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PHYLOGENETIC ANALYSIS OF THE GENUS *HAMPEA* (MALVALES: MALVACEAE: GOSSYPIEAE)

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RESUMEN

Se realizó un análisis filogenético de las 21 especies conocidas del género *Hampea* (Malvales: Malvaceae: Gossypieae), un género endémico de México (sur de 22° N), Centroamérica y Colombia. Usando características morfológicas externas, se calculó un árbol mínimo de 94 pasos con un índice de consistencia de 0.413 y un índice de retención de 0.645. Los resultados del análisis sugieren que el género se diversificó primero en el sur de México y el norte de Centroamérica, y luego se dispersó hacia el norte y hacia el sur. Aparentemente, una de las primeras divergencias del genero ocurrió dentro de las poblaciones ancestrales de *Hampea* de la costa del Atlántico con las de la costa del Pacífico. La estructura del árbol sugiere que especies de hábitats montañosos son derivados de ancestros de tierras bajas. También, varios caracteres que son útiles en diferenciar especies (flores unisexuales o flores perfectas, presencia y forma de nectarios extrafoliares, y la presencia de domacios) fueron relativamente homoplásticos en el análisis. Observaciones de campo indicaron que la homoplasticidad de estos caracteres posiblemente se deben a su valor adaptativo bajo diferentes condiciones ecológicas. Se presentan conclusiones acerca de la biogeografía del género y futuros temas de investigación relacionados con la evolución de *Hampea*.

Palabras clave: Malvaceae, filogenética, *Hampea*, Gossypieae, México, Centroamérica

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ABSTRACT

A phylogenetic analysis was conducted of the 21 known species of the genus *Hampea* (Malvales: Malvaceae: Gossypieae), a genus endemic to Mexico (south of 22° N), Central America and Colombia. Using external morphological characters, a single tree of a minimum length of 94 was calculated with a consistency and retention index of 0.413 and 0.645, respectively. Results suggest that the genus first diversified in the region of southern Mexico and northern Central America and then later dispersed southward and northward. An early divergence of the genus apparently occurred between ancestral populations on the Atlantic versus the Pacific coastal plains. Results further suggest that *Hampea* species now occurring in montane habitats are derived from lowland ancestors. Additionally, several characters (monomorphic versus dimorphic flowers, presence and form of extrafloral nectaries, and the presence of domatia) which are useful in distinguishing species proved to be relatively homoplastic in phylogenetic analysis. Observations in the field indicated that the homoplasticity of these characters was possibly due to their adaptive value under different ecological conditions. Further biogeographic conclusions and possible future research topics concerning the evolution of *Hampea* are discussed.

Key words: Malvaceae, Gossypieae, cotton tribe, phylogenetics, *Hampea*, Mexico, Central America

INTRODUCTION

The genus *Hampea* Schlechtendal is a clearly delimited monophyletic taxon within the tribe Gossypieae, family Malvaceae (Fryxell, 1968; Fryxell, 1979). Like other members of the cotton tribe, species of *Hampea* have gossypol glands, capsular fruits, decurrent stigmas, and a common basic chromosome number ($x = 13$). However, *Hampea* is unique among Gossypieae in the possession of: 1) glabrous seeds partially enclosed in a white fleshy aril; 2) dioecious flowering habit (18 of the 21 species); 3) multiple flowers per axil; and 4) relatively reduced flower size.

Plants of this genus are small to medium-sized trees endemic to Mexico (south of 22° N), Central America, and northern Colombia. The greatest diversity of Hampea occurs in the area including the state of Chiapas, Mexico and Guatemala (10 of the 21 species; Table 1). Species of *Hampea* generally occur in mesic environments, although some species are found in seasonally dry habitats. They are also found from sea level to elevations below the frost line (Fryxell, 1979). All of the species of *Hampea* have relatively restricted distributions.

Many of the plants of the lowland tropical forests in Mexico and Central America also are found in South America (Rzedowski, 1993), which has led to the conclusion that plants of the lowland tropical forests of Mexico and Central America are primarily South American (Gondwanalandian) in origin (Rzedowski, 1993;

Wendt, 1993). However, there is a small group of endemic, lowland tropical plants that are apparently Mesoamerican in origin (Wendt, 1993). The distribution of *Hampea* suggests that the genus is part of this small group. The diversity of *Hampea*, its high level of endemism in Mexico and Central America, and its clear monophyly make it an ideal candidate for study of the biogeography and speciation of plants in the tropical regions of Mesoamerica

Hampea is also the apparent original host genus of the *Anthonomus grandis* species complex (Fryxell and Lukefahr 1967, Burke *et al.*, 1986). The nominate species of this complex, the boll weevil (*Anthonomus grandis* Boheman), is the key pest of cotton in most of the Americas. Until relatively recently, no closely related species to *A. grandis* were known and it was assumed that cotton was the original host of this pest. However, four species of *Anthonomus* are now known to be closely related to *A. grandis* (Burke and Cate 1979; Jones, 1994). These four weevil species are all apparently restricted to *Hampea* for reproductive development, strongly suggesting that the ancestral host plant of this complex is *Hampea*. Understanding the phylogeny of *Hampea* will provide the evolutionary framework for understanding the evolution of the *A. grandis* species complex and its host plant ecology and give insight into how *A. grandis* has become a pest of cotton .

This study has three objectives: 1) to develop a hypothesis of the phylogenetic relationships of species of *Hampea* using external morphological characters, 2) to use the phylogenetic hypothesis to interpret biogeographic patterns of *Hampea*, and 3) to postulate evolutionary trends in character evolution and possible factors responsible for these trends.

MATERIALS AND METHODS

The external morphological features of the 21 species of the genus *Hampea* were studied and compared. Observations of *Hampea* were also made in the field for species occurring in southern Mexico and Guatemala. Additionally, pollen grains of all species were analyzed using slide mounts of pollen following acetolysis (Erdtman, 1960). Some of the specimens examined were collected during the present study, but the bulk of the material studied was from the herbaria at the Cotton Research Laboratory of the United States Department of Agriculture in College Station, TX, which was transferred in 1993 to the herbaria of the New York Botanical Garden (NY) and the University of Texas (TEX), when the Cotton Research Laboratory was closed. Material was also examined at the Herbario Nacional (MEXU) of the Universidad Nacional Autónoma de México in Mexico City.

