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Phylogenetics of Cochlostema, Geogenanthus, and an undescribed genus (Commelinaceae) using morphology and DNA sequence data from 26S, 5S-NTS, rbcL, and trnL-F loci

A phylogenetic study was conducted on a group of three small genera of neotropical Commelinaceae that exhibit a variety of unusual floral morphologies and habits. Morphological characters and DNA sequence data from plastid (*rbcL*, *trnL-F*) and nuclear ribosomal (5S-NTS, partial 26S) loci were used. In separate analyses, 26S and *rbcL* character sets each yielded cladograms that were equally or more fully resolved than those from analyses of the more rapidly-evolving 5S-NTS and *trnL-F* loci. Analysis of the molecular character sets, in combination with morphological characters, has provided a framework for the study of life form and morphological character evolution. Our studies indicate that the unusual spirally-coiled anthers and other apparent autapomorphies in the flowers of *Cochlostema* are elaborations of developmental synapomorphies shared by *Cochlostema* with *Geogenanthus* and an undescribed genus. The adaptations associated with the epiphytic habit of *Cochlostema* are best understood in light of their similarity to homologous features in the undescribed genus. Our inclusion in this study of two undescribed plesiomorphic species of *Geogenanthus* has revealed an evolutionary trend towards reduction in the inflorescence in this genus.

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Molecular systematics of Potamogeton (Potamogetonaceae)

The pondweeds, *Potamogeton* (Potamogetonaceae), display heterophyly, both within and among species. In addition, some species display seasonal heterophyly. Consequently, the genus has long been considered to be taxonomically difficult. *Potamogeton*, *sensu stricto*, has conveniently been divided into two groups, broad-leaved species and narrow-leaved species. Phylogenetic analysis of 5S nuclear ribosomal non-transcribed spacer (5S-NTS) sequences supports the monophyly of two major clades, one essentially those previously considered to be broad-leaved species and the other those previously considered to be narrow-leaved species. Within each main clade, species groups are recognized, mostly along the lines of previously accepted subsections. For example, *Potamogeton epihydrus* and *P. tennesseensis* form a clade sister to the *P. spirillus*, *P. bicupulatus*, and *P. diversifolius* clade. These two subclades are in turn sister to the species previously recognized as the narrow-leaved pondweeds.

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Ontogenetic floral evolution of Mimulus lewisii and M. cardinalis (formerly Scrophulariaceae, s.l.): allometry and morphology

Speciation in the bee-pollinated *Mimulus lewisii* and bird-pollinated *M. cardinalis* group is hypothesized to have occurred through divergence in floral form that led to a change in

breeding system. This effectively reproductively isolates the species. Previous studies have provided extensive genetic, phylogenetic and natural selection data which allow for a rare opportunity to now study and interpret ontogenetic changes as sources of evolutionary novelties in floral form. Three populations of *M. cardinalis* and four populations of *M. lewisii* (representing both described races) were studied from initiation of floral apex to anthesis using SEM and light microscopy. Allometric analyses were conducted on data derived from floral organs. Sympatric populations of the species from Yosemite National Park were compared. Calyces of *M. lewisii* initiate later than those of *M. cardinalis* relative to the inner whorls, and sepals are taller and more acute. Relative times of initiation of petals, sepals and pistil are similar in both species. Petal shapes differ between species throughout development. Corolla aperture shape becomes dorso-ventrally narrow during development of *M. lewisii*, and laterally narrow in *M. cardinalis*. In both species, the adaxial filaments curve adaxially as they elongate. In *M. lewisii*, the abaxial stamens curve away from the median while those of *M. cardinalis* are directed adaxially. Allometric analyses reveal that differences in corolla length dimensions between species are controlled by alterations in rate of growth, while differences in stamen and pistil dimensions are controlled by alterations in timing of termination of growth relative to corolla growth.

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Growth form evolution in Adenia and correlations with phytochemistry

The genus *Adenia* (Passifloraceae) provides a model system with which to investigate the relationship between growth form and phytochemistry. With ca. 90 species the genus has a diverse and varied pharmacopoeia and at least seven distinct growth forms. An association between growth form and chemistry is expected based on theoretical predictions. I mapped cyanogenesis on the phylogeny of *Adenia* to reveal that 4 of the 5 putative shifts from ancestral tendrillate vines to growth forms without tendrils are in association with low cyanogenesis as expected. The phylogeny based on ITS sequence data and an extensive sampling of African and Madagascan species of *Adenia* supports 5 main lineages. Extrafloral nectary superstructure in large part supports the molecular characterization. Individuals in the most basal lineage of *Adenia* all possess spatulate glands at the leaf blade base. The next most ancient lineage has members that are tuberous vines and herbs. Members of this lineage share paired and upturned glands at the petiole-blade junction. A more recent lineage contains a wet-tropical African lineage and a dry-habitat African and Madagascan lineage. The wet-tropical lineage has lianas and vines with paired auriculate glands at the blade-petiole junction. The dry-habitat African and Malagasy lineage possesses species with succulence and often slightly recessed glands at the base of the leaf (although some Madagascan species are autapomorphic). The lineage that is sister to this more recent branch is least characterized by gland structure, but possesses a diversity of gland structures and growth forms. Research is underway to relate anatomical features with phytochemistry to rigorously test whether changes in anatomy (hence changes in growth form) are correlated with changes in phytochemistry.

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Phylogenetics of Nemophila using molecular and morphological data

The North American endemic genus *Nemophila* (Hydrophyllaceae) consists of 11 species and six varieties of annual herbs found primarily in California. Nine species occur in the western United States as far south as Baja California, while two species (*N. phacelioides* and *N. aphylla*) are disjunct in the southeastern United States. The evolutionary relationships within *Nemophila* remain unclear despite eight previous taxonomic treatments and exploration of a variety of potentially useful kinds of characters (morphology, cytology, and development). We present a phylogenetic analysis of *Nemophila* and relevant taxa in the tribe Hydrophyllaeae using DNA sequence data from both the nuclear ribosomal DNA internal transcribed spacer, and from the chloroplast 3' trnK intron. The molecular phylogenetic analyses concur with infratribal relationships previously inferred from seed coat characters. On our phylogeny *Nemophila* and *Pholistoma* form an unresolved polytomy, but seed coat morphology suggests that *Pholistoma* is sister to *Nemophila* as a whole. Within *Nemophila* seven of the eight Californian species form a strongly supported clade; the remaining taxa occur as a second, weakly supported clade. Nonetheless, in resolved phylogenies, the two southeastern species are never sister taxa and thus may have resulted from independent dispersal or vicariant events. However, additional data are needed to confirm that these species are indeed not sister taxa.

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Angiosperm phylogeny based on matK sequence data

An angiosperm phylogeny based on sequence information from the *matK* gene is presented. Our dataset currently comprises representatives of most angiosperm lineages (approx. 350 taxa) and was analyzed using maximum parsimony with gymnosperms as outgroup. The strict consensus tree is strikingly similar to results of a recent combined analysis (18S rDNA + *rbcL* + *atpB*) both in topology and high statistical support of many nodes. Amborella branches first, followed by Nymphaeales and an *Illicium-Austrobaileya*-clade. The non-monocot eumagnoliids (Chloranthales, Magnoliales, Laurales, Winterales, Piperales) appear next as a monophyletic group. This basal grade is followed by the monocots forming a sister group to *Ceratophyllum*. Within eudicots Ranunculales branch first with the core eudicots (Saxifragales, Gunnerales, Vitales, Santalales, Berberidopsidales, rosids, Caryophyllales, asterids) being one of the best supported major clades (99%

bootstrap). A clade of asterids and Caryophyllales appears as sister to Berberidopsidales. Asterids consist of a well-supported clade composed of Ericales, Cornales, and euasterids. Within rosids most of the currently recognized orders gain good support. Moreover, *matK* sequences provide good resolution within many of the orders of angiosperms.

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Molecular systematics and biogeography of the amphibious genus Littorella (Plantaginaceae)

Littorella is a small, amphibious genus within the Plantaginaceae and is represented by three closely related, disjunct species, *L. uniflora* (L.) Ascherson in Europe including Iceland and the Azores, *L. americana* Fernald in North America, and *L. australis* Griseb. ex Benth & Hooker in southern South America. A recent phylogeny (Rahn, 1996) based on morphological, embryological, and chemical data has resulted in the reduction of *Littorella* to *Plantago* subgenus *Littorella* (P.J. Bergius) Rahn and renaming of the included species to *Plantago uniflora* L. (= *Littorella uniflora* (L.) Aschers.), *Plantago americana* (Fernald) Rahn (= *Littorella americana* Fernald), and *Plantago araucana* Rahn (= *Littorella australis* Griseb.). We compared this phylogeny to one based on DNA sequence data from the nuclear ribosomal internal transcribed spacer region (ITS). A total of four outgroup taxa, three species of *Littorella*, and 44 species of *Plantago* were included in this analysis. Our molecular phylogeny supports the generic recognition of *Littorella* as it is clearly sister to *Plantago*. Our phylogeny also rejects the conspecific recognition of *L. americana* and *L. uniflora* as proposed by recent North American authors and suggests a European origin for *Littorella*.

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Systematics of Trichostema L. (Lamiaceae): evidence from ITS, ndhF, and morphology

Trichostema L., a North American genus comprising five sections and 17 species, has long been recognized as a natural group based on its morphology. Since relationships among the species remain unclear, cladistic analyses of morphological and molecular data for *Trichostema* are needed to verify its monophyletic status and to assess the sectional classification within the genus. Both ITS and *ndhF* data indicate that *Trichostema* is monophyletic and sister to the Asian *Caryopteris* s.s. When it includes *T. brachiatum*, an eastern US species sometimes placed in its own genus, section *Orthopodium* is polyphyletic, the remainder of the species occurring in the western US. The *ndhF* data support sections *Paniculatum* and *Rhodanthum* as sister to one another. Vegetative structures, floral development, and fruit morphology have been examined in much detail in combination with characters available from the literature (pollen morphology, base chromosome, and breeding system, etc.). In particular, the characteristic trichomes (glandular and nonglandular) of *Trichostema* have been studied and assessed for their phylogenetic informativeness. The results of the morphological study support the monophyly of *Trichostema*, and are mainly congruent with relationships inferred from DNA sequence data, with the notable exception of *T. brachiatum*, which is placed in section *Orthopodium*.

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Revisiting Stapf: phylogeny of Ephedra, insights from plastid genes and morphology

Phylogenetic analyses of seed plant evolution have demonstrated the importance of the Gnetales. While these distinctive gymnosperms were initially considered a sister group to the angiosperms, all recent molecular analyses have refuted the anthophyte hypothesis, with some even suggesting a close affinity to the pines. However, a sister relationship of Gnetales to the Pinaceae is not easily reconciled with morphology. This problem is further compounded by our incomplete understanding of extant diversity in *Ephedra*, the basalmost member of the Gnetales. To test Stapf's (1889) longstanding hypothesis of relationships within *Ephedra* (*Alatae*, *Asarca*, *Pseudobaccatae*) both morphological and nucleotide sequence data sets were analyzed. These included data from the chloroplast intergenic spacer regions (*atpB-rbcL*, *trnF-trnL*) and the plastid coding region and spacer of the *rps4* gene. Our preliminary cladistic analysis suggests that New World ephedras are paraphyletic, monophyly of this group requires 32 extra steps. While the analysis provides robust support for monophyly of the *Alatae* clade, the monophyly of the *Asarca* and *Pseudobaccatae* clades are not supported. The traditionally accepted Old and New World clades are artificial. The distribution of fleshy bracts, once considered taxonomically important, requires two separate origins and a loss in the North American "*nevadensis-viridis* alliance". Hence it appears a relatively poor indicator of affinity. The topology also supports a New World origin of *Ephedra*, with a single migration event to the Old World. This scenario appears congruent with the currently known fossil evidence, and may be further supported with additional sampling. The apparent contrast between the low rate of molecular divergence and remarkably rapid rates of morphological differentiation may be tied to adaptive radiation of *Ephedra* in extreme arid environments.

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Monographic studies of Compsoeura, a Neotropical genus of the Myristicaceae

Compsoneura is a Neotropical genus of trees distributed primarily in the lowland wet forests from Bolivia and southern Brazil north to Veracruz, Mexico. Herbarium, field, and laboratory studies were conducted between 1997-2000 with the ultimate goal of producing a monographic treatment for this genus. Herbarium studies included analysis of approximately 2,500 specimens, with rigorous sampling of label and morphological data from each specimen. Geographic coordinate data for every collection were generated for use in GIS-based mapping and geospatial analysis. Stereomicroscopy and Scanning Electron Microscopy (SEM) were applied in a morphological analysis for all species in Compsoneura. Multivariate procedures of quantitative analysis were applied in order to investigate morphological variation and implications for species delimitations. Microsatellite DNA markers were used to elucidate one difficult, widespread species complex, *Compsoeura sprucei* sensu lato. A qualitative data matrix of 40 characters was analyzed using parsimony methods to investigate in-group evolutionary and biogeographic patterns. Combinations of multivariate and parsimony analyses provided a better overall view of interspecific and subgeneric patterns, respectively. A total of 20

species are currently recognized, including seven species new to science and a new combination. The classification proposed by Warburg (1897) and accepted by Smith (1937) was revised, involving the description of a new generic section (*Hadrocarpa*). Previous emphasis of the Warburgian system on androecial characteristics was found to be insufficient in light of more comprehensive information from leaves, staminate and pistillate flowers, androecia, gynoecia, fruit, aril, and seeds. Furthermore, the new section *Hadrocarpa* may represent a new genus for the Neotropics. This taxonomic hypothesis awaits further testing with outgroups and inclusion of molecular data. Results, implications, and lessons from studies of *Compsoeura* will be presented, with demonstration of the importance of basic monographic work in the Neotropics and beyond.

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Systematic research and the geospatial realm: examples from studies of Neotropical plants

Modern geospatial science integrates spatial and attribute data to visualize, manipulate, analyze, and present land-based resource patterns. Geographic Information System (GIS) technology has been applied in systematic studies of the Myristicaceae family and is now being tested, at various spatial scales, in other families of Neotropical plants, such as the Cucurbitaceae. We introduce traditional mapping of species point data, and follow with the addition of various informative geospatial data layers. We add Digital Elevation Model (DEM) grids to demonstrate the importance of this data layer in species mapping and in interpreting species distributions. Results of univariate and multivariate analysis of quantitative and qualitative morphological character data are plotted in a "geomorphospace" using GIS grid analysis. Combined results of this approach are used to demonstrate applications and implications of GIS in the future of plant systematic research, with emphasis on Neotropical species distribution and variation patterns.

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New approaches for using gene order data in phylogeny reconstruction

The rapid accumulation of whole genome sequences for a wide diversity of taxa is generating a huge amount of comparative data for biologists. The availability of whole genome sequences is providing a new set of molecular characters for phylogenetic reconstruction, which are especially useful for resolving deep branches of the tree of life. Changes in gene order are caused primarily by inversions, transpositions, and transversions. One of the major challenges for using genomic changes is the development of computational methods for handling these types of characters, especially in groups with large numbers of genes and highly rearranged genomes. We have been developing and testing a variety of methods for reconstructing phylogenies based on gene order data using both real and synthetic data. Two of the primary methods we have developed and tested are Maximum Parsimony

on Binary Encodings (MPBE) and methods for correcting previously published distance measures (inversion and transposition distances). Our simulations show that all methods perform very well when the rates of change are low relative to the number of genes and that all methods perform poorly when rates of change are high relative to the number of genes. Furthermore, corrected distance measures greatly improve the accuracy of phylogenies. We have applied these new methods to a data set for the highly rearranged chloroplast genomes of the Campanulaceae. In this group, which generally has low rates of change relative to the number of genes, all methods recover congruent tree topologies. Analyses of this data set using our new program GRAPPA (Genome Rearrangements Analysis under Parsimony and other Phylogenetic Algorithms) also produced a congruent tree topology. Gene order phylogenies for the Campanulaceae are considered accurate because they are largely congruent with trees generated from three chloroplast gene sequences (atpB, matK, and rbcL).

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Molecular rates parallel diversification contrasts between carnivorous plant sister lineages in Lentibulariaceae

In the carnivorous plant family Lentibulariaceae, the bladderwort lineage (*Utricularia* and *Genlisea*) is substantially more species-rich and morphologically divergent than its sister lineage, the butterworts (*Pinguicula*). Bladderworts have a relaxed body plan that has permitted the evolution of terrestrial, epiphytic, and aquatic forms that trap prey in intricately-designed suction bladders. In contrast, the flypaper-trapping butterworts maintain vegetative structures typical of angiosperms. We found that bladderwort genomes evolve significantly faster across seven loci (the *trnL* intron, the second *trnL* exon, the *trnL-F* intergenic spacer, the *rps16* intron, *rbcL*, *coxI*, and 5.8S rDNA) representing all three genomic compartments. Generation time differences did not show a significant association. We relate these findings to the contested speciation rate hypothesis, which postulates a relationship between increased nucleotide substitution and increased cladogenesis. Body-plan relaxation would lower selection pressure as individuals with novel phenotypes establish founder populations and diverge. In agreement with known prey specificities and interbreeding barriers among bladderworts, the strong correlation between bladder variety and phylogeny (estimated from 69 Lentibulariaceae and 10 outgroups based on *trnL-F* and *rps16* intron sequences) suggests that diversifying (disruptive) selection on trap form has further driven rate increases. Additionally, bladderwort features such as rootlessness, asymmetrical phyllotaxy, and leaf-shoot indistinction resemble phenotypes of known auxin transport mutants, suggesting that one or few genes of large effect could underlie bladderwort developmental release (see abstract by Albert and Jobson, Botany2001). Finally, we argue that molecular and speciation rate increases may amplify each other as greater genetic variation feeds into the system, resulting in "explosive" radiation (i.e., punctuational evolution).

