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Phylogenetic analysis based on structural and combined analyses of *Rhus s.s.* (Anacardiaceae)

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Structural data were combined with *trnL-F* and internal transcribed spacer sequences from other studies and with new sequences representing ten additional species to clarify the phylogenetic relationships of *Rhus s.s*. These data indicate that *Rhus s.s* and both subgenera, *Rhus* and *Lobadium*, are monophyletic. The genus *Rhus* is supported as monophyletic by the presence of red glandular hairs on the berries and inflorescence axis, cilia on the sepals and glands on the leaf blades. Subgenus *Rhus* can be identified by the presence of more than seven resin channels in the petiole, weakly percurrent tertiary veins and a type I vascular system in the mid-vein. Subgenus *Lobadium* is characterized by the presence of short bracteoles and pedicels. This subgenus is divided into four sections, *Lobadium*, *Rhoeidium*, *Styphonia* and *Terebinthifolia*. Section *Lobadium* has trifoliate leaves; section *Rhoeidium* is monotypic, including only *Rhus microphylla*; section *Styphonia* is supported by five synapomorphies, including an incomplete marginal vein, fibres in the petiole, a thick cuticle, two layers of palisade parenchyma and prismatic crystals in the mesophyll; and section *Terebinthifolia* has gelatinous xylary fibres in the petiole. Hypotheses about the evolutionary changes of these characters are presented based on the cladograms. *Botanical Journal of the Linnean Society*, 2014, **176**, 452–468.

ADDITIONAL KEYWORDS: leaf anatomy – *Lobadium* – molecular data – *Rhoeidium* – *Styphonia* – wood.

INTRODUCTION

Rhus L. has received widely varying circumscriptions over time, as outlined by Brizicky (1963) and Young (1975). Barkley (1937) recircumscribed the group by segregating many separate genera, and his circumscription of *Rhus s.s*. is generally followed today. Barkley (1940) further restricted *Rhus* by segregating a genus he called '*Schmaltzia*' (an invalid name), but most authors in recent decades have followed Young (1975, 1978, 1979) in maintaining Barkley's (1937) circumscription of the genus. Barkley (1937) and Young (1975) agreed that *Rhus s.s*. is morphologically characterized principally by the presence of red berries with red trichomes (Table 1). Barkley (1937) recognized two subgenera, subgenus *Sumac* (DC.) A.Gray and subgenus *Schmaltzia* Desv. ex Steud. Subgenus *Sumac* was characterized by, among other traits, thyrses appearing with or after the leaves, one bract per flower and short-pedicellate flowers. This subgenus was not divided into sections. Subgenus *Schmaltzia* was characterized by compound spikes appearing with or before the leaves, one bract and two bracteoles per flower, and usually sessile flowers, and was divided into five sections (Table 1).

Brizicky (1963) noted that the correct names for Barkley's subgenera are subgenus *Rhus* (for Barkley's subgenus *Sumac*) and subgenus *Lobadium* (Raf.) A.Gray (for Barkley's subgenus *Schmaltzia*), and all subsequent authors have followed Brizicky on this issue. Young (1975, 1978) added and/or refined data on secondary chemistry, morphology and wood anatomy to support Barkley's two subgenera and partially amended Barkley's (1937) sections (Table 1). Young's modified classification of the genus has been the starting point for most subsequent work. In

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Table 1. Infrageneric categories of *Rhus s.s.* by different authors

Author	Subgenus	Sections	Subsections
Barkley (1937)	*Sumac* *Schmaltzia*	None *Lobadium* *Rhoeidium* (= *Rhus microphylla*) *Pseudosumac* *Styphonia* *Pseudoschmaltzia*	
Young (1975, 1978, 1979)	*Rhus* (= *Sumac*) *Lobadium* (= *Schmaltzia*)	None *Lobadium* (*Lobadium* + *Rhoeidium*) *Terebinthifolia* (= *Pseudosumac*) *Styphonia* (*Styphonia* + *Pseudoschmaltzia*)	– *Styphoniae* *Compositae* (= *Pseudoschmaltzia*) *Intermediae*

subgenus *Lobadium*, Young recognized only three sections as opposed to Barkley's five. In Young's scheme, section *Lobadium* (Raf.) DC. was expanded to include *R. microphylla* Engelm. [the sole species of Barkley's section *Rhoeidium* (Green) Barkley] and comprised deciduous shrubs or subshrubs with flowers opening before the leaves. The remaining two sections were characterized as evergreen trees or shrubs that flower with the leaves. Section *Terebinthifolia* D.A.Young shared the circumscription of Barkley's section '*Pseudosumac*' (an invalid name) and was defined by its thinner textured, pinnately compound leaves, looser inflorescence and glandular pubescence restricted to the fruits and flowers. Section *Styphonia* (Nutt.) Barkley was expanded to include Barkley's section '*Pseudoschmaltzia*' (another invalid name) and was defined by its more coriaceous leaves that range from simple or unifoliate to pinnately compound, contracted inflorescences and often glandular pubescent leaflets. Young divided this latter section into three subsections (Table 1) (Young, 1975, 1979), adding flavonoid and wood-anatomical data to support his infrageneric classification.

The monophyly of *Rhus s.s.* has been supported recently by molecular-sequence data (Miller, Young & Wen, 2001; Pell, 2004; Yi, Miller & Wen, 2004, 2007; Pell *et al*., 2008). However, the relationships in the genus are complicated by inconsistencies between plastid and nuclear genes. For example, nuclear data support the monophyly of the two subgenera, but plastid data do not because *R. microphylla* (Yi *et al*., 2004) and *R. rubifolia* Turcz. (Yi *et al*., 2004, 2007) are nested in subgenus *Rhus*; these two species were assigned to subgenus *Lobadium* by Young (1975). Notably, Yi *et al*. (2004, 2007) recognized subgenera *Rhus* and *Lobadium* as monophyletic only if *R. microphylla* and *R. rubifolia* were excluded from their combined molecular analyses, and therefore no argument can be made about the status of these species. However, Yi *et al*. (2007: 32) argued that the varying positions of *R. microphylla* and *R. rubifolia* were 'likely an indication of hybridization between members of subgenus *Rhus* and subgenus *Lobadium*'. These authors considered that reticulate evolution played an important role in the phylogeny of *Rhus*. However, they did not discuss the possibility that poor sampling, especially in subgenus *Lobadium*, might be a problem.

At the section level and using Young's (1975) circumscriptions, section *Lobadium* has been supported as monophyletic only if *R. microphylla* is omitted (Yi *et al*., 2004). Section *Styphonia* was not recovered as monophyletic when using plastid DNA; however, combined nuclear and plastid DNA data supported this group as monophyletic, except that *R. kearneyi* F.A.Barkley appeared to belong in subsection *Compositae* rather than in subsection *Styphoniae* (Yi *et al*., 2007). Subsection *Intermediae* was not included by these authors (Yi *et al*., 2004, 2007).

Concerning the wood anatomy of *Rhus*, Heimsch (1940) noted resin canals in *R. aromatica* Ait. and *R. trilobata* Nutt., two species in section *Lobadium*, which have biseriate rays. Young (1974) found resin canals in the rays of *R. microphylla* and small vessels in a flame-like cluster in the latewood, similar to *R. aromatica* and *R. trilobata*, and no resin canals in five species of section *Styphonia*. Most genera of Anacardiaceae have wood with diffuse porosity. Although *Rhus s.s.* has ring-porous wood with libriform fibres, vessel elements with alternate pitting and helical thickenings, simple perforation plates, scanty paratracheal parenchyma (except for *R. chinensis* Mill. with diffuse apotracheal parenchyma and *R. standleyi* F.A.Barkley with diffuse-in-aggregates) and heteroge-

neous rays (Young, 1978; Terrazas, 1994; Andrés-Hernández, 2006), the quantitative characters do not appear to be statistically significant (Terrazas, 1994; Andrés-Hernández, 2006), showing a continuous variation among species of *Rhus s.s.* Leaf architecture, including venation patterns and foliar and petiolar anatomy, suggests that some traits may be phylogenetically informative (Andrés-Hernández, 2006; Andrés-Hernández & Terrazas, 2006, 2009), but these characters have not been incorporated in recent phylogenetic analyses.

Despite the advances in the taxonomy of *Rhus s.s.*, no study has tested the morphological characters traditionally used for the infrageneric classification in this group, and no study has sampled most of the species of this genus. Therefore, the present study includes 31 species, ten more than previous studies have sampled (Miller *et al.*, 2001; Yi *et al.*, 2007), and analysed such important taxonomic characters as the leaves, inflorescences, flowers and fruits. We also include new morpho-anatomical characters for species of *Rhus s.s.* and test the congruence of the structural characters with molecular phylogenetic trees generated by us and other authors.

MATERIAL AND METHODS

Taxon sampling

Thirty-one species of *Rhus s.s.* were included in this study (Appendix 1). Seven species representing other genera of Anacardiaceae that have previously been included in *Rhus s.l.* [*Actinocheita filicina* (D.C.) Barkley, *Malosma laurina* (Nutt) Abrams, *Searsia ciliata* (Licht. ex Schult.) A.J.Mill., *S. quartiniana* (A.Rich.) A.J.Mill., *Toxicodendron diversilobum* (Torr. & A.Gray) Greene, *T. radicans* Kuntze, *T. vernix* Kuntze] were included to test the monophyly of *Rhus s.s.*, and *Schinus molle* L. was used as the functional outgroup to root the tree because this genus has never been included in *Rhus s.l.* Sequences of *trnL-F*, *ndhF*, *Nia*-i3, *trnC-D* and internal transcribed spacer (ITS) were obtained from GenBank (Appendix 1) and *trnL-F* and ITS sequences were generated for *R. allophylloides* Standl., *R. andrieuxii* Engl., *R. barclayi* Standl., *R. chondroloma* Standl., *R. hartmanii* F.A.Barkley, *R. muelleri* F.A.Barkley, *R. oaxacana* Loes., *R. schmidelioides* Schtdl. (only *trnL-F*), *R. standleyi* and *R. terebinthifolia* Schltdl. & Cham. (Appendix 1).

