to form a cupule nearly as tall as the ovary itself (Rehder 1903). Bracteoles fusing to form a cupule is a feature otherwise restricted to the other major subclade of *Lonicera*, *Chamaecerasus*.

Evolution of Two Distinct Leaf Forms in Periclymenum

While variation in the degree of leaf fusion varied across *Periclymenum*, our analysis supported two distinct leaf forms for the first set of leaves that directly subtends inflorescences of *Periclymenum*—free or fused (fig. 2). The shape of the free or fused leaf ranged from lanceolate to obovate (figs. 2, 5). The amount of intraspecific variation differed, with some species, such as *L. prolifera* and *L. hispidula*, having less variation among individuals compared with *L. interrupta* and *L. implexa*, which had more lability in leaf shape.

Missing from the morphospace of leaf shape were partially fused leaves directly subtending the inflorescence, in which the leaf base or the petiole, while still discernible, is somewhat expanded. Instead, nearly all connate leaves were completely fused across the stem with no petiole-like structure, with the exception of one individual of *L. arizonica* (fig. 2). Partially fused leaves, however, were more frequently observed among the second and third sets of leaves subtending the inflorescence in herbarium specimens.

A combination of ancestral character state analysis and analysis of the phylomorphospace confidently supported the loss of fused leaves at least twice (figs. 4, 5) across *Periclymenum*, in *L. periclymenum* and *L. subspicata*. These species were placed in two independently evolving lineages, with *L. periclymenum* recovered in the European clade and *L. subspicata* in the North American chaparral clade (figs. 3, 5). A third potential loss of fused leaves was in *L. griffithii* of Afghanistan; however, inclusion of this species in a phylogenetic analysis is needed to confirm this hypothesis. Comparing the inflorescence architecture of *L. periclymenum* and *L. subspicata* does not reveal any similarities that might help to explain the parallel loss of fused leaves. *Lonicera periclymenum*, native to Europe, typically has tight clusters of inflorescences that sit directly on the leaves. This species is pollinated at night by sphinx and *Deilephila* hawk moths (Knuth 1909; Horwood 1919; Brantjes 1973). *Lonicera subspicata*, a native of the chaparral of California, has an inflorescence subtended by a peduncle, with lateral branching and distinct peduncles separating verticels. This species is primarily visited by diurnal butterflies, including *Zerene eurydice*, *Plebejus acmon*, *Aricia lupini*, *Aricia icarioides*, *Lycaeides melissa*, and *Erynnis funeralis* (J. A. Caldwell, unpublished data). Further investigation of the pollination and seed dispersal ecology of these plants, coupled with studies of the genetic and molecular mechanisms required to achieve this shift, may help identify selective pressures that underlie the reversion to free leaves.

In the context of Dipsacales, the larger clade to which *Lonicera* belongs, free leaves represent the ancestral condition, with fused leaves gained at least three times throughout the clade. Fused leaves were gained once in *Periclymenum* (followed by a parallel loss), at least once in *Triosteum* (Caprifoliaceae), and once in *Dipsacus* (Dipsacaceae; fig. 4*B*). The fused leaves of *Dipsacus fullonum* (Dipsacaceae) form a cuplike structure that can retain water, which is thought to facilitate carnivory (Christy 1923; but see Shaw and Shackleton 2011; Krupa and Thomas 2019). The fused leaves of *Triosteum* are more similar to those of *Lonicera* in that these leaves are associated with reproductive structures.

However, the inflorescences of *Triosteum*, unlike the typical terminal inflorescences of *Periclymenum*, also occur in the leaf axils (Ferguson 1966). Yet, in either case, the fused leaves create a uniform backdrop against the flowers or fruits of these plants.

Among *Periclymenum* species, multiple forms of leaves were commonly observed within an individual when fusion was present. In some cases, individuals had a single set of fused leaves representing one leaf shape and free leaves representing a second leaf shape. Among species with multiple sets of fused leaves, we typically observed that two or three (but up to five) pairs of leaves subtending an inflorescence exhibited some amount of fusion. For example, *L. prolifera* regularly displayed two or three sets of partially fused leaves below the fully fused leaves that subtended the inflorescence, while *L. tragophylla* tended to have only one additional set of partially fused leaves subtending a single set of fully fused leaves. Additionally, leaves and petioles became more distinct farther from the inflorescence, resulting in a number of leaf shapes along a stem (fig. 1C). As this trait is quite labile, there are likely multiple shifts that would be required to explain the evolution of the single and multiple sets of fused leaves observed across *Periclymenum*, though our initial findings suggest that multiple sets of fused leaves are ancestral. Shifts between numbers of fused leaves and the degree of fusion along a stem suggest possible changes in gene regulation. A hypothesized candidate gene is *CUP-SHAPED COTYLEDON* (*CUC*), which has been implicated in defining organ boundaries, as *CUC* mutants have resulted in the fusion of cotyledons into a cup in *Arabidopsis* (Aida et al. 1997; Takada et al. 2001; Vroemen et al. 2003). More recent studies have connected *CUC* activity to leaf serration (Hasson et al. 2011) and identified a potential role for *CUC* in the formation of compound leaves (Vlad et al. 2014), suggesting that *CUC* plays a significant role in leaf shape and fusion. *CUC* acts in a dosage-dependent manner, with reductions in *CUC* expression resulting in increased tissue fusion. The first step in this transition to fused leaves could have involved a decrease in *CUC* expression along the axis subtending the inflorescence that then became more canalized to only a single set of fused leaves in some clades, similar to the "fading borders" hypothesis for MADs-box genes (Chanderbali et al. 2016). Therefore, initially, this may have involved dosage of gene expression along a stem before the evolution of the ability to regulate a complete switch from the absence to the presence of leaf fusion (e.g., single fused leaves). This could also explain the absence of partially fused leaves subtending an inflorescence—the growing axis instead simply continued to produce sets of leaves until they were fully fused before triggering the production of an inflorescence. Development and expression studies of known genes involved in fusion, including *CUC*, are needed to continue this line of inquiry.

Fused Leaves Are Associated with Reproductive Structures

Our study of leaf form in *Periclymenum* has confirmed that the majority of species in this clade exhibit leaf fusion, with multiple leaf forms occurring along a single reproductive shoot. Yet, consistently among species exhibiting leaf fusion, the pair of leaves subtending the inflorescence exhibited the greatest degree of fusion. Despite a close and consistent association between fused leaves and reproductive structures, we did not detect correlated evolution among these traits.

Our study of the evolution of inflorescence architecture across *Periclymenum* did generally support that the ancestral forms of *Periclymenum* inflorescences were more compact, followed by repeated gains of lateral branching and peduncles between clusters of flowers. There are additional inflorescence features to consider to fully explore inflorescence evolution in honeysuckles as it may relate to leaf fusion, some of which (e.g., the presence of axillary branching or numbers of verticels along an inflorescence axis) should be evaluated in living plants and assessed at the population level. As an example, while species in the European clade of *Periclymenum* exhibit differences in lateral branching, this clade also varies in the positioning of the inflorescences. *Lonicera caprifolium* and *L. implexa* largely lack lateral branching within their terminal inflorescences but produce inflorescences from the axils of fused leaves (Rehder 1940). When the possible roles of fused leaves in reproduction are considered, differences in the positioning of reproductive shoots affect the overall density and distribution of flowers across a whole plant. Additionally, quantitative approaches to capturing variation in floral traits such as corolla tube size and shape or petal lobe size and positioning would better describe the inflorescence as a whole. Expanding the study of leaf shape to include additional sets of partially fused leaves while also exploring additional reproductive characters may help illuminate correlated traits.

The spatial association of fused leaves with flowers and fruits points to a possible role of reproductive ecology in the evolutionary history of this clade of honeysuckles. Given the positioning of fused leaves surrounding a developing inflorescence, a protective role for fused leaves has been suggested (Perino 1978). In mature inflorescences of *L. subaequalis* and *L. pilosa*, the fused bracts continue to form a large cuplike structure around the whorls of flowers. In *L. pilosa* the inflorescences are pendulous, and it has been noted that the fused leaves act as an umbrella shielding compact clusters of flowers (Zappi and Taylor 1993).

Fused leaves form a consistent backdrop to the reproductive structures of these honeysuckles (Perino 1978). While flower color across *Periclymenum* varies, nearly all species have red fruits (Rehder 1903). The discoverability of these fruits by a seed disperser, typically birds, in the case of *Lonicera* (Ingold and Craycraft 1983; Drummond 2005; Bartuszevige and Gorchov 2006; McCusker et al. 2010), may not be solely dependent on this red color. The "contrast hypothesis" (Schmidt et al. 2004) suggests that increasing the contrast of fruit displays increases the likelihood of disperser detection and consumption (Schmidt et al. 2004; Schaefer et al. 2006; Cazetta et al. 2009; Ordano et al. 2017), and though this is untested, perhaps fused leaves further enhance this contrast by providing a less heterogeneous surface against which reproductive structures can be viewed. Further, among the strong chromatic contrasts detectable by birds is the red-green contrast (Burns and Dalen 2002; Schaefer et al. 2006), which would be especially pertinent for these red-fruited *Periclymenum* species. Other types of modifications in red-fruited *Lonicera* species without fused leaves may also allow for such a contrast. For instance, the paired and fused red fruits of *L. alpigena* of the *Chamaecerasus* clade occur at the end of a long stalk that sits appressed to the top of a leaf. Though reproductive ecology is not at the forefront of discussions on functional differences in leaf shape (Nicotra et al. 2011; Chitwood and Sinha 2016), further studies of the intersection of leaf fusion and reproduction may prove to be important in honeysuckles.

Conclusions

While fused, or perfoliate-connate, leaves occur independently in a number of clades of flowering plants, this study is the first to consider this feature in an evolutionary context. Across Dipsacales, free leaves are ancestral, and fused leaves have been both gained and subsequently lost primarily within two clades, *Lonicera* and *Triosteum*. Fused leaf shape varies across species of the *Periclymenum* clade of *Lonicera*, with fully fused leaves always directly subtending an inflorescence. Those species with multiple sets of fused leaves exhibit successively less fusion among pairs of leaves more distant from an inflorescence. Given the close and consistent association of fully fused leaves with reproductive structures, fused leaves may protect a developing inflorescence or provide a consistent background that affects the visibility of flowers and fruits to pollinators and seed dispersers, respectively. As few studies have focused on the evolution of fused leaves, we hope that the conclusions of this study propel future work on morphological diversity and the functions of this trait across flowering plants.