Table 1. Species of the genus *Hampea* Schlechtendal and their generalized distribution

Species	Distribution
1. *Hampea albipetala* Cuatrecasas	Colombia, in Dept. del Valle, to Panama
2. *Hampea appendiculata* (J. D. Smith) Standley	Costa Rica, Nicaragua, Panama
3. *Hampea bracteolata* Lundell	Guatemala
4. *Hampea breedlovei* Fryxell	Chiapas, Mexico
5. *Hampea integerrima* Schlechtendal	Veracruz, Mexico
6. *Hampea latifolia* Standley	Chiapas, Mexico and Guatemala
8. *Hampea mexicana* Fryxell	Oaxaca and Chiapas, Mexico
9. *Hampea micrantha* Robyns	Northeastern Panama
10. *Hampea montebellensis* Fryxell	Eastern Chiapas, Mexico
11. *Hampea nutricia* Fryxell	Veracruz and Tabasco, Mexico
12. *Hampea ovatifolia* Lundell	Guatemala, Belize
13. *Hampea platanifolia* Standley	Costa Rica and Nicaragua
14. *Hampea punctulata* Cuatrecasas	Panama-Colombia border
15. *Hampea reynae* Fryxell	Northwestern El Salvador
16. *Hampea rovirosae* Standley	Tabasco and Chiapas, Mexico and adjacent Guatemala
17. *Hampea sphaerocarpa* Fryxell	Northern Honduras and extreme eastern Guatemala
18. *Hampea stipitata* S. Watson	Guatemala, El Salvador, Belize and Chiapas, Mexico
19. *Hampea thespesioides* Triana & Planchon	Central Colombia
20. *Hampea tomentosa* (Presl) Standley	Colima, Michoacán, and Guerrero, Mexico
21. *Hampea trilobata* Standley	Yucatan peninsula, Mexico, adjacent lowlands of Guatemala and Belize

The genus *Thespesia* (using the species *Thespesia populnea* (L) Solander ex Correa), was chosen as the outgroup for phylogenetic analysis for several reasons. First, in a preliminary phylogenetic analysis of the cotton tribe using character states given by Fryxell (1979), *Thespesia* was the sister group of a clade composing *Lebronnecia* Fosberg and *Hampea*. *Lebronnecia* was not chosen as the sister group because as a monotypic genus with a highly restricted distribution (Marquesas Islands), the probability is high that its only species has evolved several, highly derived autapomorphic characters that would confound analysis. Second, some species of *Thespesia*, including *T. populnea*, are found in the New World where *Hampea* is restricted, indicating that the two genera may have shared a common ancestor in the New World.

The characters chosen for phylogenetic analysis and their states are listed in Table 2. Characters were chosen based on previous descriptions and analyses of morphological traits by Fryxell (1969, 1979) and Fosberg and Sachet (1972) of *Thespesia*, as well as examination and comparisons of characters from specimens. The data matrix of the coded data for the genus *Hampea* is presented in Table 3. Unknown character states are notated as "?." Twenty of the characters had two states, nine had three states, and one had four character states. No autapomorphies were included in the analysis. The data matrix of characters for the genus and its sister group was analyzed using phylogenetic computer software (PAUP, Swofford, 1990; HENNIG86, Farris, 1989). After exploratory parsimony analysis, successive approximation procedures were used to evaluate characters using the rescaled consistency index as a weighting factor (Farris, 1989). A final analysis was conducted without the characters that had zero weight after using successive weighting procedures. All characters in these analyses were ini-tially unweighted and unordered. The random addition sequence of PAUP with fifteen passes was used with ACCTRAN optimization, tree-bisection reconnection branch swapping and "mulpars" options in effect. Analyses in HENNIG86 used multiple tree calculation procedures with branch swapping options ("mhennig*," and "bb*"). All resulting trees calculated from both PAUP and HENNIG86 using successive approximation procedures and the unweighted analyses were compared.

RESULTS AND DISCUSSION

Cladogram and support for proposed groupings. Parsimony analysis using all unweighted characters from Table 3 had little resolution and resulted in 144 trees with consistency (CI) and retention (RI) indices of 0.36 and 0.57, respectively. Successive approximation procedures in both PAUP and HENNIG86 calculated one tree after three passes through the data. This tree had a CI and RI of 0.60 and 0.81, respectively, and procedures weighted the characters as follows (character-weight[on scale of 1-10): 1-1; 2-1; 3-0, 4-0; 5-0; 6-1; 7-3; 8-10; 9-10; 10-1; 11-2; 12-2; 13-1; 14-2; 15-10; 16-2; 17-4; 18-2; 19-1; 20-0; 21-5 ; 22-1; 23-1; 24-1; 25-1; 26-2; 27-10; 28-10; 29-1; 30-1. Characters that had zero weight after successive approximation (characters: 3, 4, 5, and 20) were dropped from the matrix and trees recalculated with all characters

Table 2. Characters and character states used in the analysis of the phylogenetic relationships of the genus *Hampea*

Characters	Character States
1. Flowers	0: Perfect 1: Dimorphic
2. Involucellar nectaries	0: Absent 1: Present
3. Pedicel length[1]	0: Longer than 5 cm 1: Shorter than 5 cm
4. Calyx at anthesis[1]	0: Pentamerously split 1: Irregularly split
5. Stamens[1]	0: Punctate 1: Not punctate
6. Petals	0: Not reflexed 1: Reflexed
7. Petal length	0: Less than 1.5 cm 1: Between 1.5 to 2.5 cm 2: Greater than 3 cm
9. Petal cushion	0: Absent 1: Present
10. Number of pedicels/axil	0: Few, 1 to 4 1: Many, more than 6 common
11. Fruit size	0: Less than 10 cm^3 1: Greater than 20 cm^3
12. Fruit shape	0: Globose 1: Elongate
13. Capsule interior	0: Glabrate 1: Hirsute along suture only 2: Pubescent
14. Number of seeds locule	0: From 1 to 4 1: More than 5
15. Auriculate appendages	0: Absent 1: Poorly developed 2: Strongly developed
16. Foliar nectaries: Number and location on mid vein	0: 1, basal 1: 3, basal to mid basal 2: 3 to 5, mid leaf to upper 3: 5 to 7, top 5th of leaf
17. Leaf size	0: small, less than 200 cm^2 1: Medium, 225 to 300 cm^2 2: Large, greater than 350 cm^2

Table 2, continued

Characters	Character States
18. Leaf length/width ratio	0: 1.25 or less 1: Greater than 1.3
19. Lobes on leaves	0: Absent 1: Present
20. Domatia [1]	0: Absent 1: Present
21. Petiole pubescence	0: Glabrate 1: Stellate hairs 2: Simple hairs
22. Stellate hair length	0: Small, less than 0.15 mm 1: Large, more than 0.15 mm
23. Leaf pubescence (adaxial)	0: Glabrate 1: Veins only 2: Veins and blade
24: Leaf pubescence (abaxial)	0: Glabrate 1: Veins only 2: Veins and blade
25: Leaf margins	0: Glabrate 1: Ciliate 2: With stellate hairs
26. Calyx interior	0: Hirsute 1: Hirsute with basal tuft 2: Glabrate
27. Pentamerous calyx venation	0: Present 1: Absent
28. Calyx venation points	0: Present 1: Absent
29. Pollen spine cushion	0: Present 1: Absent
30. Capsule surface	0: Smooth 1: Ridged

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[1] Characters which had zero weight following successive weighting procedures and were thus dropped from final analysis.

unweighted and unordered. One tree resulted with both PAUP and HENNIG which was identical to that derived using successive approximation. This tree had length 94, CI and RI of 0.415 and 0.641, respectively, and is presented in Figure 1.

