

IDENTIFYING TERTIARY RADIATIONS OF FABACEAE IN THE GREATER ANTILLES: ALTERNATIVES TO CLADISTIC VICARIANCE ANALYSIS

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The fossil record shows that the legume family was abundant and taxonomically diverse in Early Tertiary tropical deciduous forests of North America. Today, woody members of this family are almost nonexistent in temperate deciduous forests. This former North American legume diversity now lies in the Tropics, including the Greater Antilles. To show the Antillean refugia, we detail a phylogenetic and biogeographic analysis of two legume groups, the *Ormocarpum* and *Robinia* clades, which have either a Tertiary fossil record in North America or a sister clade with such a fossil record. A combined analysis of molecular and nonmolecular data is used for the cladistic vicariance approaches, while an exhaustively sampled data set of nrDNA ITS/5.8S sequences is used for the molecular biogeographic analysis. Results from component, three-area-statements, and Brooks parsimony analysis are equivocal in suggesting an influence of Tertiary history on the distribution of the woody genera *Pictetia* (*Ormocarpum* clade) and *Poitea* (*Robinia* clade), two of the most speciose endemic legume radiations in the Greater Antilles. Alternatively, nucleotide diversity, evolutionary rates, and coalescent analyses of molecular phylogenies all suggest a Tertiary diversification of *Pictetia* and *Poitea*. The results are corroborated by a regression analysis that implicates both age of island biota and island area in accurately predicting numbers of endemic legume taxa. These findings, combined with the legume fossil record, suggest that both *Pictetia* and *Poitea* stem from Tertiary North American boreotropical groups. J. A. Wolfe's hypothesis that the Greater Antilles harbor boreotropical relicts is supported.

Keywords: Fabaceae, island biogeography, cladistic vicariance analysis, molecular biogeography, penalized likelihood, coalescent theory.

Introduction

The Greater Antilles are so rich in species and higher-level taxa of the legume family that Sousa and Delgado-Salinas (1993) include Cuba, Hispaniola, and Puerto Rico but neither Jamaica nor the other Caribbean islands in their Mexican legume phytogeographic province. They consider the higher-level taxonomic diversity on these islands to parallel that of Mexico. We suggest that this diversity may be related to the antiquity of legumes in the Caribbean region. After all, the Early Tertiary fossil record of legumes coincides with the western portion of the Tethys seaway (Herendeen et al. 1992) and includes the Greater Antilles (Graham et al. 2000). If extant legume diversity in the Greater Antilles is due in part to the Cenozoic age of the family in this region, historical biogeographic methods should identify those Tertiary legume lineages contributing to this diversity.

We focus on two legume genera, *Pictetia* of the *Ormocarpum* clade (Lavin et al. 2001) and *Poitea* of the *Robinia* clade (or tribe Robinieae; Lavin and Sousa 1995), that meet all the criteria as prime candidates for Caribbean vicariance analysis (Page and Lydeard 1994). These two genera comprise eight

and 12 species, respectively, all but one endemic to the Greater Antilles (table 1). If Tertiary events have determined the modern distribution of *Pictetia* and *Poitea*, then cladistic vicariance approaches should detect this by resolving area relationships compatible with those derived from geological data. For example, relevant Tertiary areas of endemism identified by Rosen (1976, 1985) are western Cuba combined with southwestern Hispaniola and eastern Cuba in association with central Hispaniola. Because *Pictetia* and *Poitea* represent two of the most speciose endemic legume radiations, the findings derived from this study could bear on the general history of legume evolution in the Antilles.

Material and Methods

Taxon Sampling

Pictetia and *Poitea* meet all the criteria of excellent study groups for Caribbean biogeography (Page and Lydeard 1994). First, both genera have been subjected to monographic and phylogenetic analysis (Lavin 1993; Beyra Matos and Lavin 1999; Lavin et al. 2000). Second, both are closely related to genera with Eocene fossil records from North America or Europe. *Pictetia* belongs to the *Ormocarpum* clade, which is sister to a clade containing *Machaerium* and *Dalbergia* (Lavin et al.

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2001) from Eocene North America and Europe (Herendeen et al. 1992); *Poitea* belongs to the *Robinia* clade (Lavin and Sousa 1995) from Late Eocene North America (Wheeler and Landon 1992; Wheeler 2001). Third, all eight species of *Pictetia* and all 13 taxa of *Poitea* have been sampled for morphological and molecular data, except *Poitea longiflora*, which is extinct and could not be sampled for molecular data. The same exhaustive sampling was performed on all close mainland relatives. Fourth, the species of *Pictetia* and *Poitea* are highly endemic to the islands of the Greater Antilles (table 1). Notably unoccupied are the Bahamas, Jamaica, and St. Croix, and only one species occurs in the Lesser Antilles: *Poitea carinalis* is endemic to Dominica. The significance here is that these islands cannot harbor Early Tertiary elements because they either are too young (Donnelly 1988; Pindell and Barrett 1990; Iturralde-Vinent and MacPhee 1999) or were inundated by the sea during the Middle to Late Tertiary (Buskirk 1985; Schubart et al. 1998). The occurrence of *Pictetia aculeata* and *Poitea florida* on Puerto Rico and the Virgin Islands exclusive of St. Croix is a consequence of these islands being directly connected to each other during the Quaternary, when sea levels were lower than at present (St. Croix is uniquely separated from Puerto Rico by a deep sea trough; Heatwole and MacKenzie 1967). Finally, certain species of *Poitea* and *Pictetia* are confined to the Early Tertiary areas of endemism described by Rosen (1976, 1985; table 1).

Although phylogenetic analysis of combined molecular and nonmolecular data has been completed for *Pictetia* (Beyra Matos and Lavin 1999; Lavin et al. 2000) and *Poitea* (Lavin 1993), additional phylogenetic analysis is presented here in order to uniformly sample for the same data all species of *Pictetia* and *Poitea*. In addition, all close relatives of both *Pictetia* and *Poitea* have been sampled exhaustively. For *Pictetia*, this includes four other genera in the trans-Atlantic *Ormocarpum* clade (*Diphysa*, *Zygocarpum*, *Ormocarpopsis*, and *Ormocarpum*; Lavin et al. 2000; Thulin and Lavin 2001) as well as appropriate outgroups identified by Lavin et al. (2001). For *Poitea*, this includes 10 other genera in the primarily North American tribe Robinieae (*Hebestigma*, *Lennea*, *Gliricidia*, *Hybosema*, *Robinia*, *Poissonia*, *Coursetia*, *Olneya*, *Peteria*, *Genistidium*, and *Sphinctospermum*; Lavin and Sousa 1995) as well as appropriate outgroups identified in a large-scale legume phylogeny derived from *matK* sequences (M. F. Wojciechowski, unpublished data). Voucher specimens of sampled species are cited in appendix A. Such exhaustive sampling of mainland relatives is suggested by Page and Lydeard (1994) for understanding the historical biogeography of Caribbean island groups.

Sequence Data and Analysis

DNA isolations, PCR amplifications, and template purifications were performed with Qiagen Kits (i.e., DNAeasy Plant Mini Kit, Taq PCR Core Kit, QIAquick PCR Purification Kit; Qiagen, Santa Clarita, Calif.). DNA sequences spanning the nrDNA 5.8S locus and the flanking internal transcribed spacers (ITS1 and ITS2) were analyzed because they provide good resolution at the species level compared with other loci (Lavin et al. 2000, 2001). PCR primers for ITS/5.8S sequences are described in Beyra Matos and Lavin (1999). DNA sequence

from the chloroplast *trnL* locus were also used in the analysis of *Poitea* because they were readily generated and phylogenetically informative; primers are described by Taberlet et al. (1991). Direct sequencing was performed in both directions. Sequencing products were run on an ABI 377 and 3700 automated sequencer at Davis Sequencing (Davis, Calif.) and DNA Sequencing and Synthesis Facility (Ames, Iowa). Multiple accessions of the same species were analyzed for ITS sequence variation when possible in order to determine intra-specific variation and its influence on larger-scale phylogenetic reconstruction.

DNA sequences were aligned manually with the aid of Se-Al (Rambaut 1996). Bias introduced by the manual alignment was evaluated with a sensitivity analysis (Delgado-Salinas et al. 1999). Missing data accounted for 1.1% of the entries in the combined *Pictetia* data set (mostly because of missing ITS1 sequences for *Pictetia spinosa*), 12.7% in the *Poitea* data set (mostly because of no molecular data for the extinct *P. longiflora*), 1.0% in the ITS/5.8S sequence data set of the *Ormocarpum* clade (mostly because of the missing ITS1 sequence for *P. spinosa*), and 0.3% in the ITS/5.8S sequence data set of the tribe Robinieae (*Robinia* clade). Maximum parsimony analyses were performed with PAUP* (Swofford 1999). Heuristic searches included 100 random addition replicates, tree bisection reconnection branch swapping, and steepest descent. Clade stability tests entailed bootstrap resampling (Felsenstein 1985). Each of 10,000 bootstrap replicates was subjected to heuristic searches as above, but with one random addition sequence per replicate and invoking neither steepest descent nor mulpars.

Cladistic Vicariance Analysis

The biogeographic analysis of Beyra Matos and Lavin (1999) is expanded to include the phylogeny of *Poitea* and to involve all traditional forms of cladistic vicariance analysis including component (Page 1993), three-area-statements (Nelson and Ladiges 1994), and Brooks parsimony analysis (Brooks and McLennan 1991). These three methods are considered standard (Morrone and Carpenter 1994). All three assumptions for treating widespread taxa (0, 1, and 2; Nelson and Ladiges 1991) were investigated.

Component 2.0 (Page 1990, 1993) performs branch swapping on the taxon area cladogram to produce an areagram that minimizes paralogy, dispersal, and extinction. Appendix B includes the data set analyzed by Component 2.0. Searches included swapping with subtree pruning regrafting, treating missing areas as uninformative, and mapping (assumption 0) or not mapping (assumption 1) widespread associates. Because widespread taxa were not positioned on the basalmost branches in the taxon area cladogram, assumption 2 was not automatically invoked (Enghoff 1998). Assumption 2 can be implemented manually in Component 2.0 by analyzing all possible combinations of widespread taxa represented by only one of the areas inhabited. Because the eight widespread taxa in this study (see app. B) require analysis of over 28 different data sets, the effects of assumption 2 were explored in the program TASS (three-area-statements analysis; Nelson and Ladiges 1991, 1994). The *Pictetia* and *Poitea* taxon area cladograms were reconciled against 1000 randomly resolved area

Table 1

Distribution of the Species of *Pictetia* and *Poitea*

Species	Distribution
<i>Pictetia aculeata</i>	Puerto Rico and the Virgin Islands excluding St. Croix
<i>Pictetia angustifolia</i>	Eastern Cuba
<i>Pictetia marginata</i>	Eastern Cuba, western Cuba
<i>Pictetia mucronata</i>	Western Cuba, eastern Cuba
<i>Pictetia nipensis</i>	Western Cuba
<i>Pictetia obcordata</i>	Central Hispaniola
<i>Pictetia spinosa</i>	Western Cuba, eastern Cuba
<i>Pictetia sulcata</i>	Eastern Cuba, southwestern Hispaniola, central Hispaniola
<i>Poitea campanilla</i>	Central Hispaniola
<i>Poitea carinalis</i>	Dominica (Lesser Antilles)
<i>Poitea dubia</i>	Central Hispaniola
<i>Poitea florida</i>	Puerto Rico and the Virgin Islands excluding St. Croix
<i>Poitea galegoides</i>	Southwestern Hispaniola, central Hispaniola
<i>Poitea galegoides</i> var. <i>stenophylla</i>	Central Hispaniola
<i>Poitea glycyphylla</i>	Southwestern Hispaniola
<i>Poitea gracilis</i>	Eastern Cuba, western Cuba
<i>Poitea immarginata</i>	Western Cuba
<i>Poitea longiflora</i>	Central Hispaniola (probably extinct)
<i>Poitea multiflora</i>	Southwestern Hispaniola, central Hispaniola
<i>Poitea pauciflora</i>	Central Hispaniola, Puerto Rico
<i>Poitea punicea</i>	Puerto Rico

Sources. Distribution of *Pictetia* and *Poitea* from Beyra Matos and Lavin (1999) and Lavin (1993), respectively. Areas of endemism are those described by Rosen (1976, 1985) for a putative Early Tertiary configuration of the Greater Antilles.

cladograms in order to estimate a confidence interval for the number of “leaves added” and “losses.” Because Component 2.0 arbitrarily resolves polytomies, fully resolved individual minimal-length trees were analyzed in addition to the consensus tree (fig. 1; app. B).

TASS (Nelson and Ladiges 1991, 1994), unlike the other cladistic vicariance approaches, automatically implements assumption 2. Terminal and interior nodes, as well as areas, were input using an alphanumeric scheme (fig. 1) to derive the TASS input file (app. C). Paralogous relationships were both minimized and maximized in order to compare results and report only common findings. The output file from TASS was converted to Nexus format (app. D) and analyzed with the branch-and-bound search algorithm in PAUP* (Swofford 1999).

Brooks parsimony analysis (BPA; Brooks and McLennan 1991, pp. 206–225) requires additive binary coding of the *Pictetia*-*Poitea* taxon area phylogeny (fig. 1). To create the area matrix (app. E), the “inclusive O-ring” was used because there is no reason to consider that different species from the same area (i.e., paralogy) are actually occupying different cryptic areas of endemism. All species of concern inhabit Neotropical seasonally dry forest dominated by the same associates, including other legumes such as *Lonchocarpus*, *Piscidia*, *Dalbergia*, and *Machaerium* (Pennington et al. 2000). Reversible and nonreversible parsimony were used to analyze the area matrix using the branch-and-bound search option in PAUP. Because BPA invokes assumption 0 (Morrone and Carpenter

1994), nonreversible parsimony can somewhat reduce the influence of widespread taxa on area relationships (Brooks and McLennan 1991, p. 217).