Acknowledgments

Our thanks to M. J. Donoghue, D. G. Howarth, E. Kulesza, K. Prudic, J. Oliver, M. Sinnott-Armstrong, E. L. Spriggs, T. J. Stammer, and the honeysuckle working group for insightful conversations and contributions to this research. We are also grateful for the assistance of and access to plant collections given by M. Dosmann and K. Richardson at the Arnold Arboretum at Harvard University, A. R. Brach at the Harvard University Herbaria, S. D'Acunto at the Mertz Library at NYBG, and B. Thiers and C. Zimmerman at the NYBG Herbarium. We acknowledge the ELSA high-performance computing cluster at the College of New Jersey for conducting the research reported in this article. This cluster is funded by the National Science Foundation under grant OAC-1828163. This work was funded by the Department of Biology and School of Science at the College of New Jersey and a National Science Foundation grant (DEB-1929670) to W. L. Clement.

Appendix A

A list of voucher specimens used in morphometric and phylogenetic analyses of the 21 species of *Lonicera* sampled in this study. Herbarium specimens are listed with the collector name and number as well as herbarium acronyms. If no collector or collector number was noted on the specimen, the specimen barcode is provided. GenBank accession numbers are listed in the following order: *LFY*, internal transcribed spacer, *trn*S-*trn*G, *rbc*L, *psb*M-*trn*D, *rpo*B-*trn*C, *atp*B-*rbc*L, *pet*N-*psb*M, and *mat*K. Most sequence data are from Smith and Donoghue (2010). A dash indicates missing data.

Herbarium abbreviations are as follows: A = Arnold Arboretum, Harvard University Herbarium; AIX = Museum d'Histoire Naturelle of Aix-en-Provence Herbarium; BG = University Museum of the University of Bergen; CHE = Société des Sciences Naturelles et Mathématiques de Cherbourg; DES = Desert Botanical Garden Herbarium; GH = Gray Herbarium, Harvard University Herbarium; GXMI = Guangxi Institute of Traditional Medical and Pharmaceutical Sciences; K = Kew Royal Botanic Gardens; KUN = Kunming Institute of Botany, Chinese Academy of Sciences; NEBC = New England Botanical Club; NEU = Neuchâtel Herbarium; NY = New York Botanical Garden; MO = Missouri Botanic Garden, Tropicos; MPU = Herbarium of Université de Montpellier; MW = Moscow State University; O = Natural History Museum, University of Oslo, OAC-BIO Herbarium, University of Guelph and University of the Basque Country; P = Museum National d'Histoire Naturelle; PE = Institute of Botany, Chinese Academy of Sciences; SM = Chongqing Municipal Academy of Chinese Materia Medica; TAA = Estonian University of Life Sciences; UBC = University of British Columbia; US = Smithsonian National Museum of Natural History; USCH = University of South Carolina, A. C. Moore Herbarium; USF = University of South Florida Herbarium; UNM = University of New Mexico Herbarium Palmer; WUK = Northwestern Institute of Botany.

L. albiflora **Torr. & A. Gray** S. Stephens 37453 (NY); D.S. Correll 21091 (NY); R. McVaugh 7233 (NY); T.F. Daniel 2757 (NY); F.S. Earle s.n. (NY); J. Reverchon 1072 (NY); E.O. Wooton s.n. (US); J. Carter & S.M. George 67 (UNM); P04333693 (P); R.A. Haughey s.n. (DES); GU269257; FJ217862; FJ217893; JN796941; -; -; -; -; -. ***L. arizonica*** **Rehder** E.A. Goldman 2118 (US); C.R. Hutchins 4990 (UNM); E. Palmer 537 (K); M. Licher 3119 (DES); GU269260; FJ217881; FJ217934; -; -; -; -; -. ***L. caprifolium*** **L.** NEU000030449 (NEU); O.R. Willis s.n. (NY); 2437409 (NY); T. Barta s.n. (NY); G. Sag 3506 (P); B. Wallnöfer 12366 (US); Dorfman s.n. (MW); S. Talts 23573 (TAA); GU269250; MG220043; FJ217891; MG224462.1; -; -; -; -; -. ***L. ciliosa*** **D. C.** M. Murley 1727 (NY); L.F. Henderson 15705 (NY); M. Ridewood 39 (NY); J.W. Thompson 11726 (NY); L.C. Wheeler 2762 (NY); E.R. Manton s.n. (UBC); C.A. Mosier s.n. (US); P03301449 (P); GU269263; MG218113; FJ217907; MG223114; -; -; -; -; KX677615. ***L. dioica*** **L.** H.A. Gleason s.n. (NY); R.F.C. Naczi 15391 (NY); 2437745 (NY); A.W. Cusick 29499 (NY); H. Gillman s.n. 2437727 (NY); H.M. Denslow s.n. 2437804 (NY); K.K. Mackenzie s.n. (NY); GU269259; GU269247; FJ217892; MG224262, EU265443, EU265507, EU265571, EU265635, MK520270. ***L. etrusca*** **Santi** J. Bornmuller 2746 (A); J. Bornmuller 13454 (A); L. Kharpal 627 (A); F. Petter 234 (A); Kammerer 2663 (GH); J. Ball 2214 (GH); J.G. Spreitzechofer s.n. (A); G. Pellanda 1765 (GH); GU269256; FJ217842; FJ217899; MG223949, EU265409, EU265473, EU265537, EU265601, -. ***L. flava*** **Sims** W.H. Lewis s.n. (NY); H.P. Sartwell s.n. (NY); S.R. Hill 36456 (NY); W.W. Denslow s.n. (NY); I.A. Lapham s.n 278506 (NY); J.G. Smyth s.n. (NY); P03708938 (P); O.W. Harbin 258 (USF); -; FJ217875; FJ217943; -; -; -; -; -; -. ***L. hirsuta*** **Eaton** H.A. Gleason 9561 (NY); C.O. Grassl 5788 (NY); C.C. Stewart 1728 (NY); E.G. Whitney 4197 (NY); P.V. Krotkov 9426 (NY); C.E. Garton 8533 (NY); H.D. House s.n. (US); W. Shumovich 718 (OAC-BIO); GU269262; FJ217821; FJ217913; HQ590166; -; -; -; -; MK520271. ***L. hispidula*** **Pall. ex Schult.** E.C. Earle 4409 (NY); A.D.E. Elmer 4596 (NY); E. Palmer 2348 (US); J. McMurphy 24 (US); G.R. Vasey s.n. (US); J. Torrey 191 (US); H.E. Brown 872 (US); R. Dennis & M. Ivie s.n. (US); GU269264; FJ217855; FJ217889; MG221342, EU265419, EU265483, EU265547, EU265611, KX676707. ***L. implexa*** **Aiton** H. Bouby 2700 (P); P03709798 (P); P02445359 (P); P02445369 (P); P0.709993 (P); Dubourg s.n. (CHE);

P03709811 (P); P03709802 (P); GU269255; FJ217861; FJ217897; -; -; -; -; -; -. ***L. interrupta*** **Benth.** B. Bartholomew 4268 (NY); C.L. Hitchcock 6498 (NY); D.E. Breedlove 62607 (NY); W.J. Williamson 186 (NY); W.C. Cusick 2898 (NY); A.A. Heller 5551 (NY); O.M. Clark 5215 (UNM); O.M. Clark 5215 (UNM); GU269266; -; FJ217909; -; -; -; -; -; -. ***L. morrowii*** **A. Gray** D.E. Atha 10262 (NY); D.E. Atha 10306 (NY); W.D. Longbottom 13169 (NY); G. Eiten 1288 (NY); W. Longbottom 10994 (US); L.J. Mehrhoff 21656 (NEBC); GU269249; FJ217859; FJ217917; KJ841385, EU265427, EU265491, EU265555, EU265619, MK520273. ***L. periclymenum*** **L.** A. Mørch s.n. (BG); T. Lillefosse s.n. (BG); R. Nordhagen s.n. (BG); J. Naustdal s.n. (BG); L. Malme s.n. (O); H. Bratli 4256 (O); P. Størmer s.n. (O); GU269254; FJ217825; FJ217928; KX677804; -; -; -; -; KJ204503. ***L. pilosa*** **(Kunth) Spreng.** No morphometric data collected. -; GU269248; FJ217900; -; -; -; -; -; -. ***L. prolifera*** **(Kirchner) Booth ex Rehder** M. McGee 818 (NY); T.G. Yuncker 18979 (NY); H.A. Gleason 9163 (NY); R.A. Davidson 448 (NY); S.R. Hill 29283 (NY); H.E. Ahles 78550 (NY); J.M. Halginger s.n. (NY); C.S. Whulia s.n. (NY); GU269258; -; -; MG222051; -; -; -; -; -. ***L. sempervirens*** **L.** D.E. Atha 9889 (NY); C. Stone 221 (NY); W.D. Longbottom 14915 (NY); 2442260 (NY); 2442269 (AIX); M. Connelly 98 (USCH); C. Aulbach-Smith 911 (USCH); C.A. Aulbach-Smith 911 (USF); GU269261; FJ217845; FJ217886; KY627129; EU265434; EU265499; EU265563; EU265627; KJ772905. ***L. stabiana*** **Guss. ex Pasq.** collector unspecified 188/10 (P); P04334309 (P); MPU1128176 (MPU); GU269261; -; -; -; -; -; -; -. ***L. subaequalis*** **Rehder** 潘超逸 850 (SM); 方鼎 姚良琪 63972 (GXMI); 方鼎 姚良琪 63972 (GXMI); 方鼎 方鼎 覃德海 63966 (GXMI); 方鼎 方鼎 覃德海 63966 (GXMI); 方鼎 陆小鸿 8158 (GXMI); 方鼎 姚良琪 63972 (GXMI); 方鼎 姚良琪 63972 (GXMI); 潘超逸 850 (SM); GU269252; EU240675; EU265341; -, EU265405, EU265469, EU265533, EU265597, -. ***L. subspicata*** **Hook. & Arn.** S. Boyd 1831 (NY); C.A. Morse 17781 (NY); T.S. Ross & S. Boyd 3542 (NY); G.R. Vasey 241 (NY); G. Collins & J.H. Kempton 279 (NY); I.L. Wiggins 11871 (US); E.Palmer 120 (MO); GU269265; FJ217843; FJ217915; -; -; -; -; -; -. ***L. tragophylla*** **Hemsl** 陈彦生、吴振海、黎斌、孙建钊等 4405 0502444 (WUK); 陈彦生、吴振海、黎斌、孙建钊等 4672 0501718 (WUK); 侯喜祥 郭友好 706 (WUK); E. Wilson 346 (US); P03302042 (P); P03302043 (P); P03302046 (P); R.P. Farges 834 (P); P03302053 (P); GU269251; FJ217874; EU265377; NC037953; EU265441; EU265505; EU265569; EU265633; NC037953. ***L. yunnanensis*** **Franch.** K.M. Feng 1047 (PE); G. Forrest 10795 (PE); collector unspecified 22913 (PE); 秦仁昌 2102 (KUN); P03301684 (P); P03301682 (P); no molecular data collected.