Structural characters

We examined the collections of *Rhus s.s.* and related taxa in the following herbaria: ANSM, ARIZ, DUKE, GH, IBUG, IEB, MEXU, NCU, NY, TEX and US. Leaves (blade and petiole) were removed for leaf architectural and anatomical studies. The methods used for these studies are described in detail elsewhere (Andrés-Hernández & Terrazas, 2006, 2009). Wood samples (one to four mature-stem samples per species) were provided by CAFw, FHOw, MADw, RSA, SJRw, TWTw and USw or were personally collected in Mexico and deposited at MEXUw (Andrés-Hernández, 2006). Wood characters are commonly diagnostic at the generic level (Carlquist, 2001); therefore, few characters provided information at the hierarchical level of interest (in subgenera). Forty structural characters (25 morphological and 15 anatomical) were coded as primary homology hypotheses (De Pinna, 1991). Sixteen characters had multiple states, and all characters were treated as unordered and equally weighted (Fitch parsimony; Fitch, 1971). The coded structural-data matrix of *Rhus s.s.* and related taxa is given in Appendix 2 and Table 2. This partition was analysed independently and in combination with molecular data to allow any secondary signal to emerge (Nixon & Carpenter, 1996).

DNA extraction, amplification and sequencing

Total DNA was extracted from silica gel-dried or herbarium leaves with a modification of the 2× CTAB procedure of Doyle & Doyle (1987). DNA was cleaned directly with QIAquick silica columns (Qiagen) or precipitated with 100% ethanol at –20 °C and purified on a caesium chloride/ethidium bromide density gradient (1.55 g mL^{-1}) with subsequent dialysis and removal of ethidium bromide with butanol.

All DNA regions were amplified in 100 μL PCR reactions including 0.5 μL 5 u μL^{-1} *Taq* DNA-polymerase (Promega), 10 μL 10× Mg-free DNA polymerase buffer (Promega), 12 μL 25 mmol L^{-1} $MgCl_2$, 2 μL 10 mmol L^{-1} each dNTP, 1 μL 0.4% bovine serum albumin (BSA), 1 μL each primer (100 ng μL^{-1}), 72.5 μL double-distilled H_2O (ddH_2O) and template DNA. Alternatively, 50-μL reactions were prepared using 45 μL 1.1× PCR Master Mix (Advanced Biotechnologies), including 1.25 μL *Taq* DNA polymerase, 75 mmol Tris-HCl (pH 8.8 at 25 °C), 20 mmol $[NH_4]_2SO_4$, 1.5 (for ITS) or 2.5 mmol (for plastid DNA) $MgCl_2$, 0.01% Tween 20 and 0.2 mmol each dNTP, to which were added 0.5 μL each primer (100 ng μL^{-1}), 0.5 μL 0.4% BSA, 2 μL ddH_2O and template DNA. The PCR mix used to amplify the ITS region included 2% dimethyl sulphoxide to reduce problems related to secondary structure and efficiency of PCR primer binding.

The *trnL-F* region, including the *trnL* intron and the intergenic spacer, was amplified either as a single piece with primers c and f or as two non-overlapping fragments using primers c-d and e-f (all from Taberlet *et al.*, 1991). The PCR profile consisted of an initial 2-min premelt at 94 °C; 28–30 cycles of 1 min

Table 2. Matrix of morphological characters

	Characters							
Taxon	1. . . .5	6. . . .10	11. . . .15	16. . . .20	21. . . .25	26. . . .30	31. . . .35	36. . . .40
Actinocheita filicina	00100	11010	00101	01101	00000	101??	?0000	1000?
Malosma laurina	2-201	03020	00001	02?10	-0000	100??	?0011	10113
Searsia ciliata	1-210	0T0??	???0?	?1?01	?0000	?????	?????	?????
Searsia quartiniana	1-012	02000	00000	01?01	?0000	?????	?????	?????
Schinus molle	01020	02002	01001	00001	00000	0000?	00000	0000?
Toxicodendron diversilobum	10002	10000	0010?	????1	?0000	200??	??0?0	??0??
Toxicodendron radicans	1-002	10000	00101	01001	00000	2100?	?0000	0000?
Toxicodendron vernix	00012	02000	00100	0???1	?0000	200??	??0?0	??0??
Rhus subgenus *Rhus*								
Rhus chinensis	0??00	11001	?0110	01001	?1101	201??	?????	?????
Rhus copallina	01100	02101	00110	01001	01101	20110	00100	10000
Rhus coriaria	0?000	11001	00111	0???1	??101	20110	00100	10000
Rhus glabra	00100	11011	00010	01001	01101	20110	00100	10000
Rhus lanceolata	01120	12001	00110	01001	01101	2?110	00100	10000
Rhus michauxii	01101	11011	01110	01001	01101	2?110	00100	10000
Rhus sandwicens	01100	11001	00110	01001	01101	2?110	00100	10000
Rhus typhina	01100	11001	01110	01001	01101	20110	00100	10000
Rhus subgenus *Lobadium* (Section *Lobadium*)								
Rhus allophylloides	1-110	11010	00110	02211	11111	20100	00100	10002
Rhus aromatica	1-000	11000	00111	02211	11111	20100	00100	10002
Rhus schmidelioides	1-110	11000	00110	02211	11111	2?100	00100	10002
Rhus trilobata	1-100	11000	01111	02211	11111	20100	00100	10002
Rhus microphylla	01110	0?110	00111	02211	11111	20100	00100	10002
(Section *Terebinthifolia*)								
Rhus barclayi	00002	02000	00111	01100	-1111	20100	10010	10002
Rhus hartmanii	00110	02000	00111	01100	-1111	20100	10010	10002
Rhus jaliscana	00111	02000	00111	01100	-1111	20100	10010	10002
Rhus palmeri	00112	02010	00111	01100	-1111	2?100	10010	10002
Rhus rubifolia	00111	02000	00111	01100	-1111	2?100	10010	10002
Rhus terebinthifolia	00110	02100	00111	01100	-1111	20100	10010	10002
(Section *Styphonia*)								
Rhus andrieuxii	00210	03002	11112	11000	-1111	20101	01011	01111
Rhus chondroloma	00200	03022	10112	12110	-1111	20101	01011	01111
Rhus choriophylla	00210	03022	11112	11000	-1111	2?101	01?11	01111
Rhus integrifolia	2-201	03022	11112	02110	-1111	21101	01012	11113
Rhus kearneyi	2-201	03022	11112	02110	-1111	20101	01012	11113
Rhus muelleri	2-211	03012	10112	02110	-1111	20101	01012	11113
Rhus oaxacana	00201	03022	21112	01000	-1111	20101	01011	01111
Rhus ovata	2-211	03022	10112	02110	-1111	20101	01013	11113
Rhus pachyrrhachis	00200	03122	10112	11000	-1111	2?101	01011	01111
Rhus schiedeana	00201	03122	11112	11000	-1111	20101	01011	01111
Rhus standleyi	2-211	0T012	10112	02110	-1111	20101	?1012	11113
Rhus virens	00200	03102	11112	11000	-1111	20101	01011	01111

denaturation at 94 °C, 30 s annealing at 48 °C and 1 min extension at 72 °C, and a final extension of 7 min at 72 °C.

The entire ITS region was amplified using primers ITS4 and ITS5 (White *et al*., 1990) and in some cases using primers 17SE and 26SE (Sun *et al*., 1994). The PCR profile for ITS5–ITS4 included an initial 2-min premelt at 94 °C; 28–30 cycles of 1 min denaturation at 94 °C, 1 min annealing at 52 °C and 2 min extension at 72 °C; and a final extension of 7 min at 72 °C. The PCR profile for 17SE–26SE differed only in using a lower annealing temperature of 50 °C.

The PCR products were cleaned with QIAquick or CONCERT (Life Technologies) silica columns accord-

ing to the manufacturers' protocols and used in cycle sequencing reactions with the ABI Prism Big Dye Terminator Cycle Sequencing Ready Reaction kit with AmpliTaq DNA polymerase (Applied Biosystems). The 10-μL cycle-sequencing reactions included 1 μL terminator mix, 3 μL 2.5× cycle-sequencing buffer (200 mmol L^{-1} trizma base, 5 mmol L^{-1} $MgCl_2$, pH 9.0), 1 μL primer (5 ng μL^{-1}) and 3–5 μL PCR product plus ddH_2O as required.

The cycle-sequencing products were cleaned by precipitation in 25 μL 100% ethanol with 1 μL 3 mol L^{-1} NaOAc (pH 4.6) on ice for 30 min, after which they were centrifuged at 12289 *g* for 25 min. The alcohol/salt mix was discarded, and the pellet was subjected to two washes with 300 μL 70% ethanol, each followed by centrifugation at 13 000 r.p.m. for 15 min. The cleaned cycle-sequencing products were allowed to dry overnight at room temperature or oven-dried at 65–70 °C for 15 min and were then protected from light until they were analysed. The forward and reverse sequences were analysed on a PE 377 automated sequencer (Applied Biosystems), and the resulting electropherograms were edited and assembled with Sequencher versions 3.1 or 4.1 (Gene Codes).

Sequence alignment and indel coding

The 3′ portion of the *trnL-F* and ITS regions were aligned with Clustal W (Thompson, Higgins & Gibson, 1994) and visually adjusted as necessary, following the guidelines of Kelchner (2000). All non-autapomorphic indels were coded as binary (presence/absence) characters using the simple indel-coding method used by Simmons & Ochoterena (2000) and appended to the sequence matrices.

