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THE PHYLOGENETIC RELATIONSHIPS OF *LEMBOCARPUS* AND *GOYAZIA* (GESNERIACEAE) BASED ON *ndhF* SEQUENCES¹

James F. Smith²

ABSTRACT

The phylogenetic relationships of *Goyazia* and *Lembocarpus* are investigated based on cladistic analysis of *ndhF* sequences. Both genera are currently classified in the tribe Gloxinieae, but both are poorly known. Based on its floral morphology, the classification of *Goyazia* in Gloxinieae is not controversial. *Lembocarpus* may be placed in Gloxinieae, Episcieae, or Sinningieae. The acaulescent, tuberous nature of *Lembocarpus* limits the number of characters available for a morphological analysis and has made its classification and phylogenetic relationships difficult to resolve. Phylogenetic analyses of *ndhF* sequences place both genera in Gloxinieae. Although the affinities within the tribe are ambiguous for *Goyazia*, *Lembocarpus* is sister to *Capanea*. The addition of *Goyazia*, *Lembocarpus*, and an additional species of *Capanea* provide better resolution of relationships within Gloxinieae and Gesnerieae than had been obtained previously from parsimony analysis. A maximum likelihood analysis is largely congruent with the parsimony tree.

Key words: cladistics, Gesneriaceae, Gloxinieae, *Goyazia*, *Lembocarpus*, *ndhF*.

Classification and phylogenetic analyses within Gesneriaceae, particularly the neotropical subfamily Gesnerioideae, have received much attention, revealing numerous relationships within genera (Smith & Sytsma, 1994a, b, c; Smith, 1994; Kvist & Skog, 1988, 1989, 1993, 1996; Kvist, 1990), within tribes (Smith & Carroll, 1997; Smith & Atkinson, 1998; Smith, 2000a, b), and among tribes (Burt & Wiehler, 1995; Smith, 1996, 2000c; Smith et al., 1997a, b). However, the classification and phylogenetic relationships of numerous genera have remained unexamined. Among these genera are *Lembocarpus*, endemic to Surinam and French Guiana, and *Goyazia* from Brazil.

Although collections of *Goyazia* are not common or well known and the plant is not in cultivation in North American or European gardens, the placement of this genus in Gloxinieae (Wiehler, 1983) has not been questioned. *Goyazia* is endemic to the Planalto of Brazil in Goiás and Mato Grosso provinces. The plant is a creeping saxicolous perennial with slender stems, scaly rhizomes, and small orbicular-ovate leaves. Flowers are borne singly in the leaf axils and are structurally the same as those of *Achimenes* Pers. and other members of Gloxi-

nieae. Wiehler (1983) placed *Goyazia* in his Gloxinieae on the basis of its scaly rhizome, annular nectary, and corolla shape.

Unlike *Goyazia*, the placement of *Lembocarpus* within Gloxinieae (Wiehler, 1983) has drawn criticism. *Lembocarpus* is a poorly known, monotypic genus that was once in cultivation in North America, and apparently is no longer. The plant is an acaulescent tuberous perennial that produces a single leaf and inflorescence each season (Wiehler, 1983). The ovary is superior and the nectary is annular but nonfunctional (Wiehler, 1983). In his treatment of the Gesneriaceae of the Guianas, Leeuwenberg (1958) considered *Lembocarpus* to be similar to both the Guianan endemic *Rhoogeton* Leeuw. (tribe Episcieae), and *Gloxinia* L'Hér. (tribe Gloxinieae).

Wiehler (1983) was the first to place *Lembocarpus* in Gloxinieae on the basis of the annular nectary and tuberous habit. Additionally, Wiehler (1983) cited hybrids between *Lembocarpus* and *Sinningia* Nees (Gloxinieae sensu Wiehler, 1983) as additional support for *Lembocarpus* in Gloxinieae. Several *Sinningia* species have tubers and nearly superior ovaries, which added further support for

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Table 1. Species sequenced in this study with GenBank submission numbers and voucher specimens. Letters in parentheses indicate herbaria where vouchers are deposited.

