INTRODUCTION

Commonly known as heathers or heaths, *Erica* belongs to the subfamily Ericoideae, comprised of approximately 25 genera of acid-loving, woody plants (Kron et al., 2002). Containing roughly 700 species, *Erica* is rivaled only by *Rhododendron* (approximately 700 species) as the largest genus in the subfamily Ericoideae. Within the Ericeae, *Erica, Calluna,* and *Bruckenthalia* formerly were referred to as the major genera and *Philippia, Ericinella,* and *Blaeria* were called the minor genera and segregated into their own subtribe. Most recently, all of the minor genera have been reduced to synonomy under the genus *Erica* due to the overlap of distinguishing characters (Oliver, 1989; Oliver, 2000).

The geographic distribution of *Erica* spans Europe, the Middle East, and Africa (Figure 1). Its range extends eastward into Turkey and Lebanon (*Erica spiculifolia*) and also into the Arabian Peninsula's southwestern tip (*Erica arborea*). In Africa, *Erica* occurs in montane scrub or grassland, forming a characteristic vegetation zone in the mountains of East Africa (Killick, 1979). The genus is additionally found at higher altitudes in Madagascar and the Mascarene Islands. *Erica arborea* L. is widespread, found in the Sahara desert as an isolated population on Emi Koussi in the Tibesti Mountains. *Erica arborea* is the only species found in both Europe and Africa. Although there are 22 recognized species in the East African mountains and 50 species from Madagascar and the Mascarene Islands, the vast majority are found in the Cape Floral region (Oliver, 1991).

Of all the Floral Kingdoms once outlined by Engler, the Cape Floral Kingdom is the smallest in the world (Oliver and Oliver, 2000), occurring between Cape Town and

Port Elizabeth (Goldblatt, 1978). Covering approximately 90,000 km^2, this region possesses one of the plant kingdom's most remarkable displays of diversity. Furthermore, the Cape Peninsula, the most southwestern portion of this kingdom, contains approximately 2000 species or one quarter of all the species in the Cape Floral Kingdom (Oliver and Oliver, 2000). Even more remarkably, this multitude of species is packed into a rugged strip of land at the foot of Africa that is only 70km long and 20km wide. *Erica* is by far the largest genus located in South Africa's southwestern Cape Peninsula, and this concentration of species belonging to a single genus is virtually unparalleled. Of the roughly 865 described species of *Erica*, nearly 760 species occur within the Cape Floral Region and all are endemic, compared to the 23 occurring in Europe (Oliver 2000). Needless to say, these species are a substantial element of the Cape Flora and of the Afromontane vegetation.

Erica is distinguished from other members of the Ericaceae by the possession of persistent corollas and by the narrow and extremely revolute 'ericoid' shaped leaves (Stevens, 1971). The sole synapomorphy for the group is the presence of stomata arranged perpendicular to the midrib in the channel on the lower surface of the leaf. Floral characters, particularly those of the anthers, have been used to identify taxa to species (Oliver, 1991). The European Ericas exhibit the bell-shaped floral morphology, while the Ericas of South Africa exhibit an exorbitant amount of diversity in both floral form and color (Schumann and Kirsten, 1992). Clad in any color except blue, the flowers showcase shapes ranging from large and tubular to small and urn-shaped. South African Ericas utilize several different modes of pollination (wind, insect, and bird) that are reflected in their corolla morphology (Oliver, 1991). The plants also vary in their habit,

growing as tall as trees or remaining as short as a clump of moss (Schumann and Kirsten, 1992).

In Europe, *Erica* species have relatively broad geographic ranges and there are fewer total species. Conversely, African Cape taxa have highly restricted ranges and extraordinarily large numbers of species in a small region. This unusual distribution has long raised questions about the evolutionary relationships of species in *Erica* with it historically believed that *Erica* originated in South Africa and later expanded its range into Europe.

Previous studies of *Erica* have concentrated on floristics (Stevens, 1971) and few have focused on evolutionary relationships (Dorr and Oliver, 1999; Oliver, 2000). This is the first study to address phylogenetic relationships based on molecular data in *Erica*. Three regions of DNA, one from the nuclear genome and two from the chloroplast, were selected as sources of molecular data. The nuclear ribosomal internal transcribed spacer region (nrITS) (Kron and King, 1996), the chloroplast (cp) atpβ-rbcL spacer region (Crayn and Quinn, 2000), and matK (Kron, 1997; Kron et al. 1999a; 1999b) were selected for use in this analysis. These regions have been proven effective in elucidating relationship within the Ericaceae.

MATERIALS AND METHODS

Taxon Sampling

Thirty-four species from Europe and Africa were sampled (Table I); 12 of the 23 European species and 15 of the 760 species in South Africa were represented. These 15 South Africa taxa were selected to represent the informative groups described by Oliver (2000). The widespread *Erica arborea* was also included in the analysis.

DNA Extraction

Total DNA from silica gel dried (Chase and Hills, 1991) leaves was extracted using a modified CTAB protocol (Doyle and Doyle, 1987). When the abundance of bioactive compounds produced by *Erica* species find their way into extractions, any efforts at DNA amplification are hampered. After incubating the ground tissue in Wendell CTAB, the resulting solution was often a shade of dark brown or black, indicating the presence of these phenolic compounds. Additional chloroform/isoamyl alcohol extractions were recommended in the literature and proved effective in eliminating the majority of the phenol compounds. To ensure purity, any future DNA DNA isolated from Ericas should be subjected to the phenol extraction suggested by Chase and Hills (1991) and purified by cesium chloride-ethidium bromide gradient.