Phylogenetic analyses

Parsimony analyses of three datasets (molecular data, including *trnL-F*, *ndhF*, *Nia*-i3, *trnC-D* and ITS; structural data; and combined data) were conducted separately with PAUP* version 4.0b10 (Swofford, 2002). All analyses consisted of 1000 replicates of random sequence addition with tree bisection-reconnection (TBR) branch swapping and the MULTREES option, saving all most-parsimonious trees. Individual gap positions were treated as missing data because the indel characters were appended to the molecular matrices. Internal clade support was evaluated using bootstrap resampling (Felsenstein, 1985), with 300 replicates using TBR branch swapping and saving up to 20 trees per replicate to reduce time spent swapping on large islands. Clade support in the combined analyses was evaluated by bootstrap and jackknife resampling (Farris *et al*., 1996), with 300 bootstrap and jackknife replicates using the searching strategy described above.

To assess the level of congruence between the data sets, we employed the incongruence length difference (ILD) test or the partition-homogeneity test (Farris *et al*., 1995), implemented in PAUP*. One hundred heuristic-search replicates were performed, with all characters equally weighted and TBR branch swapping.

RESULTS

Molecular analyses

The maximum-parsimony analysis of the sequence data yielded 4113 most-parsimonious trees with a length of 1328 steps [consistency index (CI) 0.79; retention index (RI) 0.80; homoplasy index (HI) 0.34, excluding uninformative characters]. The percentage of potentially informative characters was 6.8% (Table 3). Although 30% of the data were missing for three markers (*ndhF*, *Nia i*3 and *trnC-D*), the topology was well supported. The bootstrap analysis recovered *Rhus s.s*. as monophyletic with maximum (100%) bootstrap support (BP). Both subgenera were monophyletic with high support: 96% BP for subgenus *Lobadium* and 98% BP for subgenus *Rhus*. In subgenus *Lobadium*, two clades were also recovered, here named A and B. Moreover, in clade B, three lineages were recovered: *R. microphylla* was sister to subclade B1, and these lineages together were sister to subclade B2 (Fig. 1A). Clade A received moderate support, but the relationships in this clade were poorly resolved (Fig. 1A), except for the sister-taxa relationships of *R. integrifolia* Engl.–*R. ovata* S.Watson and *R. muelleri*–*R. standleyi*.

Table 3. Character diagnostics and trees resulting from the analysis of the molecular, morphological and global datasets

Data set	No. of characters	Potentially parsimony-informative characters	No. of optimal trees	No. of steps	CI	RI	HI
Molecular (*trnL-F*, *ndhF*, *Nia-i*3, *trnC-D*, ITS)	6973	448	4113	1328	0.79	0.80	0.34
Structural	40	40	5380	125	0.45	0.84	0.54
Combined	7013	488	56	1476	0.75	0.80	0.25

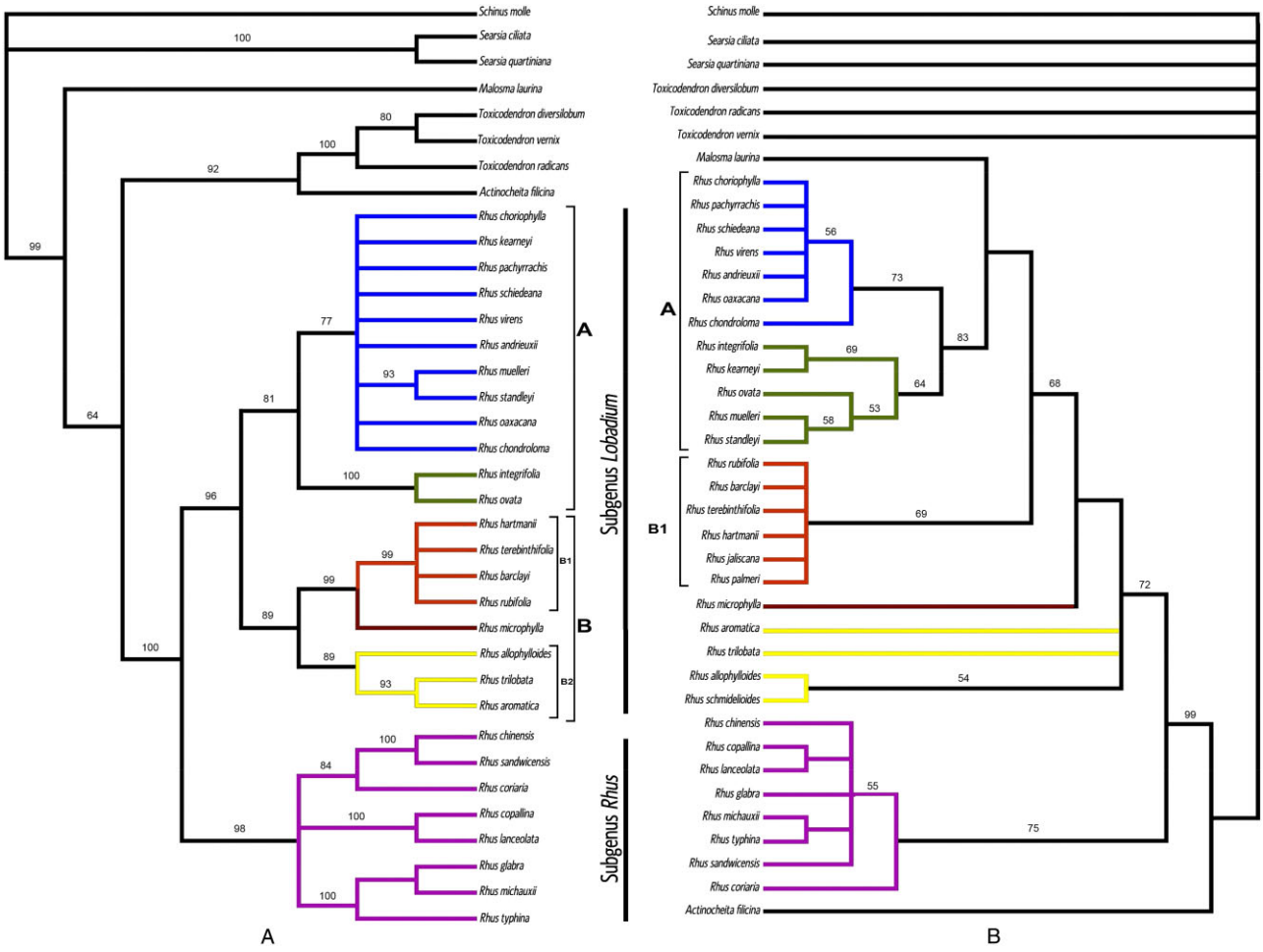

Figure 1. Strict consensus of trees resulting from the phylogenetic analyses. A, cladogram derived from the combined molecular markers, *trnL-F*, *ndhF*, *Nia*-i3, *trnC-D* and ITS (4113 trees, 1328 steps; CI = 0.79, RI = 0.80; HI = 0.34). B, cladogram derived from the structural characters (5380 trees, 125 steps, CI = 0.45, RI = 0.84, HI = 0.54). Bootstrap support values (≥ 50%) are indicated above branches. Colours correspond to subgenera or sections in Figure 2.

Structural analysis

A parsimony analysis based on 40 informative structural characters (Table 3) yielded 5380 trees of 125 steps. The bootstrap analysis (Fig. 1B) retrieved *Rhus s.s.* as monophyletic with strong support (99% BP), only if *Malosma laurina* is part of it. The characters supporting the monophyly of *Rhus* were red glandular hairs on the berries and inflorescence axis, cilia on the sepals, glands on the leaf blades and a striate cuticle on the lamina. These characters were absent in *M. laurina*. Both subgenera were recovered as monophyletic, with moderate support, 75% BP for subgenus *Rhus* and 72% BP for subgenus *Lobadium*. In subgenus *Lobadium*, clade A had the strongest support values, with *M. laurina* as its sister taxon and *R. microphylla* as sister to both plus subclade B1. However, clade B2 was not recovered; only *R. allophylloides* and *R. schmidelioides* were resolved as sister taxa. Several leaf character states are similar between *M. laurina* and members of clade A.

Combined analysis

The 40 morphological characters plus the combined molecular data contained a total of 488 potentially informative characters. The total-evidence approach yielded 56 minimum-length trees of 1476 steps (CI 0.75; RI = 0.80; HI = 0.25; 6.9% informative characters, Table 3) with a topology similar to that recovered in the analysis of the molecular data alone. In the strict-consensus tree, *Rhus s.s.* was recovered with maximum support (100% BP), including 31 species (Fig. 2), and its structural synapomorphies were the same as those found in the structural analysis, except for the striate cuticle on the leaf blade. Both subgenera were also recovered with high support. The