Species	Collection and voucher	GenBank number
<i>Achimenes skinneri</i> Lindl.	Cultivated (US)	U62177
<i>Anodiscus xanthophyllus</i> (Poepp.) Mansf.	Peru. <i>Dunn s.n.</i> (SRP)	AF040143
<i>Bellonia</i> sp.	Dominican Republic. <i>Evans s.n.</i> (SRP)	AF040144
<i>Capanea affinis</i> Fritsch	Colombia. Risaralda: Mpio. Santuario, Apr. 1998, <i>Amaya M. & Smith 393</i> (COL)	AF206201
<i>C. grandiflora</i> (Kunth) Decne. ex Planch.	Venezuela. Mérida: Sierra Nevada, Mucuy region, 26 Jan. 1989, <i>Smith 1199</i> (WIS)	AF040145
<i>Diastema racemiferum</i> Benth.	Cultivated. <i>Skog 7574</i> (US)	U62156
<i>Eucodonia andrieuxii</i> (DC.) Wiehler	Cultivated. <i>Dunn s. n.</i> (SRP)	AF040146
<i>Gloxinia sylvatica</i> (HBK) Kunth	Cultivated. <i>Dunn 9012051</i> (SRP)	U62157
<i>Goyazia rupicola</i> Taubert	Brazil. Goiás: 17 Jan. 1998, <i>Smith et al. 3722</i> (SRP)	AF257485
<i>Heppiella ulmifolia</i> (Kunth) Hanst.	Ecuador. Napo: near Baeza, 4 Apr. 1996, <i>Smith 3427</i> (SRP)	AF040147
<i>Koellikeria erinoides</i> (DC.) Mansf.	Brazil. <i>Dunn s.n.</i> (SRP)	AF013709
<i>Kohleria spicata</i> (Kunth) Oerst.	Cultivated. <i>Skog 7701</i> (US)	U62181
<i>Lembocarpus amoenus</i> Leeuw.	French Guiana. Haut Oyapock, Mt. St. Marcel, 21 Mar. 1976, <i>Sastre 4478</i> (US)	AF257486
<i>Monopyle macrocarpa</i> Benth.	Cultivated (US)	U62197
<i>Moussonia strigosa</i> (C. V. Morton)	Cultivated. <i>Dunn s.n.</i> (SRP)	AF040148
<i>Niphaea oblonga</i> Lindl.	Mexico. <i>Skog 7564</i> (US)	U62160
<i>Pearcea</i> sp.	Ecuador. Napo: near Baeza, 4 Apr. 1996, <i>Smith 3425</i> (SRP)	AF040149
<i>P. hypocyrtiflora</i> Regel	South America. Cultivated. <i>Smith 3943</i> (SRP)	AF040150
<i>Phinaea albiflora</i> Rusby	Cultivated (US)	AF040151
<i>Sanango racemosum</i> (Ruiz & Pav.) Barringer	Ecuador. Wiehler (GRF)	U62144
<i>Smithiantha cinnabarina</i> (Linden) Kuntze	Cultivated (US)	AF040152
<i>Solenophora obliqua</i> D. L. Denham & D. N. Gibson	Mexico. <i>Breedlove 71542</i> (CAS)	U62202
Gesnerieae		
<i>Gesneria pedicellaris</i> Alain	Cultivated. <i>Skog 7722</i> (US)	U62192
<i>Gesneria christii</i> Urban	Cultivated (US)	U62191
<i>Rytidophyllum tomentosum</i> (L.) Mart.	Cultivated. <i>Skog 5364</i> (US)	U62200
<i>Rytidophyllum auriculatum</i> Hook.	Cultivated (US)	U62199
Episcieae		
<i>Alloplectus panamensis</i> C. V. Morton	Panama. 28 Oct. 1993, <i>Skog et al. 7641</i> (US)	AF013685
<i>Alloplectus</i> sp.	Ecuador. Napo: San Rafael Falls, 4 Apr. 1996, <i>Smith 3418</i> (SRP)	AF013686
<i>Alsobia dianthiflora</i> (H. E. Moore & R. G. Wilson) Wiehler	Cultivated. <i>Skog 7969</i> (US)	AF013687
<i>A. punctata</i> (Lindl.) Wiehler	Mexico. Chiapas: Ocozocautla, winter 1991–1992, <i>Smith 3600</i> (SRP)	AF013688
<i>Alsobia</i> sp.	Cultivated (US)	AF013689
<i>Alsobia</i> sp.	Cultivated. <i>Smith 3599</i> (SRP)	AF013690
<i>Chrysothemis friedrichsthaliana</i> (Hanst.) H. E. Moore	Cultivated. <i>Skog 7992</i> (US)	AF013691
<i>Cobananthus calochlamys</i> (J. D. Sm.) Wiehler	Cultivated (US)	AF013692
<i>Codonanthe elegans</i> Wiehler	Belize. San Jose: <i>Skog 5699</i> (US)	U62178
<i>Codonanthopsis peruwiana</i> Wiehler	Cultivated. <i>Turley s.n.</i> (SRP)	AF013693
<i>Columnnea ambigua</i> (Urban) Morley	Puerto Rico. <i>Smith 3701</i> (SRP)	AF013694
<i>C. mira</i> Morley	Panama. <i>Smith 2450</i> (WIS)	AF013695
<i>C. oblongifolia</i> Rusby	Peru. Cuzco: Prov. Urubamba, Machu Picchu, 3 Apr. 1989, <i>Smith 1721</i> (WIS)	AF013696

