

NUCLEAR RIBOSOMAL DNA PHYLOGENY AND ITS IMPLICATIONS FOR EVOLUTIONARY TRENDS IN MEXICAN *BURSERA* (BURSERACEAE)¹

JUDITH X. BECERRA AND D. LAWRENCE VENABLE

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721

The genus *Bursera* (Burseraceae) is one of the most diversified and abundant groups of plants of the tropical dry forests of Mexico. In order to provide a basis for better understanding of its evolutionary biology, we reconstructed a phylogeny of 57 species and varieties using the nucleotide sequences of the internal transcribed spacer regions (ITS1 and ITS2) of 18S–26S and the 5.8S coding region of nuclear ribosomal DNA. We used four species of the allied genera *Commiphora* and *Boswellia* and one species of *Spondias* (Anacardiaceae) as outgroups. Our results support the views that *Bursera* is monophyletic and more closely related to *Commiphora* than to *Boswellia*. The division of *Bursera* into sections *Bullockia* and *Bursera* is also strongly supported by our phylogeny. Several other subclades also had high bootstrap values, especially within section *Bursera*. We use the phylogeny as a basis for discussing evolutionary tendencies in bark, leaves, breeding systems, and fruits.

Key words: *Boswellia*; *Bursera*; Burseraceae; burseras; *Commiphora*; copal; cuajotes; evolutionary trends; ITS sequences; phylogenetic analysis.

Burseras are New World relatives of frankincense (*Boswellia*) and myrrh (*Commiphora*). The genus comprises ~100 species distributed from the southwestern United States to Peru. It reaches its maximum diversity in the Pacific slopes of Mexico where ~80 species occur and ~70 are endemic (Rzedowski and Kruse, 1979; Daly, 1993).

Burseras are typically low or medium-size trees, and some are also small shrubs or large trees. Many species have succulent trunks colored blue, yellow, green, red, or purple. The outer bark of some species exfoliates in papery flakes or sheets of bright colors often different from that of the trunk. The genus is notable for its terpenoid secretions and exudates (Mooney and Emboden, 1968; Becerra and Venable, 1990; Becerra, 1994, 1997). These secretions arise from a system of resin canals found in the cortex of the trunk and in the leaves (Guillaumin, 1909) and are known to provide chemical defense against specialized herbivores (Becerra and Venable, 1990). The shape, size, and morphology of the leaves are highly variable among species. They are alternate and usually once- or twice-pinnate, but some are unifoliolate or trifoliolate. Leaves range from <1 to 50 cm long. Leaflet size and shape are also highly variable. All species are drought deciduous and usually flower at the end of the dry season. Most burseras are dioecious or polygamo-dioecious, although a few are apomictic or hermaphrodite. The actinomorphic flowers are usually less than a centimetre long

and are arranged in inflorescences that may include as few as one or up to 70 or more flowers. The flower color is usually pale yellow, although in some species it is wine-red. Most species are generalists in terms of pollinators, being visited by bees, flies, and small wasps. The predominantly bird-dispersed fruits are small, single-seeded dehiscent drupes with the seed partially or completely covered by a cream to red pseudoaril.

In Mexico, *Bursera* is one of the most important physiognomic components of the tropical dry forests. In many places, like the depression of the Balsas River in Michoacán and Guerrero or the dry canyons of the Tehuantepec River in Oaxaca, the genus becomes the dominant or codominant woody taxon, surpassing the legumes in diversity and abundance (Miranda, 1947; Rzedowski, 1978). They are also conspicuous constituents of habitats like desertscrub and thornscrub of the Mexican central and northern deserts and occur to a lesser extent in lowland tropical rain forests and higher altitude woodland. As is true of other Burseraceae, *Bursera* is a good indicator of relatively intact natural vegetation, because few species occur in secondary growth (Rzedowski and Kruse, 1979; Daly, 1992).

Because of its importance in the Mexican vegetation, the genus has been the subject of taxonomic studies continuously since the end of last century. Nevertheless, its classification is still problematic and its phylogenetic relationships are not well understood. Part of the problem is the scarcity of herbarium specimens with flowers. Since the small, superficially uniform flowers appear in the spring before the macroscopically more variable leaves, it is unusual to have matching specimens of flowers and leaves. As a result, the taxonomy of the group has been largely inferred from leaf morphology and bark characteristics, and to a lesser extent by fruit morphology, the morphology of the cotyledons and resin chemical profiles. However, in other groups of plants, bark and, in particular, leaf characteristics have proven to be very la-

¹ Manuscript received 17 February 1998; revision accepted 8 December 1998.

The authors thank Mark Porter, Al Agellon, Dick Olmstead, and the personnel of the Laboratory of Molecular Systematics and Evolution of the University of Arizona for helping with DNA sequencing techniques, Teresa Terrazas for DNA samples of *Spondias mombin*, and Daniel Piñero and the Institute of Ecology at the National Autonomous University of Mexico for help with the logistics of plant collection. This work was supported by NSF (INT-9505941, BSR-9520888 and BSR-9815648), the Alfred P. Sloan Foundation, and the National Geographic Society. We wish to dedicate this work to Jerzy Rzedowski.

bile and often unreliable for clarifying phylogenetic affiliations (Stebbins, 1950; Donoghue and Sanderson, 1992). Also, some species like *B. schlechtendalii*, *B. bipinnata*, *B. paradoxa*, and *B. tecomaca* have very distinctive leaf characteristics making it difficult to determine their affinities with other species using leaves. Becerra (1997) has also shown that there is considerable convergence in the presence and absence of particular terpenes. Thus, this is a group for which molecular data might prove especially useful for determining phylogenetic affiliations.

The purpose of this investigation was to infer the evolutionary relationships within *Bursera* and between *Bursera* and related genera. To do this, we have conducted a phylogenetic analysis of nucleotide sequences of the internal transcribed spacer (ITS) region of the nuclear ribosomal DNA from 57 species and varieties of Mexican *Bursera* and five outgroup taxa.

Systematics of *Bursera*—The Burseraceae includes ~20 genera and >600 species of trees and shrubs from the subtropical and tropical regions of Africa, Asia, North America, and South America. Having resin ducts containing aromatic terpenes and essential oils is characteristic of the family (Standley, 1923; Gillett, 1991; Rzedowski and Guevara-Féfer, 1992). Recent studies using molecular and anatomical data suggest that the sister family to the Burseraceae is the Anacardiaceae (Terrazas-Salgado, 1994). *Bursera*, together with the tropical genera *Triomma*, *Aucoumea*, *Boswellia*, *Commiphora*, and *Beiselia* form the tribe Bursereae or Boswelliae (Engler, 1931; Lam, 1932; Rzedowski and Kruse, 1979; Forman et al., 1991), which is considered to be an advanced group within the Burseraceae. *Bursera* is distinguished from the rest of the family by having a valved, one-seeded, dehiscent drupe and a calyx that opens in the bud (Gillett, 1980, 1991).