DNA Sequencing

Three regions were amplified: nrITS, the chloroplast atpβ-rbcL spacer, and the 5' half of the cp matK gene. For this study, 33 new sequences were generated for matK, 5 for nrITS, and 5 for atpβ-rbcL. These sequences were then added to data previously obtained by an undergraduate in the Kron laboratory (Samara Mitchell, WFU, 2000). The amplifications were performed as follows: 32.0 μL sterile deionized water, 8.0 μL

dNTPs mix (at 2.5mM concentration for each dNTP), 5.5 μL of 10x magnesium-free Taq DNA polymerase buffer, 5.0 μL 25mM $MgCl_2$, 1 μL of 5mg/mL BSA, 0.5 μL of the forward primer (0.5 μg/μL), 0.5 μL of the reverse primer (0.5 μg/μL), 0.5 μL of Promega Taq DNA polymerase, and 1 μL template DNA. Primer sequences for the 5F and 4R nrITS were obtained from White et al. (1990) (Figure 2). To amplify the nrITS, the Peltier Thermal Cycler was programmed for the following: 97°C for 45 seconds, 48°C for 45 seconds, 72°C for 75 seconds. This cycle was repeated 35 times. Primers for the atpβ-rbcL spacer regions were provided courtesy of Darren M. Crayn (Royal Botanic Garden, Sydney, Australia) (Figure 3). To amplify this region, the Peltier Thermal Cycler was programmed for the following: 95°C for 30 seconds, 37°C for 60 seconds, 72°C for 90 seconds with 10 seconds added during each subsequent cycle. This sequence was repeated 35 times. Both sets of amplified products were cleaned using the QIAquick PCR Purification Kit. Nucleotide sequencing was performed on an ABI 377 Automated DNA Sequencer at Wake Forest University School of Medicine.

The first approximately 1000 base portion of the chloroplast matK region was amplified using the following: 26.0 μL of sterile deionized water, 8.0 μL of dNTPs mix (at 2.5mM concentration for each dNTP), 5.5 μL of 10x magnesium-free buffer exTaq DNA polymerase buffer, 11.0 μL of 25mM $MgCl_2$, 1.0 μL of 5mg/mL BSA, 0.5 μL of the forward primer (0.5 μg/μL), 0.5 μL of the reverse primer (0.5 μg/μL), 0.5 μL of Takara exTaq DNA polymerase, and 1.0 μL of template DNA. Although many primers have been designed for this region, none matched the 5' region of sequence well enough to be of any use. New forward and reverse primers were designed for these plants using the sequence for *Erica spiculifolia.* The sequence for the matK 1F primer is

5’ATGGAGGAATTCAAAAGAAATTTAG3’ and the sequence for the matK 1600F primer is 5’CCTCGATACCTAACATAATGC3’ (Figure 4). The amplified products were electrophoresed through a 1% agarose gel, cleaned using the QIAquick Gel Extraction Kit, and tested to be sure that their concentrations fell between 10ng and 25ng. Nucleotide sequencing was then performed on an ABI 377 Automated DNA Sequencer at Wake Forest University School of Medicine. The raw sequences were edited using Sequencher 3.0 (Gene Codes Corporation). Only unambiguously aligned portions of the sequence were included in the subsequent phylogenetic analyses.

Phylogenetic Analyses

The software package PAUP 4.0 (Swofford, 2002) was used to perform parsimony analyses. Three searches were conducted: an nrITS search; a search using chloroplast data (atpβ-rbcL spacer and matK); and a combined nrITS, atpβ-rbcL , and matK search. All of these searches utilized the program’s heuristic option (100 random replicates, TBR, uninformative characters ignored) and gaps in the sequences were treated as missing data. *Daboecia cantabrica* was used to root the tree based upon the results from the larger analysis of the Ericaceae (Kron et al., 2002). The ratio of transitions to transversion were calculated using MacClade 4.0 (Maddison and Maddison, 2000). Bootstrap values were obtained using the bootstrap option of PAUP*4.0 (Swofford, 2002) to assess internal support (Felsenstein, 1985).

RESULTS

Aligned sequences for the first analysis (nrITS) resulted in a matrix 668 bases long with 110 phylogenetically informative characters (Length (L) = 507, Consistency Index (CI) = 0.655, Retention Index (RI) = 0.590, transition/transversion ratio = 2.45). Insertion/deletions (indels) were most common in the 5' portion of the sequence. Most indels were 1 to 2bp with a 4bp as the largest. Overall the majority of variation was composed of substitutions and the size of the nrITS regions was well conserved. The chloroplast data (atpβ-rbcL spacer and matK) was less variable than the nrITS data. Only 122 phylogenetically informative characters were present, comprising only 7% of the total available information (nuclear and chloroplast). The atpβ-rbcL spacer data was equally variable throughout the sequences with few indels that were never composed of more than two or three bases. Within the Ericaceae, the 5' region (approximately 1000 bp) of the matK gene exhibits significant size variation, so it was necessary to design primers specifically for *Erica* species. However, this gene appears to be well conserved within the genus. The modest amount of variation within the matK sequences was composed primarily of substitutions. Individual analyses of these chloroplast regions yielded completely unresolved trees (Table II). The combined nuclear and chloroplast matrix was 2410 bases long and there were 334 phylogenetically informative characters (14%) (L = 589, CI = 0.482, RI = 0.545, transition/transversion ratio = 2.05). Sequences are available from the author upon request (Table I).

Analysis of Nuclear Data

Sixty-three equally parsimonious trees were found in the nrITS search (Table 2). The strict consensus of these trees (Figure 5) shows that all African taxa form a

monophyletic group (African clade). European taxa are paraphyletic with respect to the African clade. Results from a bootstrap analysis showed moderate support (76%) for the monophyly of the African clade. Relationships for *Erica australis*, *E. carnea*, *E. cinerea*, and *E. sicula* are not resolved. *Erica manipuliflora*, *E. terminalis*, and *E. scoparia* form a well-supported clade (95%) within the European taxa. Within the African clade, *Erica coccinea*, *E. imbricata*, and *E. jonasiana* form a moderately supported clade (66%), with *E. imbricata* sister to *E. jonasiana* (63%).

Analysis of Chloroplast Data

The individual trees generated for both atpβ-rbcL and matK were highly unresolved and are not shown (Table 2). However, the search using the combined chloroplast data resulted in 3 most parsimonious trees. The strict consensus (Figure 6) also indicated that the African species form a clade. A grade of European taxa was also found. *Erica arborea* was found in a polytomy with two sets of sister taxa (*E. plukenetii* and *E. urceolata* were sister taxa, as well as *E. vagans* and *E. xanthina*). *Erica australis* is sister to the African clade, and *E. cinerea* is sister to both *E. australis* and the African clade. These European species are thus more closely related to the African taxa sampled in this analysis than to the other European taxa or *Erica spiculifolia*. Despite the fact that the results of this search yielded reasonably good resolution, there was poor bootstrap support (58%) for monophyly of the African taxa. *Erica imbricata* and *E. jonasiana* remained closely related in this analysis as in the nuclear analysis. *Erica manipuliflora*, *E. terminalis*, and *E. scoparia* remained closely allied within the basal "European" clade in this analysis as well; however, *E. scoparia* and *E. terminalis* are sister taxa, based on the chloroplast data (Table 2).