Table 1. Continued.

Species	Collection and voucher	GenBank number
<i>C. sanguinea</i> (Pers.) Hanst.	Cultivated. <i>Smith 3369</i> (SRP)	AF013697
<i>C. schiedeana</i> Schlecht.	Mexico. Vera Cruz: road from Xalapa to Misantla, <i>Smith 288</i> (WIS)	U62164
<i>Corytoplectus speciosus</i> (Poepp.) Wiehler	Ecuador. Near Limón, 15 May 1994 no voucher	AF013698
<i>D. urceolata</i> Wiehler	Ecuador. Napo: San Rafael Falls, 4 Apr. 1996, <i>Smith 3416</i> (SRP)	AF013699
<i>Episcia fimbriata</i> Fritsch	Cultivated. <i>Smith 3947</i> (SRP)	AF013700
<i>E. sphalera</i> Leeuw.	French Guiana. Mte. des Nouragues, 16 June 1994, <i>Feuillet et al. 94-079</i> (US)	AF013701
<i>Nautilocalyx adenosiphon</i> (Leeuw.) Wiehler	Cultivated. <i>Skog 7847</i> (US)	AF013702
<i>Nematanthus albus</i> Chautems, ined.	Brazil. 17 Jan. 1998, <i>Smith et al. 3726</i> (SRP)	AF206197
<i>N. fritschii</i> Hoehne	Brazil. São Paulo: Mpo. Espiritu, 17 Jan. 1998, <i>Smith et al. 3720</i> (SRP)	AF206198
<i>Neomortonia nummularia</i> (Hanst.) Wiehler	Cultivated. <i>Smith 3944</i> (SRP)	AF013703
<i>N. rosea</i> Wiehler	Cultivated (US)	AF013704
<i>Oerstedina cerricola</i> Wiehler	Panama. Bocas del Toro: Cerro Pate Macho, 20 Nov. 1978, <i>Hammel 5754</i> (US)	AF206199
<i>Paradrymonia aurea</i> Wiehler	Cultivated. <i>Skog 7979</i> (US)	AF013705
<i>P. densa</i> (C. H. Wright) Wiehler	Cultivated. <i>Stewart s.n.</i> (SRP)	AF013706
<i>P. fuquaiana</i> Wiehler	Ecuador. 6 Jan. 1990, <i>Skog 7889</i> (US)	AF013707
<i>Rhoogeton viviparus</i> Lwbg.	Guyana. Potaro-Siparuni region, Kaieteur Falls, 18 Oct. 1987, <i>Kvist et al. 370</i> (US)	AF206200
<i>Rufodorsia major</i> Wiehler	Cultivated. <i>Skog 7761</i> (US)	AF013708
Outgroups: Sinningieae		
<i>Paliavana prasinata</i> (Ker-Gawl.) Fritsch	Brazil. <i>Skog 5399</i> (US)	U62174
<i>Sinningia brasiliensis</i> (Regel & Schmidt) Wiehler	Brazil. <i>Dunn 9104014</i> (SRP)	U62175
<i>Sinningia cooperi</i> (Paxt.) Wiehler	Cultivated. <i>Skog 7808</i> (US)	U62201
<i>Sinningia richii</i> Clayb.	Cultivated (US)	U62186
<i>Vanhouttea lanata</i> Fritsch	Cultivated. <i>Skog 7690</i> (US)	U62203