The genus has been divided into two subgenera or sections (McVaugh and Rzedowski, 1965; Rzedowski, 1968; Becerra, 1997). Section *Bullockia* includes species with a trivalvate fruit, four merous flowers, branch rosettes with cataphylls, and grayish-red or grey rough bark. The outer layers of the bark are, in most cases, rough and do not separate in sheets. Toledo (1982) further divided this section into two groups: the species whose fruits are completely or almost completely covered by the pseudoaril and the species in which the pseudoaril covers the fruit only partially. In species of section *Bursera*, flowers are three, four, and five merous (often five merous in the male and three merous in the female), fruits are bivalvate, leaves have no cataphylls, and the colorful bark peels off in papery sheets, giving rise to the common name “cuajote,” which means “leprous tree” in Nahuatl. There are three distinctive groups of species in this section according to Toledo (1982). In the first group (the mulatos), the cotyledons are trilobate as in the species of section *Bullockia* and trees have red-exfoliating bark. The second group, the red-barked cuajotes, includes species with multilobate cotyledons and red-exfoliating bark. In the last group, the yellow-barked cuajotes, the cotyledons are also multilobate, but the bark exfoliates in yellow sheets.

Since the early studies, evidence has suggested that

within the Burseraceae *Bursera* is very closely related to the genus *Commiphora* and also to *Boswellia*, but the relationships among these three genera are not clear. *Boswellia* includes ~30 species distributed in the drier parts of tropical Africa, Arabia, Pakistan, Iran, Ceylon, and India. They are trees with some traits shared with section *Bursera* like exfoliating bark, five merous flowers, and a usually trilobular ovary. Their main difference from the genus *Bursera* is that in *Boswellia* the locules of the ovary are all fertile, with more than one seed (Engler, 1931; Rzedowski and Kruse, 1979). *Commiphora* includes ~200 species, and their distribution is similar to that of *Boswellia*. They are trees or shrubs sharing some similarities with species of section *Bullockia*. They have a nonexfoliating bark, four-merous flowers, and bilobular ovaries. Their main difference with the genus *Bursera* is their calyx, which is closed in the bud (Gillett, 1980). Because of the morphological affinities between section *Bursera* and *Boswellia* and between section *Bullockia* and *Commiphora*, Rzedowski and Kruse (1979) hypothesized that *Bursera* might be diphyletic. Other authors have suggested that *Bursera* is not monophyletic because it includes species that should belong to *Commiphora*. Based on pollen morphology Rzedowski and Palacios (1985) and Palacios (1984) suggested that *B. tecomaca* and *B. sarcopoda* were closer to *Commiphora* than to *Bursera*.

Some systematists have also proposed that *Commiphora* and *Bursera* should be combined into a single genus (Gillett, 1980). Others consider that *Bursera* is closer to *Boswellia* and have combined them with *Triomma* into the subtribe Burserinae, leaving *Commiphora* in the other subtribe, the Commiphorinae (Lam, 1932).

MATERIALS AND METHODS

The species involved and outgroup selection—This study included 54 species of Mexican *Bursera* (Table 1). One of these species, *B. fagaroides*, has three varieties, and some authors believe they could be different species (McVaugh and Rzedowski, 1965). We included the three varieties in the analyses. We also included the species *Terebinthus acuminata* and *B. diversifolia*. McVaugh and Rzedowski (1965) recognized that *T. acuminata* should belong to *Bursera*. However, they deferred a formal name change until it could be determined whether it was distinct or conspecific to *Bursera attenuata* or *B. simaruba*. *Bursera diversifolia* has been recognized as a group of forms that resulted from hybridization, between *B. bipinnata* and usually *B. copalifera* (Toledo, 1982). Our collection would correspond to the putative *B. bipinnata* × *B. copalifera* hybrid.

Four species of the allied genera *Commiphora* and *Boswellia* and one species of the Anacardiaceae genus *Spondias* were used to elucidate the relationships among the three Burseraceae genera.

Most *Bursera* species were collected in the field, whereas the outgroups were obtained from private collections and botanical gardens (Table 1). Small branches of the plants were collected to make vouchers specimens (Table 1) and a few leaves were stored in plastic bags, which contained 20–30 g of silica gel for quick drying to preserve DNA. One set of voucher specimens was deposited at the Herbarium of the University of Arizona and another set was deposited at the National Mexican Herbarium (National Autonomous University of Mexico, Mexico City).

DNA extraction, amplification, and sequencing—Total genomic DNA was isolated from 0.1 g of the dry leaf materials following the

protocol described by Doyle and Doyle (1987). Because of the high amounts of resins present in the leaves, we substituted 4XCTAB (hexadecyltrimethylammonium bromide) for 2XCTAB. DNA was subsequently purified with the S&S Elu-Quick DNA purification kit according to the instructions of the manufacturer (Scheiler & Schuell, Keene, New Hampshire; order number 74450).

The internal transcribed spacers (ITS1 and ITS2) and the 5.8S coding region were amplified from total genomic DNA by the polymerase chain reaction (PCR). The amplifications were performed in 50- μ L reactions using a Perkin-Elmer Cetus *GeneAmp* reagents kit (Cetus Corporation, Norwalk, Connecticut; part number N808-0009). The reactions included 27.6 μ L of sterile water, 3.0 μ L of glycerol, 5.0 μ L of 10 \times PCR buffer, 5.0 μ L of 200 μ mol/L dNTPs in an equimolar ratio, 4.0 μ L of 25 mmol/L MgCl₂ solution, 0.2 μ L of AmpliTaq DNA Polymerase, 0.2 μ L of pg32 (T4 Gene 32 protein from Ambion, catalog number 2424), 2 μ L of ITS4 (TCCTCCGCTTATTGATATGC) primer, 2 μ L of ITS5 (GCAAGTAAAAGTCGTAACAAGG) primer, and 1 μ L of template. Reaction samples included positive and negative controls. The cycling amplification profile followed the one described by Baldwin (1992). PCR products were purified using Microcon 100 microconcentrators (W. R. Grace and Co., Beverly, Massachusetts; product number 42413), and then sequenced with the automated sequencer ABI-373 (Applied Biosystems, Foster City, California).

To obtain reliable sequences, all the species included in the study were sequenced at least once with primers ITS5, ITS4, and also with internal primers ITS2 (GCTGCGTTCTTCATCGATGC) and ITS3 (GCATCGATGAAGAACGCAGC). The ITS region in *Bursera* comprises ~700 base pairs, and each reading from the sequencer included ~420 perfectly readable base pairs, for most species. Thus, the central section of the ITS region (including the 5.8 cistron) was read four times (twice in each direction), and the distal sections of the region were read twice (once in each direction).

Alignment of sequences and phylogenetic analyses—Sequences were aligned with the Genetics Computer Group software package (GCG; Madison, Wisconsin), and subsequently further aligned with the program Sequencher (1995). Finally, correction of the last small misalignments was performed manually with Sequencher. Since none of the sequences were identical, we included all taxa in the analysis. Each gap position was treated as missing data to retain information about nucleotide substitutions in taxa with the insertion (Wojciechowski et al., 1993). Also, entire gaps that were unambiguous and potentially informative (shared by two or more species) were scored and entered as separate characters. All sequences were submitted to GenBank (accession numbers GBAN-AF080003 to GBAN-AF080064; the prefix GBAN- has been added for linking the on-line version of *American Journal of Botany* to GenBank but is not part of the actual accession number).