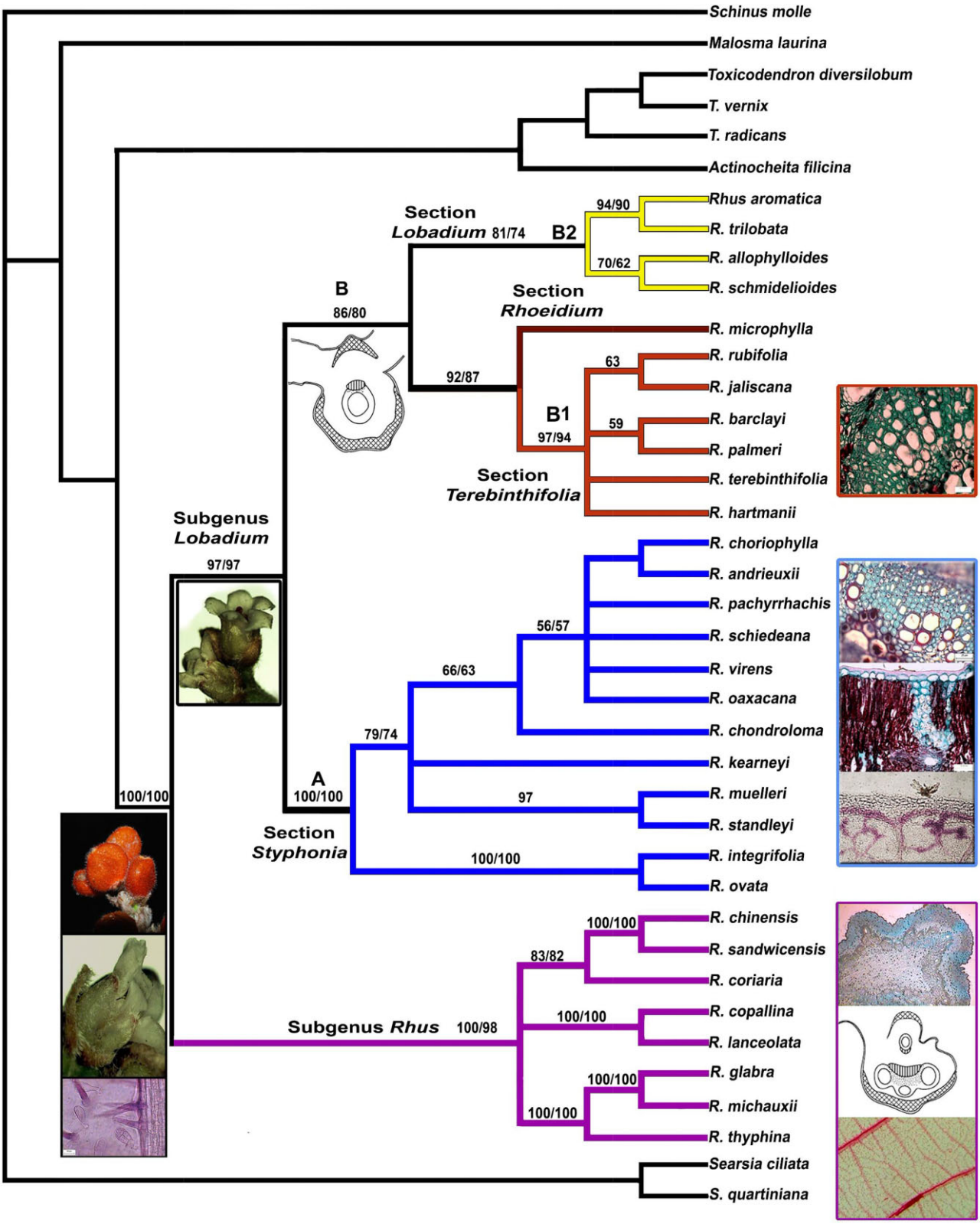

Figure 2. Strict consensus of the simultaneous analysis of structural and molecular characters (56 trees, 1476 steps, CI = 0.75, RI = 0.8, HI = 0.25). Bootstrap/jackknife support values (≥ 50%) are indicated above branches.

relationships in subgenus *Lobadium* were similar to those found in the analysis of the sequence data alone but with stronger support (Fig. 2).

DISCUSSION

Our supermatrix analysis not only supports previous findings about the circumscription of *Rhus* but also provides strong support for the subgenera and sections, delimitation of which has previously been uncertain. Both partitions (molecular and structural) supported the major lineages in *Rhus*. Therefore, combining the data did not introduce conflict but provided higher support and more resolution. Although the precise species relationships differed among analyses, the backbone relationships were supported by all partitions. Our analyses suggest that the five-sectional classification proposed by Barkley (1937) for subgenus *Lobadium* (as the incorrectly named *Schmaltzia*) is partly correct. Based on our results, we recognize Barkley's sections *Lobadium*, *Rhoeidium* and *Terebinthifolia* (incorrectly named *Pseudosumac* by Barkley) and Young's section *Styphonia* (Barkley's *Styphonia* + *Pseudoschmaltzia*).

Although our supermatrix had missing data for three genes (30%), the simultaneous inclusion of all information (additional taxa, previously available DNA sequences and structural characters) was critical in resolving the conflicting topologies generated in previous studies (Yi *et al*., 2004, 2007) especially within the genus, and revealed the phylogenetic signal of the microstructural characters. The simultaneous analysis presented here reinforces the utility of supermatrices with missing data (Pirie *et al*., 2008; Chatrou *et al*., 2012) and the value of morphological characters (Donoghue & Sanderson, 1992; Wiens, 2004).

Rhus s.s.

Total-evidence analysis yielded the strongest support to the monophyly of *Rhus s.s*. Our results confirm that the presence of red glandular hairs on the fruit surface (25) is a synapomorphy for this genus, as suggested by Barkley (1937). The occurrence of glands on the foliar blade (14), ciliate sepals (22) and red glandular hairs on the inflorescence axis and branches (23) are also synapomorphies of *Rhus s.s*. Gillis (1971) and Moffett (1993) considered *Toxicodendron* Mill. to be part of *Rhus*; however, our combined analysis does not support this circumscription. Moreover, *Toxicodendron* is recognized by its glabrous fruits and the occurrence of toxic resins (Aguilar-Ortigoza, Sosa & Aguilar-Ortigoza, 2003). Other members of *Rhus s.l*. such as *Actinocheita* F.A.Barkley and *Malosma* (Nutt.) Abrams show pilose indumenta on the fruit surface, but these hairs differ from the glandular hairs of *Rhus s.s*.

Rhus subgenus *Rhus*

Subgenus *Rhus* is monophyletic and is supported by several molecular and three structural synapomorphies: the occurrence of weakly percurrent tertiary veins (10), more than seven resin canals in the petiole (29) and type I vascular bundles in the midvein (40) (Fig. 2). These synapomorphies are conserved in the subgenus, which has a wider geographical distribution than subgenus *Lobadium*. Barkley (1937) proposed imparipinnate leaves and thyrses with pedicellate flowers as the diagnostic features for this subgenus, but these characters were not revealed as evolutionary novelties in our analyses. The sister-taxa relationship of *R. copallinum* L. and *R. lanceolata* A.Gray ex Engl. is supported by their eucamptodromous venation; other members of this clade have craspedodromous venation (7). Moreover, the *R. michauxii* Sarg.–*R. typhina* L.–*R. glabra* L. clade is supported by the presence of incomplete areoles (12), with a transformation to imperfect areoles in *R. glabra*. We found other informative structural characters to support the subgroups in subgenus *Rhus*. The sister-group relationship of *R. chinensis* Mill. and *R. sandwicensis* A.Gray was supported exclusively by molecular characters. Some authors have suggested that these species are distinguished by seed size; however, we did not include this character due to the lack of seed-size information for most *Rhus* species. These species are geographically isolated, one in Eurasia and the other in Hawaii (Yi *et al*., 2004).

Rhus subgenus *Lobadium*

Subgenus *Lobadium* was recovered as monophyletic and supported by two structural synapomorphies: short (< 1 mm) pedicels (21) and the presence of bracteoles (24) (Fig. 2). Barkley (1937) suggested the presence of bracteoles as diagnostic features for this subgenus, and our results support this hypothesis. However, the remaining diagnostic features suggested by Barkley (1937) (inflorescence in spikes and simple, trifoliolate or imparipinnate leaves) were not found to be synapomorphies. Subgenus *Lobadium* encompasses the largest number of species, most of which are distributed in the Mexican Transition Zone (Andrés-Hernández *et al*., 2006). Our results suggest that speciation associated with several anatomical and morphological features has occurred in different eco-regions: sections *Lobadium*, *Rhoeidium* and *Terebinthifolia* in temperate warm environments and section *Styphonia* in dry environments.

The combined analysis supports the recognition of four previously proposed sections (Barkley, 1937; Young, 1975, 1978), as discussed below.

Clade B

The clade here named Clade B encompasses all recognized species of the previous sections *Lobadium* (B2), *Rhoeidium* and *Terebinthifolia* (B1) and shares type III vascular bundles (40) in the midrib (Fig. 2). Subclade B2 is monophyletic and corresponds to Barkley's section *Lobadium*, with the combination of trifoliolate leaves (1) with serrate margins (6) being unique in the genus *Rhus*. This subclade does not correspond to Young's (1975) *Lobadium*, which also included *R. microphylla* (see below). The trifoliolate leaf character is acquired independently in *Searsia* F.A.Barkley and *Toxicodendron*, whereas the serrate margin represents a reversal. Moreover, serrate margins are common in species inhabiting temperate forests (Baker-Brosh & Peet, 1997), like most species of subgenus *Rhus* with imparipinnate leaves.

The species of subclade B1, section *Terebinthifolia*, share the unique combination of the following characters: three-branch inflorescences (17); a distance of 3–5 mm from the base of the second branch to the flower (18); a distance of 3–5 mm between flowers (19); the absence of a pedicel (20); a smooth cuticle on the leaf lamina (33); a papillose foliar epidermis (34); and the presence of gelatinous xylary fibres in the petiole (31) (Fig. 2). These characters were acquired independently in this clade and are not combined in other clades in *Rhus*. Barkley (1937) characterized this section as containing evergreen trees or shrubs with three to 15 leaflets and inflorescences in lax spikes. None of these characters was recovered in our analysis, although the inflorescences were represented by four informative characters rather than simple, lax spikes (see below).