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Molecular systematics of Sagittaria (Alismataceae)

The aquatic plant genus *Sagittaria* contains about 35 species and is distributed mostly in the New World but can also be found in Europe and Asia. *Sagittaria* was analyzed phylogenetically using sequences of the 5S nuclear ribosomal non-transcribed spacer (5S-NTS). Taxa that have historically been placed in *Sagittaria* subgenus *Lophotocarpus*, with the exception of members of the *Sagittaria subulata* group, were strongly supported as monophyletic and were placed basal to the remainder of the genus when using the closely related genus *Echinodorus* (Alismataceae) for outgroup comparison. Of the remaining taxa, sagittate leaved species form a group that is sister to non-sagittate leaved species. The sagittate leaved group has a disjunct distributional pattern between the New World and Asia in which the Asian species appear to be the basal members. The *Sagittaria subulata* group, within the non-sagittate leaved species, is strongly supported as monophyletic. Taxonomy, character evolution, biogeography of *Sagittaria* will be discussed in light of these findings.

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Utility of the External Transcribed Spacer (ETS) in Compositae tribe Cardueae phylogeny reconstruction and rapid evolution of North American thistles (Cirsium species)

A 21 base-pair sequence, invariant among *Carduus nutans* and *Cirsium andrewsii*, was used to design primer ETS-Car-1, beginning at base pair 561 upstream from the 3' end of ETS (referring to the sequence of *Cirsium andrewsii*). A subsequent PCR of 10 diverse Cardueae taxa using primers ETS-Car-1 and 18S-E produced products of identical length. Maximum corrected (HKY85) pairwise ETS-region sequence divergence was 14.8% between *Centaurea calcitrapa* and *Atractylodes japonica*. Within *Cirsium*, the maximum corrected (HKY85) pairwise ETS-region sequence divergence was found between *C. henryi* and *C. arvense* (5.2%). For phylogenetic analysis, 52 taxa were sequenced for ETS and ITS, including 34 North American native *Cirsium* species, 13 Old World *Cirsium* species, and two species each of *Carduus* and *Onopordum*. Divergence between the ITS and ETS sequences were similar. Phylogenetic analysis supported the monophyly of *Cirsium* and *C.* subgenus *Eucirsium* (New World thistles). Two clades of West Coast species appeared; one including Pacific Northwest and montane species with n=34 and one comprising California endemics with n=32. ETS and ITS divergence among *Cirsium* are significantly lower than in other studied groups, as determined by comparison of divergence in six California plant groups. The relatively low levels of rDNA spacer sequence divergence contrast with the great ecological diversity displayed by new World *Cirsium*.

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Chloroplast introns in plant systematics

Group II introns constitute the majority of noncoding sequence in many plant chloroplast genomes and include the commonly sequenced regions *trnK/matK*, the *rps16* intron, and the *rpl16* intron. As demand increases for nucleotide

characters at lower taxonomic levels, chloroplast introns may come to provide the bulk of plastome sequence data for assessment of evolutionary relationships in intrageneric, intergeneric, and interfamilial studies. Group II introns have many attractive properties for the molecular systematist: they are usually confined to organellar genomes in eukaryotes and the majority are single-copy; they all share a well-defined and empirically tested secondary and tertiary structure; and, they are easily amplified due to highly conserved sequence in flanking exons. Functional importance of structural conformations may be the key to understanding intron sequence evolution and enhancing their phylogenetic utility. A disparity of mutation rates among structural features of a group II intron can be exploited to recover phylogenetic signal at multiple taxonomic levels within a single intron, even between subclasses of flowering plants. Structure-linked mutational phenomena have important implications for the treatment of intron sequence data when aligning nucleotides, assessing mutational biases in the data, and selecting appropriate models of character evolution for phylogenetic analysis. A description of group II intron function and structure will be followed by a discussion of simple strategies to accommodate observed mutational biases and enhance the accuracy of phylogenies derived from intron sequence data.

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Molecular phylogenetics of the Liabeae (Asteraceae-Cichorioideae) based on ITS and ndhF sequences

Liabeae is a well-defined neotropical tribe containing approximately 15 genera and 180 species, and occupying a wide variety of habitats throughout Mexico, Central America, the West Indies, and Western South America. Despite several comprehensive studies using the morphological characters, fundamental disagreements among the morphological studies persist regarding the precise inter-generic relationships. Phylogenetic analyses of the ITS sequence data show a high level of variation with a strong support for the inter-generic relationship of the Liabeae. However the *ndhF* phylogeny is more or less incongruent with ITS phylogeny. Nevertheless, there are several important agreements regarding the recognition of the major clades: the subtribe Paranepheleinae, the clade *Munnozia/Chrysactinium*, the clade *Erato/Philoglossa*, the paraphyly of the *Munnozia*, and the new placement of the two *Munnozia* species outside the core *Munnozia*. In addition, the ITS tree implies that the genera restricted in narrow area and centered relatively in Southern South America are possibly primitive lineages in the tribe Liabeae.

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Phylogenetic relationships of Mutisieae (Asteraceae) from the Guayana Highland

The Guayana Highland has generated considerable interest among plant biologists because of their unique flora, high levels of endemism, and biogeographic isolation. The 10 genera of the tribe Mutisieae in this region are divided into two groups, one with actinomorphic florets occurring in Eastern Guayana Highland and the other with the bilabiate florets in Western Guayana Highland. The former is placed in the subtribe

Gochnatiinae and the latter in the Mutisiinae. Despite their floral dimorphism and biogeographic distinctiveness, the Guayana Highland genera have been considered to be monophyletic by previous workers. Furthermore, this regional assemblage is considered to be a basal lineage in the subfamily Cichorioideae and the Mutisieae. We examined four genera of the Mutisieae from Guayana Highland using sequences of the chloroplast encoded *ndhF* gene. Phylogenetic analyses including previously published *ndhF* sequence from the Mutisieae and other lineages of Asteraceae suggested that the Mutisieae of the Guayana Highland are not monophyletic. This phylogeny also provides a framework for reevaluation generic relationships within the Mutisieae, phylogeography of the Asteraceae, and character evolution in the family.

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Phylogeny and evolution of the Magnoliaceae implied by sequences of 10 chloroplast DNA regions

Phylogenetic analyses of 10 chloroplast DNA regions including *ndhF*, *rbcl*, *matK*, ORF350, *trnL* intron, *trnL-trnF*, *trnH-psbA*, *rbcl-atpB*, *trnK* 5' intron, and *trnK* 3' intron from 48 selected taxa were carried out to address phylogenetic questions in the family Magnoliaceae. Eleven major clades were recognized with strong support in the subfamily Magnolioideae: (1) *Michelia-Elmerrillia*-sect. *Maingola*-sect. *Alcimandra*-sect. *Aromadendron*, (2) subgenus *Yulania*, (3) *Pachylarnax*-sect. *Manglietiastrum*-sect. *Gynopodium*, (4) *Kmeria*, (5) sect. *Theorhodon* sensu stricto (excluding sect. *Splendentes* which was recently separated from sect. *Theorhodon*)-sect. *Magnolia*, (6) sect. *Gwillimia*-sect. *Lirianthe*-sect. *Blumiana*, (7) sect. *Talauma*-sect. *Splendentes*, (8) *Manglietia*, (9) sect. *Rytidospermum* sensu stricto (excluding *Magnolia fraseri*, *M. macrophylla*, and *M. dealbata*)-sect. *Oyama*, (10) *M. fraseri*, and (11) *M. macrophylla*-*M. dealbata*. Groupings were basically identical to those recognized in the previous *ndhF* study. However, the support for each clade was significantly increased in the extended data matrix based on 10 cpDNA regions. The time of divergence for major lineages was estimated, and the maximum rate of nucleotides substitution for overall 10 cpDNA regions was calculated to be 3.28×10^{-10} nucleotide substitutions per site per year. The molecular data strongly suggest that a taxonomic realignment of infra-familial delimitations and compositions should be considered.

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*The phylogeny and biogeography of the Lobeliaceae based on the chloroplast genes *atpB* and *rbcl* and their intergenic spacer sequence*

The emerging phylogenetic estimate for the Lobeliaceae based on chloroplast DNA sequence variation shows strong phylogenetic and biogeographic patterns. *Lobelia* is the 'core genus' of the family, from which the remaining genera in the family have evolved. Twenty of the 30 segregate genera have been surveyed to-date. In most cases, these segregate genera are closely related to *Lobelia* species from the same geographic area in which the segregate genus occurs. These strong biogeographic affinities are also observed within *Lobelia*, with a few notable exceptions. The Lobeliaceae originated in southern Africa, and relatively few long-distance dispersal events are needed to account for their

almost cosmopolitan, contemporary distribution. However, part of the taxonomic diversity in Australasia is due to repeated introductions, and the pantropical distribution of the giant lobelias is due to successive dispersal events.

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Phylogenetic relationships within the blueberry tribe (Vaccinieae, Ericaceae) based on matK and nrITS sequence data

The blueberry tribe is a large and morphologically diverse group that is widespread in the temperate and tropical zones of most continents. It is morphologically distinct from remaining members of Ericaceae s.l. in its possession of an inferior ovary. Among the approximately 40 genera described within Vaccinieae, *Vaccinium* is the largest and most widespread, occurring in both the Old and New World temperate and tropical latitudes. In the Neotropics 30–35 genera are recognized compared to only four or five recognized genera in the Old World tropics. This study sampled 93 species of Vaccinieae, representing 30 genera, and 17 sections (of the approximately 33 currently recognized) of *Vaccinium*. For each species, sequence data from the chloroplast *matK* gene and the nrITS were obtained. Each data set was analyzed separately and then as a combined matrix. Strict consensus trees generated from the individual data analyses did not indicate any strongly supported conflicting relationships. In the strict consensus of the combined analysis seven clades (most weakly supported) form a polytomy at the base of the tree. However, several well supported (bootstrap) clades (provisionally named for discussion purposes only) were found. These include: an Andean clade composed of representatives of 19 of the 23 Neotropical genera sampled (excluding *Vaccinium*), a Meso-American/Caribbean clade, a Malasian clade including the Old World taxa *Paphia* and *Dimorphanthera*, an *Agapetes* clade comprised of some Asian *Vaccinium* and *Agapetes*, and a *Bracteata-Oriante* clade (*Vaccinium* spp.). These results indicate that *Vaccinium* is not monophyletic and suggest that *Vaccinium* represents a grade group out of which several tropical groups have evolved. This study also indicates that several other genera currently recognized in Vaccinieae are likely not monophyletic. These include the Old World genera *Dimorphanthera*, *Paphia*, and *Agapetes*, and the Neotropical genera *Diogenesia*, *Orthaea*, *Thibaudia*, *Sphyrrosperrum*, and *Disterigma*.

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Neotropical Lobelioideae (Campanulaceae): more new species, more new characters

Botanical exploration of new areas in Andean South America by various collectors continues to generate numerous specimens of *Burmeistera*, *Centropogon*, and *Siphocampylus* (Campanulaceae: Lobelioideae). Study of these materials has revealed fifteen species new to science. These novelties, for the most part, do not differ from known congeners by simple quantitative differences. Rather, they possess characters or combinations of characters that are unique or highly unusual in their respective taxa. For example, expeditions into the Cerro Golondrinas of northern Ecuador have yielded three new species of *Burmeistera*. One is the first member of the genus to bear branched (arbusculiform) trichomes; another has flowers two to three times longer than the next largest congener and appears to be the first species of the genus adapted to pollination by hawkmoths (Sphingidae). A new species of *Centropogon* from Napo, Ecuador, is the first species of

sect. *Wimmeriopsis* with arbusculiform hairs; it is also one of the few species in that group with connate calyx lobes. Another member of the genus from the Cordillera Central of Colombia is the first to combine white arbusculiform hairs and pinnately lobed leaves. Two new species of *Siphocampylus* feature umbellate inflorescences. The one from central Bolivia is the first to combine this unusual feature with verticillate leaves, while the one from Mérida, Venezuela, is the first to combine it with arbusculiform trichomes. A *Siphocampylus* from pajonal habitats in San Martín, Peru, features a unique dimorphic habit: twining horizontal primary stems with erect whip-like branches. The continued discovery of numerous species that force us to enlarge the description of the taxa to which they belong suggests that much of the biotic diversity of the Neotropics remains to be discovered.

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Utility of microsatellites in wild potatoes

Solanum section *Petota*, the potato and its wild relatives, contains over 200 wild species distributed from the southwestern United States to central Argentina and adjacent Chile. Many taxa are similar morphologically and may be conspecific. We tested the phylogenetic utility of microsatellites in *Solanum tuberosum*, the source of the microsatellite primers, and in Mexican diploid species, the most distant clade to *Solanum tuberosum* in sect. *Petota*. We used both an infinite allele model and a step-wise mutation model with many tree building methods. The infinite allele model and Neighbor Joining produced trees most closely matching species boundaries and hypotheses of relationships, but clustered taxa very poorly in the Mexican diploids. We sequenced three microsatellite fragments from three species, and compared these to sequences of *S. tuberosum*. There were many cases of divergence among priming sites that explained some cases of non-amplification. There also was much divergence of microsatellite flanking sequences, showing non-homology of fragment sizes, explaining their reduced phylogenetic utility in the Mexican diploids.

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A molecular phylogenetic reexamination of the western North American subtribes Stephanomeriinae and Microseridinae (Compositae-Lactuceae)

Phylogenetic analysis of sequences of the ITS and ETS regions of 18S-26S nuclear rDNA for all genera of Stephanomeriinae (sensu Stebbins) except *Thamnosseris* and all of Microseridinae (sensu Stebbins) reveals that both subtribes are unnatural and identifies a series of subclades, each with very strong bootstrap support (greater than 96%). Subclade 1: *Munzothamnus*, *Pleiacanthus*, *Rafinesquia*, and *Stephanomeria*, all with $x=8$, and *Prenanthes* with $n=7$. Subclade 2: *Agoseris*, *Microseris*, *Nothocalais*, *Uropappus*, and *Stebbinsoseris*. Subclade 3: *Lygodesmia* (sensu Tomb), *Chaetadelpa*, both with $n=9$, and the annual *Shinnersoseris* with $n=6$. Subclade 4: the recently discovered monotypic *Marshalljohnstonia*, a rosette shrub from northern Mexico, and *Pinaropappus*, a genus of perennial herbs also found in Mexico. Several additional, well-supported subclades can be recognized, each including some species of *Malacothrix* (sensu lato), a genus now seen as polyphyletic with quite disparate elements. Partitioning of the two subtribes into smaller subclades

greatly simplifies the relationships among these genera. Considered as a group, the 24 genera examined represent a single, major radiation of Lactuceae mostly confined to western North America.

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A phylogenetic analysis of land plants using four genes from three genomes

Over the last several years, the phylogeny of land plants and its various associated issues have been investigated using analyses of single to multiple genes with different extent of taxon sampling, morphological data, and organellar genomic structural characters. At present, the following issues remain contentious: the first lineage of land plants, the sister lineage of vascular plants, relationships among Equisetum, Psilotaceae, euporangiata and leptosporangiata ferns, monophyly of extant gymnosperms, and the exact position of Gnetales. Here we analyze a data set of four mitochondrial (atp1 and LSU rDNA), plastid (rbcL), and nuclear (18S rDNA) genes from 150 species of land plants. We explore the effectiveness of this broad, moderately dense taxon and character sampling strategy in reconstructing the land plant phylogeny. The random outgroup rooting strategy was employed to evaluate validity of charophytes as an outgroup to land plants. We also examine substitution rates of these genes across land plants and use the sequence data to estimate divergence times of land plants as well as its various component clades.

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Systematics and taxonomy of Australian seagrasses (family Zosteraceae)

The family Zosteraceae in Australia and New Zealand currently comprises the monotypic *Heterozostera* (*H. tasmanica*) and four *Zostera* species (*Z. capricorni*, *Z. muelleri*, *Z. mucronata*, *Z. novaezealandica*) all in subgenus *Zosterella*. Species recognition in *Zostera* has always been difficult in this region due to the use of taxonomic characters that exhibit extensive intraspecific variability. Recent anatomical, developmental and molecular evidence raises further questions on generic delimitation (notably the distinctness of *Heterozostera*) and subgeneric limits. To clarify the taxonomy of Zosteraceae, we have undertaken an interspecific phylogenetic investigation that focuses on Australian species of subgenus *Zosterella*. We have examined material (including multiple accessions of many taxa) comprising all Zosteraceae genera (*Heterozostera*, *Phyllospadix*, *Zostera*), 6/7 species of *Zostera* subgenus *Zosterella* (including all Australian/New Zealand species), and one of four species of *Zostera* subgenus *Zostera*. Analyses of morphological characters and DNA sequences from nuclear (ITS) and plastid (*trnK*) genomes were used to construct phylogenetic trees of the Zosteraceae, from which taxonomic relationships might better be ascertained. Our results conclusively show 1) the nesting of "*Heterozostera*" within the genus *Zostera*; 2) the lack of molecular divergence among Australian/New Zealand *Zostera* collections formerly segregated as four distinct species; and 3) the lack of reliable morphological characters to separate these four species. We recommend the abandonment of the genus *Heterozostera* (while reinstating *Zostera tasmanica*), and the taxonomic merger of

remaining Australian/New Zealand *Zostera* within a single species *Z. capricorni* which has priority of publication.