Only four characters showed no homoplasy in the final tree (Fig.1) and 10 characters had consistency indices of 0.50 or above. However, only five characters had ambiguous state changes on the tree (characters 6, 11, 15, 26) and all nodes were supported by unambiguous character changes. The ambiguity for character 6 (reflexed or non-reflexed petals) was due simply to the undetermined status of this character in three of the members of the most derived clade (Clade B3, Fig. 1). The state of fruit size (character 11) was ambiguous at the most basal node between the outgroup *Thespesia* and *Hampea.* The state of fruit size in the outgroup is uncertain because members of *Thespesia* have small to large fruits. However, this does not affect internal tree topology. Coding this character as "1" (fruit 20 $cm^{2)}$ for *Thespesia* resolves this ambiguity in the proposed tree topology and may better reflect the actual condition of this character in the outgroup. The state of auriculate appendages (character 15) was ambiguous at the nodes between *H. trilobata* and *H. ovatifolia.* The ambiguity of character 22 (stellate hair length) is because the basal member of Clade B, *H. trilobata,* has large hairs; a character state otherwise restricted to Clade A. This arrangement means that stellate hair length of the common ancestor to Clades A and B is unresolved. Independent acquisition of long hairs on *H. trilobata* is plausible given that stellate hairs are related to water stress in leaves and this species occurs in the driest habitats of Clade B. These were the only two species which had these appendages present but in a poorly developed state. These appendages were either present in the common ancestor of Clade B (Fig. 1) and retained by *H. trilobata* and *H. ovatifolia* then later lost in the more derived species, or they developed independently in *H. trilobata* and *H. ovatifolia.* The state of the calyx interior of the ancestor of B1 (*H. montebellensis* and *H. longipes,* Fig. 1) and its sister group is ambiguous. This is because Clade B1 contains the only members with an interior tuft in the calyx. This ambiguity does not affect tree topology.

Several clades within the proposed phylogeny were well supported. The position of *H. rovirosae* as the sister species to the rest of the species of *Hampea* is supported by several characters (Fig. 1). These include the retention of the following plesiomorphic characters: irregular insertion of the involucellar bractlets (ci=1.0), calyx splitting pentamerously at anthesis (ci=0.50), glabrate petiole (ci=0.67), possession of perfect flowers (ci=0.33), glabrate ventral and dorsal leaf surfaces (ci=0.40 and 0.25, respectively).

Clade B (Fig. 1), consisting of *H. tomentosa, H. reynae, H. mexicana, H. latifolia,* and *H. platanifolia,* is supported by the possession of relatively large petals and fruit (ci=0.50 and 0.33, respectively). This clade retains the primitive characters of possession of involucellar nectaries, pentamerous venation and points (vestigial lobes) on the calyx, and large numbers of seeds per fruit. Species in the sister group of this clade have a reduction in the number of seeds per locule and loss of the in-

Table 3. Data matrix used for phylogenetic analysis of *Hampea.* The notation "?" means that character state is unknown

Taxa	Characters
	000000000111111111122222222223
Character Number	123456789012345678901234567890
H. albipetala	10100?221001112201001002201101
H. appendiculata	111011221101112201011012021101
H. bracteolata	111010220000210101010022021111
H. breedlovei	1100?01200100100010100000211?1
H. integerrima	111011220000210201000000021111
H. latifolia	101010020011100120101011 1?0000
H. longipes	110010220000120101001011011001
H. mexicana	101000120010000110111122200000
H. micrantha	11001?220000020001011001021100
H. montebellensis	101010220000210101011112011000
H. nutricia	111001220100110310101012021101
H. ovatifolia	11100?22000001110010110222 0001?
H. platanifolia	000110120011100320111012200001
H. punctulata	111010221101112201011022021101
H. reynae	011010120010110110112122000000
H. rovirosae	001110200011000200110000020001
H. sphaerocarpa	111011220000120301001022021110
H. stipitata	111011220100110301011012001110
H. thespesioides	11100?221001112201011022221101
H. tomentosa	101010110010100000101122100000
H. trilobata	111000220100111000111122000000
Thespesia (outgroup)	000000000000000000000000000000

volucellar nectaries (ci=0.40 and 0.250, respectively). The leaf size of the four species making up the sister group of *H. tomentosa* is distinctive in that leaf area is considerably greater than that of all other members of the genus, except *H. nutricia*. Leaf area forms a transformation series on the tree from moderately large leaves (225 to 300 cm^2) in *H. reynae* and *H. mexicana* to very large leaves (350 cm^2) for *H. platanifolia* and *H. latifolia* (Fig. 1).

Hampea trilobata and *H. ovatifolia* form successive basal branches to the remainder of the genus, although each branch is only weakly supported by one or two characters (Fig. 1). The apomorphic character for *H. trilobata* is the high pedicel number per axil (ci=0.33), which is also found in the more derived members of the genus. The *H. ovatifolia* branch is supported by stellate pubescence on the leaf margins and pollen spine cushions (ci=0.40, 0.33, respectively). Both species retain the primitive characters of basal floral nectaries and pentamerous calyx venation and points.

H. montebellensis and *H. longipes* form a well supported, two member clade (Clade B1, Fig. 1) sharing the synapomorphic character of an interior, basal calyx tuft (ci=1.0) and are the only species that possess calyx points without pentamerous venation. The species of the sister group to *H. longipes* and *H. montebellensis* clade do not possess either calyx venation or points.

Hampea micrantha displays several reversals in character states, including loss of dorsal and ventral leaf pubescence, and the hirsute suture in the capsule. *Hampea micrantha* retains the primitive basal floral nectary arrangement, but possesses the apparently more derived condition of a reduction in the number of seeds per locule. It is also the only species with branching (rather than fasciculate) flower arrangement.

Hampea breedlovei, H. integerrima, and *H. bracteolata* form a relatively well supported clade (Clade B2, Fig.1), the members of which each possess pubescent capsule interiors, glabrate petioles and irregular surfaced capsules (ci=0.33, 0.667, and 0.200, respectively). The characters supporting the sister group of this clade are the possession of reflexed petals and multiple and apical foliar nectary arrangements (ci=0.33 and 0.375, respectively).

Hampea sphaerocarpa, H. stipitata, and *H. nutricia* each branch separately from the tree. The evidence supporting these branching points is relatively weak. *Hampea sphaerocarpa* has a single seed per locule (ci=0.40) and differs from species of its sister group in the possession of fewer pedicels per axil. The apomorphy supporting the branch of *H. stipitata* is the reversal of the hirsute calyx interior to a glabrate one (ci=0.40). Species in its sister clade have pollen cushions and an irregular capsule surface. Apomorphies differentiating *H. nutricia* from its sister group are all reversals in leaf characters, including increased leaf size, a reduced leaf length to width ratio, and the possession of leaf lobes.