Status of *R. microphylla*

Our results support Barkley's (1937) recognition of the monotypic *Rhoeidium* (*R. microphylla*) as separate from section *Lobadium*. Young (1975, 1978) placed *R. microphylla* in section *Lobadium* based on its chemical characters and the occurrence of radial canals in its wood. However, similar resin canals are present in the wood of *R. integrifolia* of clade A, section *Styphonia* and *R. aromatica* and *R. trilobata* of clade B2, section *Lobadium*. Our molecular, morphological and combined analyses all place *R. microphylla* as sister to section *Terebinthifolia*. These lineages share eucamptodromous venation. Yi *et al*. (2004, 2007) suggested that *R. microphylla* is a hybrid between *R. copallinum* or *R. lanceolata* (subgenus *Rhus*) and *R. rubifolia* (subgenus *Lobadium*, section *Terebinthifolia*), but our results do not support this hypothesis. Conflicting sister-taxa relationships are common in phylogenetic analyses of genes such as ITS, *trnL-F* and *rbcL* (Bradford & Barnes, 2001; Arias, Terrazas & Cameron, 2003; Muellner *et al*., 2003). We suggest that poor sampling in sections *Lobadium* and *Terebinthifolia* resulted in misleading signals for *R. microphylla* and *R. rubifolia* in the analyses of Yi *et al*. (2004, 2007).

Clade A

As traditionally defined by Young (1978), members of section *Styphonia* have evergreen, coriaceous and simple or compound leaves. Our results provide strong support for this clade, which exhibits several evolutionary novelties, including incomplete marginal vein (11), xylary fibres in the petiole (30), a thick foliar cuticle (> 6 μm) (32), two equal rows of palisade-parenchyma cells (35) and prismatic crystals in the mesophyll (37). In addition to these synapomorphies, the coriaceous leaves noted by Barkley (1937) and Young (1978) constitute a unique character combination for *Styphonia*. Other characters such as cladodromous venation (7), transversely ramified tertiary veins (10), type II veinlets (15), a papillose epidermis on the midvein (38) and xylary fibres in the midvein (39) are homoplasious; these traits were acquired independently in other genera, such as *Malosma*, *Searsia* and *Toxicodendron*, and in members of other tribes of Anacardiaceae (Smith & Stern, 1962; Wilkinson, 1983; Dickison, 1989; Buijsen, 1995; Fariña *et al*., 2003; Martínez-Millán & Cevallos-Ferriz, 2005). *Styphonia* is well supported by anatomical characters that represent adaptations to xeric environments.

Young's (1975, 1978) subsections *Compositae*, *Intermediae* and *Styphoniae* were not recovered in molecular studies (Yi *et al*., 2004, 2007) and are not supported by our combined analysis, even though all recognized species have been included here. However, *R. ovata* and *R. integrifolia* (Nutt.) Engl. are sister taxa (100% BP), sharing wood with septate fibres, and *R. muelleri* and *R. standleyi* (97% BP) are sister taxa, sharing sinuous secondary veins. Moreover, the five species previously classified in *Styphoniae* are the earliest-diverging species in clade A and have a disjunct distribution pattern. *Rhus kearneyi* F.A.Barkley occurs with *R. ovata* and *R. integrifolia* in xerophytic scrublands in California and Baja California provinces, whereas *R. standleyi* occurs in the eastern Trans-Mexican Volcanic Belt and the Sierra Madre del Sur; *R. muelleri* occurs in the Sierra Madre Oriental and on the Mexican Plateau in xerophytic scrub or xerophytic scrub/temperate forest ecotones

(Andrés-Hernández *et al*., 2006). Based on this distribution pattern, we hypothesize that the foliar features shared by these five species and the other members of section *Styphonia* were acquired after subgenus *Lobadium* diverged from subgenus *Rhus* > 30 million years ago, as suggested by Yi *et al*. (2004).

Plant-organ evolution

Leaves

Eucamptodromous venation is common in Anacardiaceae (Hickey & Wolfe, 1975; Martínez-Millán & Cevallos-Ferriz, 2005). Craspedodromous and eucamptodromous venation occur in both subgenera, while cladodromous venation is unique to section *Styphonia*. The tertiary veins show a randomly reticulate condition in *Rhus*, changing to weakly percurrent in subgenus *Rhus* and transversely ramified in section *Styphonia*. Both transitions represent evolutionary novelties. Type I idioblast veinlets appear several times in *Rhus s.s*. However, type III idioblast veinlets occur only in species of *Styphonia*.

One layer of palisade-parenchyma cells is the plesiomorphic condition in *Rhus*, and two or three layers is the derived condition. The larger number of palisade-parenchyma cells is a unique feature of *Styphonia*, although two layers appear independently in *Malosma laurina*. The changes associated with the number of palisade-parenchyma layers, such as the cuticle thickness and the lignification of the midvein and petiole (Andrés-Hernández & Terrazas, 2006), may explain the maintenance of a unique type of wood porosity.

Stem

Semi-ring wood porosity is the plesiomorphic condition present in *Schinus* L.; ring porosity and diffuse porosity are derived conditions. Ring porosity occurs in all species of *Rhus s.s*. and *Toxicodendron*, whereas diffuse porosity appears in *Malosma laurina* and *Actinocheita filicina*. Ring porosity is present in all species of *Rhus s.s*. independent of their evergreen or deciduous character, even though these species are widely distributed in northern Eurasia, the United States and southward into the drier and warmer regions of southern Mexico. In the eudicotyledons with wide latitudinal distributions, wood porosity typically varies from ring to diffuse-porous as latitude decreases (Noshiro & Baas, 1998; Aguilar-Rodríguez, Terrazas & López-Mata, 2006). Contrary to expectation, the retention of ring porosity across the latitudinal range of *Rhus* does not affect conductivity due to the acquisition of several leaf-structural evolutionary novelties that favour evergreen leaves in the warmer and more xeric environments of the Mexican Sierras (Andrés-Hernández *et al*., 2006).

Inflorescences

The inflorescences of Anacardiaceae are described as thyrses and panicles. Thyrses are a distinctive trait of tribe Rhoeae, except for *Toxicodendron* species, which have panicles (Barfod, 1988). In *Rhus s.s*., Barkley (1937) recognized thyrses in *Rhus* subgenus *Rhus* and compound spikes in *Rhus* subgenus *Lobadium*. However, the diversity of the spikes in subgenus *Lobadium* is not adequately represented by these typological terms. Therefore, we coded the inflorescences using five characters (17–21). *Rhus s.s*. shows a reduction in the number of inflorescence branches. Subgenus *Lobadium* shows a reduction in the flower position along the second branch (18) and in the distance between flowers (19), whereas sections *Terebinthifolia* and *Styphonia* independently acquired the absence of pedicels.

CONCLUSIONS

This study demonstrates that more complete taxon sampling can resolve the conflicting phylogenetic relationships of certain taxa. In addition, well-understood morphological characters can be consistent with molecular phylogenetic analyses and can add support and resolution when combined with molecular data. The potential 'noise' of morphological characters due to their supposed high levels of homoplasy is not a problem when the appropriate phylogenetic levels are addressed.

Rhus s.s. contains two well-supported subgenera: *Lobadium* and *Rhus*. In subgenus *Lobadium*, four sections are recognized: *Lobadium*, *Styphonia*, *Terebinthifolia* and the resurrected *Rhoeidium*. A key to these subgeneric categories is given below. Adaptive leaf features have buffered wood evolution in *Rhus s.s*., all species of which have ring-porous wood. Thus, xerophytic leaf characters evolved once in the *Styphonia* lineage, originating in the drier environments of the Mexican provinces of California and Baja California and the scrubs of the Trans-Mexican Volcanic Belt, Sierra Madre del Sur, Sierra Madre Occidental and the Mexican Plateau.

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KEY FOR *RHUS S.S.* AND INFRAGENERIC CATEGORIES

A. Species lacking glandular hairs on inflorescences axes and fruits; sepals with entire margin ..... ***Toxicodendron, Actinocheita***

AA. Species with glandular hairs on inflorescences axes and fruits; sepals with ciliate margin ..... ***Rhus***

B. More than seven resin canals in the petiole, weakly percurrent tertiary veins, pedicel 1.5–2.5 mm, lacking bracteoles ..... **Subgenus *Rhus***

BB. Less than seven resin canals in the petiole, reticulate or transversely ramified tertiary veins, pedicel < 1 mm, bracteolate ..... **Subgenus *Lobadium***

C. Leaflets chartaceous with serrate margins; type III vascular bundles in the midrib; cuticle < 6 μm; prismatic crystals lacking in mesophyll ..... **Section *Lobadium***

D. Rachis winged; fibres lacking in the petiole ..... **Section *Rhoeidium***

DD. Rachis non-winged; gelatinous fibres in the petiole ..... **Section *Terebinthifolia***

CC. Leaflets coriaceous with entire margin; type IV vascular bundles in the midrib; cuticle > 6 μm; prismatic crystals present in the mesophyll ..... **Section *Styphonia***

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APPENDIX 1

Information for the samples of species of *Rhus s.s*. Voucher information is listed as follows: taxon, name, country, locality, collector name and number, (herbarium). For GenBank vouchers the accession numbers are given in parentheses for (ITS, *trn*L-F, *ndh*-F, *Nia*-i3, *trn*C-D). Abbreviations of herbaria according to Holmgren *et al*. (1981). *Blades that were cleared, **blades and petiole for anatomical study.

Rhus subgenus *Rhus*: ***R. copallina*** L. USA Southeast of Bamberg Dorchester, C. Ahles 31816*; Jackson Co. Illinois, L. Bastian s.n.*; Warren Co., W. Seaman 2944* (NCU); Sondy Bottom, Texas, F. Barkley 13597; Freestone, Texas, L. Do 226; Gregg Co., W. Holmes 5454; Henderson Co., A. Lundell 9565; Hardin Co., A. Lundell 11542; South of Jasper, C. Lundell 11818; Anderson Co., E. Morsh Jr. 242; Todville Road, F. Waller *et al*. 2806** (TEX); Winter State Park, R. Bochinski s.n**(US); Wake Co. N. Carolina, R. Currie 884; Hopkins Co. Texas, B. Jenning 31 (IBUG). Wen 7134, 7165, (AY641483, AY640437, AY643098, DQ382288, DQ400539).