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The utility of floral and vegetative fragrance for phylogenetic inference in three genera of Nyctaginaceae

The use of chemical information in phylogenetic studies is an under-used resource for studying evolutionary relationships. The absence of chemical data in phylogenetic inference is likely due in part to difficulties associated with coding chemical data as characters. Using floral and vegetative fragrance data from twenty species in three southwestern genera of Nyctaginaceae, we have explored several methods for handling fragrance data. Chemical data collected from several individuals within species were summarized to yield a single value per species and optimized onto a phylogeny inferred independently using molecular sequence data. Fragrance data were also coded in a variety of ways including (a) presence/absence of each compound, (b) presence/absence characters according to the biosynthetic pathway by which each compound was synthesized, and (c) multistate characters coded according to amount of floral compounds from each biosynthetic pathway. Phylogenies were inferred using these data sets, and the resultant topologies were compared to the molecular phylogeny. In addition to using fragrance data in phylogeny reconstruction, we also experimented with optimizing these fragrance data sets onto the molecular phylogeny. It appears that there is no one clear approach to handling fragrance data that retains the most phylogenetic information. Rather, the "best" coding method may differ among characters; treating biosynthetic pathways as characters may sometimes be most phylogenetically informative, whereas for other fragrance components coding specific compounds as characters might be most appropriate. Further, despite much homoplasy, results suggest that fragrance data do contain phylogenetic information.

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Genomic in situ hybridization: a useful tool for understanding genome evolution of Oryza (Poaceae)

Molecular cytogenetics opens an avenue to address old questions of biosystematics and new questions of genome evolution. Genomic in situ hybridization (GISH) was used to examine origins and evolution of the allotetraploid genomes, BBCC and CCDD, of *Oryza* (Poaceae). The results indicated that species of the BBCC genome contained two clearly distinguishable diploid genomes of BB and CC. The CCDD genome, which had a more ancient origin than the BBCC genome, has undergone extensively DNA exchange between chromosomes of the two diploid genomes. The dispersed hybridization signals consequently prevented the detection of the allotetraploid origin of the CCDD genome using GISH. The strength of GISH signals between various diploid genomes of *Oryza* was often inconsistent with phylogeny or sequence divergence of single-copy nuclear genes. This raises an important question concerning genomic and evolutionary interpretation of GISH results.

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Microsporogenesis observation and karyotype analysis of some species in genus Juglans L.

The PMC (pollen mother cell) meiosis process and pollen morphology of 4 species were observed and the pollen living activity of 2 species was measured. It was discovered that the PMC meiosis process of *J. regia*, *J. mandshurica* and *J. nigra* were basically normal, but that of *J. hopeiensis* was very irregular. The karyotypes of 7 species were analysed. According to the karyotype and pollen characters, 7 species tested were divided into 3 sections, and they are sect *Jglans*, sect *Cardiocaryon* and sect *Rhysocaryon*. The evolutionary relationships among the sections and the species in one section were approached. The authors pointed out that *J. hopeiensis* should be regarded as an independence species and the Juglandaceae was probably derived from two different plants with $x=8$ in phylogeny, and supported the view that China should be one of the original places of *J. regia*.

494 LINDQVIST, CHARLOTTE* AND VICTOR A. ALBERT

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A high elevation ancestry for the Usambara Mountains and lowland populations of African violets (Saintpaulia, Gesneriaceae)

As a follow-up to previous research, we present a cladistic analysis of 5S nuclear ribosomal DNA non-transcribed spacer (5S-NTS) sequences representing 55 *Saintpaulia* accessions and one *Streptocarpus* outgroup taxon. All formally described and potential *Saintpaulia* taxa are included except for *S. 'mafiensis'* and the possibly extinct *S. inconspicua*. Most notably, *Saintpaulia shumensis*, the highest elevation species in the Usambara Mountains, is resolved, albeit with marginal parsimony jackknife support, as the sister taxon to all remaining members of the Usambaras/lowland clade, which is otherwise poorly structured. It is hypothesized that *Saintpaulia shumensis* may show a relictual distribution in the Usambaras, as there appears to be a phylogenetic trend from higher to lower elevation among the major clades of *Saintpaulia*. Further issues discussed include the implications of intra-individual nucleotide polymorphism and the narrow genetic basis for drastic differences in trichome morphology, a cardinal characteristic for *Saintpaulia* taxonomy.

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The Hawaiian endemic mints are derived within North American Stachys (Lamiaceae)

The three Hawaiian endemic mint genera, *Haplostachys*, *Phyllostegia*, and *Stenogyne* (Lamiaceae), had been thought to be closely related to East Asian members of tribe Prasieae because of the fleshy nutlets borne by the latter two genera. Phylogenetic analyses of chloroplast *rbcl* and 5S nuclear ribosomal non-transcribed spacer (5S-NTS) sequences supported the monophyly of the Hawaiian mints and indicated that a North American *Stachys* species was a closer relative. We present further refinement of this hypothesis based on a phylogenetic survey of North American *Stachys* 5S-NTS sequences. As previously found, the Hawaiian clade consists of *Haplostachys* sister to *Phyllostegia* plus *Stenogyne*, which are unresolved with respect to each other. However, the Hawaiian taxa, which are characterized by chromo-

some number $2n=64$ or 66 , are deeply nested inside North American *Stachys*, their closest relative being *Stachys rigida*, a strictly western North American species with $2n=66$. *Stachys rigida* plus the Hawaiian mints are related to a larger clade of *Stachys* species, some of which are found mainly in the southeastern part of the United States and have $2n=34$ and/or 68 , whereas others are endemics of western North America with $2n=66$. In turn, this larger group is sister to two clades representing taxa from Texas through Mesoamerica, one of which has chromosome number $2n=32$, the other $2n=80-84$. The relationships between North American and Eurasian *Stachys* taxa are still unclear but preliminary *rbcl* data suggest that they may represent separate lineages. The chromosome number $2n=66$ recorded for *Stachys rigida*, other western *Stachys*, and some Hawaiian mints has previously been explained by centric fusion from $2n=68$, but could instead be indicative of allopolyploidy between $n=32$ and $n=34$, which in turn could help explain the radiative evolution of morphological features in the Hawaiian endemic mints.

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Sex expression, compatibility and crossing relationships in the Vittadinia group (Asteraceae)

The *Vittadinia* group is comprised of 11 genera in the *Astereae* tribe. Most members of the *Vittadinia* group occur on the continent of Australia and several of the larger genera extend their distribution across the Pacific to Hawaii and the Cook Islands. Recent studies of the phylogenetic relationships of the genera have revealed marked homoplasy in molecular data and in morphological features, particularly those associated with the breeding system. Past inter-generic hybridization events could explain, in part, the considerable degree of homoplasy observed. Here we report results of greenhouse studies on variation in sex expression, self-incompatibility and infrageneric/intergeneric cross-compatibility, in five of the largest genera: *Vittadinia*, *Tetramolopium*, *Minuria*, *Camptacra*, and *Peripleura*. *Minuria*, *Camptacra*, and one section of *Tetramolopium* are monoecious while *Vittadinia*, *Peripleura*, and the remaining two sections of *Tetramolopium* are gynomonocious. Self-incompatibility is strongly correlated with monoecy. Phylogenetic analysis indicates that monoecy has been gained and lost more than once, and hence so has self-incompatibility. Crossing studies readily obtained interspecific hybrids in all five genera with high pollen fertility in most cases. Intergeneric hybrids resulted among a majority of the attempted combinations. Intergeneric hybrids were obtained between Hawaiian and Australian taxa and possessed surprisingly high pollen fertilities. Therefore, ancient intergeneric hybridization may well have had a role in generating diversity in this group.

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Genetic diversity on the endemic Penstemon caryi Pennel. using ISSR Markers

Penstemon caryi (Scrophulariaceae) is an endemic of the Big Horn Mountains of Wyoming and the Pryor Mountains of Montana. The species is ecologically restricted to exposed limestone outcrops that occur infrequently throughout the region. Twenty-five individuals from fifteen populations of *P. caryi* were collected across the entire range of this species. Ten of these popula-

tions were collected for The Nature Conservancy's Tensleep Preserve, which occurs at the southern extent of the species range. The remaining five populations were collected from the remaining range of the species at intervals of fifteen to twenty-five miles. Five inter-simple sequence repeat (ISSR) markers were used to evaluate the genetic diversity of this species using Analysis of Molecular Variance (AMOVA). The relationship between genetic distance and geographic distance has also been investigated. Results from these analyses, in conjunction with a larger ecological study, will be used to determine conservation strategies for this species on Nature Conservancy lands.

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Molecular phylogeny of North American Asclepias (Asclepiadaceae)

The diverse floral morphology in the Asclepiadaceae historically has created taxonomic confusion in the family, especially at the generic level. In 1954, Robert Woodson sank 20 North American genera into synonymy under *Asclepias*, creating nine subgenera and an additional eight series under the largest subgenus, *Asclepias*. To clarify relationships within the genus of approximately 114 species, we have phylogenetically analyzed ITS nucleotide sequences for 76 *Asclepias* species, representing all of Woodson's subgenera and series. The data set of 152 phylogenetically-informative characters supports the monophyly of *Asclepias*. A basal clade is present, composed of species from Series *Incarinatae*. All remaining species occur in its sister clade, which has little resolution within it. Thus, it appears that there are two major lineages within *Asclepias*, one defined by erect pedicels and cup-shaped stipitate hoods (e.g., Series *Incarinatae*), while the other clade contains species with reflexed pedicels (with few exceptions) and more variable hood morphology.

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Nucleotide and amino acid sequence evolution of tasselseed2 in Poaceae and implications for estimated secondary protein structure

Unisexual flowers have evolved multiple times within Poaceae in such diverse lineages as Bambusoideae, Ehrhartoideae, Pooideae, Danthonieae, Chloridoideae and Panicoideae. The conversion from a bisexual to unisexual floral meristem in *Zea mays* is correlated with programmed cell death and the expression of *tasselseed2* (*ts2*). Based on developmental studies, *ts2* is hypothesized to act in a similar manner in other panicoid grasses. Little is known about the genetic basis of unisexual flowers in other grass lineages, although developmental studies in *Zizania aquatica* suggest that either *ts2* is not involved in the production of male flowers or is regulated differently. We have designed primers to amplify a 550 bp fragment at the 3' end of the *ts2* gene for a phylogenetically diverse array of grasses. Preliminary results suggest that *ts2* sequence is largely conserved within Panicoideae (nucleotide divergence 3.1-6.1%, amino acid divergence 1.7-6.5%) and Bambusoideae (nucleotide divergence 6.2%, amino acid divergence 4.7%), but less so within Ehrhartoideae (nucleotide divergence 17.1% amino acid divergence 16.5%), largely due to the *Zizania* sequence. Nucleotide sequence diver-

gence between *Oryza* and Bambusoideae (7.8-9.5%) and Panicoideae (7.8-9.5%) taxa, is less than the estimated divergence between *Oryza* and *Zizania*. A hot spot of sequence evolution in all sampled taxa occurs between amino acids 255 and 270 of the *Zea mays ts2* protein. *Zizania* has a large deletion within this area that maps to a helix in the estimated secondary protein structure. Other aspects of how amino acid sequence evolution affects estimated secondary protein structure will be discussed within the context of the GWPG phylogeny.

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Fusoid cells in bamboos and basal grasses (Poaceae): source of enhanced enlightenment?

Fusoid cells are large, gas-filled, thin-walled mesophyll cells of previously unknown function that occur within the basal grasses and bamboos. Study of sun-shade leaf variation in three woody bamboo species revealed not only the expected general suite of adaptations (thicker, smaller sun leaves with closer vein spacing, and thinner, larger shade leaves with wider vein spacing), but also that at least in some species fusoid cells develop normally in shade leaves but do not develop in sun leaves. Presence of fusoid cells is associated with broad leafed, forest-dwelling grasses, but sun-shade differences in the development of fusoid cells were noted even within an individual plant, indicating an environmental as well as a genetic component to their development. This strong correlation between shade and the development of fusoid cells suggests a possible role of fusoid cells in light distribution within shade leaves. Our data showed that leaves with normal gas-filled fusoid cells absorbed more light than those infused with mineral oil, supporting the novel proposal that one function of fusoid cells is to increase light absorption through the mechanism of intracellular reflectance. Further investigation should be addressed to quantifying the enhanced light absorption in leaves containing fusoid cells and to assessing the taxonomic distribution of facultatively occurring fusoid cells.

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Implications of a two-intron cpDNA phylogeny of Primula (Primulaceae) for the group's taxonomy and evolutionary history

In this, the first molecular study to sample within the genus *Primula* at such a large scale, the *rpl16* and *trnL* introns (cpDNA) have been sequenced from 95 of the ca. 450 species, covering 30 of the 37 sections and 5 of the 6 subgenera. Among the 24 additional accessions are representatives of all genera that are likely to be embedded in the primula clade, as well as outgroups from the Maesaceae, Theophrastaceae, and Myrsinaceae. In the strict consensus of the most parsimonious trees, the primula clade is sister to a clade of several genera once thought to be nested in it, including *Omphalogramma*, *Soldanella*, and *Hottonia*. A trichotomy is formed at the base of the primula clade by subgenus *Auganthus* (plus *P. dryadifolia*, an enigmatic member of subgenus *Aleuritia*), subgenus *Auriculastrum*, and the remaining subgenera. In this last clade are the following well-supported relation-

ships: (i) a clade containing some of the subgenus *Aleuritia* is sister to subgenus *Sphondylia* (and *Dionysia*, see below), (ii) the clade of i is sister to subgenus *Primula*, and (iii) the clade formed by i and ii is sister to a clade containing the remainder of subgenus *Aleuritia* (plus the unplaced section *Davidii*). Four genera are embedded in the primula clade: (i) the Eurasiatic genus *Cortusa* in subgenus *Auganthus*, (ii) the North American genus *Dodecatheon* in subgenus *Auriculastrum*, (iii) the west Asian genus *Sredinskya* in subgenus *Primula*, and (iv) the Middle Eastern genus *Dionysia* as the sister of subgenus *Sphondylia*. Homostyly is resolved as a derived condition in two sections (*Sphondylia* and *Proliferae*) currently thought to have inherited the primitive homostylous condition of the primula clade. The evolution of characters that have played a significant taxonomic role, including chromosome base number, leaf venation, and pollen type, will also be discussed in light of the phylogeny.

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Anisophylleaceae and Cunoniaceae: why are their flowers so similar?

Flowers of Anisophylleaceae and Cunoniaceae are remarkably similar. Their current phylogenetic position based on molecular studies places them in eurosids I, but in different orders, Cucurbitales and Oxalidales, respectively (APG, 1998). We studied flowers from selected genera of both families and compared them at a morphological, anatomical and histological level, with some surprising results. This study, combined with a review of previous work on these families, has revealed many shared features including the occurrence of trimerous flowers (in addition to tetra- and pentamerous flowers), digitate petals, isomery in all floral whorls, obdiplostemony, incurved filaments in bud and similar anthers, similar pollen, similar nectaries, carpels with free styles, and similar ovules with a slit-like micropyle. A timely coincidence was the recovery of well preserved fossil flowers from the Late Cretaceous of Sweden by JS and EMF that share many features with both Anisophylleaceae and Cunoniaceae (but have been placed in Cunoniaceae based on some specific traits of the gynoecium). Combined, these results suggest either that Anisophylleaceae and Cunoniaceae are more closely related than previously assumed, or if not, that they exhibit either an unusual number of symplesiomorphic features of basal rosids, or that their floral features are the result of a striking convergent evolution. In either case, it is apparent that more extensive molecular studies are needed, and if these studies confirm the current disparate position of the families, an investigation of the significance of the suite of common structural features should be made.

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Delimitation and subdivision of "Justicioids" (Acanthaceae, Justicieae)

Within the diverse (>2,000 species) and morphologically disparate lineage Justicieae, "justicioids" (i.e., members of *Justicia* and related genera in both the New and Old

Worlds) are monophyletic. These plants share a number of morphological traits (e.g., regulate corollas) such that this result is not unexpected. Our earlier results, however, unexpectedly show that the highly apomorphic Diclipterinae are also part of this group. As traditionally defined, Diclipterinae lack the morphological traits that link "justicioids" and thus have not previously been associated with them. Further, Diclipterinae are sister to New World "justicioids," and this last group is monophyletic. Old World "justicioids" are apparently not monophyletic; most are placed as a series of lineages basal to New World "justicioids" + Diclipterinae; but others are more closely related to Diclipterinae than to other "justicioids." We here test these hypotheses of relationships using substantially expanded taxon sampling and the addition of sequences from the chloroplast trnT-trnL spacer. Specifically, we test (1) the hypothesis that New World "justicioids" are monophyletic by adding representatives of all infrageneric taxa of *Justicia* and (2) the idea that OW "justicioids" are not monophyletic, again by substantially increasing our sample of infrageneric taxa of *Justicia* and related genera. This last permits us to identify the "justicioids" that are most closely related to Diclipterinae and to explore the morphological and cytological evidence for this relationship. Finally, we identify monophyletic sublineages of "justicioids," with an emphasis on Old World plants.