the placement of *Lembocarpus* in Gloxinieae. Reports of hybrids were apparently premature; no hybrids between these genera have been documented (Boggan, 1991).

Beaufort-Murphy (1983) placed *Lembocarpus* in Gloxinieae sensu Fritsch (1894) based on seed characteristics, noting that the seed shape was similar to some species of *Episcia* Mart. (tribe Episcieae) but not like any species of *Gloxinia*. Thus seed shape implies an affinity to Episcieae. Beaufort-Murphy (1983) also noted that the shape of the cells of the seed coat was similar to *Smithiantha* Kuntze, a member of Gloxinieae. Beaufort-Murphy (1983) concluded that *Lembocarpus* may have an isolated position within Gesnerioideae due to its anomalous combination of seed characteristics.

In summary, morphological data support the placement of *Lembocarpus* either in Gloxinieae or Episcieae. The similarity to Gloxinieae is based on the annular nectary, campanulate corolla, and shape of the cells of the seed coat. Its placement

in Episcieae is largely based on the many characters it shares with *Rhoogeton*: superior ovary, tuber, calyx venation, inflorescence structure, acaulescent habit, and ovules only on outer placental surfaces (Leeuwenberg, 1958). The superior ovary and tuberous habit are unknown in Gloxinieae, but are common in Episcieae. In contrast, the annular nectary is known outside of Gloxinieae and Gesnerieae only in Beslerieae, a tribe with several other defining characters that would exclude the placement of *Lembocarpus*. Tubers are more widespread among members of Sinningieae (sensu Smith et al., 1997b) than elsewhere in Gesnerioideae, implying that *Lembocarpus* may best be placed among these genera. Tubers also are known from members of Episcieae (Wiehler, 1983) but not other Gloxinieae (sensu Smith et al., 1997b).

The tribe Gloxinieae has received recent attention with regard to the phylogenetic relationships of its genera (Smith & Atkinson, 1998). However, neither *Goyazia* nor *Lembocarpus* was included in

previous cladistic analyses of molecular data due to the lack of leaf material. This study presents results regarding the phylogenetic position of these genera within the neotropical Gesneriaceae.

MATERIALS AND METHODS

Voucher information and Genbank numbers for all sequences used in this analysis are presented in Table 1. DNA for *Goyazia* was isolated from silica gel dried material (Smith et al., 1992), and the *ndhF* gene was amplified in two overlapping sections (positions 1–1350, and 972–2044). DNA for *Lembocarpus* was obtained from herbarium specimens (Savolainen et al., 1995) using the DNEasy Plant miniprep kits (Qiagen) following the manufacturer's instructions. The *ndhF* gene for *Lembocarpus* was amplified in two overlapping fragments using primers 172–1350R and 972–2044R. The first fragment is smaller than those reported previously (Smith et al., 1997b) since amplifying the DNA from herbarium specimens required successive amplifications using internal primers. Initial amplifications followed DNA procedures described elsewhere (Smith et al., 1997b) using primers 1 and 1350R for the first part and 803 and 2044R for the second part. Subsequent amplifications required the use of 172 and 972 as forward primers, although the same reverse primers resulted in successful amplifications.