Analysis of Combined Nuclear and Chloroplast Data

The analysis using the combined nuclear and chloroplast data found 2 trees (Figure 7). In accordance with the previous individual searches, the strict consensus of the combined search shows a clade of African taxa as derived within the European grade (Figure 8). *Erica arborea* was sister to the remaining African taxa included in the analysis, *E. australis* was sister to this larger clade, and *E. cinerea* was finally sister to the clade composed of *E. arborea*, *E. australis*, and the clade of Cape African taxa. *Erica spiculifolia* is sister to all remaining Ericas sampled, but most of the remaining taxa form a clade. This European clade is sister to a clade composed of 2 European taxa and the African taxa. The sole difference between the two resulting trees from the combined analysis is the rearrangement within the European clade (Figure 7). Despite these changes though, *Erica manipuliflora* and *E. terminalis* remain closely related. Results of a bootstrap analysis showed strong support (95%) for the African clade being divergent within the Erica clade, while there was a lack of bootstrap support for the *Erica carnea-E. erigena* clade.

DISCUSSION

The phylogeny constructed from this study indicates that the African taxa are more recently derived than those found in Europe, making a European origin for *Erica* a distinct possibility. The African taxa consistently form a monophyletic group that is subtended by a basal grade of European taxa. The geographic ranges of *Erica* species accurately reflect the phylogeny resulting from this study (Figure 9). *Erica spiculifolia*, sister to all other *Erica* species in the combined analysis, is unique within the genus as the only tetraploid member with 4-merous flowers within a diploid genus possessing 5-merous flowers. Appearing in northern Europe, *Erica spiculifolia* marks the genus's putative European origin. Next, *Erica australis* is found in the Iberian Peninsula and is more closely related to the Cape African despite its European distribution, appearing as sister to *Erica arborea* plus the African clade. *Erica arborea* appears in the phylogeny as sister to the African clade and has a broad, bicontinental range, suggesting it shares a widespread ancestor found in both Europe and Africa with the Cape African taxa. Evidence suggests that the Ericaceae systematically expanded its range from Europe along the African highland into the Cape Region, probably after the mid-Oligocene establishment of a connection between Europe and Africa (Levyns, 1964). The highly-specialized, endemic genera found in South Africa would have evolved rapidly upon the genus's arrival in South Africa as a result of a isolation due to a fluctuating climate, dissected topography, and numerous soil types.

Biogeography

The European and African continents came into direct contact three times since the evolution of angiosperms making the expansion of *Erica*'s range possible (Scotese,

2000). Directly adjacent to vast stretches of European coastline during the Triassic, Africa and South America separated from North America during the early Jurassic (180 m.y.a.). Africa then began to rotate counterclockwise toward Europe beginning 148 m.y.a. and continuing until approximately 80 m.y.a; this rotation continued from 80 to 53 m.y.a. as Africa moved westward. Africa briefly connected to Europe (via Spain) and Asia (via Arabia) in the late Cretaceous and early Paleocene (63 m.y.a.) before separating once more.

During the late Cretaceous and Paleogene, plate tectonic reconstructions indicate that both eastern North America and western Europe were situated in similar latitudes, producing a warm, dry climate (Scotese, 2000). Land connections between North America and Europe existed in the late Cretaceous across what is now Greenland and scattered islands along the mid-Atlantic ridge (Raven and Axelrod, 1974) and were present through the Paleocene, allowing widespread genera and making speciation possible. Adding support to this idea is the fact that islands off the western coast of the United Kingdom, such as the Azores and the Canary Islands, are still inhabited by several species of *Erica*, including *Erica arborea* and *E. scoparia*.

A cool, moist climate was established in the south Africa and a warm, humid climate prevailed over the remainder of the continent beginning in the late Cretaceous when the continent was located approximately fifteen degrees south of its present position (Goldblatt, 1978). Humid rainforest remained widespread throughout Africa, including what is now the Sahara Desert, until the beginning of the Miocene. Direct connections between Europe and Africa were established during the late Oligocene, allowing organisms to expand their ranges to the north and south. At this time, many

groups of northern plants and animals expanded their ranges into Africa and vice versa. However, *Erica* was once again unable to complete the move into Africa at this time, as the continent's climate was unsuitable.

East Africa is believed to have consisted solely of a gently undulating plain prior to the late Oligocene epoch. The continent's pattern of low relief was disrupted as uplift occurred along the east coast of Africa, creating cooler, drier belts in the south and throughout the tropical latitudes. This tectonic activity resulted in the present landscape (Lind and Morrison, 1974). Simultaneously, Australia broke away from Antarctica and moved south toward the pole, establishing a circum-Antarctic current that affected a cooler, drier climate in southern Africa. Finally, the Tethys Sea was closed in the mid-Miocene (approximately 17 m.y.a.) by the reestablishment of a direct connection between Africa-Arabia and Eurasia, making range expansion between the European and African continents possible (Goldblatt, 1978). A phase of tectonic activity was initiated during this epoch that has continued, although at considerable lower levels, to the present day. The eastern highlands and rift lakes were created, establishing Africa's present day topography. These recently uplifted highland areas spanning east Africa would provide an acceptable habitat for exploitation by *Erica* as it expanded its range into Africa (Lind and Morrison, 1974).

Fossil and Pollen Evidence

The first fossil evidence of *Erica* species appears after the last connection between Europe and Africa. A mesofossil of *Erica palaeoarborea* dating back to the late Miocene epoch was found in the North Rhine region of Germany. As only a portion of a fossil, it was identified as an *Erica* species by the characteristic "ericoid" leaf, but it was

impossible to tell whether this particular plant was in fact *Erica arborea* or one of its ancestors (Van Der Burgh, 1987). If seeds could be located in this vicinity, it might be possible to ascertain if *Erica palaeoarborea* is in fact *E. arborea* by examining the cell patterns and ornamentation. The seeds of *Erica arborea* and *E. australis* are readily distinguishable from other Erica seeds and, of the two, *E. australis* possesses fewer curved walls and greater numbers of acute angles where walls intersect (Huckerby et al., 1972).