R. chinensis Mill. Wen 6389, 7086, 7310 (AY641480, AY640435, AY643095, DQ382286, DQ 400536).

R. coriaria L. AFGHANISTAN Kabul, K. Rechinger 31176 (US). ESPAÑA Toledo, F. Meyer s.n. ISRAEL Jerusalem, D. Goldman 1080**, Amdursky 550* (NY). Wen 7150 (AY641485, AY640439, AY643099, DQ382291, DQ400540).

R. glabra L. MEXICO. Chihuahua: Mpio. Madera, A. Benítez 1417* (ANSM); Mpio. Madera, S. Rodríguez 1511* (IEB).

USA. Maple Creek Cleveland Co., H. Ahles 15244*; Stanly Co., J. Morgan 1551* (NCU); Texas: Hemphill Co., Chester & M. Rowell 4175**, 10255b; D. Correll & H. Correll 30047; Texas Co., H. Gentry 306; Palo Pinto Co., R. McVaugh 8347 (TEX). Wen 7171 (AY641486, AY640440, AY643100, DQ382293, DQ400541).

R. lanceolata A.Gray ex Engl. MEXICO. Coahuila: Múzquiz-Boquillas, J. Villareal 6944* (IEB); Sierra la Babia, M. Carranza C-3061; Rancho los potros, D. Castillo 512; Rancho las pilas Múzquiz, Vázquez-Aldape s.n.*; La Babia, J. Villareal *et al*. 8876*(ANSM); Nuevo León: Mpio. Iturbide, Hinton *et al*. 21234; San Luís Potosí: Ciudad del maíz, F. Barkley 3470; Tamaulipas: La Purificación, F. González 17227 (ANSM); Puebla: Pahuatlán, F. Salazar s.n.* (US).

U.S.A Texas: Guadalupe Mountains, A. Chose 5961; Real Co., D. Correll 38069**; Corner Co., L. Hinckley s.n.; Davis Mountains, B. Wornock 9303, 10967 (TEX). Wen 7277 (AY641487, AY640441, AY643101, DQ382299, DQ400544).

R. michauxii Sarg. USA north of Efland Orange Co., H. Ahles 58816**(NCU); Florence Co., S. Carolina, H. Bartlett 2881; Hoke Co. N. Carolina, W. Fox & R. Godfrey 4230 (TEX). Hardin 13984 (AY641488, AY640442, AY643102, DQ382307, DQ400545).

R. sandwincensis A.Gray. USA Hawaii: Maunakia, A. Hitchcook 14300* (NCU); Volcanoes Nacional Park, S. Darwin 1201**; Ola Puma, O. Deneger s.n., 9527**; Waichn Valley, H. Mann & W. Brigham 412; Galch Mahaeli, J. Rock 5837 (TEX); P. Palmer 30024 (NY). Wen 7052 (AY641491, AY640445, AY643105, DQ382316, DQ400553).

R. typhina L. CANADA Quebec, S. Blake 1984 (TEX).

USA. McDowell Co., H. Ahles 17709**; West of Tapoco, Gram. Co., A. Radford 16002**; Nilkes Co., H. Tottens s.n.* (NCU); Rolling Hills, G. Baker 555**; Stoughton N. Cork, S. Blake 10930; Franklin Co., Vermont, S. Blake 3146; Middlesex Co. Massachusetts, S. Blake 4234; Ashland Co. Ohio, J. Stevenson 8640; Sussex Co. New Jersey, H. Maldenke 25982 (TEX). Wen 7082 (AY641492, AY640446, AY643106, DQ382319, DQ400556).

Rhus subgenus Lobadium section Lobadium:

R. allophylloides Standl. MEXICO. Jalisco: Mpio. Mezquitic, C. Chávez 4999; Mazamitla, J. Machuca 7726; Los Espinos, Tapalpa, M. Macías & B. Arbayo 633; La Manzanilla, Mazamitla, R. Ornelas 1378; La Joyas, Autlán, A. Vázquez 3773; R. Vega 2509* (IBUG); Las Minas Zimapán, J. Cházaro *et al*. 911; Sierra de Manantlán, R. Guzmán 29089 (IEB); Real Alto, Hinton *et al*. 2317* (US); State of Mexico: Mina de Agua, Temascaltepec, Hinton *et al*. 2817**(US). Rzedowski 45608 (HE862264,HE862254---).

R. aromatica Ait. CANADA Ontario: Manitoulin Strait, D. Soper 8950* (NCU).

MEXICO Chihuahua: Casas Grandes, Gómez-Durán s.n**; Nuevo León: Cerro el Viejo Aramberri, Hinton *et al*. 25181 (IEB); Aramberri, Hinton *et al*. 22643, 24072 (ANSM). USA Lancaster County, H. Ahles 27466*; Riley C. Kansas, W. Baker 2565*; Bennington C., Vermont, E. Baufford 17799; Missouri, T. Croat 17119*; Pennsylvania, H. Wahlx 17406* (NCU); Texas Co., D. Corell 16214; Morion Co., D. Corell & C. Lundell 18796; Wood Co., C. Lundell & A. Lundell 9474; Red River, M. Nee 44041**; Freestone Co., B. Thorp 2908 (TEX). Wen 7086 (AY641496, AY640447, AY643107, DQ382285, DQ400535).

R. microphylla Engelm. MEXICO. Coahuila: Rancho Morteros, Múzquiz, M. Carranza *et al*. 1341; Ramos Arizpe, J. Encina 839; Mpio. G. Cepada, Hinton *et al*. 16560; Guerrero Nuevo, R. Pérez 612; Ramos Arispe, A. Rodríguez & M. Carranza 874; Sierra Paila, J. Villareal 5218 & M. Carranza (ANSM); Carr. Múzquiz-Boquillas, R. Vázquez 259* (IEB). Guanajuato: Dolores Hidalgo, Rzedowski 41071*, 41085; San Miguel Allende, Rzedowski 43470; Mpio. San Luís la Paz, Rzedowski 47060; Mesa de Jesús, E. Ventura 90204*; Cerro Sta. Cruz, E. Ventura & E. López 6817, 6824 (IEB). Nuevo León: West of Linares, C. Anderson 4624*(DUKE); San Pablo Galeana, Hinton *et al*. 21896; Aramberri, Hinton *et al*. 21968*; La Carbonera Galeana, Hinton *et al*. 25346; Mpio Galeana, Hinton *et al*. 25712 (IEB). Sonora: Cañón de la Bellota, S. White 4699*(DUKE); Durango: Mpio. Guadalupe Victoria, Ochoa-Martínez 248; San Luis Potosí: Mpio.

Charcas, J. Reyes 415; Querétaro: Vizarrón, S. Zamudio 11085 (IEB). H. Wornock s.n.**, (TEX). Wen 7288 (AY641495, AY640448, AY643108, DQ382305, DQ382305, DQ400546).

R. schmidelioides Schltdl. MEXICO. Michoacán: San Andrés Ziracuáreriro, H. Díaz-Barriga 3516***; La Esperanza Morelia, V. Huerta 521; W. San Miguel, C. Medina 1652; Mil Cumbres, Rzedowski 45608*; Cerro Blanco Pátzcuaro, S. Zamudio 10642 (IEB). Querétaro: Tres Lagunas, H. Díaz-Barriga 3850*; El Madroño Mpio. Landa, E. González 408; Acatitlán de Zaragoza, E. González 634; La Yesca Mpio. Landa, H. Rubio 1554; Puerto Hondo, H. Rubio 609; La Parada Mpio. Jalpan, Sotero-Servín 56; Pinal de Amoles, S. Zamudio 2430 (IEB). Jalisco: Concepción de Buenos Aires, R. Ornelas & A. Flores Macías 1371, 1372; Manzanilla-Mazamitla, R. Ornelas & A. Flores Macías 1378; Ejutla, R. Ornelas & A. Flores Macías 1397 (IEB); Cerro Gordo, Arandas, R. Ramírez 1217*(IBUG).

R. trilobata Nutt. MEXICO Chihuahua: Ignacio Zaragoza Mpio. Casas Grandes, P. Tenorio & C. Romero 6491**; Puerto Colorado, G. Rodríguez 261; Ejido El Largo Mpio. Madera, A. Benítez 1443, (IEB); Coahuila: Ejido Nurias, Cuatrocienegas, M. Carranza 1867; El Cedral, Sierra Paila, J. Villareal 3949 (IEB); Sierra Paila, D. Castillo & J. Aguilera 849; Saltillo, F. Encina *et al*. 562; General Cepeda, J. Marroquín 2271; Cañón de la Carbonera, Mpio. Arteaga, J. Villareal 3742; Saltillo, J. Villareal, 1537 (ANSM). Querétaro: 6.5 km to the SW of Vizarrón, Mpio. Cadereyta, S. Zamudio 2760, 8 km to the NE of Vizarrón, S. Zamudio 2854, Peña Azul, El Jabalí, S. Zamudio 3044* (IEB). Huapanguillo Mpio. Miquihuana, Tamaulipas, L. Hernández 2086* (IEB).

U.S.A: Lawrence Co. C. Bennett s.n.*; Medora North Dakota D. Stevens 2413*; Henry Co. Illinois, Sears 1065* (NCU). Miller 21 (AY641497, AY640449, AY643109, DQ382317, DQ400555).

Section *Terebinthifolia*: *R. barclayi* Standl. MEXICO Jalisco: Autlán, R. Ornelas *et al*. 1506, 1585, Lagunillas de Ayotitlán, F. Santana *et al*. 4307*; Autlán de Navarro, R. Delgadillo *et al*. 1109 (IEB); Autlán, R. Cuevas & M. Rosales 1823; Ayotitlán, S. Guerrero 247; Arroyo la Calera, A. Guzmán *et al*. 977; Ayotitlán, R. Ornelas 1604**; Puerto los Mazos Autlán, R. Ornelas 1614** (IBUG); Talpa, E. Palmer s.n.* (US). Cochrane 12157(HE862264, HE862253---).