Phylogenies were inferred from the sequence matrix using parsimony analysis with PAUP 3.1.1 (Swofford, 1993) under the Fitch criterion. We performed heuristic searches because of the large number of species included. To maximize the probability of finding the shortest possible trees our phylogenetic analyses implemented several combinations of sequence-addition and branch swapping. We did (1) SIMPLE addition and tree bisection reconnection (TBR) branch swapping; (2) CLOSEST addition and TBR branch swapping; (3) 20 replicates of RANDOM addition and nearest-neighbor interchange (NNI) branch swapping; and (4) 400 replicates of RANDOM addition and TBR branch swapping. Character state changes were weighted equally. The amount of phylogenetic information in the analysis was estimated using the consistency index (Kluge and Farris, 1969), the retention index (Farris, 1989) and the g1 statistic (from 10 000 random trees; Huelsenbeck, 1992).

To estimate the relative robustness of individual clades, we implemented a bootstrap analysis, which involved 500 bootstrap searches with 40 replicates of RANDOM addition and TBR branch swapping.

RESULTS

Alignment of the nucleotide sequences resulted in a matrix of 799 nucleotide characters plus 29 characters corresponding to gaps. Of the nucleotides and gaps 385 (53%) were potentially informative phylogenetically.

The searches generated four maximally parsimonious trees that involved 1326 evolutionary steps. All the random-addition replicates converged on the same four trees, suggesting that we probably did find the optimal trees (Swofford, 1993). Their consistency index was 0.57 and their retention index was 0.74. The g1 statistic was -0.22, suggesting significant phylogenetic signal (Huelsenbeck, 1991). Only the search that involved NNI branch swapping converged on longer trees (six trees of 1327 steps).

The strict consensus tree is highly resolved (Fig. 1), which suggests that ITS was a good choice for this molecular study. The four most parsimonious trees differed topologically in the resolution of the position of *B. heteresthes* and *B. mirandae* from section *Bullockia*. In two of these maximally parsimonious trees, the root of the clade with these two species is unresolved, whereas in the other two trees their root is resolved and situated as the sister clade of the clade that includes *B. palmeri*, *B. infernidialis*, *B. penicillata*, *B. stenophylla*, and *B. hindisiana*. Also, *B. palmeri* appears in two of the trees as the sister species of the four other species in its clade, whereas in other two trees it is the sister species of only *B. penicillata* and *B. infernidialis*.

Many clades had relatively high bootstrap values, especially the clades including the major lineages and the subgroupings in the section *Bursera* (Fig. 1). Sequences of species belonging to section *Bullockia* appear to have lower divergence (Fig. 2), which results in lower bootstrap values.

DISCUSSION

Relationship of the principal lineages—Our most parsimonious trees do not support the hypothesis that *Bursera* is a diphyletic genus with one section related to *Commiphora* and the other to *Boswellia* (Rzedowski and Kruse, 1979). Rather, our results are consistent with previous arguments that *Commiphora* and *Bursera* are closely related (Rzedowski and Kruse, 1979; Gillett, 1980). The members of *Commiphora* and *Bursera* sampled resolve as a monophyletic sister groups, with considerable ITS sequence differentiation between them and 100% bootstrap support for each. Even *B. tecomaca*, which has been repeatedly suggested to belong to *Commiphora* (Palacios, 1984; Rzedowski and Palacios, 1985), clearly falls within the clade of *Bursera* section *Bullockia* with 100% bootstrap support. Although our sampling of *Bursera* was extensive, our analysis includes only three of the 200 species of *Commiphora*. Thus, while these *Bursera* species are clearly more related to each other than to the three species of *Commiphora*, a broader taxonomic sample of *Commiphora* is desirable to confirm separate monophyly. However, further sampling is unlikely to place *Bursera* section *Bursera* closer to *Boswellia* than to *Commiphora*.

The division of the genus into two sections is strongly

TABLE 1. Species of *Bursera* and related taxa included in the analysis.

Species	Collection site	Distribution	Voucher specimen ^a
Burseraceae			
<i>Bursera</i>			
Section <i>Bursera</i> (Cuajiototes)			
Mulatos group			
<i>B. arborea</i> (Rose) Riley	Playa de Oro, Colima, Mex	Pacific Coast	247,240
<i>B. attenuata</i> Rose	Compostela, Nayarit, Mex	Pacific Coast (Nayarit and Sinaloa)	231,230
<i>B. grandifolia</i> (Schlecht.) Engler	Alamos, Sonora, Mex	Pacific Coast, Balsas Depression	339,340
<i>B. longipes</i> (Rose) Standl.	Izucar de Matamoros, Puebla, Mex	East side of the Balsas Depression	384,383
<i>B. instabilis</i> Rzedowski	Chamela, Jalisco, Mex	Pacific Coast (from Jalisco to Oaxaca)	504,246
<i>B. simaruba</i> (L.) Sarg.	Alamos, Sonora, Mex	South East US to South America	511,512
Red Cuajiototes group			
<i>B. arida</i> (Rose) Standl.	Zapotitlan, Puebla, Mex	Narrow endemic, Tehuacan Desert	127,133
<i>B. chaemepodiata</i> Rzedowski & Ortiz	Xochipala, Guerrero, Mex	Narrow endemic, Zopilote Canyon	304,302
<i>B. crenata</i> P.G. Wilson	Apatzingan, Michoacan, Mex	West Side of the Balsas Depression	215,214
<i>B. denticulata</i> McVaugh & Rzedowski	Achuato, Michoacan, Mex	West Side of the Balsas Depression	318,334
<i>B. fagaroides</i> (H.B.K.) Engl. var. <i>elongata</i> McVaugh & Rzedowski	Hermosillo, Sonora, Mex	Sinaloa and Sonora	502,503
<i>B. fragilis</i> S. Watson	Mazatlan, Sinaloa, Mex	Nayarit, Sinaloa, and Sonora	504,505
<i>B. galeottiana</i> Engl.	Tamazulapan, Oaxaca, Mex	Tehuacan-Cuicatlan Desert and Bajío region	272,271
<i>B. kerberi</i> Engler	Ceboruco, Nayarit, Mex	West side of the Balsas Depression to Nayarit	239,238
<i>B. lancifolia</i> (Schlecht.) Engl.	La Laja, Puebla, Mex	East side of the Balsas Depression to Oaxaca	348,347
<i>B. microphylla</i> A. Gray	Hermosillo, Sonora, Mex	Baja California and Sonora	507,508
<i>B. morelensis</i> Ramirez	San Pablito, Puebla, Mex	East side of the Balsas Depression to Oaxaca	350,112
<i>B. multijuga</i> Engl.	El Refilion, Nayarit, Mex	From Sinaloa to Colima	237,241
<i>B. paradoxa</i> Guevara et Rzedowski	San Pedro Barajas, Michoacan, Mex	Infiernillo region in Michoacan	205,206
<i>B. schlechtendalii</i> Engl.	Zapotitlan, Puebla, Mex	From Tamaulipas and Jalisco to Guatemala	509,510
<i>B. suntui</i> Toledo	Xochipala, Guerrero, Mex	East side of the Balsas Depression to Oaxaca	359,360
<i>B. trifoliolata</i> Bullock	Luvianos, Mexico, Mex	West side of the Balsas Depression	369,136
<i>B. trimera</i> Bullock	Placeres del Oro, Guerrero, Mex	West side of the Balsas Depression	167,153
Yellow Cuajiototes group			
<i>B. aptera</i> Ramirez	Zapotitlan, Puebla, Mex	East side of the Balsas Depression to Oaxaca	282,501
<i>B. ariensis</i> (H.B.K.) McVaugh & Rzedowski	Salto Valadez, Guerrero, Mex	From Nayarit to Oaxaca	124,121
<i>B. discolor</i> Rzedowski	Salto Valadez, Guerrero, Mex	Balsas Depression	319,320
<i>B. fagaroides</i> (H.B.K.) Engl. var. <i>fagaroides</i>	Atotomilco, Jalisco, Mex	High Plateau	330,329
<i>B. fagaroides</i> (Brandeg.) var. <i>purpusii</i> McVaugh & Rzedowski	La Pera, Mexico, Mex	From Veracruz to Michoacan	333,102
Section <i>Bullockia</i> (Copales)			
Copales with fruits covered by the pseudoaril			
<i>B. asplenifolia</i> T.S. Brandeg	Huajuapán de Leon, Oaxaca, Mex	Oaxaca	277,276
<i>B. bicolor</i> (Wild. ex Schlecht.) Engler	La Laja, Puebla, Mex	Balsas Depression	275,274
<i>B. bipinnata</i> (Sesse & Moc.) Engl	Atotomilco, Jalisco, Mex	Pacific slopes from Sonora to Guatemala	256,236
<i>B. copallifera</i> (Sesse & Moc. ex DC) Bullock	Salto Valadez, Guerrero, Mex	Balsas Depression	113,110
<i>B. cuneata</i> (Schlecht) Engl.	La Pera, Mexico, Mex	From Guanajuato to the State of Mexico	309,310
<i>B. diversifolia</i> Rose	Alquitran, Guerrero, Mex	Pacific slopes from Jalisco to Oaxaca	120,119
<i>B. excelsa</i> (H.B.K.) Engl.	Mazatlan, Sinaloa, Mex	Pacific Coast	
<i>B. hintoni</i> Bullock	Zicuiran, Michoacan, Mex	Pacific Coast, Balsas Depression	219,218
<i>B. palmieri</i> S. Wats	Queretaro, Queretaro, Mex	High Plateau from Durango to Michoacan	163,162
<i>B. sarukhanii</i> Guevara et Rzedowski	Ziquiran, Michoacan, Mex	Infiernillo region in Michoacan	212,213
<i>B. submoniliformis</i> Engler	Izucar de Matamoros, Puebla, Mex	East side of the Balsas Depression to Oaxaca	264,282
<i>B. vejar-vazquezii</i> Miranda	Izucar de Matamoros, Puebla, Mex	East side of the Balsas Depression	269,268
<i>B. velutina</i> Bullock	Placeres del Oro, Guerrero, Mex	West side of the Balsas Depression	377,140