The next fossil evidence consists of fossilized seeds of no less than eight different species of *Erica* located in southwest France from a range of Pleistocene sites (Huckerby et al., 1972). Of particular interest in light of the phylogeny, evidence of *Erica arborea* was discovered in the Tibesti Massif in northern Africa dating back to the Pleistocene and the current range of these plants extends southward into its current location in the Ethiopian highlands, suggesting that this species was once far more widespread than it is today (Quezel, 1978). *Erica arborea* appears to have undergone range reduction that has resulted in numerous island refugia found in the Sahara Desert and the eastern highlands of Africa. Supported by its position as sister to the clade of African taxa, *Erica arborea* may represent an early branching lineage from a widespread, common ancestor that was found in both Europe and Africa, eventually giving rise to the Cape Africa taxa.

Modes of Range Expansion

Wind appears to have been the most important mechanism of range expansion in this species. For a seed to be dispersed a modest distance by wind, it must not exceed 0.2mm in diameter or have a density of more than 2.6g/cm^3 (Lind and Morrison, 1974). *Erica* species produce large aaa peaah ds 0 iceTs m

(Huckerby et al., 1972) and seeds of the closely related *Calluna* (Kron et al., 2002) average 0.6 by 0.44mm and weighing approximately 10 micrograms (Gimingham, 1960). The seeds of *Calluna* have been reported to disperse a distance of 100 meters (109 yards) away from the mother plant in a wind of 10 meters per second (22 miles per hour). (Beijerinck, 1940) and the distance of dispersal increases to 250 meters (273 yards) in a wind of 30 to 40 meters per second (67 to 89 miles per hour). (Nordhagen, 1937).

Very little is known about the interactions between *Erica* species and animals, with the exception of pollination syndromes, but range expansion by way of animal migration does not seem to have contributed significantly to this genus's current distribution. *Calluna* has been noted for its value as a food source for grouse and sheep (Gimingham, 1989), while the Cape species of *Erica* are rarely grazed by large animals due to the presence of toxic compounds (Oliver, 1991). The allelopathic potential of Ericas has been documented and their extracts were recognized as often containing salicyclic acid, scopoletin, and p-hydroxybenzaldehyde (Ballester et al., 1979).

The range expansion of these species may have been facilitated during the Miocene and Pleistocene when the altitudes of the vegetation belts were decreased by as much as 100m due to a cooler climate. Temperatures in Africa appear to have experienced a decrease from the maximum at 26 m.y.a. and remained approximately 5.1 to 8.8^{o}C below our present temperatures until 14 m.y.a. (Coetzee, 1967). This tremendous expansion of the upland biomes would have encompassed a much greater portion of tropical East Africa, as well as South Africa (Moreau, 1963). It is suggested that the ericaceous belt, existing today as island refugia on high mountains in East Africa, would have been more typical of tropical Africa than the present lowland vegetation

when the European and African continents came into contact for the last time in the mid-Miocene and the area suitable for exploitation by *Erica* species along the recently-uplifted areas would have been much larger than it is today making the modest dispersal distances of the seeds more than adequate to move into the adjacent continent.

Modes of Speciation

Once *Erica* expanded its range into southern Africa geographic speciation became of primary importance for the flora of southern Africa and the montane areas of the east. Alternating mesic and arid phases occurred in southern Africa as a result of the fluctuating world climate of the late Tertiary and Quaternary periods. Beginning in the Miocene, Africa assumed its present-day, relatively arid climate under the influence of the westerlies and cold water from Antarctica. The climate in southern Africa began its ongoing reduction in overall humidity and drought-adapted plants started to evolve rapidly at this time. Uplift occurred along Africa's southern coast at the end of the Pliocene, resulting in the Drakensburg Mountains. Thus the modern landscape of southern Africa was created and can be characterized by plateaus and escarpments bordered by a narrow coastal belt that runs along the southern end of the continent (Goldblatt, 1978). It has been hypothesized that these plant communities were isolated into numerous, relictual populations over extended periods of time by a fluctuating climate, dissected topography, and numerous soil types, creating conditions that accelerate divergence, such as genetic drift and strong selection in extreme conditions (Schumann and Kirsten, 1992). As evidence, the high species per genus ratios that occur in southern Africa also occur in other arid regions of the world (Goldblatt, 1978).

The creation of interfertile hybrids has been cited as another significant means of speciation in southern Africa that is extremely likely. Woody and perennial plants predominate there and have been shown to do this in other Mediterranean areas. In addition, many South African taxa exhibit features suggestive of a hybrid origin (Goldblatt, 1978). Hybrids are well known in Ericas, particularly in Europe where they are prized horticulturally (Oliver, 1991). However, the formation of polypoids in Ericas has never been reported (Goldblatt, 1978).

Finally, the three pollination syndromes (bird, insect, and wind) found in this genus are highly correlated with the flower morphology (Rebelo et al., 1984). In a survey of avian pollination conducted near Stellenbosch, the orange-breasted sunbird, *Nectarinia violacea*, was almost enti94w 0 Td (e)Tj ET Q Q q W 62.4998 3204.u

resulting in a number of relictual species found along the coast and belts of mountains that extend from the Cape to Natal.

Conclusion

The African taxa form a monophyletic group derived from a single widespread ancestor whose ancestors were European in origin. Uplift and a modern climate were established in Africa during the early Miocene epoch putatively creating conditions in Africa that would be conducive to colonization by *Erica* species when the Tethys Sea closed and Europe and Africa reconnected in the mid-Miocene. *Erica arborea*, sister to the African clade, appears to have once had a much broader range that encompassed much of northern Africa and most of Europe before experiencing reduction to its current range seen as island refugia in the Sahara Desert and the eastern African mountains. The geographic speciation of *Erica* occurred rapidly upon its arrival in South Africa and produced uneven rates of evolution with the appearance of a multitude of species, evidenced by the short internal branch lengths and longer branches at the crown of the trees. This unparalleled speciation appears to have resulted from a combination of factors: a once broad range reduced by a warming climate, restriction of available land by water availability and soil type, and the creation of interfertile hybrids by indiscriminate feeding by certain pollinators.