Molecular Biogeography

Historical influences on modern distributions were assessed by various approaches to tree shape analysis of DNA sequence phylogenies, which do not require an interpretation of branching order per se. Precedence for this is found in studies such as Cunningham and Collins's (1994, 1998) use of reciprocal

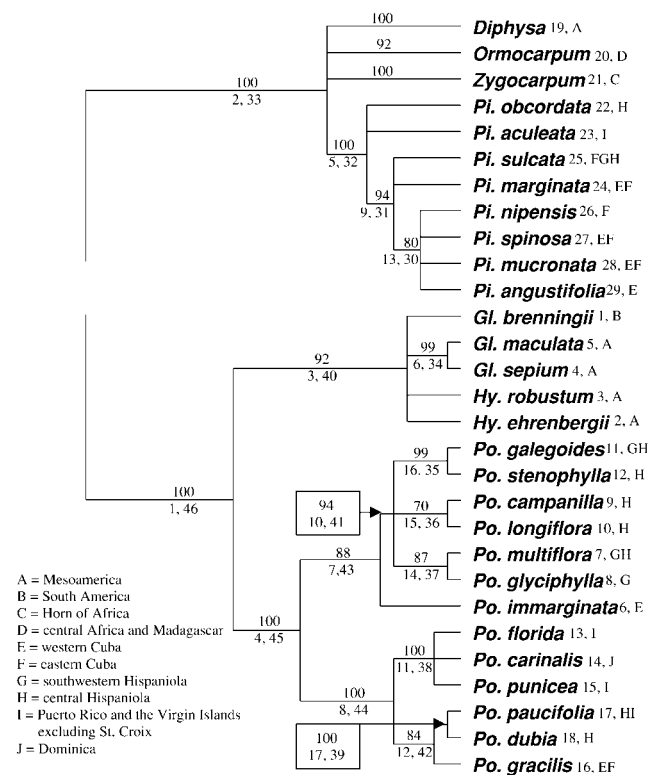


Fig. 1 Strict consensus trees of *Pictetia* (*Pi.*), *Poitea* (*Po.*), and relevant outgroups—*Gliricidia* (*Gl.*) and *Hybosema* (*Hy.*)—derived from analysis of combined molecular and nonmolecular data. The subtree with *Pictetia* and outgroups is a strict consensus of 30 minimal-length trees, each with a length of 983, a consistency index of 0.56, and a retention index of 0.75. The subtree with *Poitea* and outgroups is a strict consensus of two minimal-length trees, each with a length of 479, a consistency index of 0.81, and a retention index of 0.84. Values above the branches are parsimony bootstrap values obtained during analyses of the individual *Pictetia* and *Poitea* data sets. Bootstrap values are provided for the terminal taxa *Diphysa*, *Ormocarpum* (for the purposes of this article, this clade also includes the genera *Ormocarpopsis* and *Peltiera*), and *Zygocarpum* because they actually represent more than one species (Lavin et al. 2000; Thulin and Lavin 2001). Below each of the branches are two numbers. The first represents the node number assigned during the three-area-statements analysis (TASS; Nelson and Ladiges 1994; see app. C and app. D), and the second represents the node number assigned during Brooks parsimony analysis (BPA; Brooks and McLennan 1991; see app. E). Each terminal is provided a unique number (1–29) and an area code (A–J), both of which are used identically in component, TASS, and BPA. Area codes are listed on the figure.

Table 2

Total and Endemic Legume Taxa of Islands

Island	Biota	Area (km ²)	Distance (km) from mainland	Median latitude	Total taxa	Endemic taxa	Reference
Aleutians	0	192,062	75	52°00'N	8	0	Hultén 1937
Antigua	0	287	700	17°10'N	95	0	Howard et al. 1988
Azores	0	76,045	1645	38°70'N	57	1	Palhinha 1966
Bahamas	0	13,939	200	24°60'N	122	9	Correll and Correll 1982
Barbados	0	430	360	13°20'N	98	0	Gooding et al. 1965
Borneo	1	744,100	530	1°00'N	175	46	Merrill 1921
Britain	0	230,737	25	55°00'N	161	0	Stace 1991
Corsica	0	8720	83	42°20'N	273	0	Greuter et al. 1989
Crete	0	8259	100	35°30'N	229	5	Gandoger 1916
Cuba	1	110,800	230	21°65'N	389	117	Sauget and Liogier 1951
Cyprus	0	9251	70	35°00'N	210	8	Meikle 1977
Dominica	0	790	514	15°42'N	106	2	Nicolson 1991
Falkland	0	12,173	505	51°75'S	12	0	Moore 1968
Fiji Islands	0	18,274	2800	17°20'S	206	13	Smith 1985
Galápagos	0	73,251	1000	0°30'S	47	1	Wiggins and Porter 1971
Great Barrier	0	277	20	36°20'S	3	0	Bartlett and Gardner 1983
Greenland	0	341,600	890	72°00'N	14	0	Böcher et al. 1968
Grenada	0	344	145	12°10'N	98	1	Howard et al. 1988
Guadeloupe	0	1702	590	16°20'N	161	1	Howard et al. 1988
Guam	0	541	2950	13°40'N	81	1	Stone 1971
Hawaii	0	10,448	3700	20°50'N	124	15	Wagner et al. 1990
Hispaniola	1	76,200	580	18°90'N	392	84	Liogier 1985
Hong Kong	1	76	1	22°25'N	171	10	Bentham 1861; Hong Kong Herbarium 1967
Iceland	0	103,000	975	64°80'N	13	0	Löve 1983
Ireland	0	84,400	30	53°40'N	48	0	Webb et al. 1996
Jamaica	0	11,000	630	18°20'N	237	16	Adams 1972
Japan	0	377,750	175	37°50'N	157	24	Ohwi 1965; R. C. Barneby, personal communication
Juan Fernandez	0	146	600	33°70'S	10	3	Marticornena et al. 1998
Madagascar	1	587,041	420	19°00'S	573	450	Du Puy and Labat 2001
Madeira	0	753	670	32°75'N	122	8	Short and Turland 1994
Majorca	0	3616	175	39°60'N	153	3	Bonatè Barceló 1979
Marion	0	290	1800	46°54'S	0	0	Gremmen 1982
Martinique	0	1128	430	14°65'N	173	1	Howard et al. 1988
Mauritius	0	1876	1800	20°25'S	141	2	Polhill 1990
Montserrat	0	103	660	16°75'N	77	0	Howard et al. 1988
New Caledonia	1	16,192	1260	21°40'S	169	26	Guillaumin 1948; Nielsen 1983
Newfoundland	0	108,860	18	48°80'N	25	0	Rouleau and Lamourex 1992
New Guinea	1	828,800	155	5°00'S	521	152	Verdcourt 1979
New Zealand	0	270,534	1650	40°50'S	147	18	Webb et al. 1990
North Marianas	0	477	2600	18°30'N	33	0	Fosberg et al. 1975
Philippines	1	300,000	650	12°50'N	275	115	Merrill 1923
Pitcairn	0	5	5400	25°07'S	12	0	St. John 1987
Pohnpei	0	333	1900	6°85'N	41	1	Glassman 1971
Prince Edward	0	44	1720	46°80'N	0	0	Gremmen 1982
Puerto Rican Bank	1	9217	710	18°30'N	195	21	Britton and Wilson 1924
Queen Charlotte	0	34,272	65	52°10'N	18	0	Calder and Taylor 1968
Reunion	0	2545	1670	21°10'S	137	5	Polhill 1990
Rodrigues	0	104	2400	19°50'S	46	1	Polhill 1990
San Juan	0	889	7	48°58'N	55	0	Atkinson and Sharpe 1993
Santa Cruz	0	254	30	34°00'N	45	2	Junak et al. 1995
Sardinia	0	24,090	185	40°10'N	118	8	Cossu 1968; Greuter et al. 1989
Scilly	0	159	40	49°94'N	37	0	Lousley 1971
Seychelles	1	462	1290	4°55'S	78	1	Baker 1877; Robertson 1989
Sicily	0	25,709	3	37°60'N	264	6	Pojero 1891; Greuter et al. 1989
Socorro	0	210	580	18°80'N	10	1	Levin and Moran 1989
Socotra	1	3632	233	12°50'N	86	12	A. Miller, unpublished data
Sri Lanka	1	64,600	50	7°80'N	310	30	Trimen 1894; Kostermans 1980; Rudd 1980, 1991a, 1991b; Maxwell 1991

Table 2 (Continued)

Island	Biota	Area (km ²)	Distance (km) from mainland	Median latitude	Total taxa	Endemic taxa	Reference
St. Helena	0	127	1850	15°95'S	0	0	Cronk 2000
St. John	0	57	860	18°35'N	70	0	Acevedo-Rodriguez 1996
St. Kitts	0	180	720	17°35'N	66	0	Howard et al. 1988
St. Lucia	0	616	345	13°90'N	111	1	Howard et al. 1988
St. Vincent	0	351	280	13°25'N	126	0	Howard et al. 1988
Taiwan	1	36,000	160	23°50'N	226	22	Huang and Ohashi 1993
Tristan de Cunha	0	104	2800	37°10'S	5	0	Dickson 1965

Note. Total and endemic legume taxa of islands for which exist taxonomic accounts of the legume family. Island biota is scored "1" if it harbors Early Tertiary elements, i.e., the island is continental, lies between the tropics of Cancer and Capricorn, and has never been completely inundated since the Early Tertiary.

monophyly for identifying areas containing clades of persistent populations of marine invertebrates, Sanderson's (1997, 1998, in press) analyses of variation of nucleotide substitution rates and divergence times in seed plants, and Price et al.'s (2000) coalescent approach to the biogeography of Old and New World warblers.

Sister clades, each marked by a long basal branch length, define reciprocal monophyly (Cunningham and Collins 1994, 1998). Reciprocal monophyly is indicative of a long history in the area occupied by the clades. This is especially true if sister diversifications are determined to be coeval, or of the same approximate age. That is, contemporaneous sister diversifications are not a necessary outcome of vicariant history, but if detected, they can only be explained by a long vicariant history. In contrast, sister diversifications of very different ages, where one is of recent origin, for example, could be explained just as well by Quaternary dispersal as by Tertiary vicariance. Quantifying nucleotide diversity within and among sister clades, as determined with the program *Sendbs* (Nei and Jin 1989), is one way to determine the relative ages of sister diversifications.

The programs *Lintre* (Takezaki et al. 1995) and *r8s* (Sanderson 2001) were used to assess rate variance in the nrDNA ITS/5.8S data set. In addition, *r8s* allows an estimation of relative or absolute time from nucleotide diversity. The program *Lintre* identifies terminal or internal nodes that deviate significantly in substitution rate, and these are then manually pruned. The program *r8s* incorporates rate variation directly into phylogenetic inference procedures (Sanderson 1997, 1998, 2001, in press) and incorporates three methods for reconstructing divergence times in the absence of rate constancy. Penalized likelihood (PL) identifies a single optimal-rate smoothing parameter to arrive at substitution rates (optimality is achieved by the ability of the smoothing parameter to predict observed overall terminal branch lengths); nonparametric-rate smoothing (NPRS) imposes substitution rates to be autocorrelated (the difference in the "local" rate at one branch and those of the immediate descendant branches is minimized over the entire phylogeny); and Langley and Fitch (LF; 1974) performs a maximum likelihood estimation of a globally constant substitution rate. Penalized likelihood can identify an optimal-rate smoothing parameter that is clocklike at one extreme or neither clocklike nor autocorrelated at the other extreme. For each data set, branch lengths were initially estimated on a single maximum parsimony tree. Ages were estimated for each

node in the phylogeny of the *Ormocarpum* clade using the Caribbean or GAARlandia vicariance event (Late Eocene to Early Oligocene or 35 Ma; Rosen 1976, 1985; Iturralde-Vinent and MacPhee 1999) to fix the age at the root of the trees (geological time lines for the Tertiary follow Berggren et al. 1995). Ages were estimated for the phylogeny of the *Robinia* clade using the fossil record of a *Robinia*-like legume (Late Eocene to Early Oligocene or 35 Ma; Wheeler and Landon 1992; Wheeler 2001) to fix the age at the root of the trees. Standard errors of the divergence times were estimated by a nonparametric bootstrap procedure (Sanderson 1997). A total of 100 resampled data matrices was generated using the SEQBOOT program in PHYLIP (Felsenstein 1999); the matrices were imported into PAUP* 4.0 and divergence times were estimated on a single maximum parsimony tree derived from the analysis of each ITS data set as described above. The resulting trees with estimated node ages were processed by *r8s*, which summarizes the bootstrap distribution of divergence times for each node.

Coalescent approaches to the study of tree shape provide a means of detecting clades that are in random birth-death equilibrium or deviating from it. Equilibrium is defined as the waiting times between branching events having an exponential increase toward the present, which is equivalent to an exponential distribution of terminal branch lengths (Uyenoyama 1997). Deviation in the direction of pure birth is detected by an excess of short terminal branch lengths, whereas deviation in the direction of persistent lineages with little, if any, replacement is detected by an excess of long terminal branches (Grassly and Rambaut 2000; Richman 2000; see Price et al. 2000 for such use of coalescent theory applied to nonrecombining alleles at the species level). The *Rsd* statistic is a measure of total terminal branch length relative to tree depth and has an expected value of 1 (Uyenoyama 1997; Richman 2000). So $Rsd = S(1 - 1/n)/D$, where S = the sum of terminal branch lengths, n = number of alleles (sequences) sampled, and D = coalescence time of all sequences (tree depth); *Rsd* is calculated for each of the mainland and island radiations. Confidence intervals for the *Rsd* statistic are estimated by simulation (e.g., *TreeEvolve* program of Grassly and Rambaut 2000) with population parameters set for values expected for random birth and death. Significant differences among sister clades are estimated with jackknife resampling approaches (Richman 2000).