The focus of this analysis was on Gloxinieae since both *Goyazia* and *Lembocarpus* are currently classified in this tribe (Burt & Wiehler, 1995). However, since there is considerable question regarding the tribal position of *Lembocarpus*, initial analyses were conducted using representatives of all tribes of the neotropical subfamily Gesnerioideae. Members of the Old World tribe Epithematae were used as the outgroup because some preliminary results implied a potential relationship to this tribe. Results from this preliminary analysis (not included) allowed for a more restricted taxon sampling that would permit greater analytical flexibility as well as minimizing homoplasy in the data set. Subsequent analyses used only Gloxinieae, Gesnerieae, and Episcieae as well as Sinningieae as outgroup. The choice of taxa for the reduced analysis considered all possible tribes where *Lembo-*

carpus may have affinities (Gloxinieae, Episcieae, and Sinningieae). Taxonomic choice derived from previous tribal analyses with Episcieae sister to Gloxinieae/Gesnerieae but Sinningieae sister to these three tribes (Smith et al., 1997b). The data matrix for all taxa contains 1.54% missing cells based on total sequence alignments.

PHYLOGENETIC ANALYSIS

Phylogenetic divergence was reconstructed using PAUP version 4.0d64 to implement maximum parsimony (MP) (Farris, 1970; Farris et al., 1970; Swofford & Maddison, 1987) and maximum likelihood (MLE). In this study, trees were generated using the general heuristic option. To search for islands of equally parsimonious trees (Maddison, 1991), the search strategy of Olmstead and Palmer (1994) was implemented searching for 1000 trees each in five subsequent analyses with the nearest neighbor interchange (NNI) search option in effect and mulpars "off." Each of the results from the five NNI searches was used as the starting tree(s) for a search with tree bisection reconnection (TBR) and mulpars "on." This search strategy was used for all MP analyses.

Because of the greater time involved in MLE analysis, a smaller sampling was utilized. In this analysis, a full sampling of Gloxinieae was used and one species each of *Gesneria* L. and *Rytidophyllum* Mart. (Gesnerieae). Representatives of Episcieae were used as the outgroup with taxa selected to include possible relatives of *Lembocarpus* (most notably *Rhoogeton*). MLE trees were generated using the heuristic search option with TBR and mulpars "on." Under the MLE option, the Hasegawa et al. (1985) model was used, which allows for unequal nucleotide frequencies and differential rates for transitions and transversions. The assumed nucleotide frequencies were estimated from the data: A = 0.27809, C = 0.15598, G = 0.17529, and T = 0.39063. MLE trees were compared to MP trees using the Kishino-Hasegawa test (Kishino & Hasegawa, 1989). Additional MP trees were generated using the same search criteria described above with the same taxa utilized in the MLE analysis.

Branch support analysis was performed to ex-

←

Figure 1. One of 48 maximum parsimony trees of 3998 steps each, CI = 0.38, RI = 0.33. These trees were rooted using Sinningieae. Numbers above clades are decay values; numbers in parentheses are branch lengths using the acctran option of PAUP. Numbers below clades indicate bootstrap values. Terminal branch lengths are not shown. Branches shown with dashed lines indicate nodes that are not supported in a strict consensus of all 48 trees. Abbreviations for tribes are: Ep = Episcieae, Ge = Gesnerieae, Gl = Gloxinieae, Si = Sinningieae.

amine trees that were one or two steps longer than the most-parsimonious trees (Bremer, 1988, 1994; Donoghue et al., 1992). Clades that persisted in strict consensus trees two steps beyond the most-parsimonious trees were examined using the constraints option to search for the shortest tree that did not contain that clade. Bootstrap analysis (Felsenstein, 1985) was performed using 100 replicates with TBR and mulpars "off" and "on." Because there is substantial morphological and biogeographic data that imply a relationship between *Lembocarpus* and *Rhoogeton*, the constraints option was used to assess the most-parsimonious tree with these genera as a monophyletic group. The trees generated from the constraints analysis were compared to the unconstrained trees using the Kishino-Hasegawa test (Kishino & Hasegawa, 1989).