The most strongly supported clade in the phylogeny is that containing *H. appendiculata, H. punctulata, H. albipetala,* and *H. thespesioides* (Clade B3, Fig. 1). Members of this clade share a distinct petal cushion (ci=1.0), distinct auriculate

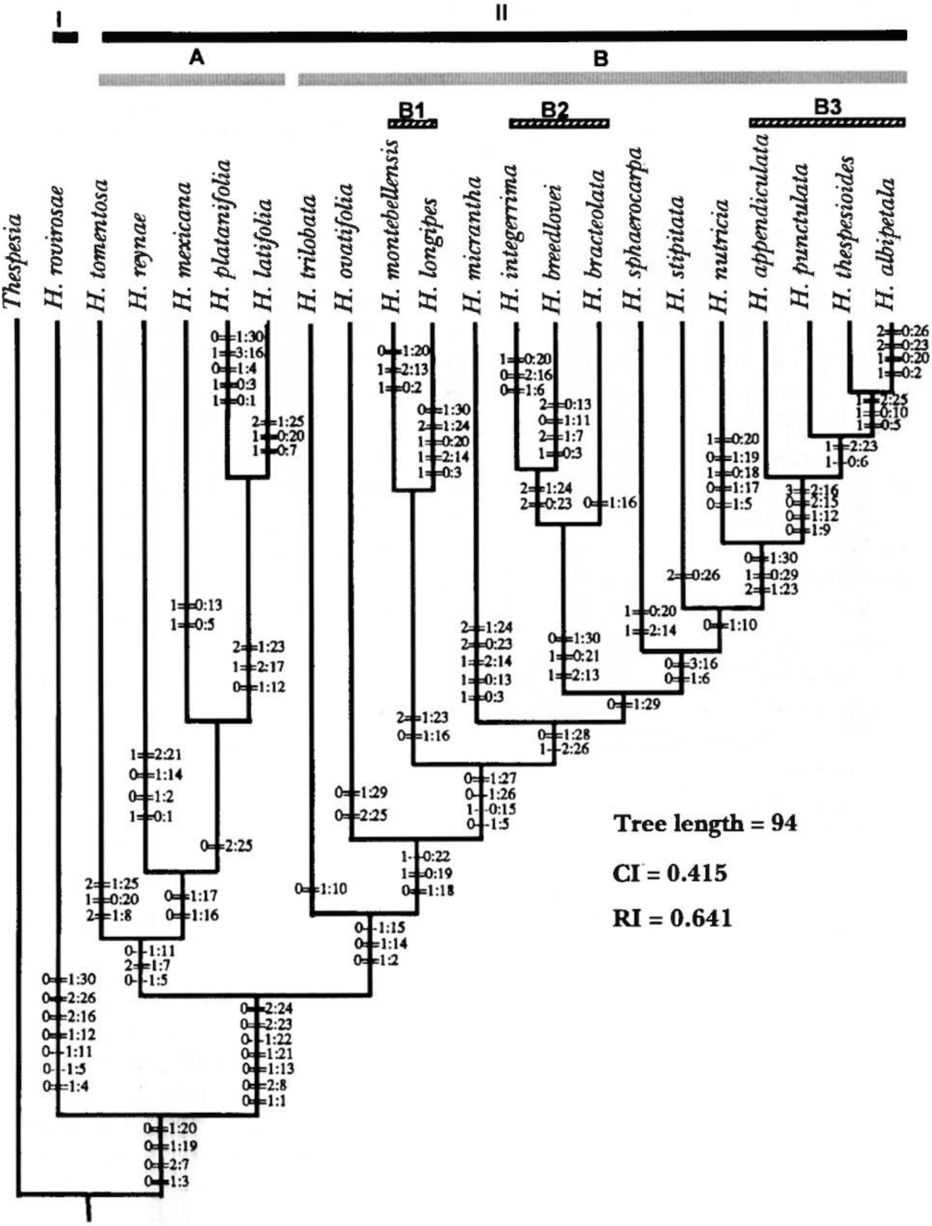

Fig. 1. Phylogeny of *Hampea* and notation of clades used in text. The number of states changes is given per branch with unambiguous changes indicated as double line, ambiguous changes indicated by a single line.

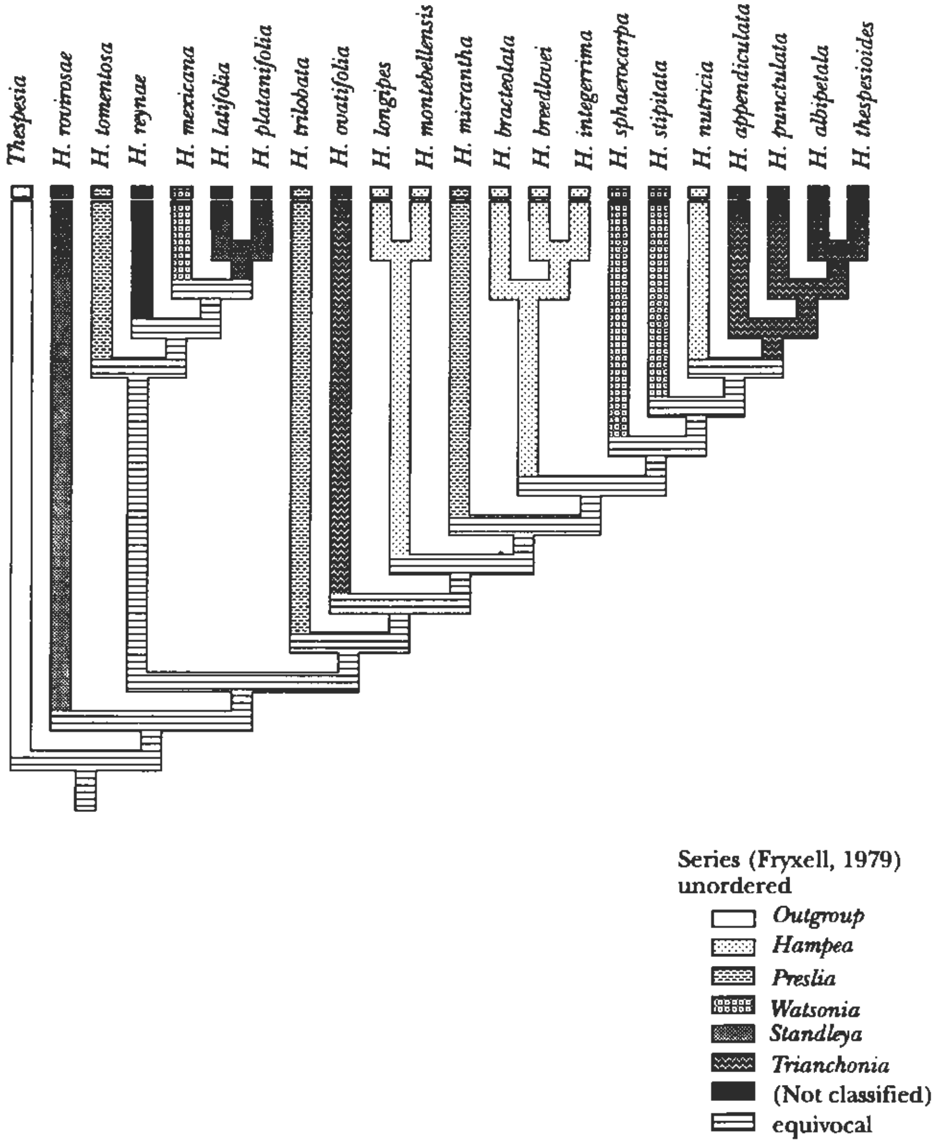

Fig. 2. Phylogeny of the genus *Hampea* with taxa with taxa coded as the infrageneric classification of Fryxell (1979).

appendages on the leaves (ci=0.67), elongate fruit shape (ci=0.33), and similar foliar nectary arrangements (ci=0.375). The clade of *H. punctulata, H. albipetala,* and *H. thespesioides* is supported by the possession of greater leaf pubescence (ci=0.25). *Hampea albipetala* and *H. thespesioides* have a reversal to fewer numbers of pedicels per axil and have leaf margins with stellate pubescence. *Hampea albipetala* has three character reversals in the possession of involucellar nectaries, glabrate dorsal leaf surface, and glabrate capsule interior.