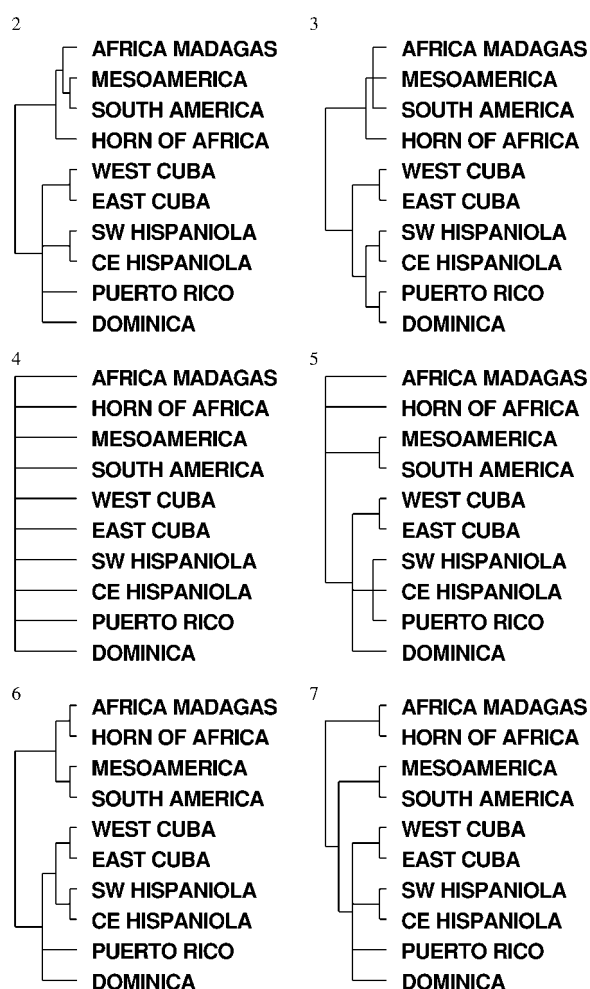


Fig. 2 Area relationships. Fig. 2.2, Strict consensus from a component analysis using either assumption 0 or 1 but using leaves added as the criterion to minimize (see table 1 for tree statistics). Fig. 2.3, Strict consensus from a component analysis using either assumption 0 or 1 but using losses as the criterion to minimize (see table 1 for tree statistics). Fig. 2.4, Strict consensus from a three-area-statements analysis invoking assumption 2. Fig. 2.5, Adams consensus from a three-area-statements analysis invoking assumption 2. In each of figs. 2.4 and 2.5, this is the consensus from 546 trees, each with a length of 12, a consistency index of 0.91, and a retention index of 0.94. Fig. 2.6, Strict consensus from a Brooks parsimony analysis (BPA) in which reversals are allowed. This is a consensus from two minimal-length trees, each with a length of 53, a consistency index of 0.87, and a retention index of 0.79. Fig. 2.7, Strict consensus from a BPA in which reversals are prohibited. This is a strict consensus from three minimal-length trees, each with a length of 56, a consistency index of 0.82, and a retention index of 0.79.

Species-Area Relationships

A relationship between taxonomic diversity and island area was explored to determine whether parameters such as island area adequately predict diversity (MacArthur and Wilson 1967). Floristic data were sampled from 64 island legume floras (table 2). Data from each of the floras listed in table 2 were modified according to recent taxonomic monographs (Irwin

and Barneby 1982; Barneby 1991, 1998; Lavin 1993; Barneby and Grimes 1996, 1997; Lewis 1998; Beyra Matos and Lavin 1999). Response variables were either the total or endemic number of legume taxa. Total numbers of legume taxa included human introductions because in many instances it was difficult to distinguish when a species was present only because of human activity. Predictor variables were island area, distance of island to mainland (mostly available from references cited in table 2), latitude, hemisphere (north or south), and age of island biota (Early to Middle Tertiary or Late Tertiary to Quaternary). The last two represent the only categorical predictors.

Age of island biota is an estimation of whether an island could serve as a museum for an Early Tertiary boreotropical biota. Islands are assigned to this “museum” category if they are continental, have no evidence of post-Eocene submergence (e.g., Jamaica; Buskirk 1985; Schubart et al. 1998), and occur at tropical latitudes (between the tropics of Cancer and Capricorn). Islands at high latitudes have suffered extinction of Early Tertiary tropical biotas (e.g., Greenland; Boyd 1992) and so, like reemerged continental islands, have had to reconstitute their biotas in more recent times.

Linear regression was preceded by log transformation of species numbers, island areas, and distances to mainland (MacArthur and Wilson 1967). The models evaluated included certain combinations of predictor variables, as well as some interaction terms, that are relevant to the equilibrium theory of island biogeography (MacArthur and Wilson 1967; Brown and Lomolino 1998; see table 7). Age of island biota was evaluated as a categorical substitute for the continuous variable latitude. Given the moderate sample sizes obtained (table 2), we chose to evaluate <30 models for each of the two response variables (Burnham and Anderson 1998). We estimated the log likelihood for each model and coefficients for model parameters using generalized linear models in Statistica (StatSoft 1999) with the identity link function (McCullagh and Nelder 1989). We selected the best approximating model from the candidate list of models using Akaike’s information criterion (AIC) for small sample sizes (AICc; Burnham and Anderson 1998). For each data set, we considered the model with the lowest AICc value to be the best. Differences between the AICc value for the best model and the AICc value for all models yielded a Δ AICc for each model. This was used to evaluate the relative plausibility of each model. We considered a model with Δ AICc of <2, 2–4, 4–7, and >7 to be strongly, somewhat, weakly, and not supported, respectively, by the data (Burnham and Anderson 1998, p. 128). We calculated the AICc weight for each model and weight of evidence in favor of a given model, according to Burnham and Anderson’s procedure (1998, p. 124). The weights for all models sum to 1 and thus provide relative weights for each model considered.

Results

A phylogenetic analysis of the *Ormocarpum* clade with 223 parsimony-informative characters from a combined morphological and ITS/5.8S sequence data set (app. A) yielded 30 minimal-length trees each with a length of 983, a consistency index of 0.56, and a retention index of 0.75. Although the

Table 3

Assumptions 0 and 1 with Criteria That Were Minimized

	Leaves added (fig. 2)	Losses (fig. 3)
Assumption 0	2 trees with minimum value of 47 ($P < 0.0000$); 540 rearrangements tried	2 trees with minimum value of 26 ($P < 0.0000$); 544 rearrangements tried
Assumption 1	2 trees with minimum value of 47 ($P < 0.0000$); 540 rearrangements tried	2 trees with minimum value of 26 ($P < 0.0000$); 544 rearrangements tried

Note. Results from Component 2.0 analysis (Page 1990). Branch swapping in all cases invoked subtree pruning and regrafting. Significance was estimated with a distribution of values derived from random trees.

root was determined with *Dalbergia congestiflora* and *Aeschynomene pfundii* as outgroups, only the results relevant to the biogeographical analysis are depicted (fig. 1). That is, only branches with high bootstrap values ($\geq 80\%$) are resolved. *Pictetia* is monophyletic, as are the other genera in the *Ormocarpum* clade. Relationships among the genera, however, are not well resolved and are thus depicted as a polytomy. Similarly, within *Pictetia*, relationships among most species are not well resolved.

A phylogenetic analysis of the *Robinia* clade, which includes *Poitea*, with 169 parsimony-informative characters from a combined morphological, ITS/5.8S, and *trnL* sequence data set (app. A), yielded two minimal-length trees each with a length of 479, a consistency index of 0.81, and a retention index of 0.84. The root was determined with the genera *Lennea* (three species) and *Hebestigma* (monotypic) as outgroups (fig. 4). The results relevant to the biogeographical analysis are depicted in figure 1 (i.e., outgroups are not shown). Again, only branches with high bootstrap values are resolved (the one low value of 70% was accepted because *Poitea longiflora* is extinct and could not be sampled for molecular data). *Poitea* is monophyletic, as is the clade containing the species of *Gliricidia* and *Hybosema*. Together these two clades form a well-supported monophyletic group. In contrast to *Pictetia*, the relationships among species of *Poitea* are mostly well resolved. Whereas *Pictetia* has several sister clades ranked as genera, the sister clade to *Poitea* is a single well-supported one localized in Mesoamerica and northern South America (figs. 1, 4).

Component Analysis

Component 2.0 analysis of the taxon area cladogram (fig. 1) described in nexus format (app. B) yielded two consensus trees (figs. 2.2, 2.3), depending on the criterion minimized. Table 3 lists the relevant statistics associated with each tree. The areas of endemism from the Greater Antilles form a closely related group, and eastern Cuba is consistently related to western Cuba, as is southwestern Hispaniola to central Hispaniola. The relationships of Puerto Rico are confounded by the widespread *Poitea pauciflora* distribution, by the presence of the Dominican *Poitea carinalis* in a clade with the Puerto Rican *Poitea punicea* and *Poitea florida*, and by the association of *Pictetia aculeata* with both Cuban and Hispaniolan species.

Three-Area-Statements

The taxon area cladogram (fig. 1) was input into TASS using the automatic prompts for the tree description. This yielded an input file (app. C) that produced the area matrix, which

was converted to nexus format (app. D). Analysis of this matrix with the branch-and-bound search algorithm resulted in 546 minimal-length trees, each with a length of 12, a consistency index of 0.91, and a retention index of 0.94. The results are shown as a strict (fig. 2.4) and as an Adams (fig. 2.5) consensus. Because assumption 2 is invoked, more resolved area cladograms were generated, and a strict consensus of these is completely unresolved. However, the Adams consensus reveals that Dominica is equivocally placed, and the emergent pattern is of close relationships of Puerto Rico to both areas of Hispaniola, which is seen in many of the individual area-grams. The Adams consensus also reveals that the Antillean areas are each more closely related to one other than to a mainland area and that eastern and western Cuba are most closely related to each other.

Brooks Parsimony Analysis (BPA)

Additive binary coding of the taxon area cladogram (fig. 1) resulted in 10 areas of endemism by 46 area characters (app. E). Analysis by reversible parsimony of this matrix resulted in two minimal-length trees each with a length of 53, a consistency index of 0.87, and a retention index of 0.79. A strict consensus (fig. 2.6) reveals a close relationship between eastern and western Cuba and between southwestern and central Hispaniola. In contrast, Puerto Rico is equivocally placed among the Antillean areas of endemism. Analysis with irreversible parsimony resulted in three minimal-length trees each with a length of 56, a consistency index of 0.82, and a retention index of 0.79. A strict consensus (fig. 2.7) reveals similar results as just described for the Antillean areas of endemism. BPA analysis reveals similar area relationships to those of Component 2.0 analysis (assumptions 0 and 1) whether or not irreversible parsimony is invoked.

Molecular Biogeography

Parsimony analysis nrDNA ITS/5.8S sequences of *Pictetia* and relatives in the *Ormocarpum* clade resulted in 5000 minimal-length trees each derived from analysis of 61 terminals by 672 sites in the aligned data set (205 phylogenetically informative sites) and each with a length of 916, a consistency index of 0.54, and a retention index of 0.80 (fig. 3). Parsimony analysis of the same sequences for *Poitea* and relatives in the *Robinia* clade resulted in 5000 minimal-length trees each derived from analysis of 103 terminals by 728 sites in the aligned data set (352 phylogenetically informative sites) and each with a length of 1634, a consistency index of 0.48, and a retention index of 0.86 (fig. 4).

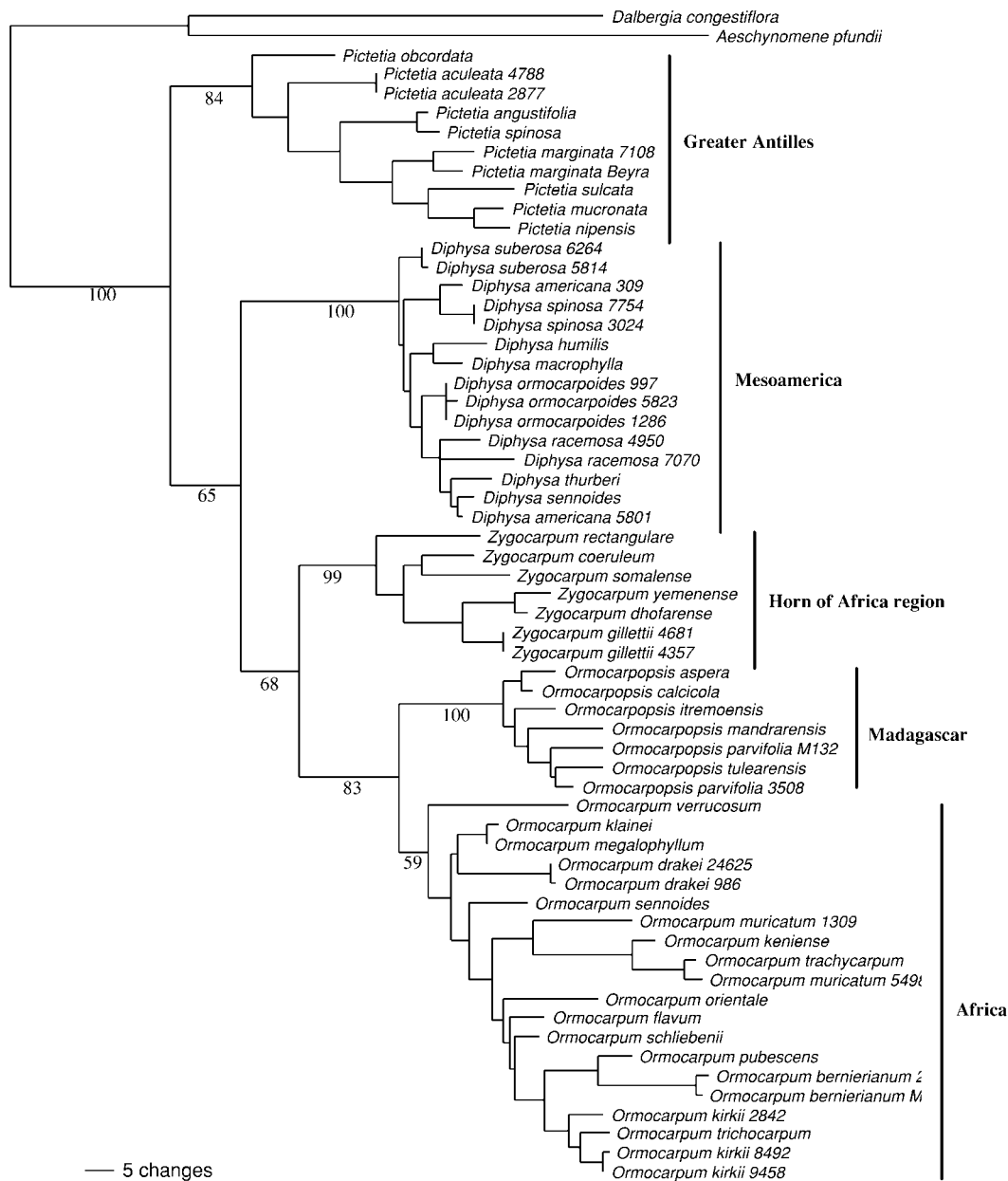


Fig. 3 Phylogram of *Pictetia* and relatives in the *Ormocarpum* clade. This tree is one of 5000 minimal-length trees derived from analysis of 61 terminals by 672 sites in the aligned nrDNA ITS/5.8S data set. The length is 916, parsimony-informative sites are 205, the consistency index is 0.543, and the retention index is 0.799. Bootstrap values lie below selected branches that were resolved in the strict consensus. The predominant geographical distribution is provided for relevant clades.