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Inference of Asparagales phylogeny using a large chloroplast data set

The order Asparagales (*sensu* APG 1998) is pivotal to our current understanding of monocot taxonomy and phylogeny. Recent morphological and molecular analyses have provided major new insights into its circumscription and internal phylogenetic structure, but various aspects of its evolutionary history remain elusive or poorly supported. To address further the higher-order relationships within Asparagales, we examined chloroplast sequence data from 15 families chosen to exemplify the phylogenetic diversity of the order (Agavaceae, Alliaceae, Amaryllidaceae, Anthericaceae, Aphyllanthaceae, Asparagaceae, Asphodelaceae, Boryaceae, Convallariaceae, Hyacinthaceae, Iridaceae, Laxmanniaceae, Orchidaceae, Phormiaceae and Tecophilaeaceae). Eight disjunct locations in the chloroplast genome were sequenced (spanning 17 chloroplast genes, three introns and three slowly evolving intergenic spacer regions), providing a total of 15 kb (unaligned) of DNA sequence data per taxon. Outgroup taxa included representatives from the other major monocot lineages. A parsimony-based phylogeny inferred from these data was largely congruent with previous studies, within the limits of current taxon sampling. Bootstrap analysis (performed under the Fitch parsimony criterion) provided moderate to strong support for most of the tree. The order's monophyly was strongly upheld, as was its division into a lower Asparagales grade and a higher Asparagales clade, as indicated by Chase et al. (1995) and Rudall et al. (1997). The family Hyacinthaceae was indicated as the sister taxon of the distinctive monotypic family Aphyllanthaceae. Alliaceae and Amaryllidaceae were supported as sister taxa. Boryaceae and Orchidaceae were weakly supported as sister taxa; Boryaceae-Orchidaceae was the sister-group of the remaining Asparagales. In addition to addressing relationships within the order, we briefly discuss the identity of the sister-group of the Asparagales. We also discuss the molecular evolution of the regions examined, providing evidence of intron loss and gene deactivation in Asphodelaceae and Orchidaceae, respectively.

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Austral biogeography: the evolution of subalpine Ourisia (Veronicaceae/Scrophulariaceae s.l.) in a phylogenetic context

The austral biogeographic pattern refers to the presence of congeneric organisms in South America, Australasia and/or Africa and is generally considered to be a classic vicariant scenario associated with the breakup of Gondwana. Results from phylogenetic studies and fossil record evidence of *Nothofagus* and *Araucaria*, both woody forest genera, are congruent with this hypothesis. However, the same history may not apply to all genera in austral areas. It has been hypothesized that higher elevation herbaceous taxa may be of more recent origin, suggesting that long-distance dispersal may have played a role in their historical biogeography. An extensive phylogenetic study of austral, subalpine *Ourisia* (Veronicaceae/Scrophulariaceae s.l.) based on molecular and morphological data is currently underway to investigate the biogeography and evolution within the genus. The approximately 30 species of *Ourisia* are distributed equally between the South American Andes (Venezuela to Tierra del Fuego) and the New Zealand Southern Alps. One species is also endemic to high-elevation habitats in Tasmania, Australia. Historically, *Ourisia* has been divided into two subgenera (each with a bihemispheric distribution) based on calyx symmetry and corolla tube curvature. Our current data sets include the nuclear Internal Transcribed Spacer (ITS1, 5.8S, ITS2) and chloroplast *matK-3'trnK* sequences for 22 species and subspecific entities of *Ourisia*. The inferred phylogenies from both separate and combined data sets show that: 1) *Ourisia* is monophyletic, 2) the subgenera as currently circumscribed are not monophyletic, 3) three suffruticose Andean taxa are sister to the rest of *Ourisia*, and 4) the New Zealand taxa form a monophyletic clade embedded within the Andean *Ourisia*. These findings suggest that it is highly unlikely that a vicariant event is responsible for the current biogeography of the genus, and instead long-distance dispersal from South America to New Zealand is a more plausible explanation.

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Fruit dispersal and character evolution in the Neotropical genus Tococa (Melastomataceae)

Tococa is a genus of 45 species of shrubs, small trees and vines from Neotropical rain forests and savannas. In 39 species the fruits are dispersed by birds, as it is the case in most other species in the family. However, a monophyletic group of six species, restricted to river banks and flooded forests of the Amazonas and Orinoco basins, have fruits that are dispersed by either water or fish (ichthyochory). Water/fish-dispersed fruits present several morphological characteristics that differentiate them from bird dispersed fruits. Bird-dispersed taxa have smaller, round, black fruits that do not fall off the plant when mature, while water/fish-dispersed taxa have large, blue fruits that fall off when mature. The seeds of water/fish-dispersed taxa are club shaped and larger than those of bird dispersed species, which are ovoid to round or pyramidal. Additionally, the seeds of water/fish-dispersed species are covered with glandular trichomes, which are absent from bird-dispersed taxa. Moreover, glandular trichomes are not known from any other Melastomataceae, including taxa that have been shown to be ichthyochorous. There are also differences in the phenology of bird dispersed and water/fish dispersed taxa. Even though ichthyochory has not been demonstrated to be the main mode of fruit dispersal for any of these six species of *Tococa*, many

of the characters that differentiate them from ornithochorous species could be easily interpreted as adaptations to fish dispersal and not water dispersal.

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Towards an understanding of the Mulga complex (Acacia aneura): polyploidy, hybridization and apomixis create dynamic population structures

Acacia aneura, also known as mulga, is the core species of the mulga complex, a widespread group that is dominant in much of arid Australia. *Acacia aneura* and the 10-15 other species that comprise the complex are taxonomically difficult, due to the morphological variability that occurs within populations, over its entire range and within *A. aneura* itself. These species vary in phyllode, fruit and seed characters, as well as flowering time and growth habit. It is not unusual to find five or six obviously different forms, with or without intermediates, growing side by side in a population. This complexity has made taxonomic treatments of the group difficult. This study utilizes morphology, cytogenetics and microsatellites on material collected throughout the range of mulga. Results indicate the morphological variation is being caused by periodic hybridization among morphotypes buffered by the effects of polyploidy and is being maintained by apomictic seed production. From field work it appears that the retention of juvenile characters, such as plant architecture and phyllode morphology is also complicating our understanding of the complex. These new data have given an insight into the population structure and overall variation within mulga. In addition these results shed light into the on evolutionary mechanism affecting the Australian arid-zone flora.

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The biogeography of South American Jaltomata (Solanaceae)

The forty or so South American species of the genus *Jaltomata* are morphologically and ecologically diverse and widely distributed in the Andes from Venezuela to Bolivia. Both herbs and shrubs are represented; corollas are rotate, campanulate or tubular, or even urceolate with a revolute limb. In South America the genus has a broad altitudinal distribution, from sea-level to over 4,000 m. Five species grow in widely separated fog-dependent islands of vegetation (*lomas* formations) in the otherwise hyper-arid coastal desert of Peru. *Lomas* species do not constitute a monophyletic group, suggesting repeated colonization events to *lomas* formations from the Andes. Four of the *lomas* species are endemic while one *lomas* species (*J. aspera* (R. & P.) Mione) also grows in the Andes. Two of the *lomas* species (*J. umbellata* (R. & P.) Mione & M. Nee, and *J. aspera*) have copious red/orange nectar, as do 8 exclusively Andean species. Although red/orange nectar occurs only in certain *Jaltomata* species of Peru and northern Bolivia, its presence is not correlated with habitat, nor altitude nor with a particular corolla form. A decade ago only three species of *Jaltomata* were known from northern Peru. Now, we know of 29 species of this genus in this region, 23 of which S. L. G. and T. M. collected during recent field work. The increase in taxa is attributable to the discovery of entirely new distinct and defensible biological entities, not to the division of previously named species.

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Phylogenetic relationships in Haloragaceae emphasizing the aquatic genus Myriophyllum

Phylogenetic analyses using parsimony and maximum likelihood methods were conducted with data from the plastid genome (*rbcl*, *matK* and *trnK* introns) to assess relationships among Haloragaceae genera and among species in the aquatic genus *Myriophyllum*. The Haloragaceae consist of 8 genera, three of them aquatic (*Proserpinaca*, *Laurembergia*, and *Myriophyllum*). *Myriophyllum* (55 species) is the largest genus in the family and has its greatest species diversity centered in Australia. Relationships among many aquatic plants have been notoriously difficult to assess due to their convergent and highly plastic vegetative morphology and reduced flower size. All of these factors have made it difficult to determine species limits and relationships among *Myriophyllum* or to assess its relationship to other genera in the family. *Rbcl*, *matK* and the *trnK* introns have been very informative in delimiting relationships among Haloragaceae genera and among species of *Myriophyllum*. Results indicate an Australian origin for the family with possible multiple origins of the aquatic habit. Results also suggest a monophyletic *Myriophyllum* consisting of two well supported clades. A clade of North American endemics (Schindler's Subgenus *Tessaronia*) is well supported and has its closest sister taxa in Australia.

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GRAPPA: a high-performance computational tool for phylogeny reconstruction from gene-order data

With the rapid accumulation of whole genome sequences for a wide diversity of taxa, phylogenetic reconstruction based on changes in gene order and gene content is showing promise, particularly for resolving deep branches. However, reconstruction from gene order data is even more computationally intensive than reconstruction from sequence data, particularly in groups with large numbers of genes and highly rearranged genomes. We have developed a software suite, GRAPPA, that extends the breakpoint analysis (BPanalysis) method of Sankoff and Blanchette while running much faster: in a recent analysis of the Campanulaceae dataset (reported by Robert Jansen) on a 512-processor supercluster, we achieved a one-million-fold speedup over BPanalysis. GRAPPA currently can use either breakpoint or inversion distance (computed exactly) for its computation, runs on single-processor machines as well as parallel ones, and has been ported to all Unix and Windows OS. Our next release will support analysis of genomes with repeats (using the exemplar strategy proposed by Sankoff) and with (mildly) unequal gene content (using induced breakpoints), while also supporting refinements of promising candidate trees with TBR techniques, and incorporating the IEBP and EDE distance corrections (presented by Robert Jansen).

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Nuclear rDNA ETS sequence data and the systematics of Machaeranthera (Asteraceae)

Previous research on the systematics of *Machaeranthera* and its relatives using chloroplast DNA and ITS sequence data have left several questions unresolved. New sequence data from the external transcribed spacer of nuclear rDNA (ETS) were generated in an attempt to resolve these questions. ETS sequence data were obtained from the same taxa that were used for previous analyses with chloroplast DNA and ITS sequences. ETS evidence provides greater resolution than does ITS evidence, and greater support for monophyletic groups, permitting further resolution of the relationships of *Machaeranthera*. Phylogenetic analysis of these data supports relationships that differ substantially from those supported by chloroplast DNA for several species and groups of species. These taxa include *Machaeranthera gypsitherma*, *M. viscida*, *M. heterophylla*, the *Machaeranthera* section *Arida*, and the genus *Pyrrocoma*. The relationships that the molecular data support for these taxa suggest that their chloroplast DNA and their nuclear rDNA have come from separate lineages, and that they may have experienced reticulate evolution in their phylogenetic history.

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Phylogenetic relationships of Aurantioideae (Rutaceae): a cladistic analysis using the Nuclear Internal Transcribed Spacer region

The subfamily Aurantioideae is one of seven subfamilies of the Rutaceae (Engler 1931). It is comprised of 33 genera divided into two tribes, the Clauseneae, containing five genera and the Citreae, containing 28 genera. Each of these two tribes are divided into three subtribes (Swingle 1943). Of the 33 genera belonging to Aurantioideae, 29 are native to the Monsoon region extending from west Pakistan to the western Polynesian Islands. Five genera are native to tropical Africa and only one genus, *Clausena*, is native to both the Monsoon region and tropical Africa. We analyzed cladistically ITS DNA (nuclear) sequences for 19 genera representing both tribes and most subtribes of the subfamily. The resulting tree support that the Aurantioideae are monophyletic, but indicate that the tribes and subtribes need re-circumscription. These results are in general agreement with Greger et al. unpublished data from the plastid *atp/rbcL* spacer region.

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Molecular systematics of the Chiococceae-Catesbaeeae Complex (Rubiaceae): phylogeny and biogeography

The classification of the Catesbaeeae and Chiococceae tribes, along with the entire Rubiaceae, has been intensely debated in recent years. This debate has focused on a few key morphological characters (corolla shape and aestivation, anther shape and position, fruit placentation, and number and position of ovules) and one set of molecular data (*rbcl*). Several phylogenetic analyses in the Rubiaceae based on nucleotide sequences of the *trnL-F* and

rps16 regions of the plastid genome and the nuclear ribosomal internal transcribed spacers (ITS1&2) suggest that none of the previously proposed classifications are entirely correct. Molecular data suggest that the traditionally defining flower and fruit features of the Catesbaeeae and Chiococceae are actually phylogenetically homoplastic, leaving present generic boundaries and relationships within the Catesbaeeae-Chiococceae Complex in doubt. The Catesbaeeae-Chiococceae Complex is a group that includes approximately 27 genera and 196 species primarily concentrated in the Greater Antilles (nearly 70% of the taxa) but also occurring in Malesia and the South Pacific (3 genera). Phylogenies using trnL-F and rps16 have identified one major monophyletic group. However, the ITS data provides more resolution and additional taxa have been surveyed. Presently the ITS data is not congruent with the other data sets and does not support the monophyly of the Catesbaeeae-Chiococceae Complex. Additionally, Pacific genera which have been absent in previous molecular studies have been sampled and included in the analyses in the hope to better understand the disjunct biogeographic distribution of these Caribbean and Pacific taxa. Based on ITS data some genera, i.e. *Exostema* and *Bikkia*, do not appear to be monophyletic. The Pacific taxa form two distinct clades, suggesting that there have been apparently two separate introductions of the Catesbaeeae-Chiococceae Complex into the Pacific basin.

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The evolution of carnivory in the Lamiales: evidence from matK and adjacent noncoding regions

The Lamiales comprise about 20 families with approximately 18000 species. The relationships of the carnivorous families (Lentibulariaceae, Byblidaceae) remained uncertain in previous phylogenetic analyses and so did the evolution of characters being part of the carnivorous syndrome. Also, the question of how many times carnivory evolved in the Lamiales remained unanswered. To address these issues, we sequenced the *matK* gene and the noncoding parts of the *trnK* intron (about 2700 bp) of nearly 100 species representing all major groups of the Lamiales with an emphasis on both the taxa with accepted carnivory and taxa with presumed preadaptations (e.g., Martyniaceae). In the trees obtained from parsimony analyses, the deeper nodes that show the branching order of the major groups receive low statistical support due to short branches. This is a phenomenon also found in all previous studies using other molecular datasets. However, Oleaceae are resolved as sister to all other Lamiales with high statistical support and in addition are characterized by several long insertions. The monophyly of most of the included families is well supported statistically, with the exception of the non-monophyletic former Scrophulariaceae and Pedaliaceae. The data indicate that carnivory evolved independently in Lentibulariaceae and the other carnivorous taxa. Within the Lentibulariaceae the majority of nodes gain very high statistical support. *Pinguicula* is sister to a clade comprising *Utricularia* and *Genlisea*. The sequence variability of the *matK* coding region proved to be equally high as that of the adjacent intron parts. The transition/transversion ratios in both coding and

noncoding sequences are close to 1.0. The variability of the 3rd codon position is only slightly higher than of 1st and 2nd positions. Within Lentibulariaceae *Utricularia* and *Genlisea* display a five times greater sequence variability than *Pinguicula*.

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Peppers and pipevines: phylogenetic relationships within Piperales

In most broadscale studies Piperales are recognised as one of the best supported clades within basal angiosperms. Although small in number of genera, the group displays a surprisingly high morphological diversity, so that a close phylogenetic relationship is not obviously supported. Based on a dense sampling, representing all genera of Saururaceae and Aristolochiaceae, Lactoridaceae as well as a selection of Piperaceae, we present an analysis inferred from different coding and non-coding regions of the chloroplast genome: the two spacers and the intron of the *trnT-trnF* region, the *matK* gene and adjacent regions of the *trnK* intron. The data show a sister group relationship between Saururaceae and Piperaceae, which both appear to be monophyletic. In previous studies the position of Lactoridaceae and the subfamily Asaroideae of the Aristolochiaceae was not clearly resolved. This ambiguity is considered to arise from long branches leading to either Piperaceae as well as to Asaroideae, and will be addressed in detail. Within Aristolochiaceae subfamily Aristolochioideae, a fully resolved and well supported phylogeny could be obtained. The genus *Thottea* branches first, followed by two clearly monophyletic clades: One comprises the Asian/American species that are often recognised as genus *Isotrema*, the other the rest of the family comprising of *Pararistolochia*, a group of woody lianas and geophytes of Central and South American species of *Aristolochia*, the Mexican genus *Einomeia* as well as the old world species of *Aristolochia* sensu stricto. Within Saururaceae two clades are inferred, one consisting of *Saururus* and *Gymnotheca*, the other of *Houttuynia* and *Anemopsis*.