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Table I

Taxon Sampling

Erica scoparia L.	√	√		Europe
Erica sicula Guss.	√	√	√	Europe
Erica terminalis L.	√	√	√	Europe
Erica tetralix L.	√	√	√	Europe
Erica vagans L.	√		√	Europe
Erica cinerea L.	√	√	√	Europe
Erica australis L.	√	√		Europe
Erica arborea L.	√	√	√	Europe, Middle East, Africa
Erica axillaris Salis.		√	√	Africa
Erica cetrata E. G. H. Oliver	√	√	√	Africa
Erica coccinea L.	√	√	√	Africa
Erica embothrifolia Salis.	√	√	√	Africa
Erica hispidula L.	√	√	√	Africa
Erica imbricata L.	√	√	√	Africa
Erica jonasiana E. G. H. Oliver	√	√	√	Africa
Erica muscosa (Aiton) E. G. H. Oliver	√	√	√	Africa
Erica oakesiorum E. G. H. Oliver	√	√	√	Africa
Erica paniculata L.	√	√	√	Africa
Erica plukenetii Berg.	√	√	√	Africa
Erica rigidula (N. E. Br.) E. G. H. Oliver	√	√	√	Africa
Erica tristis Bartl.	√	√	√	Africa
Erica urceolata (Klotzsch) E. G. H. Oliver		√	√	Africa
Erica xanthina Guthrie and Bolus	√	√	√	Africa

Table II

Statistical Information

Matrix	Matrix Length	Inform. Characters	%	Trees	Length	CI	RI	Ti/Tv
nrITS	668	110	16	63	507	0.655	0.590	2.45
atpB-rbcL spacer	867	74	9	912,000	404	0.819	0.614	0.82
matK	855	48	6	16,383	275	0.630	0.756	1.14
Combined Chloroplast Data	1722	122	7	3	698	0.722	0.570	1.05
Total Data	2390	232	10	2	589	0.482	0.545	2.05

Figure 1. Narrow north-south geographic distribution exhibited by *Erica* species in Europe and Africa. Modified from WorldAtlas.com and Oliver (2000), with number indicating numbers of species in a given region. The numbers for tropical Africa taxa have been estimated due to the need of an overall revision in this region.

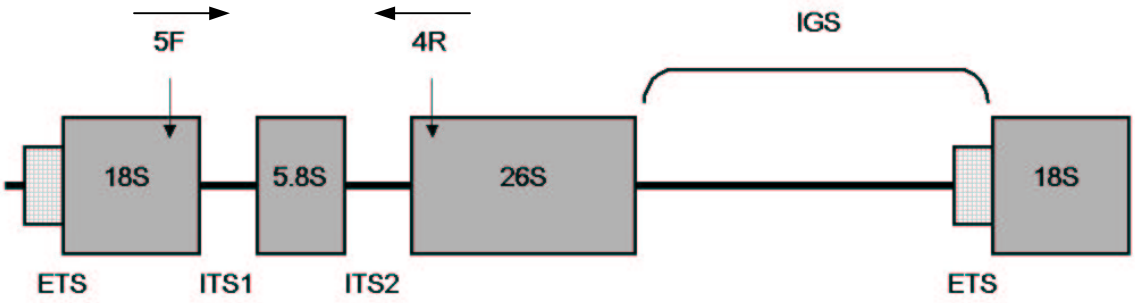

Figure 2. This diagram depicts the nrDNA repeat found in plants. The ribosomal rRNA genes are indicated as 18S, 5.8S, and 26S. The internal transcribed spacer regions, ITS1 and ITS2, were amplified in this analysis using the 5F and 4R primers. The intergenic spacer (IGS) and external transcribed spacer (ETS) are also labeled. Modified from Soltis, Soltis, and Doyle (1998).

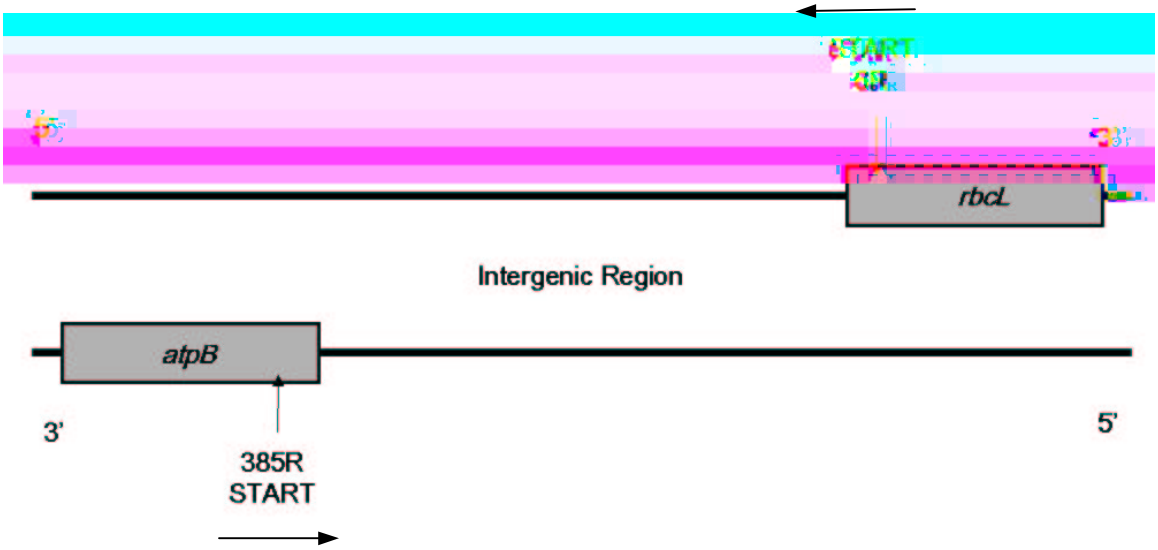

Figure 3. This diagram depicts the portion of the chloroplast genome containing the *atpβ* and *rbcL* genes. Located in close proximity, these genes are transcribed in opposite directions and house the primers used in amplification and sequencing. Modified from Soltis, Soltis, and Doyle (1998).