Comparison of cladogram with the infra-generic classification of Fryxell (1979). Fryxell (1979) presented a classification of *Hampea* in which he divided the genus into three sections: *Hampea, Standleya,* and *Trianchonia.* Fryxell's classification is compared to the proposed phylogeny in figure 2. He considered *Standleya* as the most primitive group, within which he placed the three perfect flowered species, *H. platanifolia, H. rovirosae,* and *H. latifolia.* However, in his later description of *H. reynae* (Fryxell, 1980), Fryxell commented on the problematic relationship of this species with members of *Standleya* because, although *H. reynae* has perfect flowers and pentamerous calyces, it lacks the involucellar nectaries and has only two seeds per locule, unlike members of *Standleya.* Additionally, observations of *H. latifolia* in the field confirmed that the species is dioecious and does not possess perfect flowers (Fryxell, 1980). Fryxell (1980) therefore recommended a reconsideration of the infra-generic classifications.

The phylogenetic analysis conducted here suggests three principal sub-generic groups. The first group is made up of the single species of *H. rovirosae* (Clade I, Fig. 1). The second group consists of the clade including the rest of the *Hampea* (Clade II, Fig. 1). This group is composed of two sister clades which subdivide Clade II, the first of these contains *H. tomentosa, H. reynae, H. mexicana, H. latifolia,* and *H. platanifolia* (Clade A, Fig. 1). The second clade (Clade B) consists of *H. trilobata, H. ovatifolia, H. longipes, H. montebellensis, H. micrantha, H. bracteolata, H. breedlovei, H. integerrima, H. sphaerocarpa, H. stipitata, H. nutricia, H. appendiculata, H. punctulata, H. albipetala, and H. thespesioides.*

We therefore wish to provide a revised infrageneric classification of the genus, as follows:

Hampea sect. *Hampea*

Type species: *H. integerrima* Schldl.

Included species: *H. albipetala, H. appendiculata, H. bracteolata, H. breedlovei, H. integerrima, H. longipes, H. micrantha, H. montebellensis, H. nutricia, H. ovatifolia, H. punctulata, H. sphaerocarpa, H. stipitata, H. thespesioides.*

Hampea sect. *Standleya* Fryxell.

Type species: *H. platanifolia* Standl.

Included species: *H. latifolia, H. mexicana, H. platanifolia, H. reynae, H. tomentosa.*

Hampea sect. ***Eohampea*** R.W.Jones, Fryxell et D.M.Baro, sect. nov.
Type species: *H. rovirosae* Standley
Included species: *H. rovirosae.*

Plantae glabrescentes; pedicellis solitariis (vel binatis) in axillis foliorum, nectariis tribus prominentibus cum 3-6 bracteis involucellorum irregulariter et distaliter insertis; floribus perfectis, calycibus leniter 5-nervatis, saepe 5 dentatis; capsulis duplo longioribus quam latioribus, ellipsoideis, obtusis vel retusis.

This classification represents a considerable revision of the earlier one presented by Fryxell (1969) but seems amply justified by the present analysis. The most striking features of the new classification are the recognition of the basal position of *H. rovirosae* as sect. *Eohampea* and the clear unity of the species now included in sect. *Standleya* with its revised circumscription. The remaining species (sect. *Hampea*) are quite diverse, but do not at the present time seem to be further divisible into subgroups.

Character evolution: dioecism. One of the most characteristic features of the genus *Hampea* is that the majority of the species are dioecious (18 of 21 species). Only one other species of the cotton tribe, *Cienfuegosia heteroclada* Sprague, is fully dioecious (Fryxell, 1979). The relative rarity of dioecy in the cotton tribe suggests that although this is not a novel evolutionary trait, it requires some significant genetic rearrangements for its expression.

Phylogenetic analysis of *Hampea* indicates that the dimorphic, unisexual flowers of dioecious species evolved only once in the genus in Clade II (Fig. 1). However, analysis also suggests that a reversal from dimorphic to perfect flowers occurred twice in Clade A (Fig. 1) in *H. platanifolia* and *H. reynae.* Such reversals initially seem improbable given that they not only require regaining a lost or atrophied androecium or gynoecium, but also involve a major change in the pollination ecology. However, within Clade B (Fig. 1), female flowers of the dioecious species *H. tomentosa* and *H. latifolia* still retain partial development of anthers and some pollen grains are produced (Fryxell, 1979). Given this partially dioecious condition, the reversal of the dioecious condition is plausible if selection began to favor individuals with perfect flowers.

One factor that may favor individuals capable of self fertilization is low population densities. The two species for which reversals to perfect flowers are postulated, *H. platanifolia* and *H. reynae,* are presently two of the least common members of the genus. *Hampea reynae* is known from one locality in the mountains of El Salvador where it is very rare (Reyna, 1979). *Hampea platanifolia* has been only infrequently collected and was difficult to find while conducting field studies within its reported area of distribution in Costa Rica

Further evidence of the difficulty in classifying some species of *Hampea* as either dioecious or monecious was found from observations of some populations of *H. trilobata* in the field. Several plants were found south of Escarcega, Campeche