RESULTS

The initial analysis utilized all members of the Gesnerioideae with the Old World tribe Epithematae as the outgroup (not shown). The MP analysis resulted in 14 trees of 5128 steps each (trees not shown). In all of these trees both *Lembocarpus* and *Goyazia* were within Gloxinieae. MP analysis of the reduced data set resulted in 48 trees of 3998 steps each from three different islands of most-parsimonious trees, with consistency index (CI) = 0.38, and retention index (RI) = 0.33. One of these trees is presented in Figure 1 with dashed lines to indicate clades that collapse in the strict consensus of all trees. This tree is more resolved than prior results from *ndhF* analyses (Smith & Atkinson, 1998). These trees place both *Goyazia* and *Lembocarpus* within Gloxinieae although the position of *Goyazia* is not resolved; *Lembocarpus* is sister to *Capanea* Decne. ex Planch. As demonstrated in simulation studies (DeBry & Olmstead, 2000), the bootstrap values with mulpars "off" or "on" differed only by a few points (data not shown). The values on Figure 1 are from the analysis with mulpars "off."

An additional 14 steps beyond the most-parsimonious trees were necessary to force *Lembocarpus* and *Rhoogeton* into a monophyletic group (not shown). When forced together, *Lembocarpus* and *Rhoogeton* together are sister to *Nematanthus* Schrader (Episcieae). The Kishino-Hasegawa test (Kishino & Hasegawa, 1989) did not indicate a significant difference between the constrained and unconstrained trees.

MLE analysis resulted in a $-\ln$ likelihood of 16118.64716 (Fig. 2). *Goyazia* and *Lembocarpus* are both in Gloxinieae, and *Lembocarpus* is sister

to *Capanea* as indicated by parsimony. Further, *Goyazia* is sister to a clade containing *Moussonia* Regel, *Anodiscus* Benth., and *Koellikeria* Regel (Fig. 2). An MP analysis of the same taxa used in the MLE analysis resulted in two islands for a total of four trees of 2076 steps each (trees not shown). The Kishino-Hasegawa test (Kishino & Hasegawa, 1989) did not indicate a significant difference between the MP and MLE trees.

DISCUSSION

GOYAZIA

The results of this study support the placement of *Goyazia* in Gloxinieae (Figs. 1, 2). Wiehler (1983) was the first to place *Goyazia* in his Gloxinieae, where it has remained in a modern revised version of the classification system (Burt & Wiehler, 1995). Although *Goyazia* is always in a clade with *Moussonia*, *Anodiscus*, and *Koellikeria*, its exact relationship to these other genera is unresolved (Fig. 1). One of the trees from the MP analysis (Fig. 1) and MLE analysis indicate that *Goyazia* is sister to these three genera (Fig. 2), and *Koellikeria* is sister to *Moussonia* and *Anodiscus*. However, *Goyazia* and *Koellikeria* are both found in Brazil, whereas *Moussonia* is endemic to Central America, and *Anodiscus* is native to the Andes of Peru. Since the majority of Gloxinieae are found west of the Andes, the most-parsimonious explanation for this distribution would be two separate migrations to Brazil, one each for *Goyazia* and *Koellikeria*, if the relationships among these genera are accurate as seen in Figure 2. However, weak bootstrap and decay index support herein for these relationships implies that more data are necessary before conclusions regarding the biogeography of these taxa can be made.

LEMBOCARPUS

As with *Goyazia*, the results of this analysis confirm the placement of *Lembocarpus* in Gloxinieae (Figs. 1, 2). This placement is more controversial since early descriptions of *Lembocarpus* noted its disparate calyx venation, inflorescence, acaulescent habit, outer ovule placentation, superior ovary, and tubers (Leeuwenberg, 1958) as shared with *Rhoogeton* (Episcieae).