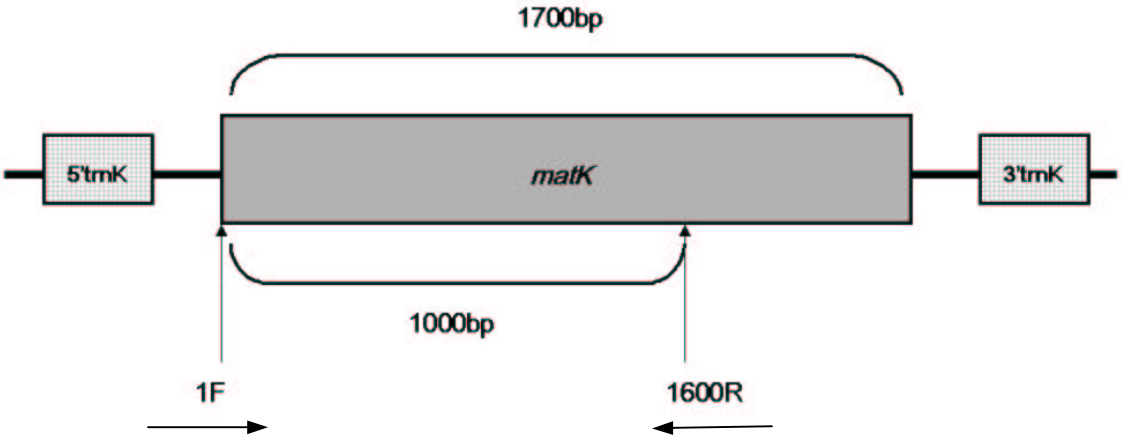

Figure 4. This diagram depicts the portion of the chloroplast genome containing the *matK* gene. Approximately 1000bp from the more variable 5' end were amplified and sequenced from this gene using the 1F and 1600R primers (Kron, 1997), designed specifically for these plants. Modified from Soltis, Soltis, and Doyle (1998).

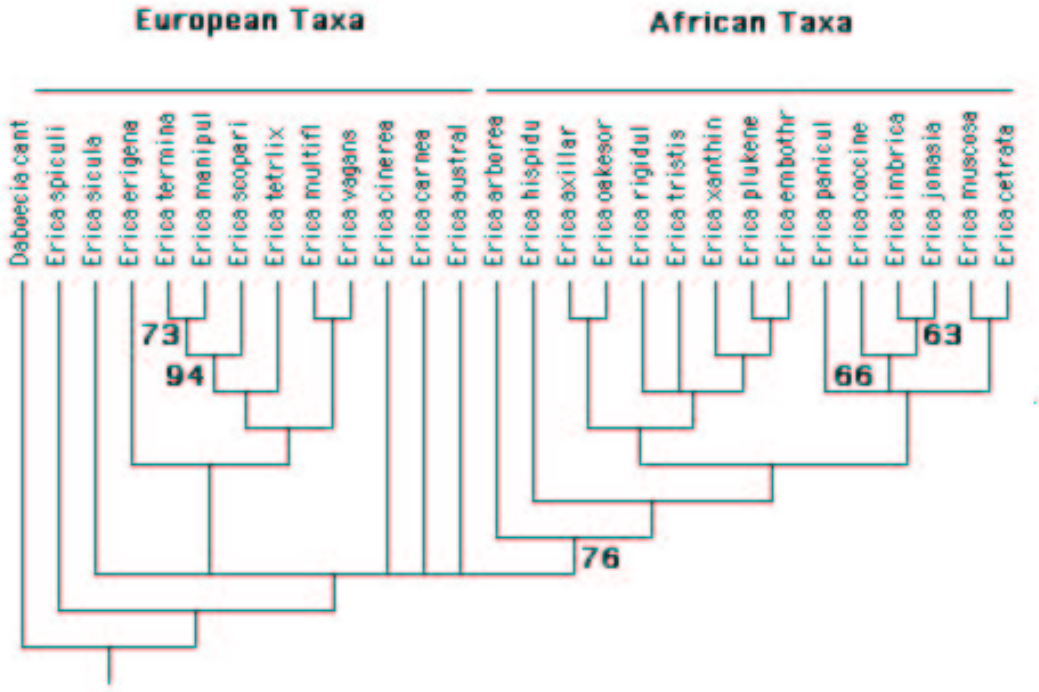

Figure 5. Strict consensus of the 63 most parsimonious ITS trees [L = 507, CI = 0.655, RI = 0.590].