R. hartmanii F.A. Barkley. MEXICO Sonora: Las Chinazas, M. Fishbein *et al*. 102a; Barranca Huicochic, M. Fishbein *et al*. 121; Río Mayo, H. Gentry 3682; Santa Rosa, L. Toolin 310***; Yecora, L. Toolin 1376* (ARIZ); Nacore Chico, C. Muller 3689 (GH). Felger 95-181, (-HE862260---).

R. jaliscana Standl. MEXICO Jalisco: Barranca Huentitlán, R. Acevedo *et al*. 1632; A. Flores & M. Cházaro 2531; Ornelas 1429*; Barranca de Oblatos, M. Cházaro *et al*. 6743*; Cerro de Lima Mpio. Jocotepec, H. de Alba & M. Cházaro 10; Las Siete Cascadas, A. Flores 2422; 2 Km to the E. of Juanacatlán, R. Ornelas & J. García Castañeda 1456 (IEB); Cerro Amatitlán, E. Estrada, 8555; Siete Cascadas, Tonalá, M. Huerta & S. Guerrero 256**; La Primavera, Zapopan, O. Reyna 551; Laguna de Chapala, L. Villareal 3176, Las Tinajas Tonalá, L. Villareal 7223; Ixtlahuacán, L. Villareal 9401; Teocaltiche, F. Zapata 10 (IBUG); Guadalajara, C. Pringlei s.n.*** (US).

R. palmeri Rose. MEXICO Sinaloa: Sierra Tacuichamona, H. Gentry 5672; Los Pucheros, Sierra Surotato, H. Gentry 7203; along hwy, R. Worthington 7939 (GH); Chihuahua: Canyon Tarahumara, H. Gentry 7296; Mina El Bravo, P. Martin *et al*. s.n. (GH); Sonora: Vicinity of Alamos, P. Standley *et al*. 1310*; La Huerta Sierra Alamos, J. Wiens *et al*. 93-121(GH).

R. rubifolia Turcz. MEXICO Jalisco: Mpio. Hostotipaquillo, R. Ornelas 1545***; 10 km before Corcovado, R. Ornelas & J. García 1461 (ANSM); 3 km to the N of Tecolotlán, R. Ornelas & A. Flores 1388*; 8 km to the N. of Ayutla, 1391*; Unión de Tula 1392, Los Pilares, Mpio. Ameca, 1513* (IEB). Steinmann *et al*. 3146 (AY641508, AY640459, AY643119, DQ382315, DQ400552).

R. terebinthifolia Schltdl. & Cham. MEXICO Chiapas: Amatenango del Valle, Shilom Tom 1845*; Tenejapa, Shilom Tom 4041* (DUKE); Tenejapa, Breedlove 12669; Lagos de Monte Bello, Breedlove 9676; Lagos de Montebello, Tziscao, M. Lavin *et al*. 4578; Amatenango del Valle, Shilom Tom 1128 (TEX); Oxchuc, F. Gómez 296 (IEB). Guerrero: Chilpancingo, W. Anderson 4338* (DUKE). Oaxaca: Sola de Vega, Breedlove 12284 (ARIZ); Grutas de San Sebastian Sola de Vega, R. Cedillo 1745*(IEB). Querétaro: Las Mesitas to the SW of El Rincón, E. González 1401*; Tongojo El Rincón, A. Herrera 56; 1.5 km to the NW of La Mesa de Corozo, H. Rubio 1750 (IEB).

GUAEMALA El Petén, E. Contreras 10464* (DUKE); Honduras N. of Teguzigalpa T. Croat 63933*(DUKE). Calzada 19102 (HE862259, HE862269---).

Section *Styphonia* subsection *Styphonia*:

R. integrifolia Engl. MEXICO Baja California: Bahía de Todos los Santos, Carter 3181; Ensenada, S. Stephenson 67-135* (DUKE); Punta Banda, M. Dillon *et al*. 1829; Rancho Morron, R. Moran 17211 (TEX). Punta Banda J. Elizondo 311 (ANSM).

USA California: La Habra Heights, S. Myer s.n.; San Bernardino Valley, S. Parish 6890; Santa Barbara, H. Pollard s.n**; Santa Monica Mountains, P. Raven s.n.; San Luis Obispo Co., D. Keil 13688**; San Diego, Wallace & D. Thompson 108 (TEX). Millar, 28 (AY641499, AY640451, AY643111, DQ382294, DQ400542).

R. kearneyi F.A.Barkley. MEXICO Sonora: Sierra Niña, R. Felger 89-47 (TEX). Baja California: San Pedro Martir, R. Moran 18308***; Canyon Diablito, G. Webster 18261 (TEX). Modson 6979* (NCU); Paniel 2312* (NCU). Ickert-Bond, 1298 (AY641500, AY640452, AY643112, DQ382295, DQ400543).

R. muelleri F.A.Barkley. MEXICO Nuevo León: Galeana, K. Nixon 4008; San Isidro y Lirios, C. Peterson 1277; Montemorelos, Sierra Cebolla, T. Petterson *et al*. 7164**; El Fraile, R. Smith M657, M683 (TEX); El Sauce, Mpio. Galeana Hinton *et al*. 18082, 19208*, Los Lirios, Mpio. Santiago, Hinton *et al*. 25584 and 24937*; NW of Galeana, M. Poole *et al*. 2476***; between Rayones and Galeana, S. Zamudio *et al*. 6220 (IEB); on the road to Madero, J. Marroquín 3705; Villa Santiago, V. Valdez 790; J. Villa 4787 (ANSM). Coahuila: El Cedral, Sierra Paila, J. Villareal 3942*, (IEB); Sierra Paila, J. Villareal *et al*. 5263 (ANSM). Hinton 24937 (HE862265, HE862255---).

R. ovata S.Watson. MEXICO Baja California: Sierra San Francisco, Mpio. Mulege, M. Domínguez 2236; 9 miles E of Mission Borja, K. Nixon 960*(IEB); Punta Prieta H. Gentry 8979*** (US).

USA California: Azuza, K. Murata & E, Lee 20; San Bernardino, S. Parish 6802; Sta. Barbara, M. Pollard s.n.; Santa Monica, T. Ross & A. Ross 5989; Liebre Mountains, Ross *et al*. 4946; Riverside Co., D. Seigier *et al*. DS-2200; Orange Co. R. Thorne 32857; San Diego Co., Wallace & D. Thompson 111; Sentenac Canyon, T. Crovello 270** (TEX); S. Boyd 6744* (NY). Miller, 6, 22 (AY641501, AY640453, AY643114, DQ382308, DQ400547).

R. standleyi F.A.Barkley. MEXICO Oaxaca: Estación Microondas, P. Guerrero 135; Santiago Teotongo, Mpio. Ayutla, Salinas Dorado s.n.*(IEB); Cuicatlán, Stone 2785*(DUKE), Tepelmeme, Tamazulapan, Breedlove & B. Bartholomew 60721; Nochixtlán, M. Luckow 2538**(TEX). Puebla: Santa Lucia Atlixco, J. Jiménez 1678; Tepoxtlan, Mpio. San Martín, P. Tenorio 4918 (IEB); Tehuacán, C. Anderson 5318* (DUKE). Salinas 8087 (HE862258, HE862268---).

Section *Styphonia* subsection *Compositae*:

R. andrieuxii Engl. MEXICO Coahuila: Sierra Rancho Nuevo, Mpio. Santiago, Carranza *et al*. 1802; Estación de Microondas Saltillo, E. Rodríguez & J. Villareal 1751; Rancho Demostrativo Saltillo, J. Valdés s.n.; 12 km to the S of Saltillo, J. Villareal *et al*. 2705 (ANSM). Oaxaca: Juxtlahuaca, Calzada 21794* (IBUG); detour toward Jaltepec, Nochixtlán, M. Cházaro *et al*. 7065*; before the Jaltepec detour, Nochixtlán, M. Negrete 7065* (IEB). Puebla: Nicolás Bravo Chapulco, M. Cházaro *et al*. 6090*; P. Tenorio 5137 (IEB). Medrano 4285 (-HE862262---) MEXU.

R. choriophylla Wooton & Standl. MEXICO Sonora: Tepehuanes, E. Torrecillas 35 (IEB); Coahuila: La paila, B. Hinton 16514**, L. Lundell 12477** (US). Miller 27 (AY641498, AY640450, AY643110, DQ382287, DQ400534).

R. oaxacana Loes. MEXICO Oaxaca: San Carlos Yautepec, T. Croat 46237*** (DUKE); Topanala Mpio. Yautepec, S. Acosta 947; Santa María Albarrados, Ayutla, M. Cházaro *et al*. 6801; San Pedro Tabiche, R. Robles 84; Tapónala, Mpio. San Carlos Yautepec, A. Flores 1168* (IEB). Juárez 567 (HE862256, HE862266).

R. pachyrrhachis Hemsl. MEXICO Coahuila: Mpio. De Candela M. Carranza 2727, Carranza *et al*. 2786 (IEB); W. of Palmilla, R. Moran 10021*(US). Guanajuato: Comonfort, A. Mora 913* (IEB). Nuevo León: Las Norias, Mpio. Arramberi, Hinton *et al*. 17473, 23602*; La Poza, Mpio. Galeana, Hinton *et al*. 22214 (IEB); 5 km to the south of Zaragoza, J. Villareal & M. Carranza 536; J. Villareal *et al*. 5154 (ANSM). Querétaro: 6 km to the NW of La Luz, Rzedowski 52479*, 54479; Bornalejo, Mpio. de la Paz, S. Zamudio *et al*. 11601 (IEB). Tamaulipas: Bustamante J. Henrickson 19091** (TEX). Steinmann *et al*. 3724 (AY641503, AY640455, AY643115, DQ38239, DQ4005448).