Placement of *Rhoogeton* in Episcieae is in itself controversial. Although morphological data and *ndhF* sequences (Smith, 2000b) provide evidence for its placement there, ITS sequences imply its position outside of Episcieae and possibly within Gloxinieae (Smith, 2000b). Unfortunately, ITS se-

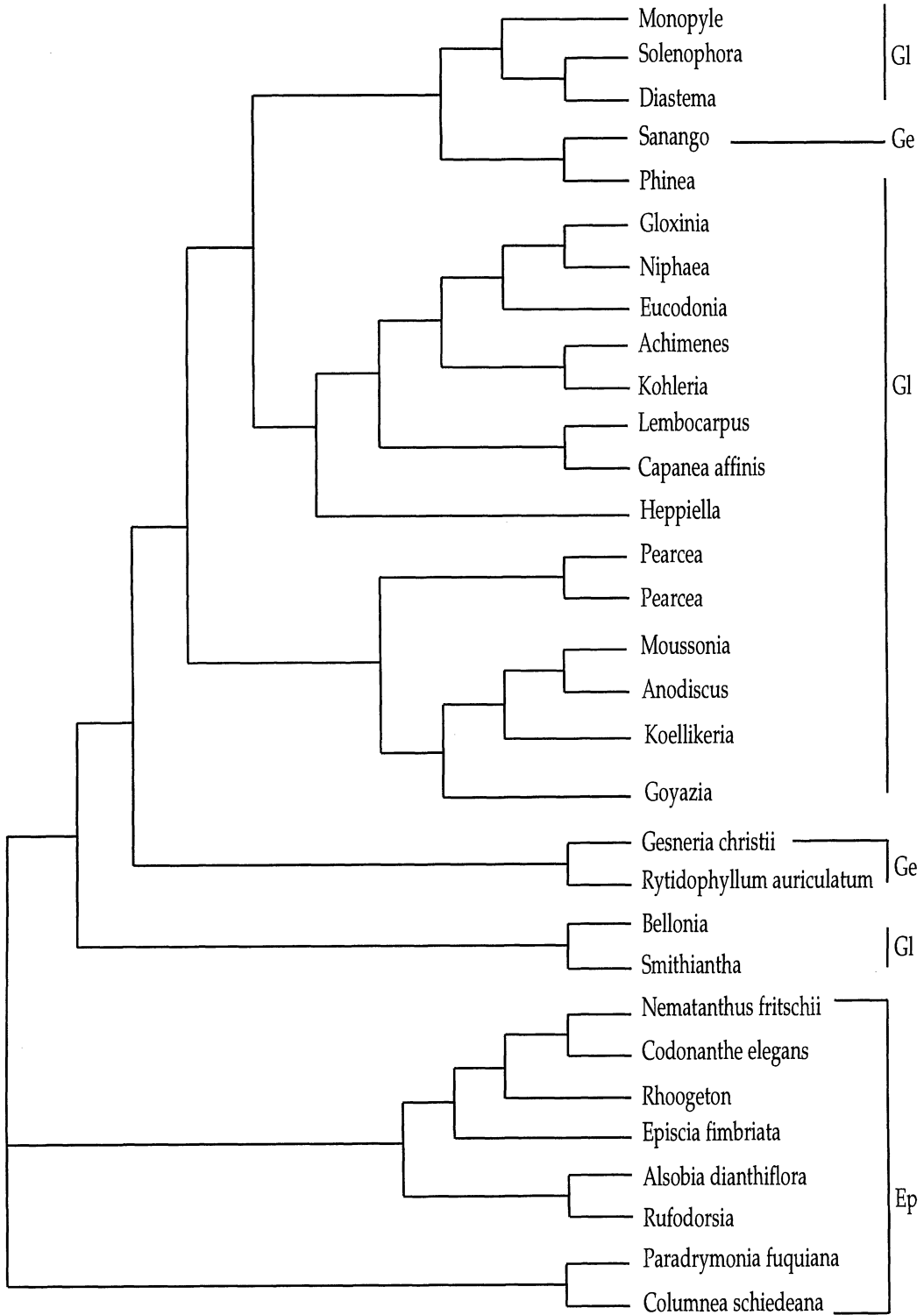


Figure 2. Maximum likelihood estimate tree, $-\ln$ likelihood = 16118.64716. To minimize computer time this analysis used only representative taxa of Episcieae as outgroups. Abbreviations for tribes are: Ep = Episcieae, Ge = Gesnerieae, Gl = Gloxinieae.

quences could not be obtained using the DNA from herbarium material used for *Lembocarpus* in this study. Despite the several morphological character states shared between *Lembocarpus* and *Rhoogeton*, 14 additional steps beyond the most-parsimonious trees are necessary to place *Lembocarpus* and *Rhoogeton* in a monophyletic group using *ndhF* sequence data. Thus, regardless of the tribal affinity of *Rhoogeton*, it does not appear to be closely related to *Lembocarpus* based on *ndhF* data.