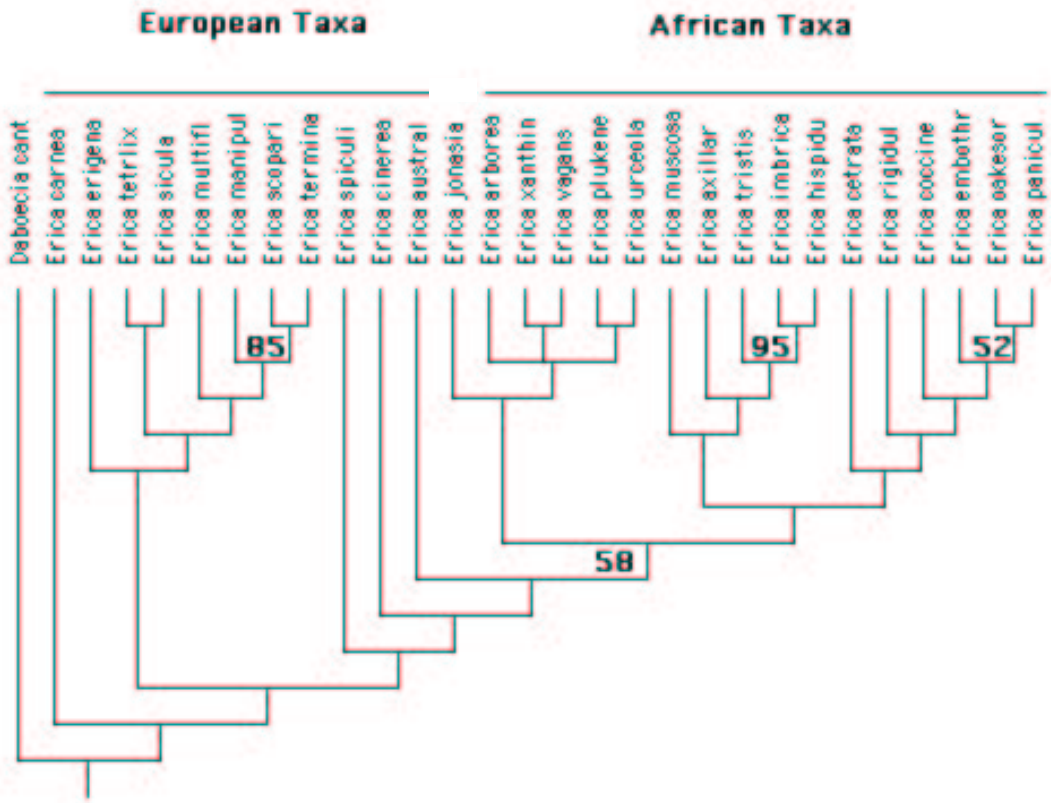

Figure 6. Strict consensus of the 3 most parsimonious trees produced from the combined chloroplast data [L = 698, CI = 0.722, RI = 0.570].

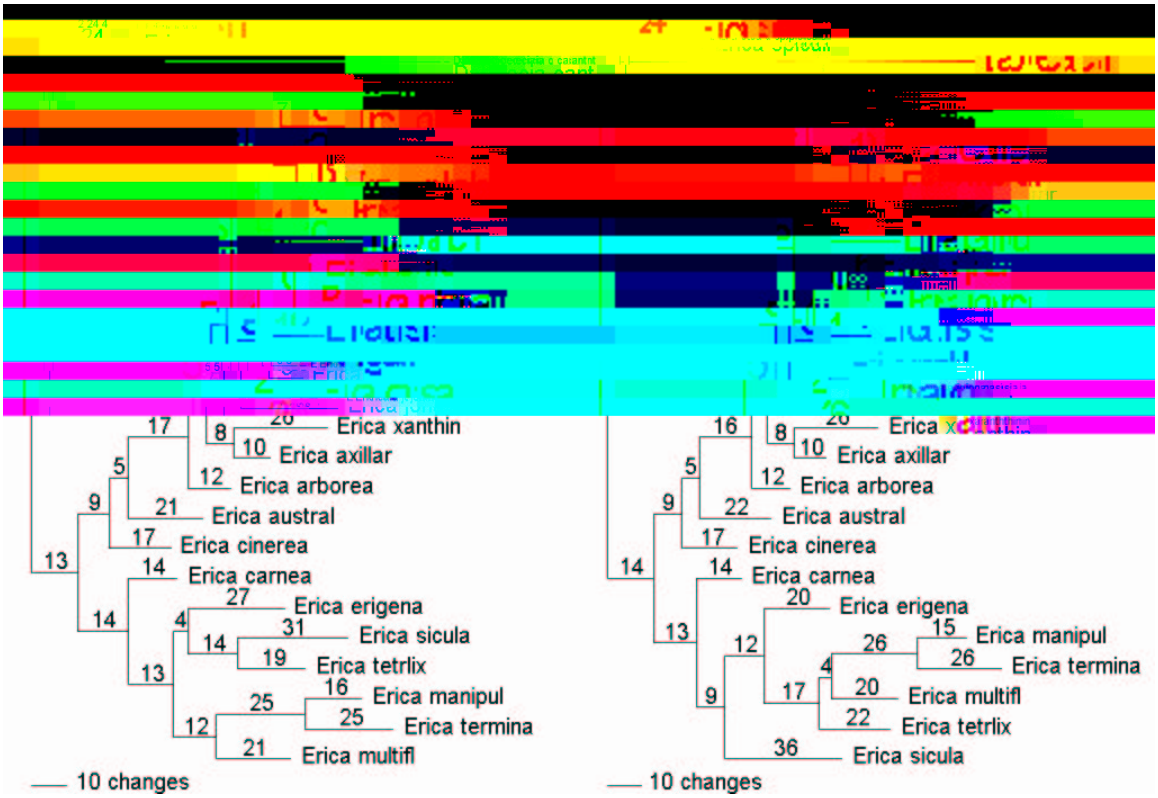

Figure 7. The two most parsimonious trees resulting from a combined analysis of nuclear and chloroplast data [L = 589, CI = 0.482, RI = 0.545]. The branch lengths are indicative of the number of changes.