Appendix B

Additional specimens examined for scoring morphological traits of *Lonicera*. For each herbarium specimen examined, the collector name and number (or herbarium barcode when collector information was absent) as well as the herbarium acronym are provided. Species are listed in alphabetical order. Herbarium abbreviations are as follows: A = Arnold Arboretum, Harvard University Herbarium; AIX = Museum d'Histoire Naturelle of Aix-en-Provence Herbarium; B = Botanic Garden and Botanical Museum Berlin-Dahlem; BG = University Museum of the University of Bergen; BNU = Beijing Normal University; CDBI = Chengdu Institute of Biology, Chinese Academy of Sciences; CHE = Société des Sciences Naturelles et Mathématiques de Cherbourg; CSH = Shanghai Chenshan Botanical Garden; DES = Desert Botanical Garden Herbarium; FR = Herbarium Senckenbergianum; GH = Gray Herbarium, Harvard University Herbarium; GXMI = Guangxi Institute of Traditional Medical and Pharmaceutical Sciences; GOET = University of Goettingen; IBSC = South China Botanical Garden; HX = Chinese Academy of Sciences, Huaxia Mountain Botanical Garden Herbarium; K = Kew Royal Botanic Gardens; KHD = Kathryn Kalmbach Herbarium (Denver Botanic Gardens); KUN = Kunming Institute of Botany, Chinese Academy of Sciences; LBG = Lushan Botanical Garden; NAS = Institute of Botany, Jiangsu Province and Chinese Academy of Sciences; NBIC = Norwegian Biodiversity Information Centre; NEBC = New England Botanical Club; NEU = Neuchâtel Herbarium; NY = New York Botanical Garden; M = Vascular Plant Collection at the Botanische Staatssammlung München; MO = Missouri Botanic Garden, Tropicos; MPU = Herbarium of Université de Montpellier; MW = Moscow State University; O = Natural History Museum, University of Oslo, OAC-BIO Herbarium, University of Guelph and University of the Basque Country; P = Muséum National d'Histoire Naturelle, Paris (France); PE = Institute of Botany, Chinese Academy of Sciences; PEY = Peking University; SLA = Société des Lettres, Sciences et Arts de l'Aveyron; SM = Chongqing Municipal Academy of Chinese Materia Medica; SZ = Sichuan University, Jianghong Ran; TAA = Estonian University of Life Sciences; UBC = University of British Columbia; US = Smithsonian National Museum of Natural History; USCH = University of South Carolina, A. C. Moore Herbarium; USF = University of South Florida Herbarium; UNM = University of New Mexico Herbarium Palmer; WUK = Northwestern Institute of Botany; XBGH = Xian Botanical Garden.

L. albiflora **Torr. & A. Gray** Aven Nelson 2006 (NY); O.B. Metcalfe 870 (NY); Palmer 157 (NY); B.C. Tharp s.n. (NY); E. Whitehouse 19500 (NY); H.H. Rusby 149 (NY).

L. arizonica **Rehder** R.T. Schuh 14 (NY); L.M. Pultz 1031 (NY); R.C. Barneby 3105 (NY); T.F. Daniel 1582 (NY); B. Maguire 121249 (NY); B. Maguire 11868 (NY); T.F. Daniel 1762 (NY); G.J. Goodman 1170 (NY); E.A. Mearns 244 (NY); D.T. MacDougal 104 (NY).

L. caprifolium **L.** Rehder Piaget s.n. (NEU); NEU000030445 (NEU); NEU000030453 (NEU); NEU000030457 (NEU); NEU000030458 (NEU); NEU000030450 (NEU); C. Coaz s.n. (NEU); J. Berset s.n. (NEU); NEU000030455 (NEU); NEU000030456 (NEU); NEU000030448 (NEU); H.P. Sartwell s.n. (NY); 2437410 (NY); 2632935 (NY); 3240473 (NY); 1688370 (NY); J. Hale s.n. (NY); A. Wood C.B. 299? (NY); 2437415 (NY).

L. ciliosa **D. C.** A.D.E. Elmer 347 (NY); T.E. Wilcox s.n. (NY); D.T. MacDougal 297 (NY); D.E. Boufford 23789 (NY); M.W. Lyon 22 (NY); F.H. Rose 911 (NY); D.T. MacDougal 104 (NY); H.T. Rogers 966 (NY); H.E. Brown 401 (NY); A.D.E. Elmer 786 (NY); J.H. Christ IV 10121 (NY); M. Parks 27 (NY); J.A. Calder 29514 (NY); N.H. Holmgren 2703 (NY); R.R. Halse 3599 (NY);

A.N. Steward 6903 (NY); C.L. Hitchcock 17229 (NY); Q. Jones 50 (NY); L.C. Wheeler 2762 (NY); J.H. Christ IV 683006 (NY); R.S. Ferris 11731 (NY); F.E. Lloyd s.n. (NY); C.C. Eugberg s.n. (NY); L.F. Henderson 417 (NY); E.P. Sheldon 10418 (NY); H. St. John 6347 (NY); J.M. Grant s.n. (NY); D. Griffiths 217 1 (NY); 30434 (NY); J.H. Sandberg s.n. (NY); V. Rattan s.n. (NY); G. Davidse 606 (NY); A.J. Cronquist 6650 (NY); W.W. Eggleston 22100 (NY); M.W. Gorman s.n. (NY); M.B. Dunkle 13605 (NY); J.H. Sandberg 390 (NY); T.J. Howell s.n. (NY); J.H. Christ IV 12098 (NY); S.M. Zelle 787 (NY); J.M. Macoun 42695 (NY); J.H. Christ IV 7374 (NY); E.K. Balls 21714 (NY); T.S. Brandegee 807 (NY); J.M. Macoun 64647 (NY); B.T. Butler 2264 (NY); R.R. Halse 8873 (NY); E. Hall 224 (NY); C.W. Sharsmith 3582 (NY); J.H. Christ IV 6866 (NY); O.D. Allen 113 (NY); B.L. Richards s.n. (NY); M.L. Conrad 6895 (NY); W.H. Baker 756 (NY); J.H. Christ IV 86 (NY); J.H. Sandberg 554 (NY); E.W. Hammond 179 (NY); J.H. Christ IV 3834 (NY); 2437534 (NY); J.A. Calder 10239 (NY); H.J. Rust 74 (NY); R.S. Williams s.n. (NY); F.O. Kreager 200 (NY); R.J. Davis 291 -37 (NY); A. Kellogg 340 (NY); W.B. Cooke 16019 (NY); A.A. Heller 13253 (NY); A.A. Heller 3316 (NY); A.A. Heller 3938 (NY); J. Grimes 1877 (NY); J.W. Thompson 17005 (NY); J.W. Thompson 11726 (NY).