Nucleotide diversity analysis. For both the *Ormocarpum* and *Robinia* clades, the program r8s identified an optimal smoothing parameter that was nearly or exactly clocklike (table 5, col. PL). In contrast, the program Lintre identified for the *Ormocarpum* clade a rate increase in some *Ormocarpum* species and a rate decrease in some *Pictetia* species. For the *Robinia* clade, a rate increase was detected by Lintre in a subclade of *Poitea* defined by the most recent common ancestor of *P. punicea* and *Poitea dubia*.

Regardless of whether the rate-variable species were man-

ually pruned (Lintre) or left intact (r8s), the nucleotide diversity of *Pictetia* (table 4) is as great as or greater than any of its sister clades. This is particularly remarkable when compared to *Ormocarpum*, a genus of ca. 15 species widespread in many different forests and woodland habitats of Africa. As such, the *Pictetia* diversification must be older than any of its sister mainland radiations. The nucleotide diversities within each of the five main subclades of the *Ormocarpum* group are significantly smaller than the among-subclade diversity (table 4). This suggests that each subclade diversification has long been isolated



Fig. 4 Phylogram of *Poitea* and relatives in the *Robinia* clade. This tree is one of 5000 minimal-length trees derived from analysis of 103 terminals (not all *Coursetia* are shown) by 728 sites in the aligned nrDNA ITS/5.8S data set. The length is 1634, parsimony-informative sites are 352, the consistency index is 0.480, and the retention index is 0.856. Bootstrap values lie below selected branches that were resolved in the strict consensus. The predominant geographical distribution is provided for relevant clades.

from the others and that any one subclade did not serve as the source for another.

Similar to *Pictetia*, analysis with either Lintre or r8s shows the *Poitea* subtree to be as genetically diverse as its sister mainland diversification, the clade comprising *Gliricidia* and *Hybosema* (table 4). Like *Pictetia*, sequence variation adjusted for rate variance suggests that the *Poitea* diversification is coeval with that of the *Hybosema*-*Gliricidia* diversification. Also similar to *Pictetia*, the nucleotide diversity within each of the two subclades *Gliricidia*-*Hybosema* and *Poitea* is significantly less

than the between-subclade diversity (table 4). Again, this suggests that each of the two subclade diversifications has long been isolated and neither can be viewed as a source or founder population of the other.

Evolutionary rates analysis. By setting the root of the *Ormocarpum* clade at 35 Ma, all three forms of rates analysis, penalized likelihood, Langley-Fitch, and nonparametric rate smoothing (PL, LF, NPRS), put the age of the *Pictetia* diversification older than any of its sister diversifications (i.e., *Diphysa*, *Ormocarpum*, *Zygocarpum*, and *Ormocarposis*; table

Table 4
Within- and Among-Clade Nucleotide Diversity

	Diversity	SE
<i>Pictetia</i> and sister clades	0.08019	0.00692
<i>Pictetia</i>	0.04587	0.00575
<i>Diphysa</i>	0.02139	0.00345
<i>Ormocarpum</i>	0.04124	0.00582
<i>Ormocaropsis</i>	0.02664	0.00411
<i>Zygocarpum</i>	0.04175	0.00582
<i>Poitea</i> and sister clade	0.07688	0.00311
<i>Poitea</i>	0.03045	0.00206
<i>Gliricidia-Hybosema</i>	0.03093	0.00259

Source. Source for analytic methods is Nei and Jin (1989).

Note. For the *Ormocarpum* group, 500 sites of the 695 aligned nrITS/5.8S sites not scored for missing data or gaps were compared. *Pictetia spinosa* was excluded from the reported results because ITS1 sequences were missing, but including the ITS2 sequence of this species does not change the interpretation. For *Poitea* and sister clade, *Poitea florida*, *Poitea carinalis*, and *Poitea punicea* were omitted in order to obtain a sequence data set with no significant rate variation; the principal conclusions do not change by including these species, however. Here, 484 of the 662 original sites were compared. Diversity is the average number of nucleotide substitutions per site among species within a designated clade, which were exhaustively sampled at the species level. Kimura two-parameter distances were used, and standard errors (SE) were estimated with 500 bootstrap replicates.

5; fig. 5). Of the younger clades, the Gulf of Aden clade (ADEN in fig. 5) was estimated by all three methods at about or just less than 10 Ma, suggesting that a significant water gap formed in this rift valley by at most 10 million years ago.

The root of the *Robinia* clade was set at 35 Ma, according to the fossil record. Similar to the r8s analysis of *Pictetia*, all three methods (PL, LF, NPRS) estimate the age of the *Poitea* diversification to be as old as or older than its sister mainland diversification (*Gliricidia-Hybosema*; table 5; fig. 6). Notably, the age estimate of the *Poitea* diversification is about one-half that of *Pictetia* (e.g., ca. 10 Ma vs. ca. 20 Ma; table 5). Regardless, all age estimates of these Antillean diversifications are Tertiary in age. Furthermore, the vicariant event involving *Poitea* (node POGL in fig. 6) is estimated at ca. 14–23 Ma, depending on the method of rate estimation (table 5). Such an age was estimated from a rate calibrated against the fossil record, which contrasts to *Pictetia*, where the only calibration available was the assumed Caribbean or GAARlandia vicariance event at ca. 35 Ma. Regardless, estimated ages of the presumed vicariant events are all well into the Tertiary, and the different calibrations utilized for the *Ormocarpum* and *Robinia* clades yield similar estimates of substitution rates (table 5).

Coalescent analysis. All but the *Zygocarpum* subtree of the *Ormocarpum* clade have Rsd values (i.e., a ratio of terminal tip lengths to tree depth) significantly greater than 1 (table 6). This suggests that the *Ormocarpum* clade is not at a birth-death equilibrium but, rather, is deviating from it in the direction of persistent species that are not being replaced. More important, *Pictetia* is shown to be equivalent in Rsd to the largest mainland radiation, *Ormocarpum* in Africa. The

Ormocarpum subtree was jackknifed 100 times for the seven available *Pictetia* species, each time deriving tree statistics from the resulting phylogeny, and a frequency distribution of tree statistics was generated and compared to the actual statistics for *Pictetia* (figs. 7.12–7.15). This approach corrects for differences in clade size and reveals that the Rsd statistic calculated for *Pictetia* is not significantly different from that of *Ormocarpum*. Thus, the *Pictetia* diversification comprises an excess of old species, similar to the other mainland diversifications. For *Poitea* and its sister clade, the coalescent approach revealed no significant deviation from a birth-death equilibrium (table 6). Furthermore, jackknifing the *Poitea* subtree to correct for its larger size revealed a significantly lower Rsd value compared with the *Gliricidia-Hybosema* clade. This resulted, however, from a greater tree depth in *Poitea* as compared to the *Gliricidia-Hybosema* subtree and not from a difference in terminal tip length (figs. 8.16–8.19). Because of the tree shape similarities between island and sister mainland clades for both *Pictetia* and *Poitea*, neither island diversification can be viewed as a recent (e.g., Quaternary) founder event from a mainland source population.

Species-Area Relationship

Distance to mainland and hemisphere are poor predictors of endemic legume diversity on islands, and age of island biota is a better predictor than latitude of endemic legume diversity (table 7). Indeed, the best model for predicting endemic diversity included area and an interaction term of area and age of island biota. That is, endemism on the tropical continental islands, particularly New Guinea, Madagascar, Sri Lanka, Taiwan, Borneo, Philippines, New Caledonia, Cuba, Hispaniola, Puerto Rico, and Socotra is significantly greater than on the other islands (table 2; fig. 9). It is these islands that are the potential museums for Early Tertiary tropical biotas given that they still occupy tropical latitudes and have never been completely submerged. The inference is that legume diversification on islands is dependent on time. In contrast, for total legume diversity, area, latitude, and distance were all determined to be important predictors (results available upon request). While total numbers of island taxa fit the prediction of the equilibrium theory of island biogeography, endemic numbers of legume taxa do not.

Discussion

Cladistic vicariance methods fail to detect a Tertiary influence on the modern distribution of *Pictetia* and *Poitea*. Importantly, the failure is not necessarily due to a lack of resolution in the areagrams (figs. 2.2–2.7). The results derived from vicariance methods either do not corroborate Caribbean vicariance hypotheses or are difficult to interpret against the predictions of geological hypotheses. Rosen's (1976, 1985) hypothesis predicts Tertiary area relationships between western Cuba and southwestern Hispaniola and between Central Hispaniola and eastern Cuba. Such area relationships were not detected with vicariance approaches in this study. Iturralde-Vinent and MacPhee's (1999) GAARlandia hypothesis, which

Table 5

Estimated Ages (Ma) and Substitution Rates (per Site per Ma) of Selected Clades Based on Penalized Likelihood (PL), Langley-Fitch (LF), and Nonparametric-Rate Smoothing (NPRS) Analyses

	PL	LF	NPRS
<i>Ormocarpum:</i>			
NATL	29.60 ± 1.21 0.002135 ± 0.000183	28.63 ± 1.22 0.002273 ± 0.000174	30.50 ± 0.86 0.004333 ± 0.000509
PICT	21.47 ± 1.92 0.001602 ± 0.000188	18.77 ± 1.97 0.002273 ± 0.000174	24.01 ± 1.96 0.002199 ± 0.000327
DIPH	9.07 ± 1.77 0.001898 ± 0.000241	7.78 ± 1.20 0.002273 ± 0.000174	13.79 ± 2.66 0.002328 ± 0.000343
ZYGO	15.33 ± 1.85 0.002084 ± 0.000220	13.60 ± 1.30 0.002273 ± 0.000174	19.39 ± 1.97 0.002744 ± 0.000297
ADEN	7.49 ± 1.61 0.002056 ± 0.000238	6.64 ± 1.25 0.002273 ± 0.000174	10.95 ± 2.24 0.001943 ± 0.000261
OPSI	8.51 ± 1.58 0.002216 ± 0.000319	8.41 ± 1.04 0.002273 ± 0.000174	12.84 ± 1.83 0.003096 ± 0.000390
ORMO	17.11 ± 2.11 0.002028 ± 0.000274	15.71 ± 1.36 0.002273 ± 0.000174	19.83 ± 1.53 0.003390 ± 0.000510
<i>Robinia:</i>			
POGL	16.45 ± 1.77 0.002996 ± 0.000421	14.47 ± 1.46 0.003691 ± 0.000231	23.27 ± 1.58 0.003660 ± 0.000419
POIT	9.20 ± 1.31 0.002996 ± 0.000422	7.80 ± 0.92 0.003691 ± 0.000231	14.85 ± 1.58 0.003098 ± 0.000392
GLIR	7.40 ± 1.32 0.002996 ± 0.000421	6.14 ± 0.98 0.003691 ± 0.000231	15.83 ± 2.06 0.002077 ± 0.000241
HEBE	22.04 ± 1.64 0.002996 ± 0.000421	20.37 ± 1.35 0.003691 ± 0.000231	22.39 ± 1.36 0.004941 ± 0.000359
ROBB	15.00 ± 1.94 0.002996 ± 0.000422	12.65 ± 1.18 0.003691 ± 0.000231	18.89 ± 1.36 0.004086 ± 0.000370
COUR	15.93 ± 1.89 0.002996 ± 0.000422	13.41 ± 1.00 0.003691 ± 0.000231	16.88 ± 1.17 0.006107 ± 0.000579

Note. This analysis was performed on nrDNA ITS/5.8S sequences from the *Ormocarpum* and *Robinia* clades. Numbers = mean ± standard error (derived from 100 bootstrap replicates). Estimated age is listed above the associated substitution rate. See chronograms (figs. 5, 6) for phylogenetic positions of specific clades.

involves the Greater Antilles (GA) and Aves Ridge (AR), posits Tertiary fragmentation of a Caribbean land span. The predicted Tertiary area relationships of the GAARlandia fragmentation are vague and essentially indistinguishable from Quaternary area relationships. Most troubling about the vicariance approach to detecting historical influence is that different geological hypotheses involving either Tertiary or Quaternary events in the formation of the Caribbean islands can equally explain the branching patterns of the area cladograms derived from the analysis of the *Pictetia* and *Poitea* taxon area cladograms (figs. 2.2–2.7). For example, a close area relationship between eastern and western Cuba is a prediction of the Tertiary GAARlandia hypothesis as well as the Quaternary configuration of Cuba.

Cladistic vicariance methods were designed to detect historical influences on modern distributions (Nelson and Platnick 1981). Such methods, however, may be limited to rare cases in which neither extinction nor dispersal has occurred among areas of endemism, including dispersal mediated by secondary contact of areas of endemism (i.e., composite areas; Platnick and Nelson 1984). If *Pictetia* and *Poitea* have a long history in the Greater Antilles, it has been obscured by dis-

persal among areas of endemism (e.g., *Pictetia sulcata* on Cuba and Hispaniola and *Poitea pauciflora* on Hispaniola and Puerto Rico), as well as by secondary contact among Early Tertiary areas of endemism (i.e., central and southwestern Hispaniola and eastern and western Cuba). Sensitivity to widespread taxa has been recognized as the major source of ambiguity for component, three-area-statements, and BPA (Morrone and Carpenter 1994).

Analyzing monophyletic radiations that have a greater degree of endemism than *Pictetia* and *Poitea* in the Greater Antilles is a possible solution (Page and Lydeard 1994). Finding such cases is unlikely, however. A sampling of the literature involving Greater Antillean radiations reveals that widespread taxa or endemics to areas such as the Lesser Antilles, the Bahamas, Jamaica, and the North and South American mainland complicate the detection of Tertiary influence (Judd 1981; Kluge 1988; Liebherr 1988; Lydeard et al. 1995; Moynihan and Watson 2001).