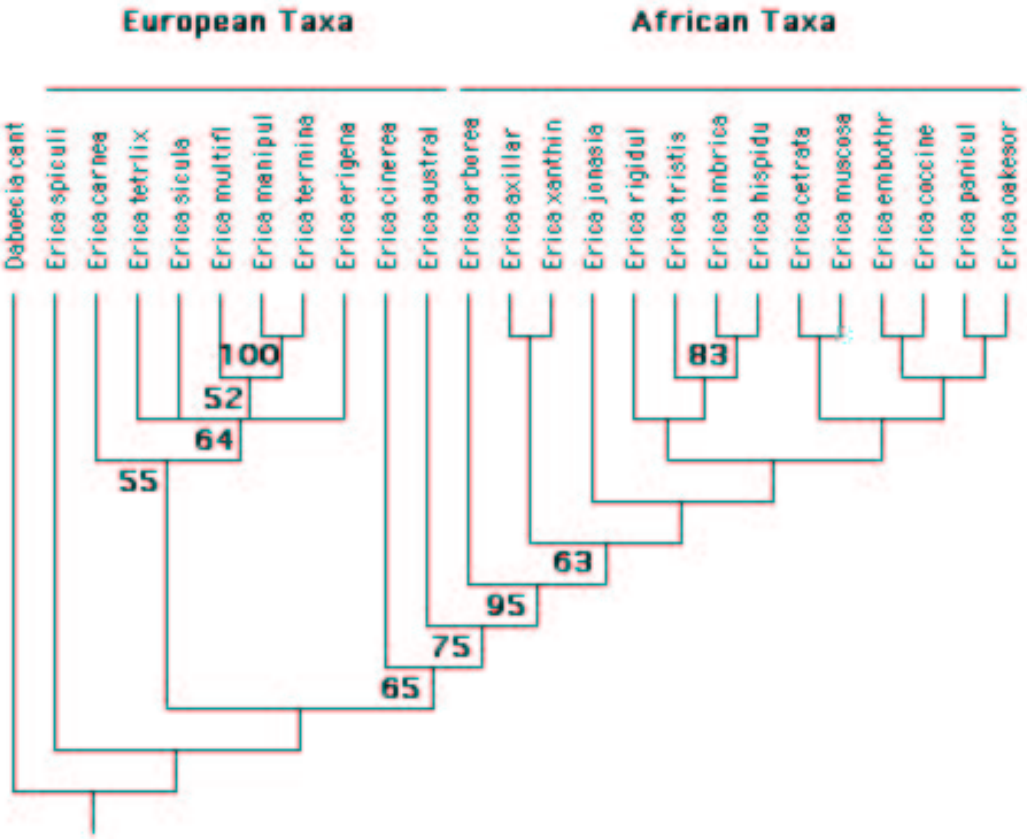

Figure 8. Strict consensus of the three most parsimonious trees found in the combined analysis of both nuclear and chloroplast data [L = 589, CI = 0.482, RI = 0.545].

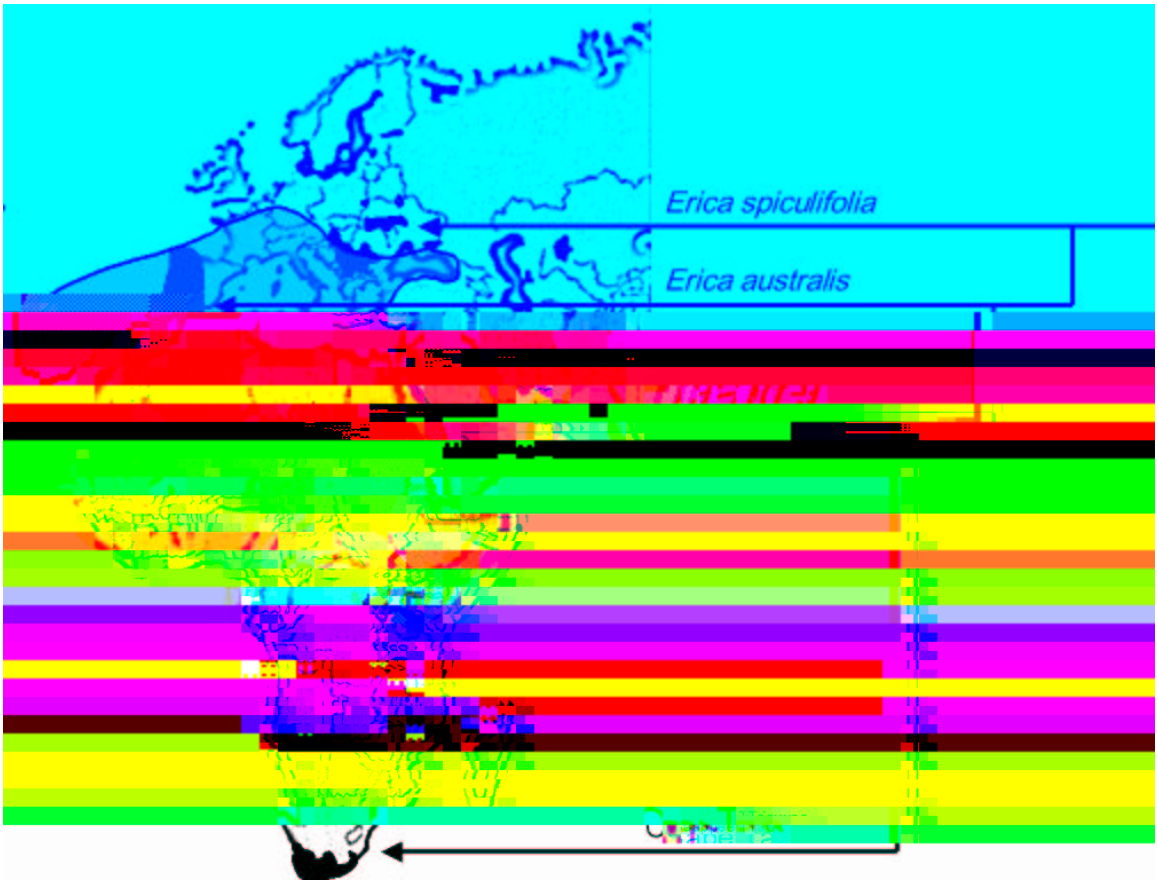

Figure 9. The phylogeny of *Erica* species accurately reflects the geography of this group, beginning with the putative origins of the genus in northern Europe with *Erica spiculifolia*.

CURRICULUM VITAE

Avery Faye McGuire
5040B Eltha Drive
Winston-Salem, NC 27105
(336) 776-1559
email: mcguaf1@wfu.edu

Personal: Born August 1, 1979, Concord, North Carolina

Education:

MS Wake Forest University, Winston-Salem, NC, 2003
BS Catawba College, Salisbury, North Carolina, 2001

Positions Held:

Biology Tutor for Biology 111 and 112 (introductory biology for nonmajors and majors), Wake Forest University, Winston-Salem, NC, 2001-2003
Lab assistant, Catawba College, Salisbury, NC, 1998-2001
Assisted in planning of the First Annual Watershed Conference, Catawba College, Salisbury, NC, 1998

Teaching Experience:

Wake Forest University-Biology 214 lab (cellular and molecular biology)
Activity Director for S.P.E.C. Camp for Academically Gifted Youth, Catawba College, Salisbury, NC, 1998-2000
Activity Director for Environmental Science Day for High School Seniors, Catawba College, Salisbury, NC, 1998-2000

Awards and Grants:

Teaching Assistantship, Wake Forest University, 2001 to 2003
Research Assistantship, Wake Forest University, Spring 2001
Catawba College (2001) - Whitener Medal for outstanding scholarship, service, and character awarded to two students (one male and one female) of the graduating class as elected by both students and faculty
Catawba College (2001) - Daniel E. Kirk Biology Award – for outstanding performance among the graduating class
ASB (2001) - Second place in the John C. Johnson Award poster competition at a regional conference
Alpha Chi Academic Honor Society-Treasurer in 1999, President in 2000
Tri Beta Biological Honor Society-Historian in 1999, President in 2000
Junior Marshall (awarded to the top ten GPAs in the junior class), Catawba College, 1999

Presentations:

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