***L. dioica* L.** V.L. Harms 17368 (NY); E.J. Grimes 383 (NY); E.J. Grimes 662 (NY); E.J. Grimes 1050 (NY); O.K. Lakela 1424 (NY); J.W. Moore 12871 (NY); W.L. Stern 578 (NY); P. Wilson s.n. (NY); F.A. Gilbert 829 (NY); M.H. Nee 52326 (NY); J. Torrey s.n. (NY); E.M. Kittredge s.n. (NY); W. Hartmann 11546 (NY); W.W. Eggleston s.n. (NY); H.M. Raup 2692 (NY); J.E. Parsons s.n. (NY); A.J. Grout s.n. (NY); N.L. Britton s.n. (NY); J.A. Steyermark 22132 (NY); W.H. Leggett s.n. (NY); G. Thurber s.n. (NY); N.L. Britton s.n. (NY); A.M. Vail s.n. (NY); E.J. Hill s.n. (NY); C.A. Darling s.n. (NY); A.A. Tyler s.n. (NY); W. Hill 22 (NY); J.C. Arthur s.n. (NY); J. Fowler s.n. (NY); A. Hayden 2054 (NY); C.D. Richards 4715 (NY); A.J.J. Breitung s.n. (NY); T.R. Robinson 29 (NY); S.L. Clarke s.n. (NY); A.M. Vail s.n. (NY); 2437688 (NY); 2437691 (NY); N.L. Britton s.n. (NY); K.K. Mackenzie s.n. (NY); K.K. Mackenzie 4659 (NY); K.K. Mackenzie s.n. (NY); H.N. Moldenke 11046 (NY); W.M. Benner 6711 (NY); G.T. Hastings s.n. (NY); Biltmore Herbarium 554 f (NY); J.R. Gardner 661 (NY); 2437708 (NY); Biltmore Herbarium 554 b (NY); J. Lunell s.n. 2437712 (NY); T.G. Yuncker 10314 (NY); L. McCaskey s.n. (NY); W.G. Dore 9800 (NY); F.H. Blodge s.n. (NY); A.M. Vail s.n. (NY); M.A. Vincent 13958 (NY); C.T. Frye 5914 (NY); P.A. Rydberg s.n. (NY); H. Gillman s.n. (NY); C.D. Richards 2111 (NY); E.J. Palmer 34801 (NY); J. Macoun 72603 (NY); O.K. Lakela 1423 (NY); L.H. Pammel s.n. (NY); P.V. Krotkov 9424 (NY); J.L.C. Marie-Victorin 55133 (NY); F. Fabius 522 (NY); W.N. Denike 122 (NY); J. Murdoch Jr. 4062 (NY); A.J.J. Breitung 17623 (NY); 2437744 (NY); F.W. Hunnewell 8254 (NY); K.M. Wiegand s.n. (NY); F.D. Lawton s.n. (NY); M. Heatley s.n. (NY); H.M. Raup 3728 (NY); C.D. Richards 1910 (NY); E.S. Burgess s.n. (NY); J.F. Kemp s.n. (NY); B. Barlow s.n. (NY); H.F. Bergman s.n. (NY); 2437768 (NY); H.A. Gleason 9653 (NY); 20611 (NY); A.J. Mc Clatchie s.n. (NY); 2437775 (NY); N. Taylor 1301 (NY); N. Taylor 1959 (NY); A.T. Beals s.n. (NY); C.H. Bissell 89 (NY); N.L. Britton s.n. (NY); C.C. Freeman 3367 (NY); J.D. Dwyer s.n. (NY); E.S. Anderson 26020 (NY); A.H. Brinkman 3440 (NY); J. Macoun 20615 (NY); C.C. Curtis s.n. (NY); W.N. Denike 140 (NY); W.H. Leggett s.n. (NY); J. Lunell s.n. (NY); E.S. Steele 17 (NY); T.A. Williams s.n. (NY); E.W. Wood 4212 (NY); C.E. Garton 24082 (NY); C.E. Garton 24082 (NY); H.M. Denslow s.n. (NY); H.R. Bennett s.n. (NY); 2437810 (NY); 2437811 (NY); I.A. Lapham s.n. (NY); J.B. Moyle 185 (NY); N. Taylor 174 (NY); K.E. Rogers 44103 (NY); B. Shimek s.n. (NY); R.D. Dorn 4052 (NY); R.D. Dorn 3994 (NY); G.H. Turner 13 (NY); S. Stephens 20007 (NY); E.T. Moldenke 9646 (NY); I.A. Lapham s.n. (NY); K.O. Foltz s.n. (NY); H.N. Moldenke 2376 (NY); H.E. Ahles 43985 (NY); T.J.W. Burgess s.n. (NY); J.M. Macoun 59980 (NY); Biltmore Herbarium 554 (NY); F.E. Fenno 182 (NY); C.C. Deam 14425 (NY); J.M. Holzinger s.n. (NY); L.R. Moyer 5 Je. 1909 (NY); J.H. Lehr 332 (NY); H.M. Denslow s.n. (NY); R.D. Dorn 4052 (NY); 1072 (NY); O.A. Phelps 1203 (NY); Biltmore Herbarium 554 (NY); I.A. Lapham s.n. (NY); A.J.J. Breitung 557 (NY); H.A. Gleason 9814 (NY); F.W. Rapp 4332 (NY); H.A. Gleason 9810 (NY); A.C. McIntosh 1413 (NY); B. Rawlinson 49-193 (NY); W.H. Camp 1300 (NY); 2437869 (NY); F.W. Hunnewell 6903 (NY); N.L. Britton s.n. (NY); 2437873 (NY); J. Kezer s.n. (NY); F.H. Blodgett s.n. (NY); 2437876 (NY); Biltmore Herbarium 554 f (NY); J.M. Holzinger s.n. (NY); Oakes s.n. (NY); C.A. Kofoid s.n. (NY); C.D. Richards 2097 (NY); F.J. Hermann 7774 (NY); C.D. Richards 692 (NY); M.E. Moodie 11 (NY); E.J. Palmer 37179 (NY); H.M. Raup 3096 (NY); H.M. Raup 3090 (NY); H.M. Raup 3095 (NY); M.E. Moodie 929 (NY); F.K. Butters 868 (NY); S. Stephens 5967 (NY); P. Johnson 209 (NY); C.D. Richards 2099 (NY); J.F. Poggenburg s.n. (NY); E.J. Alexande s.n. (NY); E.T. Moldenke 11628 (NY); Z.E. Murrell 229 b (NY); H. Hapeman s.n. (NY); J.K. Small s.n. (NY); J.K. Small s.n. (NY); J.K. Small s.n. (NY); 2437854 (NY); 2437651 (NY); 2437642 (NY); 2437815 (NY); 2437806 (NY); 2437810 (NY); 2437814 (NY); 2437850 (NY); R.C. Schneider 3602 (NY); G.T. Hastings s.n. (NY); 2437626 (NY); 2437655 (NY); V.H. Chase 12495 (NY); V.H. Chase 12608 (NY); W.W. Eggleston 231 (NY); W.L. Stern 615 (NY).

***L. etrusca* Santi** Amat, R. s.n. (AIX); G. Sag 5 (P); H. Bouby s.n. (P); P. Jovet s.n. (P); S.V. Dudov Eur 14 034 (MW); S.V. Dudov Eur 14 034 (MW); M.N. Kozhin s.n. (MW); A.V. Popovich s.n. (MW); E.E. Gogina s.n. (MW); G. Grosset s.n. (MW); Ivanova s.n. (MW); Litvinova s.n. (MW); Avvakumova s.n. (MW); Novichkova s.n. (MW); Korobkov s.n. (MW); P. van Royen 11890 (US); J.A. Calder 36678 (NY); M.E. Peck 8828 (NY); B. Verdcourt 4562 (USF); E. McClintock s.n. (USF).

***L. flava* Sims** Steven R. Hill 39155 (NY); 2437900 (NY); R.M. Harper 216 (NY); G.T. Robbins 2913 (NY); D. Demarée 22857 (NY); M. Pyne 94- 42 (NY); W.C. Coker s.n. (NY); A.M. Huger s.n. (NY); D. Demarée 22768 (NY); 2437924 (NY); H.E. Wheeler s.n. (NY); D. Demarée 6531 (NY); D. Demarée 14336 (NY); C.F. Wheeler 1071 (NY); A.J. Cronquist 4440 (NY); A.J. Cronquist 5054 (NY); W.H. Duncan 20046 (NY); R.M. Harper 330 (NY); H.K.D. Eggert s.n. (NY); S. Boykin s.n. (NY); A.M. Huger s.n. (NY); N.E. Mullens 68027 (NY); A.M. Huger s.n. (NY); E.J. Alexander s.n. (NY); J.K. Small 769 (NY); 2437960 (NY); P.L. Redfearn Jr. 4155 (NY); J.K. Small s.n. (NY); J.K. Small s.n. (NY); J.K. Small s.n. (NY); J.K. Small s.n. (NY); J.K. Small s.n. (NY); 2437952 (NY); 2437966 (NY); G.V. Nash 1042 (NY); R.C. Schneider 1042 (NY); W.S. Sullivant 80 (NY); I.A. Lapham s.n. (NY).

***L. griffithii* Hook.f. & Thomson** W. Griffith 752 (K); W. Griffith 3408 (K); W. Griffith, 3408 (K); W. Griffith 752 (K); W. Griffith 1165 (K); W. Griffith s.n. (K); W. Griffith 3408 (P); J.E.T. Aitchison 535 (P); W. Koelz 11510 (US); W. Koelz 11695 (US); W. Koelz 11657 (US); W. Griffith 3408 (M); W. Griffith 3408 (M).

***L. hirsuta* Eaton** H.A. Gleason 9574 (NY); C.E. Garton 1831 (NY); 2438021 (NY); O.K. Lakela 1303 (NY); E. Brainerd s.n. (NY); E.M. Round s.n. (NY); F.W. Hunnewell s.n. (NY); A.M. Keefe s.n. (NY); E.J. Palmer 36833 (NY); H.P. Sartwell s.n. (NY); T.W.

Edmondson s.n. (NY); 2438031 (NY); J.W. Moore 20281 (NY); J. Fowler s.n. (NY); C.E. Garton 1192 (NY); H.P. Sartwell s.n. (NY); A.Eaton s.n. (NY); B. Barlow s.n. (NY); A. Brown s.n. (NY); Sartwell s.n. (NY); H.R. Bennett s.n. (NY); J.B. Moyle 206 1 (NY); J.H. Shuette 12. 4 .66 (NY); J.H. Eby 1 (NY); J. Macoun s.n. (NY); W.H. Welch 9730 (NY); C.A. Ballard s.n. (NY); J. Macoun 62954 (NY); I.B. Crawe s.n. (NY); E.L. Hankenson s.n. (NY); C.W. Mulford s.n. (NY); P.A. Rydberg 7824 (NY); O.A. Farwell 1073 (NY); Hadley 13 (NY); H. Gillman s.n. (NY); H.A. Gleason 9812 (NY); A.P. Garber s.n. (NY); 2438070 (NY); C.F. Austin s.n. (NY); J. Macoun s.n. (NY); A.P. Garber s.n. (NY); N.L. Britton s.n. (NY); N.L. Britton s.n. (NY); 2438077 (NY); 2438076 (NY); H.D. House 20345 (NY).

***L. hispidula* Pall. ex Schult.** E. Hall 225 (NY); C.E.O. Kuntze 3174 (NY); J. Macoun 87926 (NY); E.K. Balls 18625 (NY); M.E. Peck 8581 (NY); E. Hall 226 (NY); T.J. Howell s.n. (NY); L. Constance 959 (NY); M.W. Gorman 4161 (NY); C.C. Eugberg s.n. (NY); R.A. Plaskett 153 (NY); J.H. Dickson s.n. (NY); E. Hall 225 (NY); J. Torrey 191 (NY); J. Macoun 87924 (NY); C.F. Baker 1533 (NY); C.C. Eugberg s.n. (NY); R.A. Plaskett 153 (NY); A.D.E. Elmer 4255 (NY); L.S. Rose 39278 (NY); T.F. Daniel 2938 (NY); B. Crampton 3127 (NY); H.H. Smith 3930 (NY); E.C. Smith 771 (NY); L.R.J. Dennis s.n. (NY); G.H. True 6829 (NY); J.M. Coulter 8489 (NY); J.M. Grant s.n. (NY); R.R. Halse 7281 (NY); J. Torrey 191 (NY); A.M. Ottley 1556 (NY); G.R. Vasey 241 (NY); G.K. Helmkamp 14899 (NY); G.L. Jenks s.n. (NY); H.E. Hasse 4060 (NY); W.M. Canby s.n. (NY); 2438123 (NY); G.R. Vasey s.n. (NY); E. Hall 225 (NY); F.R. Fosberg S 4851 (NY); J.I.W. McMurphy 24 (NY); G.B. Grant 3789 (NY); B. Trask 197 (NY); S.M. Zeller 882 (NY); 2438143 (NY); J. Torrey 191 (NY); R.R. Halse 4094 (NY); W.C. Cusick 2858 (NY); H.T. Edwards s.n. (NY); C.E.O. Kuntze 231 (NY); T.G. Lammers 11074 (NY); L. Abrams 5921 (NY); 2438090 (NY); 2438124 (NY); Hartweg s.n. (NY); H.E. Brown 872 (NY); A. Kellogg 838 (NY); J. Macoun s.n. (NY); M.T. Cook s.n. (NY); A.A. Heller 5723 (NY); A.A. Heller 5767 (NY); A.A. Heller 13799 (NY); A.A. Heller 7478 (NY); J.W. Thompson 9961 (NY).