In contrast to cladistic vicariance approaches, molecular biogeographic methods use more than the branching order of clades to make inferences about ages of lineages and clade diversifications. Furthermore, molecular methods are not nec-

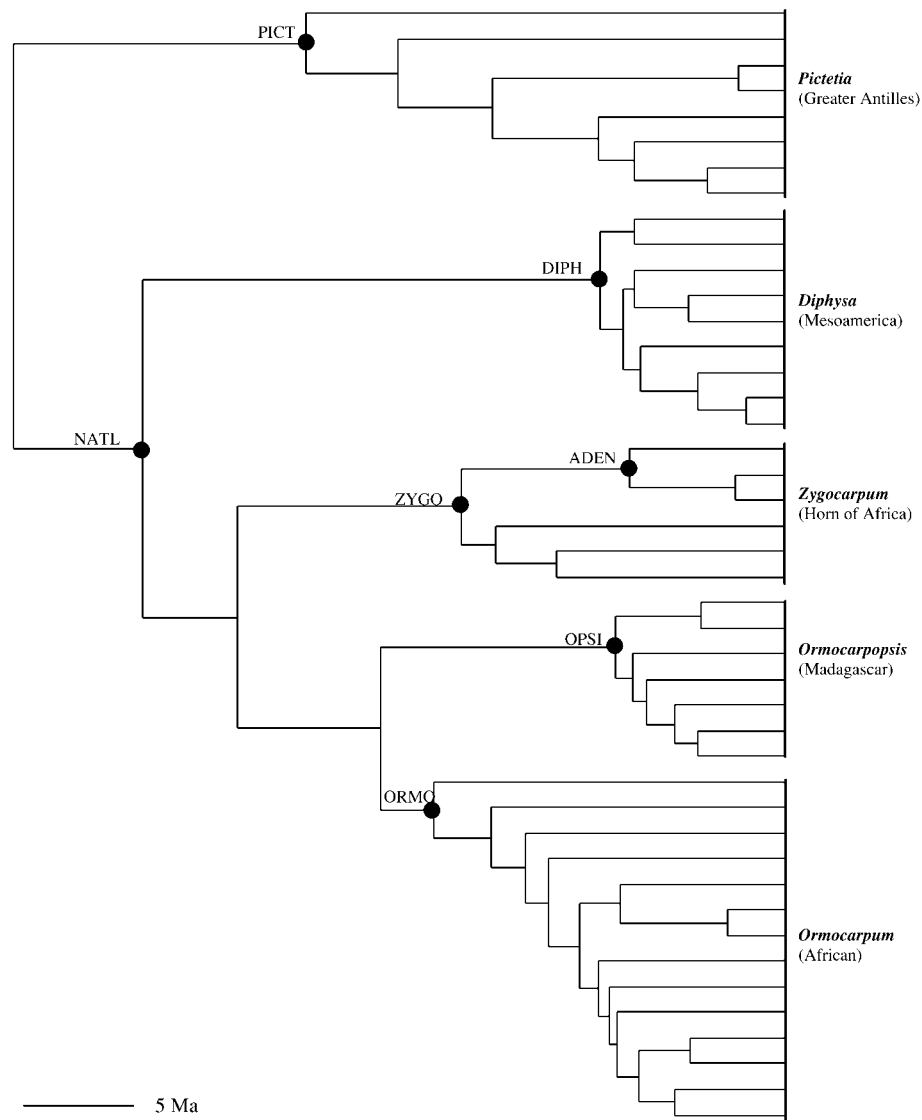


Fig. 5 Chronogram derived from the phylogram of the *Ormocarpum* clade in fig. 3 and using a time constraint at the root of 35 Ma, the estimated age of the primary vicariant event involving the Greater Antilles (Rosen 1976, 1985; Iturralde-Vinent and MacPhee 1999). Mean age, substitution rates, and standard errors for the marked clades are provided in table 5.

essarily dependent on geological hypotheses that bear on relationships among historical areas of endemism. Theoretical and empirical advances allow for historical inference directly from the shape of molecular phylogenies (Nee et al. 1995, 1996).

Nucleotide Diversity and Reciprocal Monophyly

In both *Pictetia* and *Poitea*, the pattern of reciprocal monophyly (Cunningham and Collins 1994, 1998) is found with respect to the island and sister mainland diversifications. Long branch lengths separating sister groups are detected with both high bootstrap values (figs. 1, 3, 4) and nucleotide diversity statistics that are significantly less within than among sub-clades (table 4). Reciprocal monophyly suggests long persist-

ence in the respective areas occupied by each of the coeval sister diversifications (Riddle 1996; Cunningham and Collins 1998). Importantly, such a pattern is not suggestive of a source mainland population and a founder island population, as is found most commonly with oceanic island biotas like that of Hawaii (Baldwin 1996, 1997; Vargas et al. 1998) or of extinction in the island population followed by population reconstitution by migration from the mainland (Cunningham and Collins 1998). In the source-founder relationship, there is not a discrete sister mainland diversification subtended by a long branch, and the island diversification is nested well within a larger mainland diversification. In the source-founder example, nucleotide diversity values are often as great within a continental clade as between the continental and its closely related island clade (Baldwin 1996, 1997; Vargas et al. 1998; Wagstaff et al. 1999).

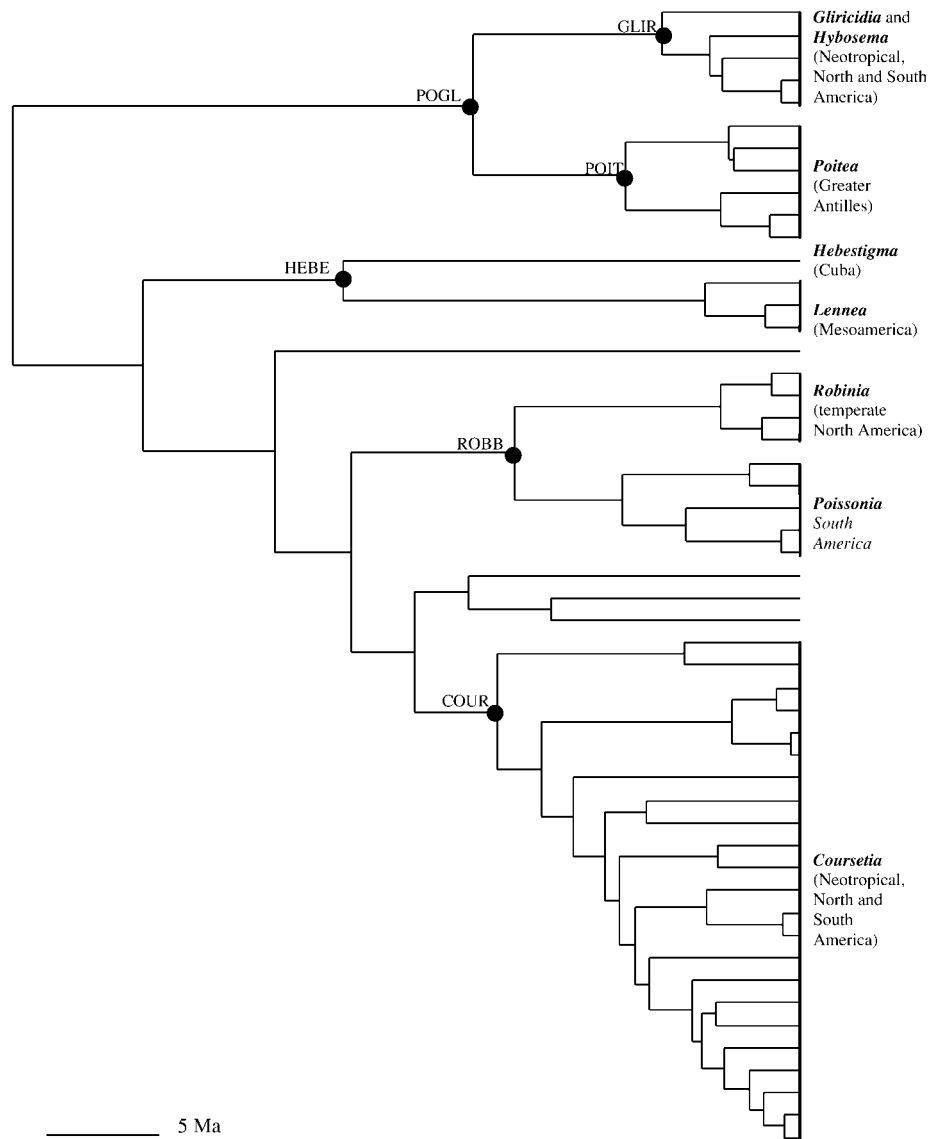


Fig. 6 Chronogram derived from the phylogram of the *Robinia* clade in fig. 4 and using a time constraint at the root of 35 Ma, the estimated age of fossil robinoid wood (Wheeler and Landon 1992; Wheeler 2001). Mean age, substitution rates, and standard errors for the marked clades are provided in table 5. Unlabeled branches are continental North American endemic genera (e.g., *Olmeia*, *Peteria*, *Genistidium*, and *Sphinctospermum*).

Analysis of Substitution Rates

By assuming the age of the Caribbean vicariance event to be Late Eocene/Early Oligocene, or ca. 35 Ma (Rosen 1976, 1985; Iturralde-Vinent and MacPhee 1999), analysis of substitution rates was performed by assuming rate variability with an optimal smoothing parameter (PL; Sanderson, in press), a molecular clock (LF; Langley and Fitch 1974), and autocorrelated rate changes among lineages (NPRS; Sanderson 1997, 1998). Regardless of which of these specific assumptions is operating, the estimated ages of both the *Pictetia* and *Poitea* diversifications are well into the Tertiary (table 5; figs. 5, 6). The accuracy of these age estimates in the *Ormocarpum* clade is corroborated by the maximum 10-million-year-old estimated

age of the clade that spans the Gulf of Aden (ADEN in table 5 and fig. 5; see *Zygocarpum gillettii*, *Z. dhofarensis*, and *Z. yemense*). This agrees with geological evidence, which posits an approximate maximum date of 10 Ma for the first major water gap that filled this rift valley (Purser and Bosence 1998; see Thulin and Lavin 2001). Also in agreement is the estimated age of the tropical North Atlantic Land Bridge (NATL in table 5 and fig. 5), which could be as young as the Oligocene (Parrish 1993). The estimated ages in the *Robinia* clade are calibrated with fossil wood specimens (Wheeler and Landon 1992; Wheeler 2001). Validation of ages estimated for the *Robinia* clade comes from another potential Caribbean vicariance event in the *Robinia* clade, the node labeled HEBE (fig. 6), which is

Table 6
Tree Shape Statistics

Subclade	Tip length	Tree depth	Rsd	SD	CV
<i>Ormocarpopsis</i>	0.07975	0.01974	3.36661 ^a	0.00578	2.30056
<i>Ormocarpum</i>	0.26053	0.03689	6.59225 ^a	0.01043	1.66569
<i>Zygocarpum</i>	0.09934	0.03134	2.64146	0.00859	1.92827
<i>Pictetia</i>	0.14850	0.03413	3.72933 ^a	0.00814	2.60506
<i>Diphysa</i>	0.09129	0.01780	4.55883 ^a	0.00494	2.05192
<i>Poitea</i>	0.05324	0.03462	1.38398	0.00294	1.80814
<i>Gliricidia-Hybosema</i>	0.05207	0.02057	2.02479	0.00620	1.67969

Sources. Sources for statistics are Uyenoyama (1997) and Richman (2000).

Note. Tip length is the sum of the terminal branch lengths (Kimura two-parameter distances). Tree depth is length or depth of the clade from its base to the average terminal tip. Rsd is sum of the terminal tip lengths scaled to the number of alleles $(1 - 1/n)$ and divided by the tree depth. SD is the standard deviation of the variation in terminal branch length. CV is the coefficient of variation (mean/SD) of terminal branch lengths.

^a Rsd values deviating significantly from 1.00 ($P < 0.01$).

dated at just over 20 Ma, as well as by the subclades with a North and South American tropical radiation (GLIR, COUR, ROBB in fig. 6), which are estimated at ca. 6–16 Ma (table 5). All of these estimated ages for subclades in the *Robinia* clade that combine North America, the Greater Antilles, and South America are consistent with the GAARlandia hypothesis (Iturralde-Vinent and MacPhee 1999), which posits a land path from the Greater Antilles region south to South America via the Aves Ridge. GAARlandia formed at 32–35 Ma but became progressively fragmented throughout the Middle to Late Tertiary.

Another form of validation of the estimated ages (table 5; figs.

5, 6) is the magnitude of the estimated substitution rate for the nrDNA ITS/5.8S locus in the *Ormocarpum* and *Robinia* clades. The penalized likelihood method, for example, yields an average substitution rate of ca. 2.0×10^{-9} and 3.0×10^{-9} substitutions per site per year for the *Ormocarpum* and *Robinia* clades (table 5), respectively. These rates are very close to those estimated for other legumes. The substitution rate for the nrDNA ITS locus of the herbaceous genera *Astragalus* and *Lupinus* is estimated at 3.5×10^{-9} at 3.3 – 3.6×10^{-9} substitutions per site per year, respectively (Wojciechowski et al. 1999), and that of the arborescent *Inga* is estimated at 2.4×10^{-9} substitutions per site per year (Richardson et al. 2001).

Coalescent Theory

Coalescent analysis of *Pictetia* clearly suggests that the species of this genus are generally old and the diversification is presently at a stage with little species birth. Species of *Pictetia* are separated by long terminal branch lengths relative to subtree depth. Furthermore, similar subtree shape is observed for nearly all of the mainland sister diversifications (table 6; figs. 3, 7.12–7.15). Although *Poitea* and its mainland sister clade are each close to a species birth-death equilibrium, according to coalescent analysis, the pattern exhibited in this group, like that of *Pictetia* and sister clades, still contrasts with a mainland source and island founder relationship. For the latter, the founder population is expected to be at a stage of active species birth relative to the source mainland, where longer terminal branch lengths are commonly observed between species. For example, analysis of the silversword nrDNA ITS data from Baldwin and Sanderson (1998) reveals that the silversword radiation comprises many short or zero-length terminal branches relative to the subtree depth. Although the endemic Jamaican crab radiation described by Schubart et al. (1998) suggests that occasional recent diversifications can have the tree shape described for *Pictetia*, the subtree shape described for the silverswords is most common for Late Tertiary to Quaternary island diversifications (Meyer 1993; Wagstaff et al. 1999).