TABLE 1. Continued.

Species	Collection site	Distribution	Voucher specimen ^a
Copales with fruit partially covered by the pseudoaril			
<i>B. aloexylon</i> (Shiede ex Schlecht.) Engler	Izucar de Matamoros, Puebla, Mex	East side of the Balsas Depression to Oaxaca	261,260
<i>B. biflora</i> (Rose) Standl.	Zapotitlan, Puebla, Mex	Narrow endemic, Tehuacan Desert	296,297
<i>B. bonetti</i> Rzedowski	Chilpancingo, Guerrero, Mex	Narrow endemic, Chilpancingo region	298,299
<i>B. coyucensis</i> Bullock	Placeres del Oro, Guerrero, Mex	West side of the Balsas Depression	312,313
<i>B. filicifolia</i> Brandegee	Arizona-Sonora Desert Museum	Narrow endemic, Cape Region	342,115
<i>B. glabrifolia</i> (H.B.K.) Engler	Salto Valadez, Guerrero, Mex	Balsas Depression	203,202
<i>B. heterosthes</i> Bullock	Uruapan, Michoacan, Mex	Pacific Coast, Balsas Depression	
<i>B. hindstiana</i> (Benth.) Engler	Arizona-Sonora Desert Museum	Baja California and Sonora	
<i>B. infernalis</i> Guevara <i>et</i> Rzedowski	Zicuiran, Michoacan, Mex	Infernillo region in Michoacan	208,209
<i>B. laxiflora</i> S. Wats	Microondas La Colmena, Sonora, Mex	Baja California and Sonora	505,506
<i>B. mirandae</i> Toledo	Xochipala, Guerrero, Mex	East side of the Balsas Depression to Oaxaca	349,351
<i>B. penicillata</i> (Sesse & Moc. ex DC) Engl.	Ceboruco, Nayarit, Mex	Pacific slopes from Sonora to Colima	253,251
<i>B. stenophylla</i> Sprague & Riley	Alamos, Sonora, Mex	Sonora, Chihuahua, and Sinaloa	513,514
<i>B. tecomaca</i> (D.C.) Standl.	Alquitran, Guerrero, Mex	Narrow endemic, Chilpancingo region	366,367
<i>B. xochipalensis</i> Rzedowski	Chilpancingo, Iguala, Mex	East side of the Balsas Depression	380,124
<i>Commiphora</i>			
<i>C. monstruosa</i> (Perrier) Capuron	Private collection of Charles Hanson	Madagascar	
<i>C. simplicifolia</i> Perrier	at Arid Lands Greenhouse, Tucson, AZ	Madagascar	
<i>C. virgata</i> Chiov.		South Africa	
<i>Boswellia</i>			
<i>B. hildebrandtii</i> Engl.	Arid Lands Greenhouse, Tucson, AZ	Northeast Africa	
<i>Terebinthus</i>			
<i>T. acuminata</i> Rose	Tejupilco, Mexico, Mex	Nayarit to Michoacan	228,227
Anacardiaceae			
<i>Spondias</i>			
<i>S. Mombin</i> L.	Fairchild Tropical Gardens	Mexico to South America, Africa	

^a First number corresponds to the voucher specimen deposited at the University of Arizona Herbarium (ARIZ) and the second to the one deposited at the Mexican National Herbarium at the Autonomous National University of Mexico (MEXU). All accession numbers are Becerra and Venable. We did not make vouchers from species whose leaf tissues were donated by botanical gardens and private collections.