R. schiedeana Schltdl. MEXICO Chiapas: Teopisca Mpio. Totolapa, Breedlove 26174*, 46237*; Amatenango del Valle, Shilom Tom 1844* (DUKE). Guanajuato: Chupaderos, Mpio. La Paz, Steinmann *et al*. 3696; Puerto Gallo, Mpio. Atarjea, E. Ventura 6493*(IEB); Atarjea, E. Ventura & E. López 9121 (ANSM). Querétaro: 4 km to the NE of Acatitlán de Zaragoza, E. Carranza 786; to the S of La Parada Jalpan, E. Carranza 820; Laguna Colorada, Mpio. Jalpan, M. Chávez 112**; 7 Km to the W of Tilaco, R. Fernández 3101, 3112; Acatitlán de Zaragoza, E. González 59*; Cerro Fresnos and La Barrada, C. Guzmán 64, 114*; Puerto Sabino, H. Rubio 320; El Rincon, Rzedowski 42980; El Lobo Landa, Rzedowski 43997; 3 km from La Parada, B. Servin 1863; S. Zamudio *et al*. 10480 (IEB). Steinmann *et al*. 3696 (AY641504, AY640456, AY643116, DQ382313, DQ400554).

R. virens Lindh. ex A.Gray MEXICO Coahuila: Sierra La Encantada, M. Carranza *et al*. C- 682, C-865, C-2279, 2126; Ramos Arizpe, J. Encina 836*; Sierra Paila, J. Marroquín 1388; Muzquiz J. Villareal 3545, 16948*; Sierra de la Madera, J. Villareal *et al*. 7313, (ANSM); Limeston Canyon, D. Flyr 1149* (DUKE). Nuevo León: Mpio. Bustamante, M. Carranza C-3643; Santa Catarina, Hinton *et al*. 24984 (ANSM). Tamaulipas: Near Villagran, C. Lundell 12477* (US). Querétaro: Mpio. Tolimán, Rzedowski 50139*; Sierra Peña Azul Vizarrón, S. Zamudio 2762; Jabalí Mpio. Cadereyta S. Zamudio 3027 (IEB). Zacatecas: 14 mi W of Sombrerete, D. Ward 5786*, (DUKE). Wen 7282 (AY641505, AY640457, AY643117, DQ 382320, DQ 400557).

R. chondroloma Standl. MEXICO Oaxaca: Tamazulapan, Teposcolula, L. Rico *et al*. 329; Sn Pedro Nopala, T. Salinas *et al*. s.n., (ANSM). Huajuapan de León, F. McCarten 2976*** (US). Tehuacán, Rzedowski 33957 (IEB). Hunn 59 (HE862257, HE862267---).

Actinocheita filicina (D.C) F.A.Barkley. MEXICO Guerrero: Iguala, C. Catalán *et al*. 783; Xochipala, E. Martínez 711, (IEB), Rzedowski 18652 (TEX). Oaxaca: Justlahuaca, S. Zamudio & G. Ocampo 11057 (IEB). Puebla: Izúcar de Matamoros, E. Guízar, 914, (IEB); Chapulco, J. Panero 7354; Tehuacán, Rzedowski 19130 (TEX). Panero s.n. (AY641509, AY640460, AY643120, DQ382321, DQ400558).

Malosma laurina (Nutt) Abrams. USA California: Rancho Sta. Ana, Gillis 9009; P. C. Everet, 2163; San Gabriel Mountains, T. Ross 3698; La Jolla, San Diego, J. Thorner s.n. (TEX). Miller 34 (AY641510, AY640461, AY643121, DQ382322, DQ400559).

Toxicodendron diversilobum Torr. & Gray. MEXICO Baja California: El Mandadero, Mpio. Ensenada, Tenorio & Romero 13397; El Observatorio, San Pedro Martir, Tenorio and Romero 13231* (IEB). Wen 6693 (AY677202, AY677208, AY677205, DQ382328, DQ4005689).

Toxicodendron radicans (L.) Kuntze. MEXICO Baja California: Sierra de La Laguna, R. 944 (IEB). Chihuahua: Municipio de Madera, Bravo-Bolaños, 890 (ANSM). Jalisco: Zapopan, Santana F. *et al*. 3178 (IEB). Nuevo León Sierra de Anahuac, Sánchez Vega,640 (ANSM). Sonora: Mpio. Yecora, Tenorio L. 4566; Tamaulipas: Gómez Farias, Avendaño R. & Naruve F. 1701; Veracruz: Chicantepec, Duran E.C. *et al*. 290; Chiconquiaco, Gutíerrez C. 3232 (IEB). USA. River at Co. H. E. Ahles 59889*; Northeast of Pollocksville, Jones Co. M. N. Sears 6736 (NCU). Wen 6236 (AY677203, AY677207, AY677206, DQ382329, DQ400569).

Toxicodendron vernix L. USA. Chowan river, Gates Co. H. E. Ahles 40371; Swampy Roads, road to Morston H.E. Ahles 24843; Swampy Hollow, Wake Co. W. B. Fox 3806 (NCU). Woodfort C. Illinois, H. Chase, 16013 (ANSM). Wen 7146 (AY541520, AY640471, AY643131, DQ382330, DQ400570).

Searsia ciliata Miller 47 (AY641513, AY640464, AY643124--). *Searsia quartiniana* Miller 51 (AY641517, AY640468, AY643128, DQ382331, DQ400566). *Shinus molle* Wen 6686 (AY641512, AY640463, AY643123, DQ382333, DQ400565).

APPENDIX 2

Structural characters and character states of *Rhus s.s*. analysed in this work.

Morphological characters:

(**1**) Leaf organization: 0 = multifoliate, 1 = trifoliate, 2 = simple.
(**2**) Rachis (midrib) winged: 0 = absent, 1 = present.
(**3**) Texture: 0 = membranaceous, 1 = chartaceous, 2 = coriaceous.
(**4**) Leaflets or leaf shape: 0 = ovate, 1 = elliptic, 2 = lanceolate.
(**5**) Leaflets or leaf base: 0 = obtuse, 1 = rounded, 2 = acute.
(**6**) Margin of leaflets: 0 = entire, 1 = serrate.
(**7**) Venation pattern: 0 = brochidodromous, 1 = craspedodromous, 2 = eucamptodromous, 3 = cladodromous.
(**8**) Course midvein: 0 = right, 1 = sinous.
(**9**) Course secondary veins: 0 = recurved, 1 = sinous, 2 = zig-zag.
(**10**) Tertiary veins pattern: 0 = irregular reticulate, 1 = weakly percurrent, 2 = transversely ramified.
(**11**) Marginal ultimate venation: 0 = looped, 1 = incomplete, 2 = fimbriate.
(**12**) Type of areole: 0 = imperfect, 1 = incomplete.
(**13**) Pilose indument: 0 = absent, 1 = present.
(**14**) Glands: 0 = absent, 1 = present.
(**15**) Freely ending veinlets terminals: 0 = without idioblast, 1 = idioblast type I, (veinlets simple to widening in spherical form at the end), 2 = idioblast type II (widened veinlets form spherical group due to the association with brachysclereids).
(**16**) Fiber in the freely ending veinlets: 0 = absent, 1 = present.
(**17**) Number of branches in the inflorescences: In mature inflorescences, the number of inflorescence axes are considered branches: 0 = more than three branches, 1 = three branches, 2 = two branches.
(**18**) Distance from base of the secondary branch to the first flower (measured with caliper at least three samples for species): 0 = 5–10 mm, 1 = 3–5 mm, 2 = 0.5–1.5 mm.
(**19**) Distance between flowers: 0 = 3–5 mm, 1 = smaller than 0.5 mm.
(**20**) Pedicel: 0 = absent, 1 = present.
(**21**) Pedicel length: 0 = 1.5–2.5 mm, 1 = smaller than 1mm.
(**22**) Ciliate sepals: 0 = absent, 1 = present.
(**23**) Red glandular hairs on principal axis of inflorescences and branches: 0 = absent, 1 = present.
(**24**) Bracteoles: 0 = absent, 1 = present.
(**25**) Red glandular hairs on the fruit surface: 0 = absent, 1 = present.

Anatomical characters:

Wood:

(**26**) Porosity: 0 = semi-ring, 1 = diffuse, 2 = ring-porous.

(**27**) Septate fibers: 0 = absent, 1 = present.
(**28**) Ray number of cells width: 0 = more than 4 cells wide, 1 = 1–3 cells wide.

Petiole:

(**29**) Number of canals in petiole: 0 = fewer of seven, 1 = more than seven.
(**30**) Xylary fibres in petiole: 0 = absent, 1 = present.
(**31**) Gelatinous fibre in xylem: 0 = absent, 1 = present.

Lamina:

(**32**) cuticle thickness: 0 = 6 μm or less, 1 = more than 6 μm.
(**33**) Cuticle surface: 0 = smooth, 1 = striate.
(**34**) Papillose epidermis : 0 = absent, 1 = present.
(**35**) Number of layer of palisade parenchyma: 0 = one layer, 1 = two unequal layers, 2 = two equally long layers, 3 = three layers.
(**36**) Presence of druses in mesophyll: 0 = absent, 1 = present.
(**37**) Prismatic crystals in mesophyll: 0 = absent, 1 = present.

Midvein:

(**38**) Presence of papillose epidermis: 0 = absent, 1 = present.
(**39**) Fibres in xylem: 0 = absent, 1 = present.
(**40**) Arrangement of vascular tissue of midvein: 0 = type I (simple, open arch with one, additional vascular bundle in the adaxial region without fibre encircling the bundle), 1 = type II (simple, open arch with one additional vascular bundle in the adaxial region with fibres encircling the bundle), 2 = type III (simple, open arch with fibres encircling the vascular system), 3 = type IV (closed arch).