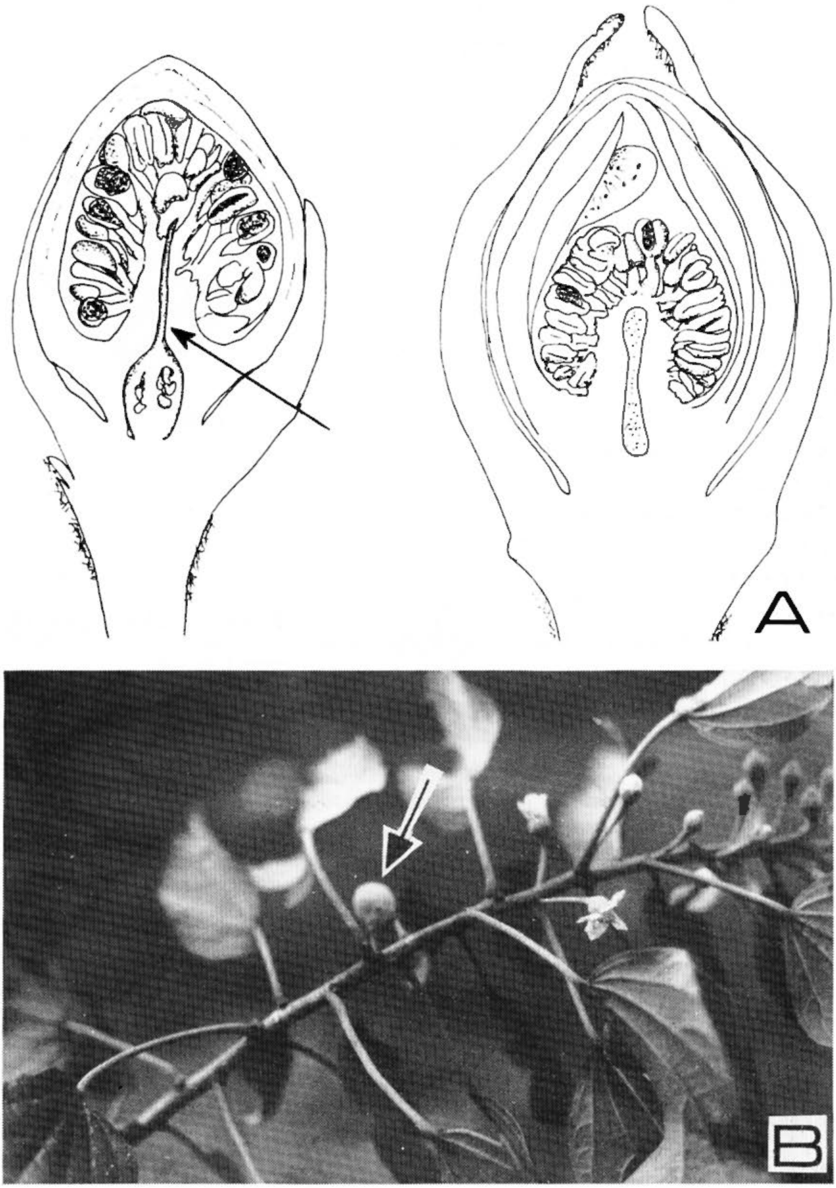

Fig. 3. Evidence of indeterminate floral morphology of *H. trilobata.* A. Dissected flowers of *H. trilobata* (left) showing partial development of style (arrow) and ovary when compared to fully unisexual male flower of *H. latifolia* (right). B. Branch of *H. trilobata* found near Escárcega, Campeche, Mexico with apparent male flowers in bloom but with maturing fruit (arrow) on lower portion of branch.

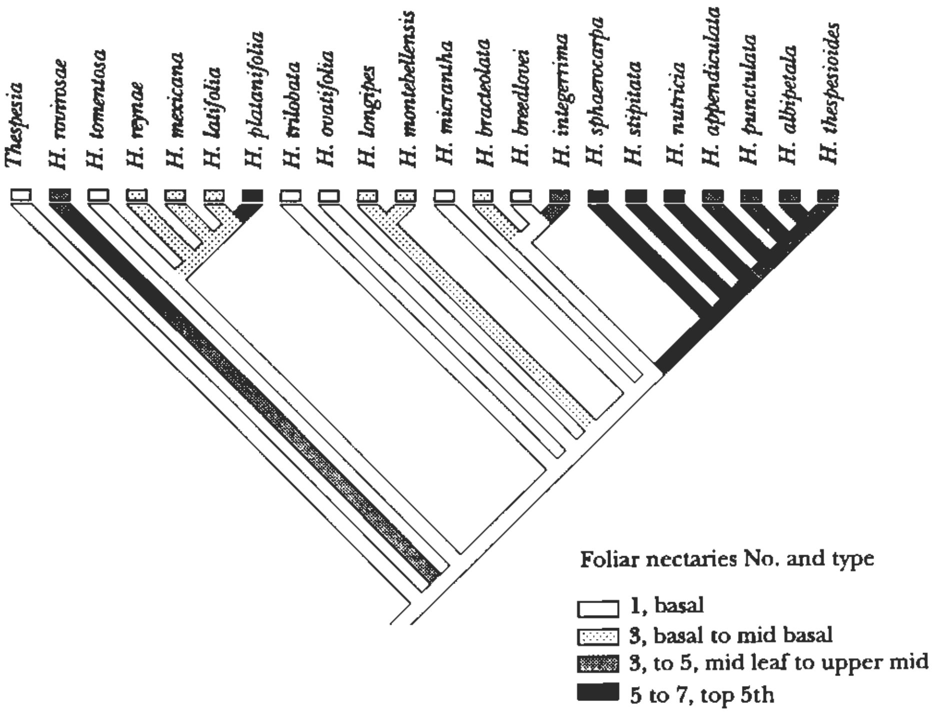

Fig. 4. Proposed phylogeny of the genus *Hampea* showing state changes in foliar nectary arrangement.

(Fig. 3 A) which had both fruit and apparently male flowers on a single branch. Dissections of buds from these plants and other plants with apparent pistillate flowers from the same area revealed significant development of an ovary and style, but without an apparent stigma (Fig. 3 B). Whether these flowers were functionally bisexual at some later point in flower development or simply imperfect is unknown. Further study is needed on the floral biology of *H. trilobata* and other species of *Hampea*.

Character evolution: extrafloral nectaries. Extrafloral nectaries are useful in distinguishing species of *Hampea*, but were found to be relatively homoplastic (ci=0.375, with four states for foliar nectaries and ci=0.250 for involucellar nectaries) in the phylogenetic analysis. A single basal nectary is clearly ancestral for foliar nectaries, but the evolution of multiple nectaries along principal veins appears to have arisen independently several times in the genus (Fig. 4). The low consistency index calculated for extrafoliar nectaries is probably due to their adaptive value. This is suggested because nectaries are found on all *Hampea* species despite the possible metabolic cost of nectar excretion.

Extrafloral nectaries have adaptive significance to plants because they attract predators, especially ants, which in turn attack injurious herbivorous insects on the secreting plant (Bentley, 1977). The benefits to both plant and insect have evolved into obligate mutualism in several plants and insects species in the tropics (Janzen, 1967; Kricher, 1989). The correlation of increased ant predators with the presence of foliar nectaries is hypothesized to have resulted in the independent development of multiple foliar nectary arrangements in *Hampea*. Ants were observed many times feeding on the foliar nectaries of various species of *Hampea* and some ants were observed in apparent searching behavior on leaves with several nectaries. Foliar nectaries that are numerous and scattered on the leaves will probably lead to greater searching by ants and increase the probability of them encountering insect herbivores. This is supported by the fact that *Hampea* species with the greatest number of nectaries all occur in lowland, moist, tropical habitats where herbivore pressure is probably greatest.

Character evolution: domatia. The term domatia, meaning "house" refers to a flap of tissue that forms over the base of the junction of two principal veins. The presence of domatia on plants was highly homoplastic, suggesting the structures evolved independently several times in the genus *Hampea*. Like extrafloral nectaries, the presence of domatia on *Hampea* leaves may be the result of evolution of mutualistic associations with arthropods. Walter and O'Dowd (1992) found that tropical plant species with domatia had greater numbers of phytoseiid predatory mites on leaves than species without domatia, apparently because of the shelter the domatia afforded the mites. *Hampea* is often heavily infested with phytophagous mites on which phytoseiids are likely to prey. The development of domatia may have been selected for in several lineages of *Hampea* because of the benefits in maintaining high predatory mite densities on leaves.

Biogeography of *Hampea*. The distributions of the closest relatives of *Hampea* suggest that the genus evolved from plants that had colonized Middle America via oceanic dispersal. *Lebronnecia* and *Kokia* are both restricted to volcanic Pacific islands (Fryxell, 1979) and must have evolved from an ancestor that had crossed large oceanic distances. *Thespesia* is a pantropical genus and some members are common in the strand habitat adjacent to the sea, including Middle America and the Caribbean (Fosberg and Sachet, 1972; Fryxell, 1979). The distribution of the least derived *Hampea* species, *H. rovirosae*, suggests that the common ancestor of the genus may have been a littoral-adapted species like *Thespesia*. *Hampea rovirosae* is often found in the littoral zone along the Pacific Coast of Chiapas and the Gulf Coast of Tabasco (R. Bodegas, personal communication; Stansly, 1985) suggesting that it has partially retained this ecological preference for littoral habitats.