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Diversification in the endemic Hawaiian subfam. Alsinoideae (Caryophyllaceae): evidence from nrDNA ITS, ETS sequences and morphology

The endemic Hawaiian Alsinoideae genera *Schiedea* and *Alsiniidendron* (Caryophyllaceae) comprise the fifth largest radiation of flowering plants in the Hawaiian Islands, and one of the most diverse lineages in terms of morphology, habit, breeding system and habitat preference. The Hawaiian Alsinoideae have served as a model system for studying shifts from hermaphroditism to dimorphic breeding systems (dioecy, subdioecy and gynodioecy). Because of the possibility that habitat shifts have led to the evolution of dimorphism, the Hawaiian Alsinoideae may provide information on causal mechanisms underlying the evolution of

sexual dimorphism. Despite the importance of phylogenetic approaches for understanding the relationship of habitat and breeding system evolution, recent phylogenetic analyses have failed to identify the closest relatives of the Hawaiian clade, confounding questions of monophyly, character state polarization and ancestral breeding system state reconstruction. Relationships within the Hawaiian Alsinoideae have remained unresolved, due, in part, to low genetic divergences among closely related species, and extremely rapid radiation following colonization of the Hawaiian Islands. In this study, we combine three data partitions (nr ITS and ETS sequences and morphology) for reconstructing phylogenetic relationships using maximum parsimony and maximum likelihood. Our results suggest 1) the Hawaiian Alsinoideae are strongly supported as monophyletic; 2) *Schiedea* is paraphyletic with *Alsinidendron* derived within a lineage containing *S. verticillata* from Nihoa; 3) *S. membranacea* and *S. helleri* comprise the sister clade to all other members of the lineage in Hawaii; 4) two primarily dimorphic clades identified in morphological analyses (*adaman-tis* and *globosa* clades) form a single clade in analyses based on all three data partitions, suggesting a single origin of dimorphic breeding systems in Hawaiian Alsinoideae. Analyses based on nucleotide partitions alone support two separate origins of dimorphism.

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Origin of the Hawaiian subfam. Alsinoideae and preliminary relationships in Caryophyllaceae inferred from matK and trnL C-F sequence data

Relationships within the Caryophyllaceae have never been examined explicitly using phylogenetic methods, despite the central position and well-defined nature of the family in the order Caryophyllales among the eudicots. Within Caryophyllaceae, the Hawaiian Alsinoideae are an important model system for studying the insular adaptive shift in breeding system from hermaphroditism to dimorphic breeding systems. The relationships of the Hawaiian genera of subfam. Alsinoideae *Schiedea* and *Alsinidendron* to the rest of the family and relationships within the subfam. Alsinoideae are poorly known. Previous studies suggested that the native Hawaiian Alsinoideae are strongly supported as monophyletic and the result of a single ancestral colonization to the archipelago. These studies suggested that western North American members of the genus *Minuartia* are sister to the Hawaiian clade, based on the shared presence of similar, unique, nectary projections. Additionally, the monophyly and relationships of the three main subfamilies, (Paronychoideae, Caryophylloideae and Alsinoideae) are in question. The current classification of the subfam. Alsinoideae has been based largely on potentially highly labile characters, such as type of locule dehiscence and number of styles relative to number of capsule teeth; i.e. characters which may be homoplastic. A molecular phylogenetic analysis using *matK* and *trnL C-F* sequences reveal that: (1) the closest relatives of the Hawaiian Alsinoideae are a pair of monotypic, circumboreal genera, *Honckenia* and *Wilhelmsia*, (2) the subfamilies as currently delimited are not natural groups; (3) the species-rich alsinoid genera *Arenaria* and *Minuartia* are not natural groups and will likely require nomenclatural reorganization to better reflect phylogenetic relationships.

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Phylogeny of Bupleurum (Apiaceae) based on ITS sequence data

Bupleurum L. (Apiaceae: Apioideae) is a genus of ca. 150 species with broad distribution in the N Hemisphere (except the S African *B. mundii*), but with many species that are rare or restricted to small areas. The genus is easily recognized within the family because of its simple and entire leaves, but unusually includes woody members as well as the more usual annual and perennials herbs. *Bupleurum* has for long been regarded as a natural group but its infrageneric classification has been problematic. Phylogenetic relationships of the genus were investigated using sequences of the internal transcribed spacers (ITS) of nuclear ribosomal DNA, from 32 species (35 taxa) representing all sections and subsections of the genus. Phylogenies generated by maximum parsimony, maximum likelihood, and neighbour joining methods show very similar topologies, unequivocally demonstrating monophyly of *Bupleurum* and the division of the genus into two major clades (100% bootstrap support in all analyses). The most basal clade is formed by all the species of the genus with pinnate-reticulate veined leaves, and surprisingly also includes *B. rigidum*, which itself has a unique type of leaf venation. The other major clade comprises most of the species studied, all of which have ± parallel-veined leaves. These results do not agree with any previous classifications of the genus. Relationships within the major clades are not fully resolved, and a larger sampling and further data from other gene regions is required. Nevertheless, three other strongly supported clades were identified; one of these clades correspond to a group that includes all NW African endemic species, and the low nucleotide variation in this group suggests a recent radiation. The S African *B. mundii* seems to be a neoendemic closely related to *B. falcatum*, an Eurasian species.

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Paleoherb status of Hydnoraceae supported by multigene analyses

Uttilization of molecular phylogenetic information over the past decade has resulted in clarification of the position of most angiosperm orders, as demonstrated by the classification produced by the Angiosperm Phylogeny Group. A group of 11 families was listed at the beginning of the APG classification because "they belong neither in any of the phylogenetically basal orders at the beginning nor in the monocots or eudicots." The phylogenetic positions of most of these families (e.g. Amborellaceae, Nymphaeaceae, Winteraceae, etc.) have since been clarified, however, the positions of two holoparasitic families, Hydnoraceae and Rafflesiaceae, have remained enigmatic. To address the question of phylogenetic position of Hydnoraceae, nuclear SSU and LSU rDNA and mitochondrial *atp1* and *matR* sequences were obtained for *Hydnora* and *Prosopanche*. These sequences were used in a combined analysis that included the above four genes as well as chloroplast *rbcl* and *atp* (these plastid genes are missing in Hydnoraceae and were hence coded as missing). Three data sets were analyzed

using maximum parsimony: 1) 3 genes/461 taxa; 2) 5 genes/77 taxa; and 3) 6 genes/38 taxa. All of these analyses support the monophyly of Hydnoraceae and the association of that clade with the "paleoherb" families Aristolochiaceae and Lactoridaceae. These results suggests that either Aristolochiaceae are paraphyletic or that Hydnoraceae should be included (along with Lactoridaceae) in a more broadly defined family Aristolochiaceae. In contrast to most traditional classifications, molecular phylogenetic analyses do not suggest a close relationship between Hydnoraceae and Rafflesiaceae s. lat.

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Phylogenetic relationships in tribe Neillieae (Rosaceae) inferred from DNA sequences

Tribe Neillieae, characterized within Rosaceae by stipulated simple leaves, ovoid seeds, and copious endosperm, comprises three taxonomically difficult genera, *Neillia*, *Stephanandra*, and *Physocarpus*. As part of a comprehensive systematic study of the tribe, nucleotide sequences of the ITS and 3' partial ETS regions of nrDNA, *trnL-trnF* and *trnD-trnT* regions of cpDNA, and the second intron of a floral homeotic gene, *LEAFY*, were determined to elucidate phylogenetic relationships in the tribe Neillieae. The maximum parsimony analyses of nrDNA and cpDNA data set indicate that two major clades (*Physocarpus* and *Neillia/Stephanandra*) are strongly supported in tribe Neillieae, but the relationship between *Neillia* and *Stephanandra* is inconsistent. The level of sequence divergence of the second intron of *LEAFY* is about 5-fold higher than that of nrDNA and the intron sequences are phylogenetically useful. Separate phylogenetic analyses of three data sets (nrDNA, cpDNA, and *LEAFY*) suggest that the *P. opulifolius* complex may have been originated by a hybridization between *P. monogynus* and *P. capitatus*. The results also suggest that *Stephanandra* may be of hybrid origin.

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A molecular phylogeny of the Boraginaceae/ Hydrophyllaceae

We conducted a molecular phylogenetic study of the Boraginaceae and Hydrophyllaceae using the chloroplast genes *rbcl* and *ndhF* and including 90 species previously assigned to the two families. Results indicate that most of the taxa assigned to these families together form a monophyletic group, but that neither of the two families, as traditionally circumscribed, are monophyletic. *Hydrolea* (Hydrophyllaceae) and *Pteleocarpa* (Boraginaceae) do not belong in this group and are better placed elsewhere. Two major clades are identified. The first major group includes the predominantly temperate herbaceous subfamily Boraginoideae and the genus *Codon* (Hydrophyllaceae; S. Africa). The other major monophyletic group includes clades that correspond roughly to subfamilies Cordioideae, Ehretioideae, and Heliotropoideae of Boraginaceae and tribes Nameae and Hydrophyllaeae/Phacelieae of Hydrophyllaceae. Within this second clade, the predominantly woody and tropical members of Boraginaceae (Cordioideae, Ehretioideae, and Heliotropoideae) are monophyletic and these are sister to tribe Nameae, which also contains the only woody and tropical members of Hydrophyllaceae (along with other temperate species). *Pholisma*, representing the small parasitic plant family, Lennoaceae in our study, is sister to *Tiquilia* (Ehretioideae), with which it co-occurs in the deserts of North America. The primary characteristic that dis-

tinguishes Boraginaceae from Hydrophyllaceae is the reduced number of ovules (2 per carpel). The most parsimonious interpretation of this character on our tree requires two independent reductions in ovule number, once in the ancestor of the Boraginoideae (with the characteristic nutlet fruits) and once in the ancestor of the tropical, woody clade (mostly drupes).

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Preliminary phylogenetic studies in the Menyanthaceae

The Menyanthaceae are a relatively small family of aquatic and semi-aquatic flowering herbs with a center of diversity in Australia. The five genera comprising the family are *Menyanthes*, *Fauria*, *Liparophyllum*, *Nymphoides*, and *Villarsia*, and are often cultivated as ornamentals. Evolutionary patterns within the Menyanthaceae remain unclear despite previous studies utilizing anatomy, flavonoid, seed, and pollen morphology data. Parsimony analyses of *rbcl* sequences strongly resolve two major lineages within the family. These results portray a close relationship between the monotypic *Menyanthes* and *Fauria*, both of the Northern Hemisphere. The other clade depicts a strong alliance between *Nymphoides*, *Villarsia*, and *Liparophyllum*. The positioning of the monotypic *Liparophyllum* within a clade of *Nymphoides* species implies the present recognition of this Tasmanian-New Zealand endemic at the generic level may be unwarranted.

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Molecular phylogenetic studies of members of tribes Helenieae, Heliantheae, and Eupatorieae (Asteraceae).

1. Introduction

Past molecular studies aimed at elucidating tribal relationships in the Asteraceae have revealed a Helenieae-Heliantheae-Eupatorieae (HHE) clade in a somewhat terminal position in subfamily Asteroideae. This interesting result and our interest in elucidating further relationships among these tribes have been the stimulus for the present study. We believed a comprehensive DNA sequencing effort would provide a more robust hypothesis of relationships among the genera of the HHE clade. Sequencing studies have focused on completing data matrices for 26 primers for several genes, introns and spacer regions of the chloroplast genome. The final data matrix contains 16,650 bp for 127 genera of the HHE clade. The regions of the chloroplast genome sampled include the genes *matK*, *ndhF*, *ndhD*, and *accD*; the introns of *rpl16*, *petB*, *petD*, *trnL*, and 5'*trnK-matK*, and the spacers between *rpl20-rps12*, 23S-16S, *accD-rbcL*, *trnT-trnL*, and *trnL-trnF*. Phylogenetic studies based on this data matrix reveal the polyphyletic composition of tribes Helenieae and Heliantheae as currently circumscribed, with members of tribe Eupatorieae in a highly nested position within a clade with the Peritylinae and Galeana-Villanova clade. Moderate to strong jackknife support has been obtained for most clades in the strict consensus tree.

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Molecular phylogenetic studies of members of tribes Helenieae, Heliantheae, and Eupatorieae (Asteraceae)
2. Tribal/generic relationships

Molecular phylogenetic studies of 123 genera belonging to tribes Helenieae, Heliantheae and Eupatorieae of the HHE clade reveal novel relationships for several members of these tribes. The genera *Phaneroglossa* (Senecioneae) and *Inula* (Inuleae) were chosen as outgroups. Parsimony analysis of the data matrix produced 8640 trees of 11090 steps (CI 0.5654 excluding uninformative characters, RI 0.6605). After analysis of the data matrix and the resulting phylogenetic hypothesis we conclude that the genera *Athroisma* and *Blepharisperrum* are not members of the HHE clade and should either be recognized as a separate tribe or reincorporated into the Inuleae, as they share numerous synapomorphies with the outgroup. The basalmost lineage of the HHE clade contains the genera *Psathyrotes*, *Marshallia*, *Helenium*, *Hymenoxys*, and *Psilostrophe*. These genera, along with a few others classified by previous authors in either subtribes *Marshalliinae* or *Gaillardiiinae*, are here included in a narrowed interpretation of tribe Helenieae. *Dahlia* and *Coreopsis* are sister and constitute the next sublineage to diverge. Their basally divergent position is somewhat surprising although morphologically they are a very distinct group that we recognize as tribe *Coreopsideae*. In some of the most parsimonious trees we observed that a majority of the epaleate genera centered about *Bahia*, *Chaenactis*, and *Hymenopappus* and previously classified in tribe Helenieae s. l., the traditional helianthoid taxa *Polymnia*, *Enydra*, and subtribe *Neurolaeninae* are grouped in a clade sister to a large clade containing most members of tribe Heliantheae, Eupatorieae and the tarweeds and relatives. In the strict consensus tree this intriguing clade collapses leaving a polychotomy with the genera *Varilla* and *Jaumea* as single lineages, *Enydra* sister to *Neurolaeninae*, the epaleate helenioid genera grouped in a clade with moderate support, and *Polymnia* sister to *Oxyappus*.

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Molecular phylogenetic studies of members of tribes Helenieae, Heliantheae, and Eupatorieae (Asteraceae)
3. General systematics and proposed taxonomic changes in current classification

Most genera of the HHE clade are grouped in two major sister clades. One of the two clades contains the core Heliantheae genera and in turn has two major clades. Each of the two core Heliantheae clades has as its basalmost lineage a white ligulate genus. The monotypic genus *Rojasianthe* and *Montanoa* share white ligules, acresent pales after anthesis, and a chromosome number of $x = 19$. *Rojasianthe* is basal to the lineage

containing the *Verbesiniinae* s. str., the *Engelmanniinae* sister to the *Rudbeckiinae*, and this sister to a terminal clade containing selected members of the *Ambrosiinae*, *Helianthinae*, *Zaluzaniinae*, *Zinniinae*, the conical receptacle genera of the *Ecliptinae* (exemplified by the genus *Acmella*), and the epaleate genus *Trichocoryne*. The genus *Parthenium* is sister to *Dugesia*; both genera share a similar achene dispersal mechanism and floral sexuality pattern. The genus *Ambrosia* in some of the trees is sister to *Encelia* and basal to most genera of this clade. *Encelia* is not the immediate sister taxon of the *Helianthinae*. The other clade of core *Heliantheae* has the genus *Montanoa* as its basalmost lineage sister to the core *Ecliptinae*. The major clade sister to core *Heliantheae* contains a disparate group of taxa ranging from traditionally helianthoid paleate taxa such as those classified under subtribes *Galinsoginae*, *Melampodiinae*, *Milleriinae*, and *Guardiolinae*, along with epaleate taxa such as *Galeana/Villanova*, the *Peritylinae*, and the *Madiinae*. Support for deeper clades of the major group of paleate and epaleate taxa that includes *Eupatorieae* is weak, but the component taxa are probably closely related based on strong support for other deep clades of the HHE tree. The results outlined here provide support for changes in the classification of tribes Helenieae and Heliantheae. A tentative classification scheme for the HHE clade will be presented.

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Tribal relationships and character evolution in the cashew family (Anacardiaceae): inferences from three regions of the chloroplast genome

The cashew family, *Anacardiaceae*, includes about 600 species and has traditionally been subdivided into five tribes (*Anacardiaceae*, *Dobineae*, *Rhoeae*, *Semecarpeae*, and *Spondiadeae*). Results from analysis of sequence data for *matK*, *trnL*, and the intergenic spacer between the *trnL* exon and *trnF* indicate that this five tribal system is artificial and instead supports two major clades within the family. The larger clade contains members of tribes *Rhoeae*, *Semecarpeae*, *Dobineae*, and *Anacardiaceae* while the smaller clade contains tribe *Spondiadeae* and a few members of tribe *Rhoeae*. The results, generated from sequence data for these three regions of the chloroplast genome, also support a monophyletic *Anacardiaceae*, distinct from its sister group, the *Gumbo-Limbo* family, *Burseraceae*. The sequence data appear congruent with floral structure characters that distinguish these two families. Within each of the families floral structure is relatively uniform but *Anacardiaceae* differs from *Burseraceae* by the number and orientation of the ovules. Conversely, fruit type in *Burseraceae* is rather invariable while *Anacardiaceae* has a wide variety of fruit types. There are many unusual fruit characteristics found within the cashew family, such as, the presence of specialized seed germination structures known as opercula and a diversity of evolutionary adaptations for wind dispersal. Preliminary phylogenies generated in this study indicate that opercula have evolved twice and wind dispersed taxa group together in a single clade.