***L. implexa* Aiton** K. Larsen et al. 36175 (USF), G. Sag 3506a P00040794 (P). L. Mercurin 1652 P00101127 (P). V. Raquet vr 41 P00735646 (P). J. Raynal 4305 P00699267 (P). J. Guillet s.n. P 00699270 (P). C. Legros s.n. P00699271 (P). L. Rotereau s.n. P00699272 (P). A. Beaugé B184 P00789323 (P). C. Dupin s.n. P00791082 (P). R. Grasl & P. Excobar García 1761 P00263628 (P). C. Billot s.n. P04360057 (P). P04310058 (P). P04360061 (P). P04360063 (P). P04360064 (P). P04360065 (P). P04362288 (P). P04362290 (P). P04362291 (P). P04362344 (P). P04364027 (P). P04364592 (P).

***L. interrupta* Benth.** K.T. Hartweg 1759 (NY); J.B. Walker 1306 (NY); 2438155 (NY); L.C. Wheeler 2784 (NY); E. Anderson 7473 (NY); T.S. Ross 2779 (NY); T.S. Ross 3975 (NY); H.D.D. Ripley 6989 (NY); B. Maguire 11387 (NY); W.R. Dudley 544 (NY); H.E. Hasse 6056 (NY); R.T. Schuh s.n. (NY); R.T. Schuh s.n. (NY); L.R. Landrum 6861 (NY); J. Peñalosa 2067 (NY); C. C. Bruce 2472 (NY); L.A. McGill LAM 1410 (NY); C.H. Quibell 1949 (NY); J. Torrey 190 (NY); J.D. Culbertson 5044 (NY); J.I.W. McMurphy 26 (NY); C.C. Parry 151 (NY); S.R. Hill 38551 (NY); G. Hansen 137 (NY); H.E. Brown 232 (NY); L.C. Higgins 18111 (NY); T.S. Ross 2885 (NY); E.C. Twisselmann 9477 (NY); F. Shreve 13 (NY); A. Nelson 1876 (NY); T.C. Bridges 137 (NY); G. Hansen 137 (NY); J. Torrey 190 (NY); T. Elias 8503 (NY); K. Reichhardt 90-01 (NY); B Maguire 11306 (NY); B. Maguire 12076 (NY); G.K. Helmkamp 14698 (NY); A.D.E. Elmer 4346 (NY); C.C. Parry 151 (NY); R.E. Collom 13 (NY); D.J. Keil 3956 (NY); J.H. Barnhart 2977 (NY); J.M. Bigelow 1- 2 (NY); E. Hall 226 (NY); C.C. Parry 151 (NY); L. Abrams 136 (NY); L. Abrams 4537 (NY); L. Abrams 326 (NY); L. Abrams 4537 (NY); A. Kellogg 339 (NY); H.M. Edwards s.n. (NY); E.B. Copeland 3492 (NY); W.B. Cooke 15161 (NY); A.A. Heller 11408 (NY); A.A. Heller 7881a (NY); A.A. Heller s.n. (NY).

***L. periclymenum* L.** A. Kirchhoff s.n. (B); J. Kohava s.n. (TAA); J. Kohava s.n. (TAA); H. Hupke s.n. (FR); H. Hupke s.n. (FR); J. Ratzloff s.n. (KHD); G. Dominicique 3504 (P); F. R. Fosberg 57732 (P); Changy 42 (AIX); P. Pedersen & B. Øllgaard 254 (US); G.V. Nash 5747 (NY); H.P. Statwell s.n. (NY); Morong s.n. (NY); I.T. Worthley 5747 (NY); M.L. Fernald s.n. (NY); R.R. Halse 5223 (NY); E. Jahr s.n. (NBIC); L. Sekse 605.2 (BG); G.B. Straley 5550 (UBC); K and S.S. Larsen 38542 (USF); E. Fremstad 6052 (BG); P. Pedersen and B. Øllgaard 254 (BG); A. Danielsen 966-99 (BG); J. Kohava s.n. (TAA).

***L. pilosa* (Kunth) Spreng.** A.B. Ghiesbreght 699 (MO);. 2331682 (MO); J. Gregg 699 (MO); J.C. Hinton 17127 (MO); G.S. Hinton 20270 (MO); J.C. Hinton 23262 (MO); J.C. Hinton 23320 (MO); G.S. Hinton 25425 (MO); C.C. Parry & Edward Palmer 297 (MO).

***L. prolifera* (Kirchner) Booth ex Rehder** E.N. Plank s.n. (NY); B.F. Bush 10135 (NY); C.S. Sheldon s.n. (NY); W.H. Welch 908 (NY); W.H. Welch 847 (NY); O.K. Stark 457 (NY); F.J. Hermann 8948 (NY); J.H. Vincent 8.4.66 (NY); I.F. Holton s.n. (NY); J.W. Moore and I.W. Murphy 10038 (NY); F.J. Hermann 8832 (NY); C.C. Deam 984 (NY); E.J. Palmer 40517 (NY); H.F. Jaeger s.n. (NY); D.J. Vasey s.n. (NY); F. Hall s.n. (NY); W.H. Welch 666 (NY); M. Nee 55428 (NY); H.V. Ogden s.n. (NY); J. Hastling 26837 (NY); L.M. Umbach s.n. (NY); A. Hayden 9512 (NY); C.T. Whuler (NY); H.N. Patterson s.n. (NY); J.M. Hanginger s.n. (NY); W.A. Kellerman. s.n. (NY); F.W. Johnson 1680 (NY); W.A. Kellerman s.n. (NY); N.L. Britton s.n. (NY); W.S. Moffatt M.D. s.n. (NY); M.S. Bebb s.n. (NY); W.M. Canby s.n. (NY); T.F. Lucy 11927 (NY); R.C. Schneider 3620 (NY); G.V. Nash Sept 1 1904 (NY); H.E. Ahles 16225 (NY); G.V. Nash 3621 (NY); R.A. Howard 17956 (NY); R.C. Friesner s.n. (NY); D.B. Ward and A.R. Bechtel 17531 (NY); E.J. Palmer and J.A. Steyermark 41167 (NY); J.A. Steyermark 25977 (NY); J.A. Steyermark 71555 (NY); J.A. Steyermark 28728 (NY); G.J. Goodman 2985 (NY); H.C. Steels s.n. (NY); S.R. Hill 36681 (NY); S.R. Hill 36129 (NY); J.M. Greenman et al. 42 (NY); V.E. Chase I0774 (NY); R.C. Schneider 26837 (NY).

***L. sempervirens* L.** S.T. Olney s.n. (NY); 4159b (NY); 2442461 (NY); D.E. Atha 9480 (NY); D.S. and H.B. Correll 10086 (NY); Chapman s.n. (NY); T. Morong s.n. (NY); A. & C. Krochmal s.n. (NY); N.K. Berg s.n. (NY); J.S. Grace s.n. (NY); M. Whaily s.n. (NY); A.T. Beals s.n. (NY); E. Hall 286 (NY); L.R. Gibbs s.n. (NY); J. Pruski and K. Malin 210 (NY); J.M. Coulter 8495 (NY); E.S. Britton s.n. (NY); Biltmore 14678 (NY); A.S. Reed 266 (NY); G.B. Goodr s.n. (NY); G.B. Goodr s.n. (NY); Redford and Stuart 479a (NY); S.T. Olney s.n. (NY); 2442292 (NY); L.M. Perry s.n. (NY); Chapman s.n. (NY); S.M. Tracy 9206 (NY); W.W. Thomas 28 (NY); G.V. Nash 246 (NY); N.K. Berg s.n. (NY); F.S. Earle, C.S. Baker 419 (NY); S. McCoy 2520 (NY); T.G. Yuckner 1327 (NY); S. McCoy 961 (NY); G. Wilson s.n. (NY); 2442315 (NY); H.J. Banker 3511 (NY); M. Hitchcock 1069 (NY); J.E.