The coeval ages of the diversifications of sister clades described for *Pictetia* and *Poitea* are in contrast to empirical examples shown for mainland source and island founder populations. The Hawaiian silversword radiation, for example, is

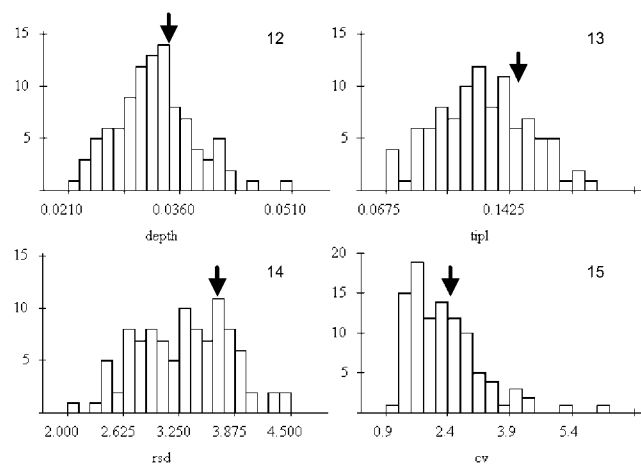


Fig. 7 Tree shape analysis. Fig. 7.12, Tree depth (*depth*). Fig. 7.13, Terminal tip length (*tipl*). Fig. 7.14, *rsd*, the sum of the terminal tip lengths scaled to the number of alleles $(1 - 1/n)$ and divided by the tree depth. Fig. 7.15, *cv* (mean/standard deviation of the variation in tip length). The frequency distribution was created by 100 random draws of seven species each (the number of *Pictetia* species with full-length ITS/5.8S sequences) from the *Ormocarpum* subtree. Each time the relevant statistic was measured, and the histogram records the frequency of trees with a given measure. The arrow indicates the actual value of the *Pictetia* subtree (table 6).

Analysis of Species-Area Relationships

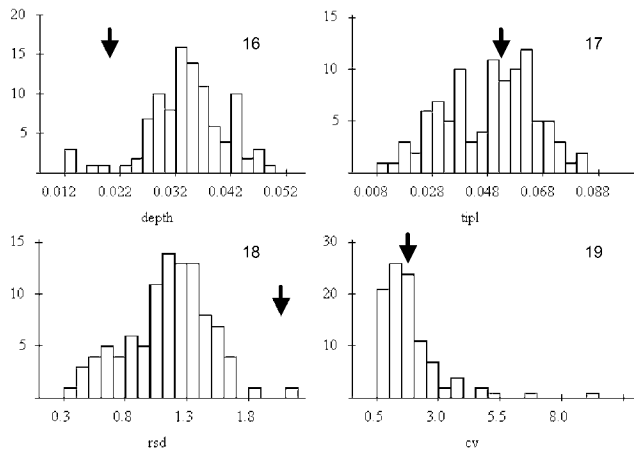


Fig. 8 Tree shape analysis. Fig. 8.16, Tree depth (*depth*). Fig. 8.17, Terminal tip length (*tipl*). Fig. 8.18, *rsd*, the sum of the terminal tip lengths scaled to the number of alleles ($1 - 1/n$) and divided by the tree depth. Fig. 8.19, *cv* (mean/standard deviation of the variation in tip length). The frequency distribution was created by 100 random draws of five species each (the number of *Gliricidia* species with full-length ITS/5.8S sequences) from the *Poitea* subtree. The arrow indicates the actual value of the *Gliricidia* subtree (table 6).

dated at less than 6 Ma, while the sister mainland diversification, tarweeds of western North America, is more than 15 Ma (Baldwin and Sanderson 1998). The pattern of reciprocal monophyly is not detected for the silverswords, and the relatively more recent island diversification is suggestive of a founder event from a continental source. Analysis of substitution rates and tree shape all point to a long, isolated history of *Pictetia* and *Poitea* in the Greater Antilles. An over-water dispersal hypothesis put forward by Hedges (1996) for the Middle to Late Tertiary origin of Antillean vertebrates is thus not a general condition of the Greater Antillean biota.

This analysis was prompted by the contrasting legume floras of Jamaica with those of the other Greater Antilles. While Cuba, Hispaniola, and the Puerto Rican Bank are rich in endemic species and genera of Fabaceae, Jamaica has a pan-tropical legume flora, and any legume taxon endemic to this island is generally a weak segregate of a fairly widespread species (Adams 1972). Jamaica is considered geologically distinct (Iturralde-Vinent and MacPhee 1999); it was inundated during the middle Tertiary (Buskirk 1985; Schubart et al. 1998). After eradication of the Early Tertiary Jamaican flora, this island biota must have been reconstituted. As such, much Tertiary history was lost, and today Jamaica has a legume flora much like those of the geologically younger Lesser Antilles (Adams 1972; Howard et al. 1988). The other Greater Antillean islands, in contrast, still harbor an Early Tertiary history.

Notably, Jamaica has a larger surface area but fewer endemic legume taxa than the Puerto Rican bank (table 2). Whether the difference is statistically significant can only be determined by analyzing the legume floras for all islands of the world in order to determine the predictive value of island area for numbers of endemic legume taxa. A disequilibrium between island area and endemic taxa has been noted for Caribbean anoles (Losos and Schluter 2000), where endemic speciation needs to be accounted for on islands greater than ca. 3000 km². In this analysis, we determined that endemic speciation is not just a factor of area but also of age of biota.

Island biotas of the world can be classified into two types. The “Cuba” or museum type refers to an island biota that has been in existence since the Eocene. This is the epoch when the modern tropical biotas began to rapidly diversify, which is the case for legumes (Herendeen et al. 1992). The “Jamaica” or young type refers to island biotas that were formed after the Eocene diversification. Generally, these are oceanic islands or continental islands that have had Early Tertiary tropical biotas eradicated by climate change (e.g., location in high northern

Table 7

Models Evaluated for the Response Variable “Number of Endemic Taxa per Island”

Δ AICc	Weight	Lmodel	Intercept	Biota	Latitude	Hemisphere	Area	Distance	Biota × area	Latitude × area	K
0.000	0.53354	1	x				x		x		3
2.702	0.13821	0.259043	x				x	x	x		4
2.978	0.12036	0.225579	x			x	x		x		4
3.102	0.11315	0.212072	x	x			x		x		4
5.979	0.02684	0.050306	x			x	x	x	x		5
6.019	0.02631	0.049321	x	x			x	x	x		5
6.197	0.02407	0.045110	x	x		x	x		x		5
9.376	0.00491	0.009204	x	x		x	x	x	x		6
9.352	0.00497	0.009316	x		x		x			x	4
9.852	0.00387	0.007256	x				x			x	3
12.602	0.00098	0.001834	x		x		x	x		x	5
11.350	0.00183	0.003431	x		x		x			x	4
12.650	0.00096	0.001791	x				x	x		x	4

Note. For each of the 13 candidate models, “x” indicates constituent predictor variables (see table 2). Models are ranked from the lowest Δ AICc (adjusted for small sample size; $-2[\ln L] + 2[K] + [2K(K+1)/(n-K-1)]$), where $\ln L$ is the log likelihood of a particular model, K is the number of parameters in the model, and n is the sample size (64 islands). Weights are calculated as $\exp[-1/2 \times \Delta$ AICc]/ Σ AICc). The likelihood of the model (Lmodel) is calculated as the weight for the model of interest divided by the weight for the best model. This value is the probability of the given model being the best given the candidate model list and data set.

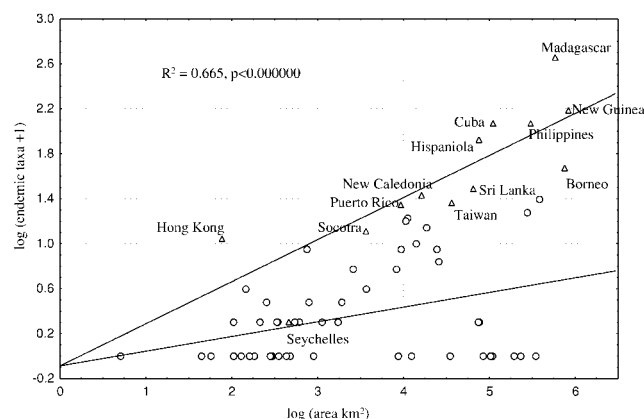


Fig. 9 Linear regression of endemic legume taxa as a response to island area (km^2) and age of biota. Islands potentially harboring Early to Middle Tertiary elements (open triangles and labeled) contrast to those with Late Tertiary to Quaternary biotas (open circles and unlabeled). The model presented for endemic taxa is the first one in table 7. The predicted number of endemic taxa on islands lacking Early to Middle Tertiary elements = $-0.0875 + 0.13056 \times \log$ of endemic taxa (95% confidence interval for the slope is $0.04773-0.21339$). The predicted number of endemic taxa for islands harboring Early to Middle Tertiary biotas = $-0.0875 + 0.3743 \times \log$ of endemic taxa (95% confidence interval for the slope is $0.29839-0.45021$, as determined with the Delta method; Seber 1982, pp. 7–9). The 95% confidence interval for the intercept of this model encompasses zero.

or southern latitudes) or complete submergence, as in the case of Jamaica. In addition to Cuba, Hispaniola, and Puerto Rico, continental islands such as New Guinea, New Caledonia, Borneo, Philippines, Taiwan, Madagascar, Sri Lanka, and Socotra can be classified into the museum type of island (fig. 9). The AIC approach to model selection implicates both age of island biota and island area in the prediction of numbers of endemic legume taxa.

As such, this study quantifies the observation that there are no spectacular cases of legume radiations on oceanic or other islands with more recent biotas. For example, on Hawaii, there are only 15 native species of legumes, and *Canavalia* with six endemic species may be the single largest legume radiation on any oceanic island (Wagner et al. 1990). It is the same situation for continental temperate islands like New Zealand, where legume endemism comprises two separate lineages of ca. 18 species of *Carmichaelias* (Webb et al. 1990; Wagstaff et al. 1999). Relatively low levels of legume endemism on islands like Jamaica, Hawaii, and New Zealand underscores the point that high levels of legume endemism, as seen on Cuba, Hispaniola, and Puerto Rico, require as much time as land area.

Distance to mainland, or isolation of island, has little influence on legume endemism on islands (table 7). This is not necessarily contrary to the findings of MacArthur and Wilson (1967) because they did not concern themselves with taxonomic distinctions within island biotas (Brown and Lomolino 1998). A perusal of island floras (table 2) points to striking differences among plant families. In contrast to Fabaceae, families such as Asteraceae and Lamiaceae have high levels of endemism on oceanic islands, temperate and tropical. The Fabaceae and certain other families (e.g., Ochnaceae, Sabiaceae,

Rutaceae, Sapindaceae, and so forth) may have a poorer ability to disperse over water on average relative to families like Asteraceae and Lamiaceae. Thus, endemic legume diversity on islands in general depends more on endemic speciation than on colonization from a mainland source.

Given that *Pictetia* and *Poitea* are sister to clades with Early Tertiary North American fossil records (see “Material and Methods”) and are also highly endemic to just the Greater Antilles, the results from the species-area analysis alone strongly indicate that these two genera have a Tertiary history in the Greater Antilles. The genetic data presented here reinforce this hypothesis.

Tropical Continental Islands as Tertiary Refugia for the Fabaceae

Modern-day centers of diversity provide weak evidence for ancestral distributions (Croizat et al. 1974; Manchester 1999). The type of results presented here, however, indicate that the diversity of the family Fabaceae in the Caribbean basin results in part from a long residence in the region. If an island has acted as a museum for Tertiary boreotropical elements (*sensu* Wolfe 1975; Tiffney 1985), only then can it have the kind of legume endemism found in Cuba, Hispaniola, and Puerto Rico. Indeed, Wolfe (1975) suggested that the Greater Antilles was a boreotropical refugium. The region of the Tethys seaway during the Early Tertiary, including continental North America, was tropical, and legumes were first diversifying during this time in this region (Herendeen et al. 1992). A modern island flora with a continental history that has remained at tropical latitudes throughout the Cenozoic and in the region of the former Tethys seaway, and has never been submerged like Jamaica, should have a rich endemic legume flora. In addition to Cuba, Hispaniola, and Puerto Rico, other tropical continental islands like Madagascar, Sri Lanka, Borneo, New Guinea, Taiwan, and the Philippines should show legume diversifications with patterns of reciprocal monophyly, estimated ages that date well into the Tertiary, and long terminal branch lengths suggesting old radiations presently not undergoing active speciation. This should contrast to islands such as Jamaica, Japan, Hawaii, and New Zealand, for example, with endemic legume radiations lacking the pattern of reciprocal monophyly, having estimated Late Tertiary to Quaternary ages, and having little if any genetic distance separating the constituent species of an endemic island clade.

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analysis: E, F, K, MEXU, MO, MONT, NY, P, QLD, and UPS. Financial support for this study came from the U.S. National Science Foundation (DEB-0075202).

Appendix A

DNA Vouchers

Each entry includes species, locality, voucher specimen, and GenBank accession number (¹ITS/5.8S accession; ²trnL accession). Combined data sets in nexus format are available from <http://gemini.oscs.montana.edu/~mlavin/data/carib.htm>.

Aeschynomene pfundii Taubert; Zimbabwe Botanical Gardens; *Lavin* s.n. (MONT); ¹AF189026.

Coursetia andina Lavin; Venezuela: Mérida; *Lavin* 5732 (TEX); ¹AF398848.

Coursetia axillaris Coulter & Rose; U.S.A.: Texas; *Lavin* 4641 (TEX: 271287); ¹AF398840.

Coursetia brachyrhachis Harms; Argentina: Jujuy; *Lewis* 2169 (MONT); ¹AF398837.