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A cladistic analysis of Charianthus (Miconieae: Melastomataceae) using morphological and molecular characters

The absence of convincingly delimited monophyletic groups within the Miconieae is well known to students of the family. The current revision of *Charianthus* represents the first genus in the Miconieae to be the subject of a molecular cladistic analysis. Molecular data was combined with morphology to analyze hypotheses of phylogeny within *Charianthus* using nine additional species as outgroups. The internal transcribed spacer (ITS) region of 18S - 26S nuclear ribosomal DNA was sequenced and provided important insights into the evolutionary relationships of the taxa under investigation. Each cladistic analysis supports the monophyly of *Charianthus* when *C. fadyenii* is excluded. A combined analysis of the morphological and molecular data sets resulted in a strongly supported *Charianthus* clade with 100% bootstrap and a decay value of 12. *Charianthus fadyenii* is in the *Tetrazygia* clade where its position as sister to *T. bicolor* is supported by a bootstrap value of 89% and decay of three. Inclusion of *C. fadyenii* in *Charianthus* makes both *Charianthus* and *Tetrazygia* non-monophyletic, therefore, this species is transferred to *Tetrazygia*. Morphological adaptations to hummingbird pollination have arisen independently in both *Charianthus* and *Tetrazygia*. *Charianthus purpureus*, as defined by previous taxonomists, is a polyphyletic species because of the inclusion of the populations on the islands of Dominica and Grenada, thus, two new species must be recognized. *Charianthus* is a morphologically well-characterized clade of six species of hummingbird pollinated shrubs and small trees found in the tropical montane rain forests and elfin forests of the Lesser Antilles. The revised circumscription of the group makes it the only plant genus endemic to the Lesser Antilles. Ongoing studies will continue to concentrate on the implementation of a phylogeny based on sequence data of both a nuclear gene (ITS) and a chloroplast gene (*trnL-F*, *matK*, or *GBSSI*) for all genera of Miconieae.

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Phylogenetics of Muhlenbergia and relatives (Poaceae: Chloridoideae) based on internal transcribed spacer region sequences (nrDNA)

A recent treatment of the subtribe Muhlenbergiinae (Eragrostideae; Peterson 2000 in *Grasses: Systematics and Evolution*, Pp. 195-212.) suggested that *Muhlenbergia* (a large genus of about 153 species) shares a common ancestor with five smaller genera: *Bealia*, *Blepharoneuron*, *Chaboissaea*, *Lycurus*, and *Pereilema*. An ongoing phylogenetic study of this group based on internal transcribed spacer (ITS) region sequences (nrDNA) shows that these five genera are nested within a paraphyletic *Muhlenbergia*. In addition, four chloridoid genera that have been classified outside of the Muhlenbergiinae are also nested within *Muhlenbergia*: *Aegopogon*, *Redfieldia*, *Schaffnerella*, and *Schedonnardus*. Some well supported clades (i.e., with many base

substitutions and high jackknife support) in the phylogeny correspond to existing formal and informal groups within *Muhlenbergia*. One clade consists entirely of species of *Aegopogon*, *Muhlenbergia* subg. *Muhlenbergia*, and *Pereilema* that exhibit PCK leaf anatomy. Another clade contains species that correspond to members of *Muhlenbergia* subg. *Trichochloa* (i.e., with sclerosed phloem in the primary vascular bundles and a crown of inflated cells just above the primary vascular bundles). Interestingly, ITS sequences within this clade have diverged little compared to other clades. Members of the *Muhlenbergia montana* complex, a group of caespitose perennials and annuals that usually have a 3-nerved and/or toothed upper glumes, form a clade. Another clade is composed entirely of annual species of *Muhlenbergia*, and *Blepharoneuron tricholepis*, a caespitose perennial. Although only 32 species of *Muhlenbergia* have been sampled at this writing, it is already clear that the ITS region will contribute much to our understanding of the diversification of this lineage.

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Phylogeny of New World riverweeds (Podostemaceae): morphology

Podostemaceae are restricted to tropical river-rapids and waterfalls. About half of the 49 genera and 60% of the species occur in the New World. This contribution focuses on phylogenetic relationships among New World Podostemoideae (the largest subfamily) based on parsimony analyses of morphological (vegetative and reproductive) characters. *Apinagia* (ca. 50 spp.), *Marathrum* (ca. 25 spp.), and *Rhyncholacis* (ca. 25 spp.) are the largest genera in the New World. Our analyses indicate that neither *Apinagia* nor *Marathrum* is monophyletic. Species of *Apinagia* occur in several clades. Some species of *Marathrum* occur closely related to those of *Rhyncholacis*, while others occur in different clades. One well-supported group is composed of one species each of *Marathrum*, *Vanroyenella* and *Macarenia*. *Mourera* is monophyletic. The genus *Oserya* is monophyletic, and occurs basal to a clade in which *Ceratolacis*, *Devillea*, *Castelnavia*, *Podostemum* and *Crenias* occur. Species of *Podostemum* and *Crenias* form a monophyletic group. *Podostemum*, however, is paraphyletic. Preliminary analyses indicate that Indian Podostemoideae arose from ancestors that are shared with the New World genera *Podostemum* and *Crenias*. Character state change will be discussed relative to the phylogenetic hypotheses. For example, the phylogenetic topology indicates that the andropodium (fused stamen filaments) and dyad pollen each evolved once.

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Taxonomy and systematics of Podostemum (Podostemaceae)

A revision of *Podostemum* (Podostemaceae) is presented based on morphological analyses of extensive field collections. A. Michaux established the genus *Podostemum* in 1803 with the description of *P. ceratophyllum* from eastern North America. Numerous species have subsequently been described from Mexico and southern South America. (Several Indian species had previously been included in *Podostemum*, although they are now placed in the Indian *Zeylanidium*. *Podostemum* is a New World genus.) Seventeen specific and subspecific taxa were recognized by P. Van Royen (1954) in *Podostemum* as part of his treatment of New World Podostemaceae. We interpret nine species and varieties recognized by Van Royen as environmental forms of the seven species recognized in our treatment: *P. ceratophyllum* Michx., *P. mülleri* Warming, *P. comatum* Hicken, *P. distichum* (v. Chamisso) Weddell, *P. irgangii* Philbrick & Novelo, *P. ricciiforme* Liebmann, *P. fruticosum* (Tulasne & Weddell) Weddell. We recognize species based primarily on stipule form (number of lobes, orientation) and to a lesser degree on leaf structure. *Podostemum distichum* is highly polymorphic in leaf and stipule form; five previously recognized species are interpreted as environmental forms of *P. distichum*. Phylogenetic analyses based on morphological characters indicate that *Podostemum* is paraphyletic. *P. mülleri* is monophyletic with species of *Crenias*. In contrast, ITS sequence data indicates a different placement of *P. mülleri*. Morphological data also place *P. ceratophyllum* and *P. comatum* as unresolved at a basal location in the topology, while *P. distichum* and the newly described *P. irgangii* are sister-species.

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Integrating molecular cytogenetics and phylogenetics: genome evolution in diploid and polyploid Tragopogon (Asteraceae)

Recent mapping and chromosome painting studies of polyploid crops indicate that extensive genomic restructuring can occur following polyploidization. For example, different patterns of rDNA evolution are found in crop allopolyploids: interlocus homogenization (gene conversion) of rDNA loci can occur in *Nicotiana* and *Gossypium*, but is not reported in *Brassica* and *Triticale*. However, while synthetic polyploids of crop plants have been used to demonstrate rapid genome evolution, a naturally occurring diploid-allopolyploid system still needs to be well characterized. *Tragopogon* provides unique opportunities to investigate recent, recurrent allopolyploidy. Previous molecular studies indicate that *T. mirus* may have evolved 12 times and *T. miscellus* may

have formed 20 times within the past 70 years. We are evaluating the two allopolyploids, *T. mirus* and *T. miscellus*, relative to their three diploid progenitors using molecular cytogenetic and phylogenetic approaches. Fluorescent *in situ* hybridization (FISH) is being used to identify several loci on individual chromosomes to detect chromosomal evolution. Probes for the 18S-5.8S-26S array, 5S array, and other repeats are being evaluated in diploids and recurrent polyploids for number of loci and activation. Nucleolar dominance is a common feature in many allopolyploids, presumably only when the units have not homogenized and remain clearly related to the diploid progenitors. Thus, the rDNA unit structure data predicts that nucleolar dominance may be a feature of *Tragopogon* allopolyploids. Also, phylogenetic studies of nrDNA show perfect additivity (no interlocus homogenization) in that all cloned ITS sequences from *Tragopogon* polyploids give sequences from the progenitor diploids. However, Southern hybridization to the diploids reveals that all units of the 18S units of an array are similar, yet there are clearly population differences amongst the diploids, showing that intralocus gene conversion (homogenizing the entire array) must be occurring. Integrating molecular cytogenetics and phylogenetics is proving a powerful approach in assessing the complex histories of these dynamic polyploid genomes.

532 PLUNKETT, GREGORY M.^{1*}, PORTER P. LOWRY², AND JONATHAN M. EIBL¹

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Evolution and speciation in New Caledonian Araliaceae

The location and geological history of New Caledonia has made this Pacific island one of the most intriguing spots on earth to study plant evolution. The island separated from Australia roughly 65 mya, carrying with it many ancient lineages of angiosperms, some of which are left nowhere else on earth (e.g., *Amborella*). Although its tectonic history has predisposed this island to high levels of paleoendemism, the unique combination of geography, geology, and ecology found in New Caledonia has also provided many opportunities for more recent speciation. Araliaceae have a near-cosmopolitan distribution, but their generic and species diversity is nowhere greater than in New Caledonia, making the family an ideal model for studying both paleo- and neoendemism. To infer the role of geological history and physical conditions on evolutionary patterns, we present data on three araliad lineages. The generic diversity of one lineage (comprising *Mydocarpus*, *Delarbrea*, and *Pseudosciadium*) appears to pre-date the late Cretaceous separation of New Caledonia from Australia, but species diversity is likely due to radiations onto ultramafic substrates, especially in *Mydocarpus*. For two other araliad lineages, *Polyscias* and *Schefflera*, our data suggest an arrival in New Caledonia via long-distance dispersal (most likely after the Cretaceous), followed by relatively recent radiations. Speciation patterns in these genera, especially in *Polyscias*, are closely correlated with the physical diversity of the island. Species pairs that are morphologically coherent and yet clearly distinguishable are allopatrically isolated on the basis of elevation, soil types, and/or local geography. The single species *Polyscias dioica*, however, combines high levels of morphological variability and a broad distribution across the island with complex patterns of phylogenetic relationships. Species "breakdown" (via hybridization among once distinct species) may account for this exceptional pattern.

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Defining the sources of Paradox: DNA sequence markers for North American walnut (Juglans L.) species and hybrids

One of the most important rootstocks in the California walnut industry is Paradox, which refers to the offspring of a California black walnut pollinized by a Persian walnut (*Juglans regia*). Paradox was developed by Luther Burbank, who did not distinguish between northern (*J. hindsii*) and southern (*J. californica*) California black walnut. Although it is generally accepted that Paradox designates hybrids between *J. hindsii* and *J. regia*, the name is commonly applied to any black walnut Persian walnut hybrid. Moreover, due to gene flow among black walnut species, the genealogy of Paradox hybrids may also include species such as Arizona (*J. major*) and Eastern black (*J. nigra*) walnut. Since the nuts from which Paradox seedlings are grown are collected from wild trees, their genetic backgrounds are not generally known. In conjunction with a large study aimed at evaluating Paradox hybrids from different industry sources, we have been working to develop molecular markers that can be used to infer the parentage of individual Paradox seedlings. Representatives of the five black walnut species from North America were screened for variability in the ITS regions of the nuclear ribosomal DNA and in three noncoding regions from the chloroplast genome, the *trnT-trnL*, *trnL-trnF*, and *trnD-trnT* spacers. Unique sequence markers were identified for each species, and total DNA extracts from 27 Paradox source trees were tested for those markers. Chloroplast DNA profiles were used to trace the maternal lineages of the Paradox source trees, while the ITS data provided evidence as to whether or not the source trees were themselves hybrids. Our results indicate that, among industry Paradox sources, there is considerable genetic contribution from species other than *J. hindsii*.

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Hawaiian blueberries and their relatives, a phylogenetic analysis of Vaccinium L. sections Macropelma (Klotzsch) Hooker f., Myrtilus Dumortier, and Hemimyrtilus Sleumer

Phylogenetic relationships among *Vaccinium* sections *Macropelma*, *Myrtilus* and *Hemimyrtilus* have been the subject of much debate but hypotheses about evolutionary relationships among these taxa have not been tested using a cladistic framework. These taxa have been proposed as close relatives and they share, along with sect. *Oxycoccoides*, the character of buds covered by two partially fused prophylls. However, the monophyly of these sections has not been assessed and there has been disagreement as to their species content. *Vaccinium* sect. *Macropelma* as currently recognized includes four species: *Vaccinium dentatum*, *V. calycinum*, and *V. reticulatum* from the Hawaiian Archipelago and *V. cereum* from southern Polynesia. While most investigators agree that the Hawaiian taxa represent a natural group, the phylogenetic position of *V. cereum* has been the subject of much discussion. Some authors place *V. cereum* in sect. *Macropelma*, while others feel that it is closer to other Pacific sections of *Vaccinium* (i.e., sect. *Bracteata*). The goals of this study were to use molecular data in a phylogenetic analysis to assess the monophyly of sections *Macropelma*, *Myrtilus* and *Hemimyrtilus* and to determine their phylogenetic position in tribe Vaccinieae. Molecular data from the

chloroplast genes *matK* and *ndhF* and nrITS for approximately 50 species of Vaccinieae and three outgroups from "Andromedeae" were analyzed, individually and in combination, using parsimony. Results show that both sect. *Myrtilus* and sect. *Hemimyrtilus* are paraphyletic. Hawaiian representatives from sect. *Macropelma* form a well-supported clade derived from within sect. *Myrtilus*. However, the Polynesian *V. cereum* may be of hybrid origin. The *Macropelma* + *Myrtilus* clade is sister to a clade which contains *V. erythrocarpon* (sect. *Oxycoccoides*) sister to the two Asian representatives from sect. *Hemimyrtilus*, *V. hirtum* and *V. smallii*. The three Mediterranean taxa from sect. *Hemimyrtilus* form a clade weakly supported as sister to the rest of tribe Vaccinieae.

535 PRATT, DONALD B.*, LYNN G. CLARK, AND ROBERT S. WALLACE

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A tale of two families: phylogeny of the Chenopodiaceae-Amaranthaceae

The Chenopodiaceae and Amaranthaceae are closely related families consisting of about 174 genera and 2,050 species of world-wide distribution. The Chen-Am alliance is ecologically important and also contains a number of economically important crop and weedy species. The alliance is further noted for C4 photosynthesis as well for adaptations to xeric and saline environments. The Chen-Ams traditionally have been considered allied based on a shared core floral formula, as well as morphological, anatomical, chemical, and molecular data. Despite their importance, the phylogeny of the Chen-Ams has not been investigated. We report here a preliminary analysis of the phylogeny of the Chen-Am alliance based on plastid *ndhF* gene sequences. All currently recognized subfamilies and tribes (except the Polycnemoideae) were sampled including over 15 genera. Parsimony analysis of *ndhF* strongly supports a monophyletic Chen-Am alliance. Based on sampling to date, the Chenopodiaceae as currently circumscribed is paraphyletic, and the Amaranthaceae is potentially polyphyletic.

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Phylogeny of the cycads and their placement in the seed plants, as inferred from a large chloroplast data set

The cycads have a central place in our understanding of the phylogenetic relationships of the seed plants. Their circumscription into two suborders (Zamiineae and the monofamilial Cycadineae) is supported by various molecular studies and is further confirmed here. We investigated higher-order relationships by sampling a large portion of the chloroplast genome for *Bowenia*, *Cycas*, *Ceratozamia*, *Dioon*, *Encephalartos*, *Stangeria* and *Zamia*, representing all the families, subfamilies and tribes in Stevenson's (1992) treatment of the cycads. We obtained ~13.5 kb (unaligned) of DNA sequence data per taxon, spanning a diverse range of coding sequences, introns and intergenic spacers dispersed throughout the chloroplast genome. Our results are largely congruent with published molecular studies, and provide substantial support for most of the inferred backbone of cycad phylogeny. *Dioon* is strongly supported as the sistergroup of the remaining members of Zamiineae. Our findings also support the novel arrangement of *Stangeria* with subfamily Zamioideae (represented here by *Zamia* and *Ceratozamia*), as was recently noted by Bogner and Francisco-Ortega. The precise placement of *Bowenia* was not fully resolved, but its membership in Stangeriaceae was strongly rejected. In con-

trast to the other seed plants, cycad chloroplast genomes share two features of their molecular evolution with *Ginkgo* – a slower rate of evolution and an apparently elevated transition: transversion ratio. The question of cycad placement within the seed plants remains unresolved, and analyses based on different gene samplings, taxon samplings and phylogenetic optimality criteria provide different arrangements of the five living spermatophyte groups. Split-decomposition analysis suggests that there is conflicting signal in the seed-plant data, possibly a function of long-branch distortion. This conflict appears to be reduced by improving the taxon sampling. None of our analyses support a sistergroup relationship between *Ginkgo* and the cycads, but this possibility could not be rejected using parsimony-based parametric bootstrapping.