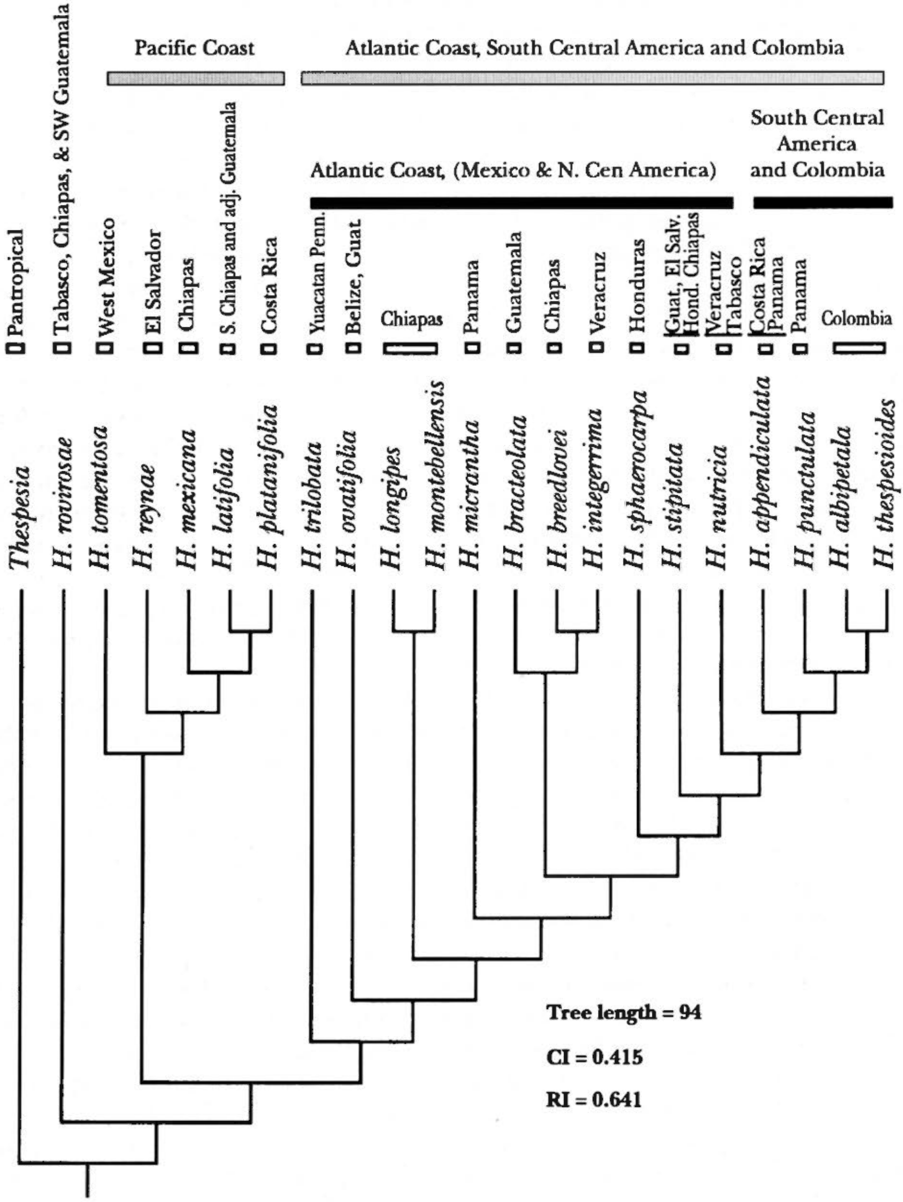

Fig. 5. Proposed phylogeny of the genus *Hampea* in relation to geographic distribution of species.

The first major split in the evolution of the genus appears to have occurred with the differentiation of populations occurring on the Atlantic versus the Pacific Coasts. The two clades corresponding to sections *Standleya* and *Hampea*, (Clades A and B, respectively in the proposed phylogeny; Fig. 1), are clearly divided into species that occur on the Pacific slope and those occurring on the Atlantic Coast and highlands (Fig. 5). Species of *Standleya* all have fairly restricted distributions and habitat type where they are found. All species of *Standleya* occur in habitats with distinct dry seasons. Two of the species of this clade, *H. mexicana H. latifolia*, are clearly deciduous during these dry periods (personal observation, RWJ), as opposed to evergreen species examined during the dry season from sect. *Hampea* (*H. longipes, H. nutricia, H. montebellensis, H. trilobata*). Although the remaining species of *Standleya* have not been examined during the dry season, a deciduous vegetative growth habit may be a further characteristic unique to this clade. Species in *Hampea* are found from the Gulf coast of northern Veracruz, Mexico to northern Colombia. With the exception of *H. trilobata*, all species of the sect. *Hampea* are found in relatively mesic environments. The species found north of Nicaragua grow exclusively on the Atlantic slope whereas the southern species can also be found on the Pacific Slope at the narrowest portions of Central America. These southern species make up the clade with greatest character support and include *H. appendiculata, H. punctulata, H. albipetala*, and *H. thespesioides*. The distinctness of sect. *Hampea* and its derived position within the phylogeny suggests that these species evolved relatively recently from a common ancestor that colonized southern Central America and perhaps northern Colombia.

The phylogeny of *Hampea* indicates that species in montane-habitats are derived (Fig. 6). This suggests that montane adapted species evolved from a lowland ancestor through colonization, or through vicariance of a species with a wide altitudinal range. The most primitive species, *H. rovirosae*, is strictly a lowland species, and the sister species to all major clades are adapted to lowland habitats (*H. tomentosa, H. trilobata, H. micrantha*, and *H. sphaerocarpa*). Species in Clade B1 occur in the Meseta Central de Chiapas and those in Clade B2 are restricted to the Atlantic slopes of the Sierra Madre Oriental, the Montañas del Norte de Chiapas and the northern ranges of Guatemala.

The question of 'center of origin'. The area encompassing southern Mexico (Chiapas and Tabasco) and Guatemala fit various criteria of Cain (1943) to classify the region as the 'center of origin' of *Hampea*. This area has the greatest variety of forms of the genus, the greatest number of species in the most varied habitats, and the most primitive species, *H. rovirosae*, is restricted here.