Coursetia caribaea (Jacq.) Lavin; Mexico: Oaxaca; *Lavin* 4603 (TEX); ¹AF398846.

Coursetia caribaea; var. *ochroleuca* (Jacq.) Lavin; Ecuador: Manabi; *Klitgaard* 564 (MONT: 1063); ¹AF398847.

Coursetia chiapensis Lavin & M. Sousa; Mexico: Chiapas; *Lavin* 8202 (MEXU); ¹AF398830.

Coursetia dubia (H.B.K.) DC.; Ecuador: Pichincha; *Humbles* 6170 (F: 926); ¹AF398851.

Coursetia elliptica M. Sousa & V. Rudd; Costa Rica: Guanacaste; *Janzen* 11558 (MO); ¹AF398828.

Coursetia ferruginea (H.B.K.) Lavin; Venezuela; *Hughes* s.n. (MONT: 613); ¹AF398836.

Coursetia fruticosa (Cavanilles) MacBride; Peru: Huanuco; *Ferreya* 6640 (F: 921); ¹AF398838.

Coursetia glabella (A. Gray) Lavin; Mexico: Chihuahua; *Lavin* 4960 (TEX); ¹AF398845.

Coursetia glandulosa A. Gray; U.S.A.: Arizona; *Lavin* 4671 (TEX); ¹AF398839.

Coursetia gracilis Lavin; Ecuador: Pichincha; *Gentry* 70194 (MONT: 629); ¹AF398854.

Coursetia grandiflora Benth.; Peru: Cajamarca; *Sagastegui* 15495 (F: 929); ¹AF398853.

Coursetia hassleri Chodat; Argentina: Tucuman; *Lavin* 5809 (TEX); ¹AF398850.

Coursetia heterantha (Grisebach) Lavin; Argentina: Salta; *Lavin* 5785 (TEX); ¹AF398842.

Coursetia hidalgoana Lavin; Mexico: Hidalgo; *Lavin* 5901 (TEX: 100588); ¹AF398844.

Coursetia hintonii V. Rudd; Mexico: Tejuipilco; *Guizar* 261 (TEX: 1030); ¹AF398855.

Coursetia hypoleuca (Spegazzini) Lavin; Argentina: Jujuy; *Lavin* 5814 (MONT: 231089); ¹AF398834.

Coursetia insomniifolia Lavin; Mexico: Coahuila; *Lavin* 5732 (TEX); ¹AF398841.

Coursetia madrensis Micheli; Mexico: Puebla; *Lavin* 4626 (TEX); ¹AF398831.

Coursetia marañona Lavin; Peru: San Martin; *Gentry* 37672 (MONT: 948); ¹AF398857.

Coursetia mollis Robinson & Greenman; Mexico: Michoacan; *Lavin* 5360 (TEX: 1039); ¹AF398856.

Coursetia oaxacensis M. Sousa & V. Rudd; Mexico: Guerrero; *MacQueen* 444 (MONT: 615); ¹AF398829.

Coursetia orbicularis Benth.; Peru: Abancay; *Vargas* 9808 (F: 923); ¹AF398835.

Coursetia paniculata M. Sousa & Lavin; Mexico: Oaxaca; *Lavin* 5320 (TEX); ¹AF398833.

Coursetia planipetiolata Micheli; Mexico: Guerrero; *Lavin* 5355 (TEX); ¹AF398832.

Coursetia polyphylla Brandege; Mexico: Veracruz; *Lavin* 8224 (MEXU); ¹AF398859.

Coursetia pumila (Rose) Lavin; Mexico: Durango; *Lavin* 5006 (TEX); ¹AF398843.

Coursetia rostrata Benth.; Brazil: Bahia; *Anderson* 36955 (F: 930); ¹AF398858.

Coursetia rostrata; Brazil: Bahia; *Klitgaard* 78 (MONT: 1062); ¹AF398860.

Coursetia rostrata; Brazil: Bahia; *Lewis* 1863 (MONT: 611); ¹AF398861.

Coursetia vicioides (Nees & Martius) Benth.; Brazil: Bahia; *Silva* 177 (TEX: 938); ¹AF398849.

Coursetia weberbaueri Harms; Peru: Arequipa; *Hutchinson* 7259 (F: 918); ¹AF398852.

Dalbergia congestiflora Pittier; El Salvador: Santa Ana. Metapan; *Hughes* 1253 (MEXU); ¹AF068140.

Diphysa americana (Miller) Sousa; Mexico: Puebla. Santiago Nopala; *Lavin* 5801 (MONT); ¹AF068160.

Diphysa americana [reported as *D. suberosa* S. Watson in Beyra Matos and Lavin 1999]; Mexico: Chiapas. San Fernando; *MacQueen* 309 (MONT); ¹AF068166.

Diphysa floribunda Benth. & Oerst.; Mexico: Oaxaca. Putla; *Sousa* S. 10616 (MO); ¹AF068161.

Diphysa humilis Oerst.; Costa Rica: Puntarenas. Santa Elena; *Haber* 1322 (MO); ¹AF068162.

Diphysa macrophylla Lundell; Mexico: Oaxaca. Salina Cruz; *Sousa* 9115 (MO); ¹AF189029.

Diphysa ormocarpoides; Mexico: Oaxaca. San Pedro Totalapan; *Saynes* V. 1286 (MEXU); ¹AF068168.

Diphysa ormocarpoides; Mexico: Oaxaca. Tehuantepec; *Torres* C. 997 (MEXU); ¹AF068169.

Diphysa ormocarpoides (Rudd) Sousa; Mexico: Oaxaca. San José; *Lavin* 5823 (MEXU); ¹AF068167.

Diphysa racemosa; Mexico: Puebla. El Coro; *Tenorio* 4950 (MO); ¹AF189030.

Diphysa racemosa Rose; Mexico: Oaxaca. El Puente; *Sousa* S. 7070 (MO); ¹AF068163.

Diphysa sennoides Benth.; Mexico: Oaxaca. Teposcolula; *García* M. 484 (MO); ¹AF068164.

Diphysa spinosa; Mexico: Chiapas. Amatenango de Valle; *Cabrera* 3024 (MO); ¹AF189032.

- Diphysa spinosa* Rydberg; Honduras: Francisco Moraza. Tegucigalpa; *Nelson* 7754 (MO); ¹AF189031.
- Diphysa suberosa* S. Watson; Mexico: Oaxaca. Santa Cruz Mixtepec; *Sousa* 6264 (MO); ¹AF189033.
- Diphysa suberosa*; Mexico: Oaxaca. Juchetango; *Lavin* 5814 (MO); ¹AF189034.
- Diphysa thurberi* (A. Gray) Rydb. ex Standley; Mexico: Sonora. Alamos; *Kearns et al.* s.n. (MONT); ¹AF068165.
- Genistidium dumosum* I. M. Johnston; U.S.A.: Texas; *Lavin* 210890 (MONT); ¹AF398826.
- Gliricidia brenningii*; Ecuador: Montalvo; *Hughes* 1194 (FHO); ¹AF398804.
- Gliricidia brenningii*; Ecuador: Palestina; *Hughes* 1009 (FHO); ¹AF398809.
- Gliricidia brenningii*; Ecuador: Palmale; *Hughes* 1012 (FHO); ¹AF398805, ²AF400140.
- Gliricidia brenningii*; Ecuador: Portovelo; *Hughes* 1015 (FHO); ¹AF398808.
- Gliricidia brenningii*; Ecuador: San Pablo; *Hughes* 1199 (FHO); ¹AF398807.
- Gliricidia brenningii* (Harms) Lavin; Ecuador: Chone; *Hughes* 993 (FHO); ¹AF398806.
- Gliricidia maculata*; Mexico: Campeche; *Hughes* 678 (FHO: 42-87-1); ¹AF398813.
- Gliricidia maculata*; Mexico: Quintana Roo; *Hughes* 675 (FHO: 42-85); ¹AF398811.
- Gliricidia maculata*; Mexico: Yucatan; *Hughes* 939 (FHO: 43-87); ¹AF398810, ²AF400139.
- Gliricidia maculata* (H.B.K.) Steudel; Mexico: Campeche; *Hughes* 678 (FHO: 42-87); ¹AF398812.
- Gliricidia sepium*; Costa Rica: Nicoya; *Hughes* 11-86 (FHO); ¹AF398816.
- Gliricidia sepium*; Costa Rica: Santa Cruz; *Hughes* 799 (FHO: 12-86); ¹AF398815.
- Gliricidia sepium*; Mexico: Jalisco; *Hughes* 622 (FHO: 41-85); ¹AF398814.
- Gliricidia sepium* (Jacq.) Steudel; Guatemala: Cuyotenango; *Hughes* 430 (FHO); ²AF400138.
- Hebestigma cubense*; Cuba: Guardalavaca; *Lavin* 7144a (MONT); ¹AF398762.
- Hebestigma cubense* (H.B.K.) Urban; Cuba: Habana; *Lavin* 5611 (TEX); ¹AF398763, ²AF400134.
- Hybosema ehrenbergii*; Guatemala: La Ruda; *Hughes* 1458 (FHO); ¹AF398769.
- Hybosema ehrenbergii* (Schlechtendal) Harms; Guatemala: Ixtahuacan; *Hughes* 1468 (FHO); ¹AF398770, ²AF400136.
- Hybosema robustum*; Mexico: Chiapas; *Sousa* 13212 (MEXU); ¹AF398768, ²AF400137.
- Hybosema robustum* M. Sousa & Lavin; Mexico: Chiapas; *Hughes* 1186 (FHO); ¹AF398767.
- Lennea melanocarpa* (Schlechtendal) Vatke ex Harms; Mexico: Veracruz; *Lavin* 8217-4 (MEXU); ¹AF398766.
- Lennea modesta* (Standley & Steyermark) Standley & Steyermark; Mexico: Chiapas; *Lavin* 8210 (MEXU); ¹AF398764, ²AF400135.
- Lennea viridiflora* Seemann; Mexico: Veracruz; *Lavin* 822a (MEXU); ¹AF398765.
- Olneya tesota*; U.S.A.: Arizona; *Lavin* 5472 (TEX); ¹AF398822.
- Olneya tesota* A. Gray; U.S.A.: Arizona; *Lavin* 4654 (MONT); ¹AF398823.
- Ormocarpopsis aspera* R. Viguier; Madagascar: Antananarivo. Mohobo; *Peltier* 4416 (MO); ¹AF068148.
- Ormocarpopsis calcicola* R. Viguier; Madagascar: Ambongo. Antsakoamanera; *Capuron* 24240-SF (K); ¹AF068145.
- Ormocarpopsis itremoensis* Du Puy & Labat; Madagascar: Fianarantsoa. Ambatofinandrahana; *Labat* 2363 (K); ¹AF068149.
- Ormocarpopsis mandrarensis* Dumaz-le-Grand; Madagascar: Toliara. Andohahela Reserve; *Phillipson* 2924 (K); ¹AF068147.
- Ormocarpopsis parvifolia* Dumaz-le-Grand; Madagascar: Toliara. Tsiombe; *Phillipson* 3508 (K); ¹AF068143.
- Ormocarpopsis parvifolia* 1; Madagascar: Toliara. Beloha; *Du Puy et al.* M132 (K); ¹AF068144.
- Ormocarpopsis tulearensis* Du Puy & Labat; Madagascar: Toliara; *Keraudren* 1369 (K); ¹AF068146.
- Ormocarpum bernierianum*; Madagascar: Antsiranana; *Du Puy et al.* M716 (P); ¹AF189036.
- Ormocarpum bernierianum* (Baill.) Du Puy & Labat; Madagascar: Antsiranana; *Labat et al.* 2882 (P); ¹AF189035.
- Ormocarpum drakei*; Madagascar: Bekopaka; *Rakotozafy* 986 (P); ¹AF189039.
- Ormocarpum drakei* R. Viguier; Madagascar: Menabe. Antsalova; *Capuron* 24625-SF (P); ¹AF189038.
- Ormocarpum flavum* Gillett; Tanzania. Iringa Distr.; *Greenway* 14054 (MO); ¹AF189041.
- Ormocarpum keniense* Gillett; Kenya: Meru; *Faden* 74/958 (MO); ¹AF068155.
- Ormocarpum kirkii*; South Africa: Kloof Forest; *Balsinhas* 2842 (MO); ¹AF068151.
- Ormocarpum kirkii* [reported as *O. mimosoides* S. Moore in Beyra Matos and Lavin 1999]; Mozambique: Momba; *Torre* 9458 (MO); ¹AF068152.
- Ormocarpum kirkii* S. Moore; Malawi: Southern Region; *Chapman* 8492 (MO); ¹AF068150.
- Ormocarpum klainei* Tisserant; Cameroon: Southwest. Lake Barombi; *J. D. Manning* 747 (MO); ¹AF189044.
- Ormocarpum megalophyllum* Harms; Cameroon: Forest Preserve; *Amshoff* 1299 (MO); ¹AF068154.
- Ormocarpum muricatum* Chiov.; Kenya: Mandera; *Gilbert & Thulin* 1309 (MO); ¹AF068156.
- Ormocarpum muricatum* [reported as *O. trachycarpum* (Taub.) Harms in Beyra Matos and Lavin 1999]; Ethiopia: Harar; *DeWilde* 5498 (MO); ¹AF068157.
- Ormocarpum orientale* (Spreng.) Merr.; Australia: Queensland. North Kennedy; *Roach* s.n. (QLD); ¹AF068159.
- Ormocarpum pubescens* (Hochst.) Cufod; Afrique occidentale; *Aubreville* s.n. (P); ¹AF189045.
- Ormocarpum schliebenii* Harms; Tanzania: Lindi Distr.; *Schlieben* 5766 (P); ¹AF189047.
- Ormocarpum sennoides* (Willd.) DC.; Tanzania: Zaraninje Forest; *CFRP* 1043 (MO); ¹AF068153.
- Ormocarpum trachycarpum* (Taub.) Harms; Ethiopia: Harar. *Amshoff* 9887 (MO); ¹AF189049.
- Ormocarpum trichocarpum* (Taub.) Burtt Davy; Natal: Gunamanini Pan; *Stephens* 820 (MO); ¹AF068158.