Fairey et al. 705 (NY); M.L. Fernald and B. Long 10433 (NY); J. Lusk 2 (NY); 2442327 (NY); J.L. Poggenberg s.n. (NY); E.L. Davis s.n. (NY); D. Gully 15 (NY); A. Staccick s.n. (NY); 2442340 (NY); 2442341 (NY); 2442342 (NY); M.B. Warner s.n. (NY); H.E. Ahles and C.R. Bell 10394 (NY); C.W. Short M.D. s.n. (NY); Morong s.n. (NY); A.H. Curtiss 4654 (NY); V.L. Cory 53388 (NY); F.W.H. 17576 (NY); R.K. Godfrey 3665 (NY); D.T. Carraway 124 (NY); G. Fletcher 163 (NY); S.B. Buckley s.n. (NY); H.E. Ahles and J. Haesloop 53309 (NY); G. and F. Haas s.n. (NY); H.E. Ahles and J. Haesloop 53309 (NY); W. Lucian 60 (NY); D. Hale s.n. (NY); A.G. Reanolds s.n. (NY); R.D. Thomas 13053 (NY); W.M. Canby s.n. (NY); A. Wood CB 299 (NY); 2442392 (NY); R.T. Worthington 12917 (NY); J. Pruski, L. Urbastch 1659 (NY); A.H. Curtiss 6375 (NY); A.M. Attley and H.J. Davis 1720 (NY); Morong s.n. (NY); T.H. Kearney Jr. s.n. (NY); 2442406 (NY); 2442407 (NY); M. Ajour 15 (NY); R. McVaugh 6569 (NY); S.R. Hill 22962 (NY); S.R. Hill 13730 (NY); P. Fryxell 2895 (NY); P. Fryxell 2477 (NY); P.R.S. s.n. (NY); S.R. Hill 13917 (NY); Rugel s.n. (NY); B.F. Bush 142 (NY); I.F. Lewis 249 (NY); 2442437 (NY); E. J. Palmer 39793 (NY); H.A. Gleason 8544 (NY); W.A. Mukhill s.n. (NY); 812 (NY); A.H. Curtiss s.n. (NY); Rev. L.H. Lighthipe 644 (NY); E.J.C. Gilbert s.n. (NY); 2442452 (NY); W.M. Canby s.n. (NY); G. McCathy s.n. (NY); E. Hall 268 or 068 (NY); A. Cronquist 4475 (NY); A. Cronquist 4991 (NY); K.K. Mackenzie 7922 (NY); K.K. Mackenzie 6984 (NY); H.A. Gleason 8445 (NY); W.D. Longbottom 14844 (NY); F.W. Pennell 6728 (NY); R.F.C. Naczi 12412 (NY); A. Ruth s.n. (NY); W.D. Longbottom 12673 (NY); W.H. Leggett s.n. (NY); N.L. Britton s.n. (NY); K.M. Wiegand s.n. (NY); W.C. Ferguson 7579 (NY); W.C. Ferguson 6650 (NY); W.C. Ferguson 7671 (NY); A.M. Vail s.n. (NY); S.L. Clarke s.n. (NY); A.M. Vail s.n. (NY); M.A. Vincent & M.W. Vincent 14831 (NY); F. Moore 71602 (NY); H. Swift 71602 (217) (NY); J.W. Tansey s.n. (NY); Arkin s.n. (NY); Gray 221 (NY); W.D. Longbottom 16908 (NY); J. Brinker 8151 (NY); Gray 2013 (NY); 2442344 (NY); E.P. Bicknell s.n. (NY); J. Grimes 2529 (NY); F.E. Egler 40-12 (NY); F.S. Earle and C.F. Baker s.n. (NY); S. Brown et al. 2035 (NY); J.E. Fairey, III et al. 717 (NY); N.L. Britton and J.K. Small. s.n. (NY); R. Dragonetti 31 (NY); J. Aloian 23 (NY); A.A. Heller 844 (NY); N.L. and E.Q. Britton and A.M. Vail. s.n. (NY); C.A. Hollick s.n. (NY); N.L. Britton s.n. (NY); W.M. Benner 64 (NY); F.W. Pennell 3920 (NY); A.R. Hodgdon s.n. (NY); J.K. Small s.n. (NY); J.K. Small s.n. (NY); J.K. Small s.n. (NY); J.K. Small and A.A. Heller 224 (NY); J.K. Small and A.A. Heller 224 (NY); M.L. Fernald and B. Long 6401 (NY); H.N. Moldenke 1212 (NY); A.D. Granger s.n. (NY); J.W. and M.F. Moore. 10274 (NY); E.J. Palmer 42242 (NY); I.M. Clute 100 (NY); S. McDaniel 2305 (NY); S. McDaniel 1783 (NY); D.S. Correll & H.B. Correll 23567 (NY); R.R. Haynes 7729 (NY); F.S. Earle and L.M. Underwood s.n. (NY); F.S. Earle and E.S. Earle 70 (NY); D.L. Curtis 133 (NY); H.D. House 3847 (NY); S.R. Hill 39156 (NY); H.D. House 1813 (NY); H.D. House 2039 (NY); R.T. Clausen and H. Trapido 3784 (NY); H.D. House 3279 (NY); C.C. Freeman 20484 (NY); R.K. Godfrey 53012 (NY); R.P. Martin 1503 (NY); B. Moore 50 (NY); R.K. Godfrey 84534 (NY); C. Easley 186 (NY); W. Kittredge 915 (NY); D.S. & H.B.Correll 53762 (NY); F.J. Hermann 10509 (NY); D. Demaiee 12025 (NY); D. Demaree 17147 (NY); D. Demaree 19897 (NY); D. Demaree 20844 (NY); D. Demaree 22074 (NY); R.D. Thomas et al. 104692 (NY); D. Demaree 16823 (NY); D. Demaree 18937 (NY); D. Demaree 16898 (NY); A.W. Cusick 27441 (NY); B.C. Tharp 49-1030 (NY); J.F. Collins s.n. (NY); S.R. Hill 36320 (NY); J.F. Poggenberg s.n. (NY); A. Staccick s.n. (NY); B.H. Long 23028 (NY).

***L. splendida* Boiss.** P.E. Boissier 95 (K); P.E. Boissier 95 (K); J. Ball s.n. (K).

***L. stabiana* Guss. ex Pasq.** V. Le Bussion 2995 (P); V. Le Bussion s.n. (P); G. Pellanda s.n. (P); M. Guadagno s.n. (P); Pellanda, G s.n. (MPU); Pellanda, G s.n. (NL); 188/10 (SLA).

***L. subaequalis* Rehder** 方鼎 覃德海 63966 (GXMI); 方鼎 覃德海 63966 (GXMI); 姚良琪 63972 (GXMI); 姚良琪 63972 (GXMI); 姚良琪 63972 (GXMI); 姚良琪 63972 (GXMI); : 陆小鸿 8158 (GXMI); 姚良琪 63972 (GXMI); 包维楷等 1830 (CDBI); 包维楷等 1830 (CDBI); 红水河植物考察队 1960 (PE); 方鼎, 覃德海 63966 (PE); 刘照光 4632 (PE); 杨开太、王方瑜等 11465 (CDBI); 印开蒲、陈庆恒 224 (CDBI); 印开蒲、陈庆恒 224 (CDBI); 716 (CDBI); 川经植 142 (PE); 川经植 142 (PE); 川经植 286 (PE); 川经植 716 (PE); 川经植 716 (PE); 管中天 8696 (PE); 李鳌、黄云珍 川经宜 142 (CDBI); 禹平华 859 (WUK); 禹平华 859 (PE); 余师珍 49506 (SZ); 俞德俊 3936 (PE); 169 (NAS); 206 (NAS); 331 (IBSC); 331 (NAS); 716 (KUN); 835 (KUN); C. W. Yao 3079 (PE); 川经江 1187 (KUN); 川经江 142 (KUN); 秦沛南 黄治平 朱树屏等 206 (PE); 禹平华 859 (KUN); 四川大学生物系植物调查队 49506 (WUK); 赵汝垲 200 (KUN); A.E. Pratt 364 (K); A. Henry 8936 (K).

***L. subspicata* Hook. & Arn.** F.E. and E.S. Clements 201 (NY); H.P. Chandler 5288 (NY); 23212 (NY); Cleveland s.n. (NY); C.R. Orcutt s.n. (NY); J.F. Allen s.n. (NY); Schwartz 24-3 (NY); LeDoux et al. 1138 (NY); F.M. Reed 5824 (NY); I.W. Clokey and B. Templeton 4554 (NY); G.H. Horn s.n. (NY); G.T. Hastings s.n. (NY); H. Edwards s.n. (NY); L. Abrams & E.A. McGregor 302 (NY); V. Durna 3496 (NY); Schuh et al. s.n. (NY); C.Ç. Parry s.n. (NY); A.J. McClatchie (NY); L. Abrams 4148 (NY); A.J. McClatchie (NY); H.M. Hall 2529 (NY); L. Abrams 2544 (NY); A. Eastwood 65 (NY); A. Eastwood 197 (NY); A.W.E. Elines 3729 (NY); H.P. Chandler 5466 (NY); E.S. Ferris et al. 6082 (NY); E. Palmer M.D. 120 (NY); G. Thurber 538 (NY); C.A. Morse 17713 (NY); L.R. Landrum 7818 (NY); E.A. Purer 6513 (NY); J.T. Howell 6278 (NY); P.A. Munz 11567 (NY); L.C. Wheeler 830 (NY); G.L. Fisher 96 (NY); G.R. Vasey 242 (NY); P.A. Munz 7128 (NY); G.T. Hastings (NY); M.F. Spencer 88 (NY); G.T. Hastings (NY); F.M. Reed 6026 (NY).

***L. tragophylla* Hemsl.** 何毅、吴磊 GSL2014050668 (BNU); 李思峰、黎斌、张莹、胡浩 17659 (XBGH); 李思峰、黎斌、张莹、王宇超 17791 (XBGH); 李思峰、黎斌、张莹、王宇超 17791 (XBGH); 李思峰、黎斌、张莹、胡浩 17149 (XBGH); 李思峰、黎斌、张莹、周亚福、胡浩 16297 (XBGH); 李思峰、黎斌、张莹、柏国清 15586 (XBGH); 李思峰、黎斌、张莹、张瑞博 13457 (XBGH); 李思峰、黎斌、张莹、张瑞博 13758 (XBGH); 李思峰、黎斌、张莹、张瑞博 13900 (XBGH); 李思峰、黎斌、张莹、张瑞博 13911 (XBGH); 李思峰、黎斌、张莹、张瑞博 14224 (XBGH); 李思峰、黎斌、张莹、陈昊、张瑞博、韩桂军 10806 (XBGH); 吴振海 WZH-08-129 (CSH); 吴振海 WZH-07-077 (CSH); 张超 20071123 (HX); 白水江考察队 124 (PE); 陈彦生、吴振海、黎斌、孙建钊等 4405 (WUK); 陈彦生、吴振海、黎斌、孙建钊等 4405 (WUK); 陈彦生、吴振海、黎斌、孙建钊等 4405 (WUK); 陈彦生、吴振海、黎斌、孙建钊等 4672 (WUK); 陈彦生、吴振海、黎斌、孙建钊等 4672 (WUK); 陈彦生、吴振海、黎斌、孙建钊等

4672 (WUK); 陈彦生、吴振海、黎斌、孙建钊等 4672 (WUK); 陈彦生、吴振海、黎斌、孙建钊等 2281 (WUK); A. Henry 685 (K); A. Henry 1707 (K); A. Henry 4010 (K).