537 RANDLE, CHRISTOPHER P.^{1*}, MARK P. SIMMONS², JOHN V. FREUDENSTEIN², AND JOHN W. WENZEL³

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Limitations of Relative Apparent Synapomorphy Analysis (RASA) for measuring phylogenetic signal

We evaluate the ability of relative apparent synapomorphy analysis (RASA) to measure phylogenetic signal, select outgroups, and identify terminals subject to long branch attraction. In all cases except for equal character-state frequencies, RASA indicated extraordinarily high levels of phylogenetic information for hypothetical data matrices that are uninformative regarding relationships among the terminals. Yet, regardless of the number of characters or character-state frequencies, RASA failed to detect phylogenetic signal for hypothetical matrices with strong phylogenetic signal. In our empirical example, RASA indicated increasing phylogenetic signal for matrices for which the strict consensus of the most parsimonious trees is increasingly poorly resolved, clades are increasingly poorly supported, and for which many relationships are in conflict with more widely sampled analyses. RASA is an ineffective approach to identify outgroup terminal(s) with the most plesiomorphic character states for the ingroup. Our hypothetical example demonstrated that RASA preferred outgroup terminals with increasing numbers of convergent character states with ingroup terminals, and rejected the outgroup terminal with all plesiomorphic character states. Our empirical example demonstrated that RASA, in all three cases examined, selected an ingroup terminal, rather than an outgroup terminal, as best outgroup. In no case was one of the two outgroup terminals considered the optimal outgroup by RASA. RASA is an ineffective means of identifying problematic long branch terminals. In our hypothetical example, RASA indicated a terminal as being a problematic long branch terminal in spite of the terminal being on a zero-length branch and having no possibility of undergoing long branch attraction with another terminal. RASA also failed to identify actual problematic long branch terminals that did undergo long branch attraction, but only after following Lyons-Weiler and Hoelzer's (1997) process to identify and remove terminals subject to long branch attraction. We conclude that RASA should not be used for any of these purposes.

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Inferring phylogenies of photosynthetic organisms from chloroplast gene orders

Distribution of gene order changes have been used successfully for estimating phylogenies within and among various land plant groups. However, such chloroplast DNA structural characters remain largely untested for phylogenetic inference at very high taxonomic levels such as between Chlorophytes and Streptophytes or among major lineages of photosynthetic organisms. When chloroplast genomes of these more distantly related organisms are compared, computational difficulties increase dramatically. Challenges include unequal gene content and high rates of change relative to the number of genes available as landmarks. We have been developing and testing a variety of methods for reconstructing phylogenies based on gene order data (see abstracts by Jansen et al and Moret et al). Here we will compare results of our methods when analyzing highly divergent gene orders. We have determined gene orders, from complete genome sequence information available in genbank, for chloroplast genomes of eleven organisms. In our data, we represent the free-living cyanelle, Cyanophora, "red algae" (Cyanidium, Porphyra), "green algae" (Chlorophytes: Chlorella, Mesostigma, Nephroselmis and Streptophytes: Marchantia and tobacco), and presumed secondary endosymbionts (putative red algal derivatives: Guillardia, Odontella and putative green algal derivative: Euglena). To analyze these data we have utilized GRAPPA and other approaches based on breakpoint and inversion distance as well as cladistic analyses using shared rearrangement endpoints as characters.

539 REE, RICHARD

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Floral diversity and phylogeny of Pedicularis

Pedicularis is a lineage of approximately 700 species of hemiparasitic angiosperms that has radiated extensively in the eastern Himalayan biodiversity "hot spot" of south-central China. This group displays substantial variation in floral morphology: corollas can be beaked, crested, toothed, and/or long-tubed. New molecular phylogenies of Himalayan *Pedicularis* resolve a long-standing source of conflict in systematic treatments regarding the use of floral versus vegetative characters in identifying primary subgeneric lineages, corroborate existing hypotheses about patterns of character evolution in the corolla, and raise intriguing questions about the role of pollinators in mediating the origin and maintenance of diversity in this group.

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A morphological and molecular cladistic analysis of Echinodorus with emphasis on the placement of E. floridanus, (Alismataceae)

The genus *Echinodorus* comprises 27 species found throughout North, Central, and South America. The most recently described species, *Echinodorus floridanus* (Haynes and Burkhalter, 1997), is diagnosable from other North American

Echinodorus species by its large size, leaf shape, hardy rhizome, and stellate pubescence, and is endemic to the Florida panhandle. We have hypothesized that *Echinodorus floridanus* is closely related to South American taxa based on shared morphological traits. From a cladistic analysis of 127 morphological characters taken from 31 *Echinodorus* species and subspecies we have hypothesized that *E. floridanus* is closely related to South American taxa. Preliminary data using the 5S ribosomal DNA non-transcribed spacer (5S-NTS), a rapidly evolving nuclear region also supports *Echinodorus floridanus* as being sister to South American taxa, specifically to *E. grandiflorus*. We discuss relationships within the genus, focusing on two major groupings, and among putative out-group taxa, providing characters uniting the various groupings therein. The first grouping consists of the 4 species of *Echinodorus* native to the United States while the second group of interest, *E. floridanus*, *E. grandiflorus*, and *E. bracteatus*, are of mixed geographic origin but appear to be closely related to one another.

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Floral diversification and phylogenetic relationships in Achimenes (Gesneriaceae)

Achimenes (Gloxinieae; Gesneriaceae) includes approximately 25 species of perennial herbs distributed from Mexico south through Central America to northern South America. Six sections are recognized: *Achimenes*, *Dicyrta*, *Guthnickia*, *Locheria*, *Plectopoma*, and *Scheeria*. These sections have traditionally been defined based on flower type/pollination syndrome. Flowers can be salverform, tubular, or funnellform in shape and red, yellow, purple, pink, or white in color. Additionally, some species have a distinct floral spur while others have no enlargement of the floral tube base. Phylogenetic relationships in the genus were explored using sequence data from the nrDNA internal transcribed spacer (ITS) and cpDNA *trnL-F* and *trnE-T* spacer regions. Results suggest that the large sections *Achimenes* and *Dicyrta* are polyphyletic. Some relationships supported by the molecular data correlate well with vegetative morphological characteristics. Patterns of floral evolution will be discussed.

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Phylogenetic investigations of the Ericameria/Chrysothamnus complex (Astereae, Asteraceae) based on nuclear ribosomal ITS and ETS sequence data

Systematic and evolutionary studies of *Ericameria* based largely on morphological and cytological data have resulted in numerous, dramatically different, concepts of relationship. *Ericameria* has been treated as a section of *Haplopappus* and as a distinct genus. At various times, species in the genus *Chrysothamnus* have been transferred to *Ericameria*. Additional proposals suggest that all species of *Chrysothamnus*, and species previously residing in *Haplopappus* sections *Asiris*, *Macronema*, and *Stenotopsis* be treated as *Ericameria*. Furthermore, the genus *Xylothamnia* was established to accommodate certain species that were once part of *Ericameria*. Inferred relationships based on sequence data of the internal transcribed spacer (ITS) and external transcribed spacer (ETS) regions of nuclear ribosomal DNA are not entirely in keeping with existing assumptions but provide the basis for additional phylogenetic hypotheses. Species of *Chrysothamnus*

sensu Nesom form a clade that includes *Solidago*, *Sericocarpus*, and certain species of *Tonestus*. *Ericameria sensu* Nesom forms a clade distinct from that containing *Chrysothamnus* and is sister to *Tracyna*, *Ragiopappus*, and *Pentachaeta*. *Xylothamnia*, as defined by Nesom, appears to represent at least two different lineages and probably is paraphyletic. *Ericameria's* subtribal affiliation with *Hinterhuberinae* is not supported by sequence data.

543 ROBERTS, ROLAND P.* AND LOWELL E. URBATSCH
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Seed plant relationships and the systematic position of Gnetales; evidence from nuclear and chloroplast DNA demonstrates the monophyly of conifers

The phylogeny of Gnetales has been debated during recent years. Traditionally, they have often been regarded as the sister group of angiosperms, but alternative opinions, mainly based on wood and stem characters, have also been put forward. Recently, several molecular studies have indicated that Gnetales might be nested within conifers. In this study more than a hundred new sequences of *rbcl*, *atpB*, 26S and 18S rDNA have been analyzed together with available GenBank sequences. Seed plant phylogeny and the systematic position of Gnetales have been investigated using parsimony methods. The four datasets were analyzed separately and combined, with different weighting schemes, and with variously sized subsets including between 20 to 750 land plant species. The aim was to thoroughly evaluate the phylogenetic information of each gene, and to study if results were influenced by taxon sampling. Our combined tree is well resolved recognizing major land plant clades, including conifers, with high support. Relationships within angiosperms, cycads, conifers and ferns are well supported, but relationships between major groups might be interpreted in several ways. The 'gne-pine' theory is clearly refuted

by our data, but before making any further conclusions on the evolution of seed plants, additional types of data need to be considered. Molecules alone might not be able to solve seed plant phylogeny.

545 RØNSTED, NINA

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Phylogenetic relationships within Plantago (Plantaginaceae) based on ITS and trnL sequence data

Plantago (Plantaginaceae) is a genus of more than 200 annual and perennial herbs and semi-shrubs with a worldwide distribution. The genus is considered monophyletic, but some of the infrageneric relationships are ambiguous. The first molecular phylogeny at the genus level is presented. About 60 representative species from the 24 series, as defined by Rahn (1996) were sequenced for nuclear ITS and chloroplast trnL regions. The phylogenetic analysis is correlated with Rahn's morphological phylogeny from 1996, and with known iridoid glucoside patterns, but subgenus *Albicans* is paraphyletic. Five monophyletic subgenera are recognised, *Plantago*, *Coronopus*, *Psyllium*, *Littorella* and *Bougeria*. *Littorella* is sister to the other subgenera of *Plantago*. Series *Hymenopsyllium* is surprisingly closer related to section *Gnaphaloides* than to section *Albicans*. Only part of the sections can be resolved into series. The DNA variation within subgenus *Plantago* is low, as also expected from morphology.

546 SAAR, DAYLE E. AND MELVIN R. DUVALL*

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Do nuclear and plastid loci in Asteraceae show substantial incongruence? A preliminary intertribal phylogenetic study of Heliantheae s. l.

Asteraceae present special technical challenges for molecular phylogenetic studies. Less sequence divergence is generally observed between composites at all taxonomic levels than between comparable taxa in other families. Combining sequences from different loci into the same analysis increases the amount of phylogenetic signal and improves resolution in phylogenetic trees. As members of the Compositae Alliance continue to coordinate their efforts the motivation for combining DNA sequences from loci in different genomes will increase. However, the relatively recent radiation of the family suggests a greater probability of character incongruence between loci, because of differential lineage sorting and/or interspecific hybridization. Reported here is a preliminary molecular phylogenetic study of Heliantheae s. l. This complex exhibits typically low levels of intergeneric sequence divergence. Selected species in 16 genera were analyzed to test the feasibility of combining data. Sequences were determined or obtained for the variable 3' portion of the plastid locus *ndhF* and the nuclear ribosomal ITS region. Interlocus congruence was assessed with two methods both of which found significant congruence between nuclear and plastid trees. The data sets were then combined and analyzed together. The combined tree had a larger measure of signal content, higher resolution, and better support values for internal nodes than trees from either of the separate data sets.

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A phylogenetic analysis of Dahlia (Asteraceae)

The genus *Dahlia* Cav. presently consists of 30 species, primarily from Mexico. Species are usually placed in four subgeneric sections: *Pseudodendron*, *Epiphytum*, *Entemophyllum*, and *Dahlia*, based largely on morphological characters, supplemented with cytological, geographical, and biochemical data. Combined molecular sequence data from both the internal and external transcribed spacer regions (ITS and ETS), located within the nuclear ribosomal gene repeat unit, were used to infer a phylogeny of the genus. Basal nodes were also supported by RAPD data. Sect. *Entemophyllum* appears to be very distinct from the remainder of the genus in almost every parameter measured. *Dahlia merckii* and *D. tubulata* are also quite distinct, both from each other and the remaining taxa. Sections *Pseudodendron* and *Epiphytum* are closely allied with each other as well as with a few species from sect. *Dahlia*, and this clade, the variable root clade (VRC), incorporates all species with unusual root forms, along with some species exhibiting the more typical tuberous type. The remaining species of sect. *Dahlia* form a well-defined clade, the core *Dahlia* clade (CDC). Comparisons of this phylogeny with morphological characters suggest some traits of an ancestral *Dahlia*.

548 SALAZAR, GERARDO A.^{1,2}, MARK W. CHASE¹, AND MARTIN INGROUILLE*

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Phylogenetic assessment of subtribe Spiranthinae and tribe Cranichideae (Orchidaceae) from four plastid and one nuclear DNA sequence datasets

We discuss the phylogeny of the predominantly Neotropical subtribe Spiranthinae, and more broadly of tribe Cranichideae, on the basis of cladistic analysis of 90 sequences each of two protein-coding plastid genes (*rbcl* and *matK*), two non-coding plastid regions (*trnL* intron and *trnL-F* intergenic spacer), and the nuclear ribosomal ITS region. These include representatives of all the subtribes currently recognized as belonging in Cranichideae (except the monotypic Manniellinae) and representatives of tribes Diurideae (identified by independent works as sister to Cranichideae), Orchideae (including Diseae), and Codonorchideae (outgroups). The five datasets produced highly congruent patterns of relationship and were thus analyzed in combination. This analysis confirms the close relation of both Chloraeinae and Pterostylidinae to the "core" Cranichideae indicated by previous studies of *rbcl* (Cameron et al., 1999; Kores et al., 1997) and *matK* sequences (Kores et al., 2000), with Chloraeinae sister to a clade including Pterostylidinae plus *Megastylis* and the core Cranichideae. Within the latter, Pachyplectroninae are strongly supported as sister to a monophyletic Goodyerinae, and this clade is sister to the rest of Cranichideae. Spiranthinae as delimited by Dressler (1993) are not monophyletic unless *Galeottiella* is excluded, and Prescottiinae are a paraphyletic grade with Cranichidinae embedded in them.

549 SAMUEL, ROSABELLE^{1*}, TOD F. STUESSY¹, AND CARLOS M. BAEZA²¹Dept. of Higher Plant Systematics and Evolution, Institute of Botany, University of Vienna, Rennweg 14, Vienna, Austria;²Departamento de Botanica, Universidad de Concepcion, Concepcion, Chile*Molecular phylogeny of Hypochaeris (Asteraceae) and relationships to other genera of Hypochaeridinae*

Nuclear internal transcribed spacer regions (ITS) and the chloroplast trnL intron and trnL/trnF intergenic spacer and matK sequences were used to assess relationships among European and South American species of *Hypochaeris*. The ITS tree shows high resolution compared to that of the maternally inherited trnL and matK. Monophyly of south American *Hypochaeris* is strongly supported by both ITS and the joint matrix of ITS, trnL and matK data. The European species lie basal to the South American taxa. This, plus small molecular divergence among South American species, suggests that they evolved from a single introduction from a European progenitor similar to *H. maculata* (or possibly *H. cretensis* or *H. oligocephala*), and not from *H. radicata* or *H. robertia* as suggested previously. *Hypochaeris* is also revealed to be paraphyletic in relation to generic relatives. ITS data indicate that *H. robertia* is closer to *Leontodon helveticus* and *L. autumnalis*, which brings its placement within *Hypochaeris* into serious question. Species of *Leontodon* form two clades based on molecular data, each also supported by chromosome numbers and morphology. Both nuclear and chloroplast markers suggest that *Leontodon*, *Picris* and *Helminthotheca* are very closely related genera and all need taxonomic re-evaluation.

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Evolution of the mesophyll in the grasses (Poaceae)

Specialization of the mesophyll in grasses is well known, especially with reference to its correlation with photosynthetic pathway. In cross-sectional view, the mesophyll has been classified as radiate or non-radiate, and several cell forms have been identified, including tabular cells, isodiametric cells, fusoid cells, and various lobed cells (e.g., arm cells). With the availability of a robust phylogeny of the grass family, we undertook a survey of the major clades in order to understand better the evolution of mesophyll in grasses. We included taxa of both forest and open habitats whenever possible and cross and longitudinal sections were examined. The results were mapped on the Grass Phylogeny Working Group phylogeny, but character distribution on an alternative topology was also explored. Our results suggest that arm cells, one of the cellular forms in which lobing/invagination shows up in cross-sectional view, is polymorphic in the Anomochlooideae, but is characteristic of Pharioideae, Puelioideae and Bambusoideae, and then is lost in the Pooideae and the PACCAD Clade. Fusoid cells show a similar evolutionary pattern. Rosette cells, previously lumped with arm cells, are interpreted as a potential synapomorphy for the Bistigmatic Clade (Puelioideae + [BEP+PACCAD]). Rosette cells are common in the mesophyll in Ehrhartoideae but usually occur in combination with arm cells in Bambusoideae. The presence of rosette cells in a few members of the Pooideae and the PACCAD clade may represent retention of this character. Longitudinally elongated lobed cells (LEL cells) previously known from a few taxa are here found to be a potential synapomorphy for the Pooideae + PACCAD Clade, under the alternative topology. We also report on some additional observations in the PACCAD Clade.

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Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach

Rates of molecular evolution vary widely between lineages, but quantification of how rates change has proven difficult. Recently proposed estimation procedures have mainly adopted highly parametric approaches that model rate evolution explicitly. Here a semi-parametric smoothing method is developed using penalized likelihood. A saturated model in which every lineage has a separate rate is combined with a roughness penalty that discourages rates from varying too much across a phylogeny. A data-driven cross-validation criterion is then used to determine an optimal level of smoothing. This criterion is based on an estimate of the average prediction error associated with pruning lineages from the tree. The methods are applied to three data sets of six genes across a sample of land plants. Optimally smoothed estimates of absolute rates entailed two- to ten-fold variation across lineages.