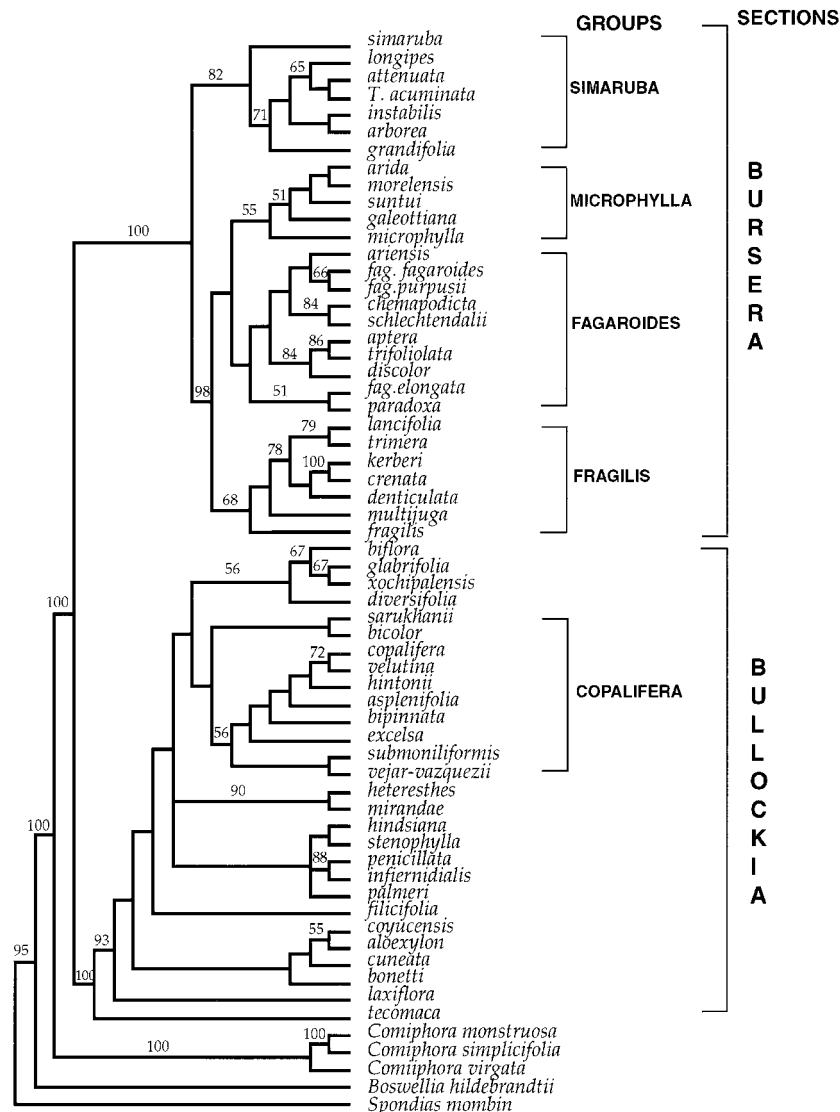


Fig. 1. Phylogeny of *Bursera* based on the nucleotide sequences of the ITS1, ITS2, and 5.8S regions of nuclear ribosomal DNA. Strict consensus tree of the four maximally parsimonious trees founded by heuristic analyses. *Commiphora monstrosa*, *C. simplicifolia*, *C. virgata*, *Boswellia hildebrandtii* (Burseraceae), and *Spondias mombin* (Anacardiaceae) were used as outgroups. Numbers above branches are bootstrap percentage values for clades supported above a 50% bootstrap value.

supported by our DNA phylogeny. McVaugh and Rzedowski (1965) stated that these sections form good natural groups. In our phylogeny they are each monophyletic with 100% bootstrap values. Traditionally, the morphological trait most frequently used to distinguish the two sections is the presence or absence of the exfoliating bark (McVaugh and Rzedowski, 1965). Yet, *B. paradoxa* and *B. mirandae* have anomalous traits. The overall morphology, including a trivalvate drupe and trilobular ovary of *B. paradoxa*, indicates its affiliation with section *Bursera* (Guevara-Féfer and Rzedowski, 1980), but its non-peeling gray bark is like that of section *Bullockia*. The opposite occurs with *B. mirandae*, which has the general morphology of a *Bullockia* species but also has a peeling bark (Toledo, 1984). Our phylogeny confirms that these species should be classified according to their general morphology, not their bark characteristics. Closer exam-

ination of the traits of these species reveals that the exfoliation in *B. mirandae* is atypical in its thickness as compared to the usually papery thinness of the exfoliation of species of section *Bursera* (Toledo, 1984). Likewise, seedlings and young juveniles of *B. paradoxa* retain their sectional traits of papery exfoliating bark (personal observation).

Subdivisions of the sections into monophyletic groups—McVaugh and Rzedowski (1965) and Rzedowski and Kruse (1979) recognized the mulato group within section *Bursera* as a natural, well-defined group (Table 1). These species are distinguished from the rest of the genus by their red exfoliating bark, leaflets with entire margins and apices mostly acuminate, and trilobate cotyledons. Monophyly is strongly supported by the molecular phylogeny (Fig. 1). *Terebinthus acuminata* falls into

this group, confirming the widely held belief that it is indeed a *Bursera*. Its position in the phylogeny suggests that it may be more closely related to *B. attenuata* than to *B. simaruba*. Further population studies are required to determine whether these two species should be combined.

Our consensus tree contains three other recognizable groups in section *Bursera*: the *fragilis* group, the *fagaroides* group, and the *microphylla* group. Until more reproductive characteristics are gathered, the most conspicuous difference between these three groups and the mulatos is that the mulatos have trilobate seedlings and the leaflets with margin entire, whereas the other three groups have multilobate seedlings. The *fragilis* group is distinguished by having generally serrate (or crenate) leaflet margins, whereas the *fagaroides* and *microphylla* groups have generally entire margins. The *microphylla* group has distinctive small linear leaflets and red trunks.

Although bootstrap support is not high for any of these groups, except the mulato group, the general outlines of these groups are consistent with previous systematic treatment. The *microphylla* group has been consistently recognized as a set of related species (Bullock, 1936; McVaugh and Rzedowski, 1965; Toledo, 1984), although reservations regarding monophyly have sometimes been expressed based on the possibility of convergence in leaf morphology (e.g., Toledo, 1982). The monophyly of this group in our strict consensus tree suggests that leaf morphology of this group is a good synapomorphy. The *fagaroides* and *fragilis* groups have also been consistently recognized as natural groupings, though *B. paradoxa*, *B. trifoliolata*, and the closely related pair *B. chemapodicta* and *B. schlechtendalii* are distinctive and have always been difficult to place (McVaugh and Rzedowski, 1965; Guevara-Féfer and Rzedowski, 1980). Nonetheless, the remaining species have been recognized as having clear affinities with one of these two groups. Thus, our strict consensus tree confirms the idea that these are likely to be good groupings with the possible exception of the four "difficult" species. All four of these difficult species have attached to the *fagaroides* clade in the molecular phylogeny. It is perhaps indicative of their distinctive status that this clade has the lowest bootstrap value of the four. Indeed, when these four species are excluded from analysis, the bootstrap value for the *fagaroides* group increases to 59%. Of the four, *B. trifoliolata* is most convincingly placed with strong bootstrap support for its close relationship to the yellow-barked *B. aptera* and *B. discolor*.

The division of the nonmulato species of section *Bursera* into red-bark cuajotes and yellow-bark cuajotes (Table 1; Toledo, 1982) is not supported by the molecular phylogeny. The red-barked *microphylla* group comes out closer to the yellow-barked *fagaroides* group than to the red-barked *fragilis* group. Also, the position of the red-barked species, *B. schlechtendalii*, *B. trifoliolata*, and *B. chemapodicta* within the *fagaroides* group, further detracts from the idea that red and yellow bark are good synapomorphies.