Morphological support for the placement of *Lembocarpus* in Gloxinieae comes from the corolla and seed. Although Beaufort-Murphy (1983) hypothesized that *Lembocarpus* may have an isolated position within the Gesnerioideae due to a unique combination of characters, this combination of seed surface characters and superior ovary is best viewed as autapomorphic. The shape of the cells of the seed coat and campanulate corolla may be synapomorphies to place *Lembocarpus* in Gloxinieae.

An additional synapomorphy for *Lembocarpus* and Gloxinieae is nectary shape. Whereas the annular nectary is widespread in Gloxinieae, it also is known from tribes Gesnerieae and Beslerieae. In cladistic analyses of Gloxinieae and Gesnerieae based on *ndhF* sequences, the position of Gesnerieae always creates a paraphyletic Gloxinieae (Figs. 1, 2; Smith & Atkinson, 1998). This implies that if not derived from within Gloxinieae, the Gesnerieae are closely related, and the annular nectary is likely a synapomorphy for both tribes Gloxinieae and Gesnerieae. The Beslerieae are more distantly related to Gloxinieae based on previous phylogenetic analyses of morphology and *ndhF* sequences. Beslerieae are best considered one of the more earlier lineages within Gesnerioideae (Smith, 1996; Smith et al., 1997b; Smith, 2000a). Therefore the annular nectary of Beslerieae is unlikely homologous to the annular nectary of Gloxinieae/Gesnerieae. Although nectary structure may be a homoplastic character, it still serves as a synapomorphy to unite Gloxinieae and Gesnerieae, as well as to place *Lembocarpus* in this group.

CAPANEA AND LEMBOCARPUS

The data presented here not only provide new evidence for the tribal placement of *Lembocarpus*, but place it as sister to *Capanea* (Figs. 1, 2). This is one of the more strongly supported clades in the tree based on decay index values. This relationship of *Lembocarpus* to *Capanea* is unusual in that *Capanea* is the only epiphytic genus of Gloxinieae, whereas *Lembocarpus* is a terrestrial, tuberous, acaulescent herb. No striking synapomorphies

unite these genera with the exception that they are among the few genera within Gloxinieae that lack scaly rhizomes. The placement of *Capanea* in Gloxinieae contradicts earlier cladistic analyses of *ndhF* sequences of Gloxinieae where it was placed in Episcieae (Smith & Atkinson, 1998). The earlier analysis based on *ndhF* sequences only used *Capanea grandiflora* (Kunth) Decne. ex Planch., and *Capanea affinis* is added to the present analysis. The source of discrepancy is as yet unknown, but based on results of ITS and *ndhF* sequences (Smith, 2000b), it is clear that *Capanea affinis* belongs in Gloxinieae.

SUMMARY

The *ndhF* data presented here confirm the placement of both *Goyazia* and *Lembocarpus* within Gloxinieae. *Lembocarpus* is strongly supported by decay index, moderate (relatively) bootstrap values, and MLE analysis as sister to *Capanea*. *Goyazia* is placed in a clade with *Moussonia*, *Anodiscus*, and *Koellikeria* in both MP and MLE analyses, although the relationships among these four genera are not fully resolved in MP trees. Because *ndhF* seems to be at the limits of its resolving power within Gloxinieae (also observed in tribe Episcieae; Smith & Carroll, 1997; Smith, 2000b), it will be essential in future investigations to add additional sequence data to resolve more fully the intergeneric relationships of this tribe.

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