***L. yunnanensis* Franch.** 蓝顺彬 435 (PE); 蓝顺彬 435 (PE); 刘照光 4632 (CDBI); 刘照光 4632 (CDBI); 刘照光 4632 (CDBI); 滇东北队 1247 (PE); 滇西北金沙江队 6248 (PE); 滇西北金沙江队 63-6248 (PE); 姜恕等 5618 (PE); 邱炳云 57914 (WUK); 邱炳云 57914 (NAS); 冯国楣 21584 (PE); 刘伟心 51250 (IBSC); 辛景三 513317 (IBSC); 云南植物 51250 (WUK); 冯国楣 50401 (IBSC); 毛品一 1453 (PE); 毛品一 1453 (PE); 毛品一 1453 (WUK); 秦仁昌 21626 (PE); 刘慎谔 21815 (PE); K. M. Feng 9069 (PE); 秦仁昌 22913 (PE); H.T Chang 207 (IBSC); 蒋英 16497 (IBSC); 吴征镒 刘德义 12208 (PE); T.T. Yu 11453 (PE); 俞德俊 11453 (PE); H.T. Tsai 53650 (LBG); H.T. Tsai 53607 (PE); H.T. Tsai 53650 (IBSC); H.T. Tsai 53650 (PE); Y. Tsiang 12010 (NAS); 445 (IBSC); 10605 PEY0040530 (PEY); 10605 PEY0040529 (PEY); 10605 PEY0040528 (PEY); 10632 (PEY); 12208 (PEY); E.E. Maire s.n. (IBSC); J.M. Delavay 229 (HUH); 蔡希陶 53650 (KUN); 毛品一 1453 (KUN); 吴征镒 刘德义 s.n. (PE); 玉溪队 89-131 (KUN).

Literature Cited

Aida M, T Ishida, H Fukaki, H Fujisawa, M Tasaka 1997 Genes involved in organ separation in *Arabidopsis*: an analysis of the cup-shaped cotyledon mutant. Plant Cell 9:841–857.

Andrade IM, SJ Mayo 1998 Dynamic shoot morphology in *Monstera adansonii* Schott var. *klotzschiana* (Schott) Madison (Araceae). Kew Bull 53:399–417.

Bartuszevige A, DL Gorchov 2006 Avian seed dispersal of an invasive shrub. Biol Invasions 8:1013–1022.

Bonhomme V, S Picq, C Gaucherel, J Claude 2014 Momocs: outline analysis using R. J Stat Softw 56:1–24.

Brantjes NBM 1973 Sphingophilous flowers, function of their scent. Pages 419–432 *in* NBM Brantjes, HF Linskens, eds. Pollination and dispersal. Botany Department, University of Nijmegen, Nijmegen, The Netherlands.

Brown JH, A Kodric-Brown 1979 Convergence, competition, and mimicry in a temperate community of hummingbird-pollinated flowers. Ecology 60:1022.

Brown VK, JH Lawton, PJ Grubb 1991 Herbivory and the evolution of leaf size and shape. Philos Trans R Soc B 333:265–272.

Burns KC, JL Dalen 2002 Foliage color contrasts and adaptive fruit color variation in a bird-dispersed plant community. Oikos 96:463–469.

Cazetta E, H Schaefer, M Galetti 2009 Why are fruits colorful? the relative importance of achromatic and chromatic contrasts for detection by birds. Evol Ecol 23:233–244.

Chanderbali AS, BA Berger, DG Howarth, PS Soltis, DE Soltis 2016 Evolving ideas on the origin and evolution of flowers: new perspectives in the genomic era. Genetics 202:1255–1265.

Chapman AW, DC Eaton 1884 Flora of the southern United States: containing an abridged description of the flowering plants and ferns of Tennessee, North and South Carolina, Georgia, Alabama, Mississippi, and Florida arranged according to the natural system. Ivison, Blakeman, Taylor & Co, New York.

Chen G, W Sun, H Sun 2010 Leaf epidermal characteristics of Asiatic *Buddleja* L. under scanning electron microscope: insights into chromosomal and taxonomic significance. Flora 205:777–785.

Chitwood DH, WC Otoni 2017 Morphometric analysis of *Passiflora* leaves: the relationship between landmarks of the vasculature and elliptical Fourier descriptors of the blade. GigaScience 6:1–13.

Chitwood DH, N Sinha 2016 Evolutionary and environmental forces sculpting leaf development. Curr Biol 26:R297–R306.

Christy M 1923 The common teasel as a carnivorous plant. J Bot 61:33–45.

Clements FE, CO Rosendahl, FK Butters 1912 Minnesota trees and shrubs: an illustrated manual of the native and cultivated woody plants of the state. University of Minnesota, Minneapolis.

Correll DS 1968 Some additions and corrections to the flora of Texas. Wrightia 4:28.

Das SK, GS Giri 1991 A new species of *Leycesteria* Wall. Caprifoliaceae from Arunchal Pradesh. J Bombay Nat Hist Soc 88:26–267.

Díaz-Valenzuela R, R Ortiz-Pulido 2011 Effects of a snowstorm event on the interactions between plants and hummingbirds: fast recovery of spatio-temporal patterns. Rev Mex Biodivers 82:1243–1248.

Dickinson TA 1986 Topodeme differentiation in Ontario taxa of *Crataegus* (Rosaceae: Maloideae): leaf morphometric evidence. Can J Bot 64:2738–2747.

Donoghue MJ, CD Bell, RC Winkworth 2003 The evolution of reproductive characters in Dipsacales. Int J Plant Sci 164(suppl): S453–S464.

Donoghue MJ, T Eriksson, PA Reeves, RG Olmstead 2001 Phylogeny and phylogenetic taxonomy of Dipsacales, with special reference to *Sinadoxa* and *Tetradoxa* (Adoxaceae). Harv Pap Bot 6:459–479.

Drummond BA 2005 The selection of native and invasive plants by frugivorous birds in Maine. Northeast Nat 12:33–44.

Edgar RC 2004 MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acid Res 32:1792–1797.

Edwards EJ, EL Spriggs, DS Chatelet, MJ Donoghue 2016 Unpacking a century-old mystery: winter buds and the latitudinal gradient in leaf form. Am J Bot 103:975–978.

Ferguson IK 1966 The genera of Caprifoliaceae in the southeastern United States. J Arnold Arbor 47:33–59.

GIMP (GNU Image Manipulation Program) Team 2018 GIMP 2.8.10. http://www.gimp.org.

Gould KR, MJ Donoghue 2000 Phylogeny and biogeography of *Triostem* (Caprifoliaceae). Harv Pap Bot 5:157–166.

Guitian P, J Guitian, L Navarro 1993 Pollen transfer and diurnal versus nocturnal pollination in *Lonicera etrusca*. Acta Oecol 14:219–227.

Hara H 1983 A revision of Caprifoliaceae of Japan. Academia Scientific Book, Tokyo.

Hasson A, A Plessis, T Blein, B Adroher, S Grigg, M Tsiantis, A Boudaoud, C Damerval, P Laufs 2011 Evolution and diverse roles of the CUP-SHAPED COTYLEDON genes in *Arabidopsis* leaf development. Plant Cell 23:54–68.

Hooker JD 1882 Caprifoliaceae to Apocynaceae. Flora Br India 3:8–17.

Horwood AR 1919 British wild flowers in their natural haunts. Vol 4. Gresham, London.

Huelsenbeck JP, F Ronquist 2001 MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17:754–755.

Ingold JI, MJ Craycraft 1983 Avian frugivory on honeysuckle (*Lonicera*) in southwestern Ohio in fall. Ohio J Sci 83:256–258.

Jarrett FM 1959 Studies in *Artocarpus* and allied genera. III. A revision of *Artocarpus* subgenus *Artocarpus*. J Arnold Arbor 40:113–155.

Jensen RJ, KM Ciofani, LC Miramontes 2002 Lines, outlines, and landmarks: morphometric analyses of leaves of *Acer rubrum*, *Acer saccharinum* (Aceraceae) and their hybrid. Taxon 51:475–492.

Johnson MF 1974 Eupatorieae (Asteraceae) in Virginia: *Eupatorium* L. Castanea 39:205–228.

Jones GN 1940 A monograph of the genus *Symphoricarpos*. J Arnold Arbor 21:201–252.

Jordano P 1990 Biología de la reproducción de tres especies del género *Lonicera* (Caprifoliaceae) en la Sierra de Cazorla. An Jard Bot Madr 48:31–52.

Klingenberg CP, S Duttke, S Wehlan, M Kim 2012 Developmental plasticity, morphological variation and evolvability: a multilevel analysis of morphometric integration in the shape of compound leaves. J Evol Biol 25:115–129.

Knuth P 1909 Handbook of flower pollination based upon Hermann Müller's work "The Fertilization of Flowers by Insects." Vol 3. Clarendon, Oxford.

Kores PJ, M Molvray, SP Darwin 1993 Morphometric variation in three species of *Cyrtostylis* (Orchidaceae). Syst Bot 18:274–282.

Krupa JJ, JM Thomas 2019 Is the common teasel (*Dipsacus fullonum*) carnivorous or was Francis Darwin wrong? Botany 97:321–328.

Kumar N, P Belhumeur, A Biswas, D Jacobs, W Kress, I Lopez, J Soares 2012 Leafsnap: a computer vision system for automatic plant species identification. Pages 502–516 *in* A Fitzgibbon, S Labebnik, P Perona, Y Sato, and C Schmid, eds. Computer Vision: ECCV 2012. 12th European Conference on Computer Vision, Florence, Italy, October 7–13, 2012, Proceedings, Part IV. Springer, Berlin.

Lanfear R, B Calcott, SYW Ho, S Guindon 2012 PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol Biol Evol 29:1695–1701.

Lázaro A, C Vignolo, L Santamaría 2015 Long corollas as nectar barriers in *Lonicera implexa*: interactions between corolla tube length and nectar volume. Evol Ecol 29:419–435.

Maddison WP, DR Maddison 2018 Mesquite: a modular system for evolutionary analysis. Version 3.61. http://www.mesquiteproject.org.

Makins FK 1937 The identification of trees & shrubs; how to recognize, without previous knowledge of botany, wild or garden trees and shrubs native to the north temperate zone. Dutton, New York.

McCusker CE, MP Ward, JD Brawn 2010 Seasonal responses of avian communities to invasive bush honeysuckles (*Lonicera* spp.). Biol Invasions 12:2459–2470.

McIntyre P, S Strauss 2014 Phenotypic and transgenerational plasticity promote local adaptation to sun and shade environments. Evol Ecol 28:229–246.

Nash DL 1976 Flora of Guatemala. Vol 24. Fieldiana Bot 11:276–295.

Nicotra AB, A Leigh, CK Boyce, CS Jones, KJ Niklas, DL Royer, H Tsukaya 2011 The evolution and functional significance of leaf shape in the angiosperms. Funct Plant Biol 38:535–552.