The classical center of origin concept has been criticized as relying too heavily on dispersal as the mechanism for explaining the distribution of organisms, whereas vicariant evolution may be more common (Croizat *et al.*, 1974). However, if the present distribution of *Hampea* was the result of a widespread ancestral species evolving vicariantly throughout its range, areas of high *Hampea* species diversity similar to that found in Chiapas and Guatemala would be expected in other parts of

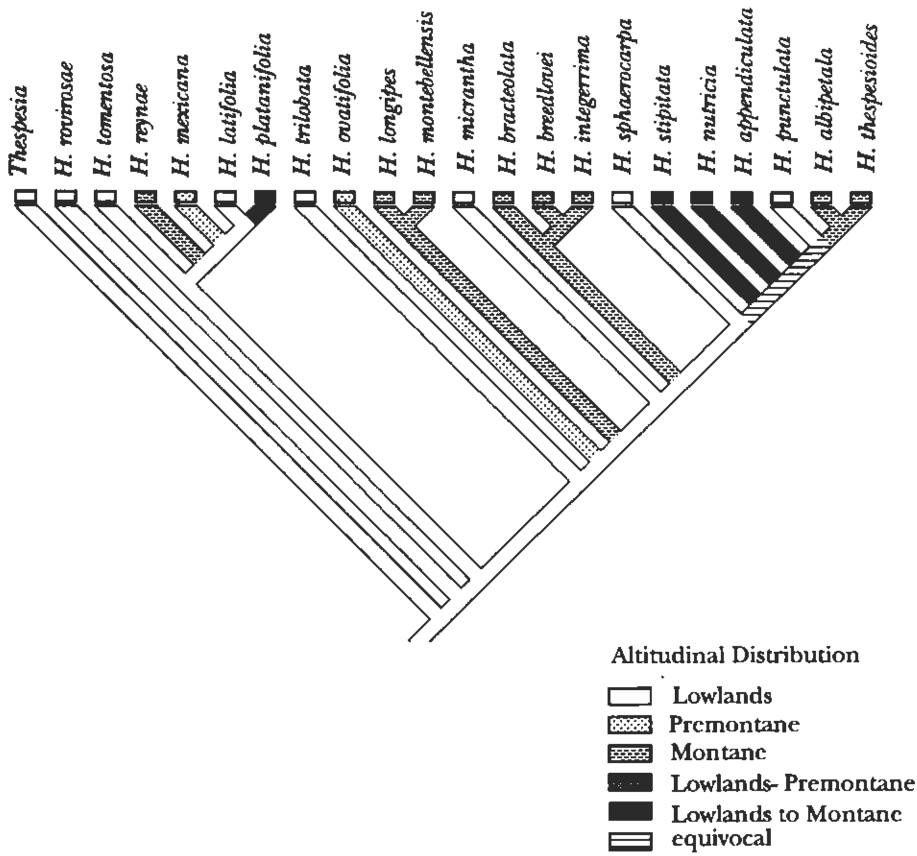

fig. 6. Phylogeny of the genus *Hampea* showing altitudinal distribution of terminal taxa.

its range, especially in areas of similar habitat diversity. This does not occur. In areas of southern Central America where our results indicate that the *Hampea* species are more derived (Fig. 1), species diversity is lower and the species present often have wide altitudinal ranges. The two species found in Costa Rica, *H. appendiculata* and *H. platanifolia*, are found from lowlands to montane forests, suggesting a relatively recent dispersal event with insufficient time for local adaptation and speciation to occur. More information is needed concerning seed dispersal of *Hampea* to evaluate dispersal routes and the possibilities of long range dispersal of members of this genus. Additionally, a comparison is needed of the biogeography of Hampea and other plants characteristic of Middle America to address more rigorously the question of whether vicariance or dispersal is the primary mechanism that has resulted in the present distribution and diversity of *Hampea.*

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LITERATURE CITED

BENTLEY, B. B. 1977. Extrafloral nectaries and protection by pugnacious bodyguards. *Annual Rev. Ecol. Syst. 8*: 407-427.

BURKE, H. R. AND J. R. CATE. 1979. A new species of Mexican *Anthonomus* related to the boll weevil (Coleoptera: Curculionidae). *Ann. Entomol. Soc. Amer.* 72:189-192.

BURKE, H. R., W. E. CLARK, J. R. CATE AND P. A. FRYXELL. 1986. Origin and dispersal of the boll weevil. *Bull. Entomol. Soc. Amer. 32*(4): 228-238.

CAIN, S. A. 1943. Criteria for the indication of center of origin in plant geographical studies. *Torreya 43*: 132-154.

CROIZAT, L., G. NELSON AND D. E. ROSEN. 1974. Centers of origin and related concepts. *Syst. Zool. 23*:265-287.

ERDTMAN, G. 1960. The acetolysis method. *Svensk Bot. Tidskr. 54*: 561-564.

FARRIS, J. S. 1989. *HENNIG86 Reference, version 1.5*, J. Farris Pub., Stony Brook, New York. 22 p.

FOSBERG, F. R. AND M. H. SACHET. 1972. *Thespesia populnea* (L.) Solander ex Correa and *Thespesia populneiodes* (Roxburgh) Kosteletzky (Malvaceae). *Smithsonian Contr. Bot. 7*:1-13.

FRYXELL, P. A. AND M. J. LUKEFAHR. 1967. *Hampea* Schlecht: possible primary host of the boll weevil. *Science 155*: 1568-1569.

FRYXELL, P. A. 1968. A redefinition of the tribe Gossypieae. *Bot. Gaz. 129*:296-308.

FRYXELL, P. A. 1969. The genus *Hampea* (Malvaceae). *Brittonia 21*:359-396.

FRYXELL, P. A. 1979. *The natural history of the cotton tribe.* Texas A&M Univ. Press, College Station, Texas. 245 p.

FRYXELL, P. A. 1980. A new species of *Hampea* (Malvaceae) from El Salvador. *Syst. Bot. 5*: 442-444.

JANZEN, D. H. 1967. Interaction of the bull's horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginenea* F. Smith) in eastern Mexico. *Univ. Kansas Sci. Bull. 47*:315-558.

JONES, R. W. 1994. *Systematics and ecology of the* Anthonomus grandis *species complex (Coleoptera: Curculionidae) and their* Hampea *host plants (Malvales: Malvaceae).* Ph.D. Dissertation, Texas A&M University, College Station, Texas.

KRICHER, J. C. 1989. *A neotropical companion. An introduction to the animals, plants and ecosystems of the New World tropics.* Princeton University Press, Princeton, New Jersey.

REYNA V., M. L. 1979. *Vegetación arbórea del bosque nebuloso de Montecristo.* Thesis (Lic. Biol.) Univ. El Salvador, San Salvador.

RZEDOWSKI, J. 1993. Diversity and origins of the Phanerogamic flora of Mexico. *In:* T. P. Ramamoorthy, R. Bye, A. Lot and J. Fa (eds.). *Biological diversity of Mexico. Origins and distribution.* Oxford University Press, New York, pp. 129-146.

STANSLY, P. A. 1985. *Life history and ecology of the boll weevil on a native host plant in southeastern Mexico.* Ph.D. Dissertation, Texas A&M University, College Station, Texas.

SWOFFORD, D. L. 1990. *PAUP^{R}: Phylogenetic analysis using parsimony.* Version 3.0. Computer program distributed by Illinois Natural History Survey, Champaign, Illinois

WALTER, D. E. AND D. J. O'DOWD. 1992. Leaf morphology and predators: Effects of leaf domatia on the abundance of predatory mites (Acari: Phytoseiidae). *Environ. Entomol. 21*: 478-484

WENDT, T. 1993. Composition, floristic affinities, and origins of the canopy tree flora of the Mexican Atlantic slope rain forests. *In:* T. P. Ramamoorthy, R. Bye, A. Lot and J. Fa (eds.). *Biological diversity of Mexico. Origins and distribution.* Oxford University Press, New York, pp. 595-680.