- Ormocarpum verrucosum* P. Beauv.; Cameroon; *Jungner* s.n. (UPS); ¹AF189050.
- Peteria scoparia*; U.S.A.: Texas; *Lott* s.n. (TEX); ¹AF398825.
- Peteria thompsonae*; U.S.A.: Idaho; *Lavin* 7048-2 (MONT); ¹AF398824.
- Pictetia aculeata*; Puerto Rico: Guanica, F. Axelrod 2877(NY); ¹AF068174.
- Pictetia aculeata* (Vahl) Urban; Puerto Rico: Cabo Rojo; *Axelrod* 4788 (NY); ¹AF068175.
- Pictetia angustifolia* Grisebach; Cuba: Camagüey. Loma de la Coca; *Beyra Matos* s.n. (MONT); ¹AF068171.
- Pictetia marginata*; Cuba: Las Villas-Camagüey; *Beyra Matos* s.n. (MONT); ¹AF068177.
- Pictetia marginata* Sauv.; Cuba: Holguín. Sierra Nipe; *Lavin* 7108 (MONT); ¹AF068176.
- Pictetia mucronata*; Cuba: Camagüey. Tagarro; *Beyra Matos* s.n. (MONT); ¹AF068173.
- Pictetia mucronata* (Grisebach) *Beyra Matos* & *Lavin*; Cuba: Camagüey. La Mina; ¹AF068172.
- Pictetia nipensis* (Urban) *Beyra Matos* & *Lavin*; Cuba: Sierra Nipe; *Ekman* 10,001 (NY); ¹AF189052.
- Pictetia obcordata* DC.; Dominican Republic: Cambita Garabita; *Zanoni* 40488 (NY); ¹AF068170.
- Pictetia spinosa* (A. Richard in Sagra) *Beyra Matos* & *Lavin*; Cuba: Santiago de Cuba; *Ekman* 8403 (NY); ¹AF203565.
- Pictetia sulcata* (P. Beauv.) *Beyra Matos* & *Lavin*; Dominican Republic: Baoruco; *García et al.* 623 (NY); ¹AF068178.
- Poitea campanilla*; Dominican Republic: Jarabacoa; *Lavin* 8033-1 (MONT); ¹AF398779, ²AF400145.
- Poitea campanilla*; Dominican Republic: Jarabacoa; *Lavin* 8033-3 (MONT); ¹AF398780.
- Poitea campanilla*; Dominican Republic: Piedra Blanca; *Lavin* 8032-2 (MONT); ¹AF398778.
- Poitea campanilla* DC.; Dominican Republic: Piedra Blanca; *Lavin* 8032-1 (MONT); ¹AF398777.
- Poitea carinalis*; Dominica; *Lavin* 011288 (MONT); ¹AF398792.
- Poitea carinalis* (Grisebach) *Lavin*; Dominica; *Lavin* 7150 (MONT); ¹AF398793, ²AF400148.
- Poitea dubia* (Poiret) *Lavin*; Dominica Republic: Las Matas de Farfan; *Lavin* 8028 (MONT); ¹AF398803, ²AF400151.
- Poitea florida*; Puerto Rico: Coamo; *Lavin* 8015 (MONT); ¹AF398784.
- Poitea florida*; Puerto Rico: El Verde; *Lavin* 8017 (MONT); ¹AF398788.
- Poitea florida*; Puerto Rico: Ponce; *Lavin* 8014 (MONT); ¹AF398787, ²AF400146.
- Poitea florida*; Puerto Rico: Susua; *Lavin* 8012 (MONT); ¹AF398786.
- Poitea florida* (Vahl) *Lavin*; Puerto Rico: Yauco; *Lavin* 8005 (MONT); ¹AF398785.
- Poitea galeoides*; Dominican Republic: Aceitillar; *Lavin* 8031-1 (MONT); ¹AF398774.
- Poitea galeoides*; Dominican Republic: Aceitillar; *Lavin* 8031-2 (MONT); ¹AF398775.
- Poitea galeoides* var. *stenophylla* *Ekman* ex *Lavin*; Dominican Republic: Rancho Arriba; *Zanoni* 45081 (NY); ¹AF398776.
- Poitea galeoides* Ventenat; Dominican Republic: Hato Damas; *Lavin* 8021 (MONT); ¹AF398773, ²AF400142.
- Poitea glycyphylla*; Dominican Republic: Pedernales; *Lavin* 8030-2 (MONT); ²AF400144.
- Poitea glycyphylla*; Dominican Republic: Pedernales; *Lavin* 8030-4 (MONT); ¹AF398782.
- Poitea glycyphylla* (Poiret) *Lavin*; Dominican Republic: Pedernales; *Lavin* 8030-1 (MONT); ¹AF398783.
- Poitea gracilis*; Cuba: Cananova; *Lavin* 7142 (MONT); ¹AF398796.
- Poitea gracilis*; Cuba: Santa Lucia; *Lavin* 7146-3 (MONT); ¹AF398794.
- Poitea gracilis*; Cuba: Santa Lucia; *Lavin* 7146-4 (MONT); ¹AF398795.
- Poitea gracilis* (Grisebach) *Lavin*; Cuba: Levisa; *Lavin* 7138 (MONT); ¹AF398797, ²AF400149.
- Poitea immarginata*; Cuba: Pinar del Rio; *Lavin* 7105 (MONT); ¹AF398771.
- Poitea immarginata* (C. Wright) *Lavin*; Cuba: Pinar del Rio; *Lavin* 7104 (MONT); ¹AF398772, ²AF400141.
- Poitea multiflora* (Swartz) Urban; Dominican Republic: Las Matas de Farfan; *Lavin* 8027 (MONT); ¹AF398781, ²AF400143.
- Poitea paucifolia*; Dominican Republic: Rio Nigua; *Lavin* 8024 (MONT); ¹AF398801.
- Poitea paucifolia*; Dominican Republic: Boca Nigua; *Lavin* 8026 (MONT); ¹AF398802, ²AF400150.
- Poitea paucifolia*; Puerto Rico: Sabana Grande; *Lavin* 8008 (MONT); ¹AF398799.
- Poitea paucifolia*; Puerto Rico: Susua; *Lavin* 8009 (MONT); ¹AF398800.
- Poitea paucifolia* (DC.) *Lavin*; Puerto Rico: Yauco; *Lavin* 8006 (MONT); ¹AF398798.
- Poitea punicea*; Puerto Rico: N of Sabana Grande; *Lavin* 8004 (MONT); ¹AF398790.
- Poitea punicea*; Puerto Rico: Yauco; *Lavin* 8007 (MONT); ¹AF398791, ²AF400147.
- Poitea punicea* (Urban) *Lavin*; Puerto Rico: Sabana Grande; *Lavin* 8003 (MONT); ¹AF398789.
- Robinia hispida* L.; U.S.A.: New York; *Lavin* 010688 (MONT); ¹AF398819.
- Robinia neomexicana*; U.S.A.: Arizona; *Wojciechowski* 717(DAV); ¹AF398818.
- Robinia neomexicana* A. Gray; U.S.A.: Arizona; *Lavin* 190789 (MONT); ¹AF398817.
- Robinia pseudoacacia* L.; U.S.A.: New York; *Lavin* 6200 (BH); ¹AF398820.
- Robinia viscosa* Ventenat; U.S.A.: South Carolina; *Nelson* 14351 (MONT); ¹AF398821.
- Sesbania (Glottidium) vesicaria* (Jacq.) Elliott; U.S.A.: Texas; *Lavin* 6194 (BH); ¹AF398761.
- Sphinctospermum constrictum* (S. Watson) Rose; Mexico: Michoacan; *Lavin* 5120 (TEX); ¹AF398827.
- Zygocarpum coeruleum* Balf. f.; Yemen: Socotra; *Thulin & Gifri* 8781 (UPS); ¹AF189037.
- Zygocarpum dhofarensis* Hillcoat & Gillett; Yemen; *Thulin et al.* 9746 (UPS); ¹AF189040.
- Zygocarpum gillettii*; Somalia: Hobyo Dist.; *Wieland* 4357 (MO); ¹AF189043.
- Zygocarpum gillettii* *Thulin*; Somalia; *Wieland* 4681 (UPS); ¹AF189042.

Zygocarpum rectangulare Thulin; Somalia; Thulin et al. 5818 (UPS); 'AF189048.
6891 (UPS); 'AF189046. *Zygocarpum yemenense* Gillett; Yemen; Thulin et al. 9267
Zygocarpum somalense Gillett; Somalia; Thulin & Warfa (UPS); 'AF189051.

Appendix B

Data Set for Analysis with Component 2.0

```
#NEXUS
[Poitea and Pictetia]
BEGIN TAXA;
DIMENSIONS NTAX = 10;
TAXLABELS
AFRICAMADAGASCAR HORNNOFRICA
MESOAMERICA SOUTHAMERICA WESTCUBA
EASTCUBA SOUTHWESTHISPANIOLA
CENTRALHISPANIOLA PUERTORICO DOMINICA;
ENDBLOCK;

BEGIN DISTRIBUTION;
TITLE = 'Pictetia_Poitea';
NTAX = 29;

RANGE
Diphysa: MESOAMERICA,
Ormocarpum: AFRICAMADAGASCAR,
Zygocarpum: HORNNOFRICA,
Pi._obcordata: CENTRALHISPANIOLA,
Pi._aculeata: PUERTORICO,
Pi._sulcata: EASTCUBA SOUTHWESTHISPANIOLA
CENTRALHISPANIOLA,
Pi._marginata: EASTCUBA WESTCUBA,
Pi._nipensis: EASTCUBA,
Pi._spinosa: EASTCUBA WESTCUBA,
Pi._mucronata: EASTCUBA WESTCUBA,
Pi._angustifolia: WESTCUBA,
Gl._brenningii: SOUTHAMERICA,
Gl._maculata: MESOAMERICA,
Gl._sepium: MESOAMERICA,
Hy._robustum: MESOAMERICA,
Hy._ehrenbergii: MESOAMERICA,
Po._galegoides: SOUTHWESTHISPANIOLA
CENTRALHISPANIOLA,
Po._stenophylla: CENTRALHISPANIOLA,
Po._campanilla: CENTRALHISPANIOLA,
Po._longiflora: CENTRALHISPANIOLA,
Po._multiflora: CENTRALHISPANIOLA
SOUTHWESTHISPANIOLA,
Po._glyciphylla: SOUTHWESTHISPANIOLA,
Po._immarginata: WESTCUBA,
Po._florida: PUERTORICO,
Po._carinalis: DOMINICA,
Po._punicea: PUERTORICO,
Po._paucifolia: CENTRALHISPANIOLA PUERTORICO,
Po._dubia: CENTRALHISPANIOLA,
Po._gracilis: EASTCUBA WESTCUBA;

TREE PictetiaPoitea = ((Diphysa, Ormocarpum,
Zygocarpum,(Pi._obcordata,Pi._aculeata,(Pi._sulcata,
Pi._marginata,(Pi._nipensis,Pi._spinosa,Pi._mucronata,
Pi._angustifolia))))),(Gl._brenningii,Hy._robustum,
Cy._ehrenbergii,(Gl._maculata,Gl._sepium)),
((Po._immarginata,(Po._multiflora,Po._glyciphylla),
(Po._galegoides,Po._stenophylla),(Po._longiflora,
Po._campanilla))),(Po._punicea,Po._florida,Po._carinalis),
(Po._gracilis,(Po._paucifolia,Po._dubia))));
ENDBLOCK;

BEGIN TREES;
RANDOM MODEL = EQUIPROBABLE NTREES =
1000;
ENDBLOCK;
```

Appendix C

Input File for Three-Area-Statement Analysis (TASS) Invoking Assumption 2 for Widespread Taxa

For area designation (A, B, C, etc.), see figure 1.

29	3	4 5	3 4	0	h	i
17	2	6	5	0	gh	ef
2	4	0	6	0	h	efgh
2	2	24 25	7 8	0	i	f
4	2	0	9	b	j	ef
4	2	13 14 15	0	a	i	ef
2	2	16	10	a	ef	e
3	0	26 27 28 29	11 12	a	hi	
2	0	7 8	13	a	h	
2	19 20 21	9 10	14 15 16	e	a	
2	1 2 3	11 12	0	gh	d	
3	0	17 18	17	g	c	
3	22 23	1 2	0	h	h	

Appendix D

Output from TASS (Three-Area-Statements Invoking Assumption 2 for Widespread Taxa) and Converted to Nexus Format

```

#NEXUS
[FROM TASS OUTPUT IN HENNIG86 FORMAT]
BEGIN DATA;
DIMENSIONS NTAX = 11 NCHAR = 11;
FORMAT MISSING = ? symbols = "01";
MATRIX

                                11
                                12345678901
OUTGROUP                        00000000000
Mesoamerica                     00000000001
South_America                   000000??01
Horn_of_Africa                  ??????000??
Africa_Madagascar              ??????000??
Western_Cuba                    101010111?0
Eastern_Cuba                    10????111?0
Southwestern_Hispaniola        ??1111110?0
Central_Hispaniola             111111100?0
Puerto_Rican_Bank             11????10010
Dominica                        ???????010

; END; BEGIN PAUP; OUTGROUP 1; END;

```

Appendix E

Nexus File Representing the Additive Binary Coding of the Areagram in Figure 1 and Invoking the "Inclusive O-Ring" for Paralogous Taxa

```

#NEXUS
BEGIN DATA;
DIMENSIONS NTAX = 10 NCHAR = 46;
FORMAT MISSING = ? symbols = "01";
MATRIX

                                1111111111222222222233333333334444444
                                1234567890123456789012345678901234567890123456
Mesoamerica                     0111100000000000000100000000000011000001000001
South_America                   10000000000000000000000000000000000000000001000001
Horn_of_Africa                  00000000000000000001000000000010000000000000
Africa_Madagascar              000000000000000000010000000000001000000000000
Eastern_Cuba                    000000000000000100000001111101111000000010111
Western_Cuba                    00001000000001000100000111111000000011111
Southwestern_Hispaniola        000001100100000000000001000001110101000101011
Central_Hispaniola             000001011110000110001001000001110110010111111
Puerto_Rican_Bank             000000000001010000001000000011000100000111
Dominica                        00000000000010000000000000000000000000100000111

; END; BEGIN PAUP; OUTGROUP 1 2 3 4; END;

```

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