Nürk NM, FR Blattner 2010 Cladistic analysis of morphological characters in *Hypericum* (Hypericaceae). Taxon 59:1495–1507.

Ohwi J 1965 Flora of Japan. Smithsonian Institution, Washington, DC.

Ordano M, PG Blendinger, SB Lomáscolog, NP Chacoff, MS Sánchez, MG Núñez Montellano, J Jiménez, RA Ruggera, M Valoy 2017 The role of trait combination in the conspicuousness of fruit display among bird-dispersed plants. Funct Ecol 31:1718–1727.

Ottosen C 1986 Pollination ecology of *Lonicercu periclymenum* L. in NE.-Zealand, Denmark: floral development, nectar production and insect visits. Flora 178:271–279.

Pagel M 1994 Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. Proc R Soc B 255:37–45.

Pagel M, A Meade 2017 BayesTraits v. 3.0.1. http://www.evolution.rdg.ac.uk/BayesTraitsV3.0.5/BayesTraitsV3.0.5.html.

Pagel M, A Meade, D Barker 2004 Bayesian estimation of ancestral character states on phylogenies. Syst Biol 53:673–684.

Paradis E, K Schliep, R Schwartz 2019 ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35:526–528.

Perino CH 1978 A revision of the genus *Lonicera* subgenus *Periclymenum* (Caprifoliaceae) in North America. PhD diss. North Carolina State University, Raleigh.

Piper CV, RK Beattie 1914 Flora of southeastern Washington and adjacent Idaho. New Era, Lancaster, PA.

——— 1915 Flora of the northwest coast, including the area west of the summit of the Cascade Mountains, from the forty-ninth parallel south to the Calapooia Mountains on the south border of Lane County, Oregon. New Era, Lancaster, PA.

Plotze RdO, M Falvo, JG Padua, LC Bernacci, MLC Vieira, GCX Oliveira, OM Bruno 2005 Leaf shape analysis using the multiscale Minkowski fractal dimension, a new morphometric method: a study with *Passiflora* (Passifloraceae). Can J Bot 83:287–301.

Pojarkova AI 1999 Caprifoliaceae. Pages 397–650 *in* BK Schischkin, ed. Flora of the U.S.S.R. Vol 23. Amerind, Janpath, India.

Premoli AC 1996 Leaf architecture of South American *Nothofagus* (Nothofagaceae) using traditional and new methods in morphometrics. Bot J Linn Soc 121:25–40.

Rafinesque CS 1836 New flora and botany of North America, or a supplemental flora, additional to all the botanical works on North America and the United States, containing 1000 new or revised species. 3. New sylva. Philadelphia.

Rambaut A, AJ Drummond, D Xie, G Baele, MA Suchard 2018 Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Syst Biol 67:901–904.

Rausher MD 1978 Search image for leaf shape in a butterfly. Science 200:1071–1073.

R Core Team 2019 R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/.

Rehder A 1903 Synopsis of the genus *Lonicera*. Mo Bot Gard Annu Rep 1903:27–232.

——— 1910 *Lonicera prolifera* and *L. flavida*. Rhodora 12:166–167.

——— 1940 Manual of cultivated trees and shrubs hardy in North America. Dioscorides, Portland, OR.

Revell LJ 2012 phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol Evol 3:217–223.

Robinson HE 1983 A generic review of the tribe Liabeae (Asteraceae). Smithson Contrib Bot 54:1–69.

Ronquist F, JP Huelsenbeck 2003 MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574.

Roxburgh W 1832 Flora indica, or descriptions of Indian plants. W Thacker & Co, Calcutta.

Royer DL, JC McElwain, JM Adams, P Wilf 2008 Sensitivity of leaf size and shape to climate within *Acer rubrum* and *Quercus kelloggii*. New Phytol 179:808–817.

Royer DL, P Wilf, DA Janesko, EA Kowalski, DL Dilcher 2005 Correlations of climate and plant ecology to leaf size and shape: potential proxies for the fossil record. Am J Bot 92:1141–1151.

RStudio Team 2015 RStudio: integrated development for R. RStudio, Boston. http://www.rstudio.com/.

Rydberg PA 1917 Flora of the Rocky Mountains and adjacent plains: Colorado, Utah, Wyoming, Idaho, Montana, Saskatchewan, Alberta, and neighboring parts of Nebraska, South Dakota, North Dakota, and British Columbia. Steinman & Foltz, Lancaster, PA.

Sanders RW 1977 Taxonomy of *Rumfordia* (Asteraceae). Syst Bot 2:302–316.

Santiago LS, S Kim 2009 Correlated evolution of leaf shape and physiology in the woody *Sonchus* alliance (Asteraceae: Sonchinae) in Macaronesia. Int J Plant Sci 170:83–92.

Schaefer HM, DJ Levey, V Schaefer, ML Avery 2006 The role of chromatic and achromatic signals for fruit detection by birds. Behav Ecol 17:784–789.

Schmerler SB, WL Clement, JM Beaulieu, DS Chatelet, L Sack, MJ Donoghue, EJ Edwards 2012 Evolution of leaf form correlates with tropical-temperate transitions in *Viburnum* (Adoxaceae). Proc R Soc B 279:3905–3913.

Schmidt V, HM Schaefer, H Winkler 2004 Conspicuousness, not colour as foraging cue in plant-animal signaling. Oikos 106:551–557.

Scoggan HJ 1979 The flora of Canada. IV. Dicotyledoneae (Loasaceae to Compositae). National Museums of Canada, Ottawa.

Shaw PJA, K Shackleton 2011 Carnivory in the teasel *Dipsacus fullonum*: the effect of experimental feeding on growth and seed set. PLoS ONE 6:e17935. https://doi.org/10.1371/journal.pone.0017935.

Silva MFS, IM De Andrade, SJ Mayo 2012 Geometric morphometrics of leaf blade shape in *Montrichardia linifera* (Araceae) populations from the Rio Parnaíba Delta, north-east Brazil. Bot J Linn Soc 170:554–572.

Small JK 1913 Flora of the southeastern United States; being descriptions of the seed-plants, ferns and fern allies growing naturally in North Carolina, South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, Louisiana, and in Oklahoma and Texas east of the one hundredth meridian. New Era, Lancaster, PA.

Smith SA, MJ Donoghue 2010 Combining historical biogeography with niche modeling in the *Caprifolium* clade of *Lonicera* (Caprifoliaceae, Dipsacales). Syst Biol 59:322–341.

Spriggs EL, SB Schmerler, EJ Edwards, MJ Donoghue 2018 Leaf form evolution in *Viburnum* parallels variation within individual plants. Am Nat 191:235–249.

Straley GB 1994 Bold-leaved Asian perennials. Wash Park Arbor Bull 57:17.

Takada S, K Hibara, T Ishida, M Tasaka 2001 The CUP-SHAPED COTYLEDON1 gene of *Arabidopsis* regulates shoot apical meristem formation. Development 128:1127–1135.

Theis N, MJ Donoghue, J Li 2008 Phylogenetics of the Caprifolieae and *Lonicera* (Dipsacales) based on nuclear and chloroplast DNA sequences. Syst Bot 33:776–783.

Torrey J 1824 A flora of the northern and middle sections of the United States, or, a systematic arrangement and description of all the plants hitherto discovered in the United States north of Virginia. T & J Swords, New York.

Tsukaya H 2005 Leaf shape: genetic controls and environmental factors. Int J Dev Biol 49:547–555.

Vaidya G, DJ Lohman, R Meier 2011 SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. Cladistics 27:171–180.

Villarreal-Quintanilla JA, AD Ruiz-Acevedo, AE Estrada-Castillón, D Jasso de Rodríguez 2016 El complejo *Lonicera pilosa* (Kunth) Spreng. (Caprifoliaceae). Acta Bot Mex 115:27–42.

Villarreal-Quintanilla JA, AD Ruiz-Acevedo, AE Estrada-Castillón, D Jasso de Rodríguez, J Méndez-González 2017 El género *Lonicera* (Caprifoliaceae) en México y Guatemala. J Bot Res Inst Tex 11:81–101.

Viscosi V, P Fortini, DE Slice, A Loy, C Blasi 2009 Geometric morphometric analyses of leaf variation in four oak species of the subgenus *Quercus* (Fagaceae). Plant Biosyst 143:575–587.

Vlad D, D Kierzkowski, MI Rast, F Vuolo, RD Ioio, C Galinha, X Gan, et al 2014 Leaf shape evolution through duplication, regulatory diversification, and loss of a homeobox gene. Science 343:780–783.

Vroemen CW, AP Mordhorst, C Albrecht, MACJ Kwaaitaal, SC de Vries 2003 The CUP-SHAPED COTYLDEON3 gene is required for boundary and shoot meristem formation in *Arabidopsis*. Plant Cell 15:1563–1577.

Wickham H 2016 ggplot2: elegant graphics for data analysis. Springer, New York.

Wiegand KM, AJ Eames 1926 The flora of the Cayuga Lake Basin, New York. Cornell University, Ithaca, NY.

Yang H, NH Holmgren, RR Mill 1998 *Pedicularis* L. Pages 97–209 *in* ZY Wu, PH Raven, eds. Flora of China. Vol 18. Science Press, Beijing.

Yang Q, S Landrein, J Osborne, R Borosova 2011 Caprifoliaceae. Pages 616–641 *in* ZY Wu, RH Raven, eds. Flora of China. Vol 19. Science Press, Beijing.

Yano S, I Terashima 2001 Separate localization of light signal perception for sun or shade type chloroplast and palisade tissue differentiation in *Chenopodium album*. Plant Cell Physiol 42:1303–1310.

Young JP, TA Dickinson, NG Dengler 1995 A morphometric analysis of heterophyllous leaf development in *Ranunculus flabellaris*. Int J Plant Sci 156:590–602.

Zappi D, N Taylor 1993 223. *Lonicera pilosa*: Caprifoliaceae. Kew Mag 10:111–113.

Zhang L, WL Clement 2021 Data from: Evolution of leaf fusion in honeysuckle (*Periclymenum*, *Lonicera*). Int J Plant Sci, Dryad Digital Depository, https://doi.org/10.5061/dryad.9p8cz8wd1.

Zwickl DJ 2006 Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. PhD diss. University of Texas, Austin.