Several smaller clades within these groups have some support. *Bursera chemapodicta* was originally described as a local endemic derived from *B. schlechtendalii*. Their close relationship is strongly supported (Fig. 1). In the

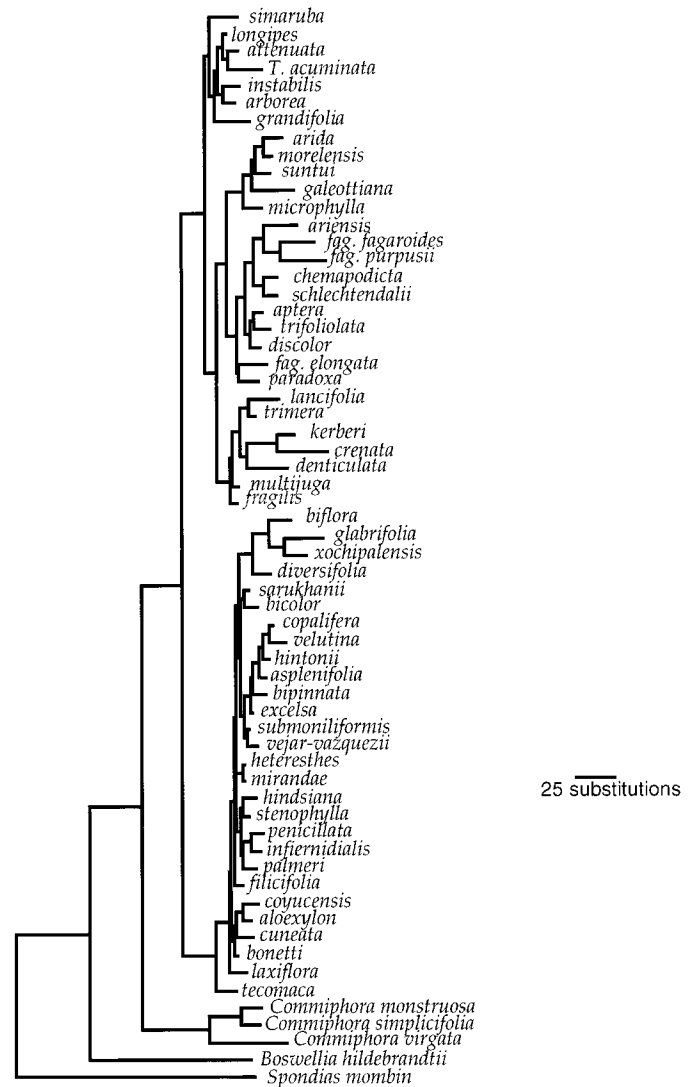


Fig. 2. One of the four maximally parsimonious trees derived from heuristic analyses of ITS and 5.8S regions among species of Mexican *Bursera*. Lengths of branches are proportional to the number of substitutions inferred.

fragilis group, *B. denticulata*, *B. crenata*, *B. kerberi*, *B. lancifolia*, and *B. trimera* appear to be closely related with two sister-species pairs involving reductions in leaflet number: the multifoliate *B. lancifolia* to tri- or unifoliate *B. trimera* and trifoliate *B. kerberi* to unifoliate *B. crenata*.

Further divisions of the *Bullockia* section based on the results of our phylogenetic analysis are less reliable because bootstrap values are low. This is somewhat expected from the lower level of DNA divergence at the lower branches of the tree, which result in lower bootstrap values even in the absence of contradictory characters (Sanderson, 1989). Nevertheless, some patterns can still be discerned. Toledo (1982) divided section *Bullockia* into two groups. The first one included species whose seeds are completely or almost completely (two-thirds or more) covered by the pseudoaril. The second group comprised species only partially covered (less than two-

thirds) by the pseudoaril. The strict-consensus tree contains a clade that consists exclusively of members of the covered-pseudoaril group, which we have labeled as the *copalifera* group (Fig. 1). Although all of the species in this clade are from the covered-pseudoaril group, several species with seeds completely or almost completely covered by the pseudoaril are not part of this clade (i.e., *B. cuneata*, *B. coyucensis*, *B. palmeri*, and *B. diversifolia* [which is probably a hybrid species]). That this clade exclusively contains plants previously posited to have close systematic affinity suggests that it may approximate a valid, monophyletic group. The rest of the section contains few monophyletic groups, and the characteristic of having a partially covered seed is not a good synapomorphy uniting them.

Several smaller clades have some support. *Bursera biflora*, *B. glabrifolia*, and *B. xochipalensis* form a monophyletic group in the strict-consensus tree, albeit with only 67% bootstrap support. Rzedowski suggests in his original description of *B. xochipalensis* (cited in Toledo, 1982) that it is closely related to *B. glabrifolia*. Likewise *B. biflora* has been posited to be a unifoliate derivative of *B. gabrifolia* (Bullock, 1936). Thus, agreement with previous systematic hypotheses suggests some validity for this clade. It is interesting that *B. diversifolia*, a putative hybrid between *B. bipinnata* and *B. copalifera* of the covering-aril clade attaches to the *B. biflora* clade. Toledo (1982) suggested that *B. cuneata*, *B. copalifera*, and *B. velutina* are closely related species that replace each other ecologically along an altitudinal gradient. Our study confirms that *B. copalifera* and *B. velutina* are sister taxa but suggests that *B. cuneata* is not closely related. *Bursera cuneata*'s positioning with *B. aloexylon* and *B. coyucensis* is supported by an unusual bifurcation of the style of females (the style divides below the stigma) in the specimens we examined of these three species (personal observation). There is strong bootstrap support for a close relationship between *B. mirandae* and *B. heteresthes*. This positioning seems reasonable on morphological grounds and Toledo (1982, 1984) previously suggested that *B. mirandae* may be close to "species such as *B. laxiflora*, *B. bonetti*, or *B. heteresthes*." *Bursera penicillata* and *B. infernialis* form a strongly supported species pair in the molecular phylogeny. Although reasonable on morphological grounds, their relationship has not been previously suggested.

Other details of the molecular analysis shed light on the taxonomy of the species. For example, *B. fragilis*, a species of northwestern Mexico, has been regarded as synonymous with *B. lancifolia* of south central Mexico (Bullock, 1936; Johnson, 1992). Although they have disjunct distributions, these two species exhibit considerable overlap in leaf and leaflet size and morphology, and in fruit characteristics. In our phylogeny, however, they are located rather far apart from each other, casting doubt on their conspecificity (Fig. 1).

The same is true of *B. laxiflora* and *B. filicifolia*, which, because of their similar morphological features, are sometimes considered synonymous (Felger and Lowe, 1970; Turner, Bowers, and Burgess, 1995). The former occurs in most of the state of Sonora, whereas the latter occurs only in southern Baja California. In our phylogeny they are quite distantly related for conspecifics.

According to the molecular phylogeny, two varieties of *B. fagaroides*, var. *fagaroides* and var. *purpusii*, form one clade, and var. *elongata* is in another more ancestral clade. This could be explained by a hybrid origin of var. *elongata*, between var. *fagaroides* and another species from the *fragilis* group (McVaugh and Rzedowski, 1965). But it is also possible that var. *elongata* is a completely different species from var. *fagaroides*. This study does not provide the best kind of evidence to resolve the placement of these three varieties, but, given their genetic differences in the ITS region (Fig. 2), perhaps they should be tentatively regarded as three separate species.

Evolutionary tendencies within the genus—There has been considerable discussion about the evolutionary tendencies of different characteristics of species of *Bursera* (Rzedowski and Kruse, 1979; Toledo, 1982). With this DNA phylogeny we can begin to make more definitive statements about evolutionary trends.

Colorful, peeling bark is probably one of the most striking features of this genus. This exfoliating bark may serve several functions (Rzedowski and Kruse, 1979). Peeling may provide light access to the photosynthetic layers of the trunk by occurring when the bark becomes opaque. It may discourage the establishment of lichens, which block light. It may impede the establishment of epiphytic seedlings, like those of *Ficus*, and it may attract fruit dispersers from a long distance. According to our phylogeny, the presence of an exfoliating bark is a primitive trait in section *Bursera*, with a subsequent independent evolution of a smooth nonpeeling bark in *B. paradoxa*. Red-peeling bark is primitive and yellow-peeling bark is derived, though there are some reversions as mentioned above. The opposite occurs in section *Bullockia* where smooth bark is ancestral, with subsequent evolution of peeling bark in *B. mirandae*.

Another interesting feature of burseras is the large variation in the size of leaves and the size, shape, and number of leaflets. Leaf size and shape are considered to be of adaptive significance in several ecological contexts (Givnish, 1979). Small, long-lived sclerophyllous leaves are considered important adaptations to nutrient stress, yet large systematic variation in nutrient availability is not readily apparent across *Bursera* habitats. Furthermore, most burseras occur in seasonally dry habitats and they produce one cohort of leaves that usually lasts the full wet season. This provides little opportunity for specialization with regard to longevity, with the possible exception of *B. simaruba*, which lives in evergreen rainforest, and *B. microphylla* and *B. hindsiana*, which occur in deserts where rainfall is more sporadic and somewhat less seasonal. However, there is a strong gradient in temperature and aridity across the habitats in which *Bursera* is found. Thus, leaf adaptations to mesic vs. arid gradients are expected. Leaf size and subdivision have important impacts on leaf energy budgets. Small leaves or leaflets can regulate their temperature to be near ambient, whereas the temperature of large leaves tends to increase above ambient upon exposure to high levels of solar radiation. The most important impact of high leaf temperature in arid habitats is greater transpirational loss of hard-to-obtain water. Reduction of leaf area or subdivision of leaves is thus favored in arid habitats.

The evolution of leaves in the section *Bursera* is instructive in this regard. The gross macroevolutionary pattern is one of reduction of leaf size as this section evolved into more arid habitats. First, the large-leaved *simaruba* clade separated from the rest (Table 2). Then, the smaller leaved *fragilis* clade separated. Finally, the even smaller leaved *fagaroides* clade separated from the smallest leaved *microphylla* clade. Species in these groups tend to live in progressively drier habitats along this evolutionary sequence (E. Huerta, J. X. Becerra, and D. L. Venable, unpublished data). Within each of these clades there was subsequent evolution of larger and smaller leaves in moister and drier habitats, respectively (e.g., *B. morelensis* vs. *B. arida* or *B. ariensis* vs. *B. schlechtendalii*).

Pinnately compound leaves represent the primitive condition in the genus. There have been repeated reductions in either number or size of leaflets in the different clades of section *Bursera* (Rzedowski and Kruse, 1979; Toledo, 1982). *Bursera instabilis* tends to have 1–3 leaflets, which is a reduction in number in the *simaruba* clade. In the *fragilis* clade *B. trimera* is, in our phylogeny, a trifoliate sister species to *B. lancifolia*, which frequently has 5–7 leaflets. *Bursera crenata* is a unifoliate sister species to the usually trifoliate *B. kerberii*. In the *fagaroides* clade *B. chemapodicta* and *B. schlechtendalii* are unifoliate derived species in contrast to *B. paradoxa*, which has evolved reduced leaflet size in the form of unusual narrowly linear leaflets. In all of these cases the derived species occur in hotter drier habitats. Leaf area of the whole *microphylla* clade is low. This condition has been achieved by the production of many small strap-shaped leaflets. *Bursera arida* represents a derived reduction in leaflet number in response to aridity within this clade.

Similar trends occur in section *Bullockia*. *Bursera biflora* is the often unifoliate sister species of pinnate *B. glabrifolia* and *B. xochipalensis* in our phylogeny. *Bursera heteresthis* is the trifoliate sister species of pinnately compound *B. mirandae*. *Bursera infernialialis* is a trifoliate sister species to pinnate *B. penicillata*. Bipinnate leaves with very small leaflets have evolved at least twice (*B. bipinnata* and *B. stenophylla*) from pinnate ancestors. The independent status of the often-bipinnate *B. laxiflora* and *B. filicifolia* from each other and from *B. stenophylla* is suggested by our most parsimonious trees. However, this part of the tree has short branch lengths and low bootstrap values, making the conclusion of independence tentative.

Basal breeding systems appear to be dioecious, though *B. simaruba* has been reported to be dioecious or polygamodioecious. At the base of section *Bullockia*, *B. tecomaca* and the clade involving *B. bonetti* are all dioecious. Although most species and populations of *Bursera* are dioecious, considerable variation in the breeding system occurs, mostly at the within-species level. In *B. fagaroides* var. *fagaroides*, we have observed all-female, presumably agamospermous populations, populations with males, females, and andromonoecious individuals (inconstant males with varying proportions of hermaphroditic flowers), and at least one population with male, female, andromonoecious inconstant males, and hermaphroditic individuals (E. Huerta and D. L. Venable, personal observations). We have observed dioecious and

hermaphroditic populations of *B. fagaroides* var. *elongata*. *Bursera medranoana* (not in our phylogeny, but putatively a hybrid between *B. morelensis* and *B. schlechtendalii*; Rzedowski and Ortiz, 1988) appears to also be agamospermous, consisting only of female individuals (Rzedowski and Ortiz, 1988; and E. Huerta and D. L. Venable, personal observations). In most populations of *B. galeottiana* the males appear to be inconstant, producing a few hermaphroditic flowers and fruits (E. Huerta and D. L. Venable, personal observation). *Bursera schlechtendalii* produces males, females, and inconstant males with hermaphroditic flowers and fruits, at least in some populations. Since *Bursera* flowers are small and often emerge before the species-identifying foliage, it is hard to gather information on the intraspecific distribution of sexual systems for the whole genus. Nonetheless, among-population variation in asexual vs. sexual or dioecious vs. hermaphrodite breeding systems present a rare opportunity for comparing these systems which typically occur in different genera or families of plants (Barrett, Harder, and Warley, 1996) and we are currently investigating these systems.

Likewise, much remains to be learned about the fruits of *Bursera*. The color and degree to which the pseudoaril covers the usually black seed are well documented (Rzedowski and Kruse, 1979; Toledo, 1982) and there are clear taxonomic patterns. All of section *Bursera* tends to have the pseudoaril completely covering the seed, and the color of the aril tends to be cream or yellow with some tendencies toward red, for example, in *B. schlechtendalii* and *B. crenata*. The pseudoaril is more variable in section *Bullockia*, with the *B. copalifera* clade having completely or almost completely covering, usually orange to red pseudoarils. Most of the remaining species have the aril covering half or less of the seed. *Bursera infernialialis* is unusual in having the pseudoaril covering half of one face of the seed, but most of the other. These seeds are attractive to birds and secondarily consumed by rodents once on the ground (Rzedowski and Kruse, 1979).

There is considerable variation in ecologically relevant fruit traits that are not well understood for the genus as a whole. Pseudoarils range from dry and papery to thick and fleshy with different water and sugar contents (Bates, 1992). Also seeds are matured either simultaneously or over a prolonged period (Rzedowski and Kruse, 1979). Bates (1992) studied *B. hindiana* and *B. microphylla* on the coast of Sonora, Mexico, and found that fruits of *B. hindiana* were used by a variety of generalist birds. It had higher dry mass of aril and higher sugar content per seed than *B. microphylla*, and fruits were matured simultaneously and eaten in the autumn. In contrast, fruits of *B. microphylla* were used by overwintering gray vireos who set up territories around them and used them almost exclusively. They matured a few at a time throughout the winter and had lower sugar content and volume. Similar patterns have been seen in the northeastern United States deciduous forest where some plants produce high-quality fruits that mature synchronously during autumn bird migration, whereas others produce lower quality fruits more gradually, which are used by nonmigrants through the winter (Stiles, 1989). Greenberg (1993) has shown that white-eyed vireos overwintering in the Yucatan Peninsula feed heavily (96% of frugivory observations) on *B. sim-*

TABLE 2. The distribution of some morphological traits in *Bursera*. The order of the species is the same as in the phylogeny of Fig. 1.

Species	Bark color ^a	Number of leaflets	Leaf size ^b	Margin ^c	Size of pseudoaril ^d	Color of pseudoaril
<i>B. simaruba</i>	E-R	5 to 9	4	E	C	red to orange
<i>B. longipes</i>	E-R	7-13	4	E	C	cream or yellow
<i>B. attenuata</i>	E-R	7	4	E	C	
<i>T. acuminata</i>	E-R	5 to 7	5	E	C	
<i>B. instabilis</i>	E-R	1 to 3	1	E	C	cream
<i>B. arborea</i>	E-R	5 to 9	4	E	C	pink
<i>B. grandifolia</i>	E-R	5 to 9	5	E	C	cream or pink
<i>B. arida</i>	E-Y	5 to 9	1	E	C	yellow
<i>B. morelensis</i>	E-R	37 to 47	2	E	C	yellow
<i>B. suntui</i>	E-R	7 to 13	1	E	C	cream
<i>B. galeottiana</i>	E-R	13 to 29	1	E	C	orange
<i>B. microphylla</i>	E-Y	7 to 35	1	E to D	C	red
<i>B. ariensis</i>	E-Y	5 to 9	3	E	C	cream
<i>B. fag. fagaroides</i>	E-Y	7 to 11	2	E to D	C	yellow to red
<i>B. fag. purpusii</i>	E-Y	5 to 11	1	E	C	cream
<i>B. chemapodicta</i>	E-R	1	1	E	C	
<i>B. schlechtendalii</i>	E-R	1	1	E	C	yellow or red
<i>B. aptera</i>	E-Y	11 to 19	1	E	C	cream or red
<i>B. trifoliolata</i>	E-R or Y	3	1	E to D	C	yellow
<i>B. discolor</i>	E-Y	5-11	2	E	C	cream
<i>B. fag. elongata</i>	E-Y	3 to 13	2	E to D	C	yellow to red
<i>B. paradoxa</i>	G	13 to 19	1	E	C	cream
<i>B. lancifolia</i>	E-R or O	5-9	3	S	C	yellow
<i>B. trimeria</i>	E-R	1 or 3	1	S	C	yellow
<i>B. kerberi</i>	E-R	3	3	S	C	cream
<i>B. crenata</i>	E-R	1	1	C	C	red
<i>B. denticulata</i>	E-R	3 to 5	3	CD	C	cream
<i>B. multijuga</i>	E-R	7 to 11	2	S	C	cream
<i>B. fragilis</i>	E-Y	3 to 9	3	S	C	orange
<i>B. biflora</i>	G	1 or 3	1	S	H	
<i>B. glabrifolia</i>	RG	7 to 11	3	S	H	yellow to red
<i>B. xochipalensis</i>	G	7 to 11	1	S	H	orange
<i>B. diversifolia</i>	G	13 to 21	2	E, C, or D	A	cream
<i>B. sarukhanii</i>	G	9 to 13	4	S	A	red
<i>B. bicolor</i>	G	13 to 17	3	S to E	A	orange to red
<i>B. copalifera</i>	G	15 to 29	3	SC	A	orange to red
<i>B. velutina</i>	B	11 to 25	1	S	A	orange
<i>B. hintonii</i>	G	9 to 15	4	S	A	orange
<i>B. asplenifolia</i>	G	15 to 25	3	SC	A	orange to red
<i>B. bipinnata</i>	G	7 to 12	1	E	A	red
<i>B. excelsa</i>	G	9 to 15	4	2D	C	cream
<i>B. submoniliformis</i>	G	9 to 17	3	S	C	yellow-pale orange
<i>B. vejar-vazquezii</i>	G	13 to 15	4	E to CD	A	red or yellow
<i>B. heteresthes</i>	G	3 to 5	2	S	H	orange
<i>B. mirandae</i>	E-B	9 to 17	1	D	H	red
<i>B. hindsiana</i>	RG	3	1	C	H	orange
<i>B. stenophylla</i>	RG	13 to 15	2	E	H	orange
<i>B. penicillata</i>	G to RG	7 to 11	2	SD	H-L	red to yellow
<i>B. infernidialis</i>	RG	3	2	D	H-A	red
<i>B. palmeri</i>	G to RG	7 to 11	3	S to D	H	yellow to red
<i>B. filicifolia</i>	G	5 to 15	2	D to E	A	orange
<i>B. coyucensis</i>	G	7 to 11	2	S	H	orange
<i>B. aloexylon</i>	RG	5 to 7	2	CD	H	orange
<i>B. cuneata</i>	G	7 to 9	4	S	A	orange or yellow
<i>B. bonetti</i>	G	13 to 19	2	D	H	pale orange
<i>B. laxiflora</i>	G	5 to 15	2	D or E	H	orange or red
<i>B. tecomaca</i>	G	3	4	S	L	orange

^a The bark of most species of section *Bursera* exfoliates (E) in red (R), yellow (Y), or orange (O) papery sheets. Most species from section *Bullockia* do not exfoliate. Their bark can be grey (G), reddish grey (RG), or brown (B).

^b Size of typical leaves can be (1) ten or less, (2) between 10 and 30, (3) between 30 and 50, (4) between 50 and 100, or (5) between 100 or 200 cm².

^c Leaf margin can be entire (E), dentate (D), twice dentate (2D), serrate (S), or crenate (C).

^d The pseudoaril may cover the seed completely (C), almost completely (A), cover only half the seed (H), or less than half (L).

aruba throughout the winter. These birds have territories that include *B. simaruba* trees, and they defend their trees against conspecifics as well as other species of vireos. *Burseria simaruba*'s fruits ripen slowly for a 7–8 mo period coinciding with the white-eyed vireo overwintering (September–early April). Rzedowski and Kruse (1979) list *B. fagaroides*, *B. longipes*, and *B. morelensis* (representing three of the four section *Burseria* clades) as other species that slowly ripen fruits over many months and *B. bipinnata* and *B. copalifera* (both members of the covering-pseudoaril clade of section *Bullockia*) as examples of simultaneous maturing fruits. Yet, the general distribution of these and other frugivore-related traits such as quantity and quality of fleshy pseudoaril, as well as the quantity and quality of dispersal provided by different dispersal agents, is not yet known.

Thus, *Burseria* exhibits high lability in many ecologically interesting traits and provides a good opportunity to test hypotheses on their evolutionary tendencies. Such tests using this phylogeny will also help in understanding the evolutionary success of this highly diverse and abundant group of the dry tropics of Mexico.

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