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Utility of low-copy nuclear genes in plant phylogenetics

Low-copy nuclear genes in plants are a rich source of phylogenetic information. They hold a great potential to improve the robustness of phylogenetic reconstructions at all taxonomical levels, especially where universal markers such as cpDNA and nrDNA are unable to generate a strong phylogenetic hypothesis. Low-copy nuclear genes, however, remain underused in plant phylogenetic studies due to practical and theoretical complications in unraveling evolutionary dynamics of a nuclear gene family. The lack of the universal markers or universal PCR primers of low-copy nuclear genes has also hampered their phylogenetic utility. It has recently become clear that low-copy nuclear genes are particularly helpful in resolving close interspecific relationships and in reconstructing allopolyploidization in plants. Gene markers that are widely, if not universal, useful have begun to emerge. Although utilizing low-copy nuclear genes usually requires extra lab work such as designing PCR primers, PCR-cloning, and/or Southern blotting, rapid accumulation of gene sequences in the databases and advances in cloning techniques have continued to make such studies less labor-intensive. The growing number of theoretical studies devoted to the gene tree and species tree problem began to build a solid foundation for reconstructing complex plant phylogenies based on multiple gene trees. It is also increasingly realized that fast evolving introns of the low-copy nuclear genes will provide much needed phylogenetic information around the species boundary, and allow us to address fundamental questions concerning processes of plant speciation.

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Rare plants species on the Russian Far East

As the result of flora analysis 200 rare vascular plants species were determined with different categories and statuses of rarity. All of them require special measures of monitoring or protection. The number of centers of the species concentration can be observed in the territorial distribution of the rare plants. Partly, because of detailed flora studies were maintained unevenly in certain areas of the vast region. Estimation of the species rarity and

evaluation of the protection requirements involve a number of methodic approaches. Within the group 52 species are east-asian relicts, inhabiting mostly in southern part of the region: *Taxus cuspidata*, *Microbiota decussata*, *Dioscorea nipponica* and others. Also rare aquatic species reach the northern limits of distribution in Asian continent: *Nuphar japonica*, *Nelumbo komarovii*. In the subgroup of rare endemic forest and alpine plants there are 60 species whose ancestors could be typical mountainous species or genera, such as *Leontopodium blagoveshczenskyi*, *Saussurea kitamuraana*, *Saxifraga astilbeoides*. In the southern and central parts of the region 70 rare plants species are situated on the limits of natural distribution: *Acanthopanax sessiliflorus*, *Smilax maximowiczii*, *Sanicula rubriflora*. Another large subgroup of rare species requiring protection includes plants with decorative and medicinal substances – 116 species and 48 respectively. It is important to underscore that the subgroups mentioned above embrace relict and endemic species. A human or anthropogenic type of impact in the natural habitats of these species could often be selective. About 50% of the rare species populations occur in the areas with multiple impacts of mining industry activities, land reclamation, or complete vegetation cover destruction. Almost all of the rare plants species habitats are under the threat of massive forest fires, timber harvesting, excess of recreation, illegal gathering or collection. It is significant that the number of the rare relict species have weak ecological amplitude.

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Insights into the origin and evolution of Myristicaceae (Magnoliales), based on morphological and molecular data

All recent molecular phylogenetic analyses restrict Magnoliales to a monophyletic order of six families, whose closest relatives are Laurales, Winterales, and Piperales. We present a morphological cladistic study of all 20 genera of Myristicaceae and a broad sample of outgroups, emphasizing the contribution of palynological characters. This analysis placed the Malagasy genus *Mauloutchia* at the base of Myristicaceae. However, a detailed species-level study of *Mauloutchia* reveals unexpected intrageneric variation for the most important characters in the family (including stamen fusion, exine structure, and aril development), calling into question the putative primitiveness of this enigmatic genus. In addition, we generated sequences of the *trnK* intron (including *matK*), the *trnL* intron, the *trnL-trnF* spacer, and the *ndhF* gene from all families of Magnoliales (including 15 genera of Myristicaceae) and major lineages of all three related orders. Parsimony and maximum-likelihood analyses of these data sets strongly support a basal position of Myristicaceae in Magnoliales and a sister-group relationship between *Eupomatia* and Annonaceae, as suggested in higher-level angiosperm analyses with less intensive sampling in Magnoliales. Within Myristicaceae, these data support several groups found in the morphological analyses, especially an Asian clade including *Myristica* and *Knema*, but not the basal position of *Mauloutchia*, which belongs instead to an Afro-Malagasy clade. However, these usually fast-evolving

sequences provide much less informative variation than expected for this diverse and widely distributed family. Annonaceae show at least three times as much variation as Myristicaceae in the same genes. Whether these results indicate an unexpectedly recent origin of Myristicaceae or major changes in molecular rates during the history of Magnoliales remains unclear. In either case, rooting of Myristicaceae using DNA sequences turns out to be a difficult problem, due to the very long stem branch leading to the extant family.

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Systematic analysis of Liatrinae (Asteraceae)

Phylogenetic analyses of DNA sequence data were undertaken to address systematic questions involving subtribe Liatrinae. Molecular phylogenetic results placed Liatrinae among the relatively derived $x = 10$ lineage of Eupatorieae as sister to the *Eupatorium* + *Eupatoriadelphus* clade. This result is in agreement with biogeographic distributions (the two clades are unique in Eupatorieae for their distributions centered in eastern North America), although not with traditional taxonomic treatment. Molecular results supported separation of *Trilisa* and *Litrisa* as distinct from *Carphephorus*, and also provided confirming evidence for placement of the anomalous *Garberia* and *Hartwrightia* within Liatrinae. The shrubby *Garberia* is placed basally as the sister group to the remainder of the otherwise herbaceous subtribe. There is, however, incongruence in the placement of *Hartwrightia*. Results based on the chloroplast encoded *matK* placed it as sister to *Carphephorus*, whereas those based on the nuclear ITS placed it with *Trilisa*. Combined *matK* + ITS results for the entire subtribe gave little resolution, but with *Hartwrightia* (and *Litrisa*, another anomalous genus) removed, there was strong support for a sister group relationship between *Liatris* and *Carphephorus*, with *Trilisa* sister to that clade. *Hartwrightia* may thus be an example of a morphologically distinct genus that has arisen through phylogenetic reticulation.

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Molecular systematics and floral structure of a Western Gondwanan clade of Myrtales

Recent order-wide phylogenetic studies in the Myrtales strongly supported a clade comprising the three African taxa Oliniaceae, Penaeaceae, and Rhynchocalycaceae plus the Central and South American family Alzateaceae. Inter- and intrafamilial relationships however, remained unclear. A phylogenetic hypothesis based on chloroplast and nuclear DNA sequences of most of the species within the clade will be presented and discussed in connection with important floral features. Preliminary results suggest a sister relationship of Oliniaceae and Rhynchocalycaceae, a clade which in turn is sister to the Penaeaceae. First results based on the chloroplast gene *rpl16* suggest that intrafamilial relationships in Penaeaceae are different from traditional conceptions.

557 SCHUETTPELZ, ERIC J.* AND SARA B. HOOT

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Phylogenetic and biogeographic relationships of Caltha (Ranunculaceae) based on DNA sequence data and morphology

Caltha consists of ten species of perennial herbs found in the moist temperate and cold regions of both hemispheres. Past treatments had divided the genus into two sections based primarily on the presence of distinctly inflexed leaf auricles in the Southern Hemisphere species. Through a cladistic analysis of three DNA sequence data sets and morphology, we evaluate this classification as well as biogeographical implications and character evolution. We find that *Caltha natans* (N. America, Asia) is sister to all other species; *Caltha palustris* (circumboreal) and *Caltha scaposa* (Asia) are well supported as sister; and *Caltha leptosepala* (western N. America) and the Southern Hemisphere species together form a well supported group. We suggest a historical dispersal event from North to South America, with a subsequent dispersal event to New Zealand and Australia. A reexamination of leaf morphology supports this hypothesis.

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ITS sequence variation in Tragopogon (Asteraceae): phylogeny and gene evolution in allopolyploids

Over half of all plant species are derived through polyploidy. However, despite the prevalence of polyploid speciation little is known about the genetic consequences of polyploidy. Three diploid species of *Tragopogon* were introduced from Europe to the Palouse region of eastern Washington and adjacent Idaho in the early 1900s. These species hybridized, and two allotetraploid species were formed: *T. mirus* and *T. miscellus*. The parentage of these tetraploid species is well documented, and the tetraploids are serving as models for the study of various aspects of polyploid evolution. We have reconstructed the phylogeny of *Tragopogon*, a largely Eurasian genus of about 50 species, using sequences of the internal transcribed spacers (ITS) of the nuclear ribosomal DNA. Our results suggest that the three diploid progenitor species of the Palouse tetraploids are distantly related. We also used DNA sequence variation in the ITS regions of *T. mirus*, *T. miscellus*, and their diploid parents to determine whether or not concerted evolution had homogenized the rDNA arrays in the tetraploids during the approximately 70-80 years since their formation. Two populations of each allotetraploid and its diploid parents were sampled, and each population was represented by three or more individuals, with four or more clones per individual. The ITS sequences of the diploid parents of *T. mirus* differed at 18 nucleotide positions; those of the parental species of *T. miscellus* differed at 16 sites. Cloned PCR products from each tetraploid match the sequence of the respective parents. These results indicate that the rDNA arrays of the recent tetraploids *T. mirus* and *T. miscellus* do not appear to have undergone concerted evolution.

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The effects of increasing genetic distance on alignment of, and tree construction from, rDNA internal transcribed spacer sequences

We examined how alignment of internal transcribed spacers (ITS) of rDNA changes with increasing genetic distance between sequences, using four fungal and four plant datasets. Increasing genetic distance can negatively affect the tree topology and branch-support values in two ways. First, it may cause errors in the alignment and therefore the homology of the characters that are based on the misaligned positions. Second, it may cause errors in the homology assessments of positions that underwent multiple hits as genetic distance increased, therefore causing errors in homology assessments of the states for those characters. These two causes of error in phylogenetic inference were distinguished from one another in our analysis. The errors in alignment caused by increasing genetic distance were primarily due to inserting too few gaps and inserting them at the wrong positions. We suggest that terminals on branches that represent genetic distances of over 0.118 are likely to have negative effects on tree construction caused by misaligned positions and multiple hits. Significant errors in tree resolution, topology, and/or branch-support values were more often caused by multiple hits (and/or absence of interaction of the excluded terminals with the included terminals) than by misaligned positions. This suggests that increasing genetic distance negatively affects our primary homology assessments of character states (due to multiple hits) more severely than our primary homology assessments of characters (due to misaligned positions). We suggest that increasing taxon sampling with the aim of subdividing long branches is the preferred strategy for obtaining reliable alignments; manual adjustment of alignments and/or eliminating ambiguously aligned positions from the analysis are of lesser benefit.

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Amino acid vs. nucleotide characters: challenging preconceived notions

The Soltis et al. (2000) 567-terminal simultaneous analysis of *atpB*, *rbcl*, and 18S rDNA was used as an empirical example to test the use of amino acid vs. nucleotide characters for protein-coding genes at deeper taxonomic levels. Nucleotide characters for *atpB* and *rbcl* have 6.5 times the amount of possible synapomorphy as amino acid characters. The nucleotide-based jackknife tree is much more resolved than the amino acid-based tree, for both large and small clades. Nearly twice the percentage of well supported clades resolved in the 18S rDNA tree are resolved using nucleotide characters (88.5%) relative to amino acid characters (47.5%). The well supported clades resolved by both character types are much better supported by nucleotide characters (98.6% vs. 83.3% average jackknife support). Nucleotide characters outperform amino acid characters even when both matrices are reduced to the same amount of possible synapomorphy (236 randomly selected informative nucleotide characters vs. all 411 informative amino acid characters). For the reduced nucleotide-based matrix, 72.1% of the well supported clades are resolved, and the well supported clades resolved by both character types are better supported by nucleotide characters (92.7% vs. 85.9% average jackknife support). Although the performance of nucleotide char-

acters decreased with reduced sampling of terminals, amino acid characters did not improve. Nucleotide characters outperformed amino acid characters even with 90% of the terminals deleted, in order to increase genetic distance between clades. Of the 14 cases of conflicting resolution between the amino acid and nucleotide-based jackknife trees, there is independent evidence for the phylogeny of 11 these groups. For 10 of the 11 cases, the independent evidence supports the nucleotide-based topology. There is evidence of convergence to the same amino acid specified by different codons and/or artifacts caused by the use of composite characters for the amino acid characters supporting eight of these contradictory clades.

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*Phylogeny and biogeography of Staphyleaceae (DC.)
Lindl*

One of the most interesting facets of angiosperm biogeography is the disjunct distribution of closely related plant groups. When seeking plausible explanations for the origins of biogeographical patterns, analyses of the phylogenetic relationships of disjunct taxa are critical. It is particularly important to seek a phylogenetic framework when morphological data is sparse or ambiguous, as is the case for the family Staphyleaceae. The family, (composed of three genera, *Staphylea*, *Euscaphis*, and *Turpinia*, totaling 50-60 species) exhibits two intriguing biogeographical patterns. *Staphylea* is distributed in temperate North America, Europe and Asia, while *Turpinia* is disjunct between the tropics of the new world (Mexico to South America) and the old world (central Asia to Papua New Guinea). The genus *Euscaphis* is monotypic and occurs in eastern Asia. The three genera of Staphyleaceae are delimited primarily on the basis of fruit type, with few other characters to distinguish them. This raises additional questions: is the presence of fleshy fruits (*Turpinia*) the result of a relictual distribution of a wider ranging fleshy-fruited taxon, or are the fruits a misinterpreted result of convergence? To answer questions regarding biogeographical patterns, generic circumscription, phylogenetic relationships within the genera, and character convergence we initiated a study using sequence data from one nuclear (ITS 1 and 2) and two chloroplast (*matK-psbA* and *trnT-trnL*) regions. Results from comparative studies based on sequence data revealed that traditional generic groupings are polyphyletic and a re-evaluation of the generic limits is necessary. Data gathered to date and its implications for the interpretation of the biogeographic history of Staphyleaceae will be discussed.

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*Evolution of the Bouteloua curtipendula complex
(Gramineae: Chloridoideae) based on molecular data*

Based on the most recent revision, the *Bouteloua curtipendula* complex is a group of 11 grass species and 5 varieties native to the New World. Non-coding nuclear ribosomal and chloroplast DNA sequences (ITS and *trnT-L-F* regions, respectively) subjected to parsimony cladistic analysis show that the complex is monophyletic, though most of the species are para- or polyphyletic. Both phylogenies have three major clades. The largest clade includes mostly polyploids with more than one spikelet per branch and usually orange, red, or purple anthers. The other two clades group mostly diploid taxa with yellow anthers, however the number of spikelets per branch varies from one to many. The phy-

logenies suggest that diploidy is ancestral. Samples showing incongruencies between the ITS and *trnT-L-F* phylogenies were found to be polyploids and in possession of several different copies of the ITS region, indicating that hybridization via allopolyploidy has played a role in the diversification of the complex. Homoplasia, hybridization, polyploidy, and the reported occurrence of apomixis combine to make circumscription of taxa in this group challenging.

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*A re-evaluation of the infrageneric classification of
Clematis (Ranunculaceae) using chloroplast DNA
sequences*

Clematis is a large cosmopolitan genus of more than 300 species. With a distribution that spans all continents save Antarctica, members of the genus have been sought after by horticulturalists the world over. Due to such intense interest the classification of *Clematis* has been revised numerous times over the last 300 years. The most widely accepted, current, classification based on traditional morphology was put forth by Tamura in 1968, revised in 1989, and modified further by Johnson in 1997. This classification is based largely upon floral characteristics such as size, shape and color as well as minor differences in vegetative and inflorescence morphology. Essig in 1990 suggested an alternative classification scheme based upon seedling morphology and reproductive compatibility. Essig proposed two natural groups which would encompass the traditional sections. Sequences of the chloroplast encoded *trnL* intron and *trnL-F* intergenic spacer were examined to test which hypothesis accurately represents the phylogenetic relationships within the genus. The two chloroplast regions (approx. 720 bp.) will be augmented with *matK*, also chloroplast encoded, sequence data as well as a morphological data set. Preliminary sequence analysis of ten ingroup taxa and one outgroup taxa (*Anemone spp.*), utilizing the *trnL* intron and *trnL-F* intergenic spacer regions, shows moderate support for Essig's "seedling hypothesis". These findings provide insights into characters that could potentially hold vast amounts of phylogenetic information within this group.

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Population genetics in Iliamna using ISSRs

Two species in *Iliamna* Greene, *I. corei* and *I. remota*, have been questioned as to their designation as separate species. *Iliamna remota*, the Kankakee Mallow, is found in several disjunct populations in eastern Illinois, Indiana, and western Virginia. It is speculated that *I. remota* was introduced into Virginia during the early 1900s via human activity and railways. *Iliamna corei*, the Peters Mountain Mallow, is known from one population located in southwest Virginia on Peters Mountain. Currently, their populations do not overlap and their habitats differ greatly. Both *I. corei* and *I. remota* are classified as endangered at the state level and *I. corei* is federally listed as well. Conservation efforts are underway to preserve populations in both species. Inter-simple sequence repeats (ISSRs) have been shown to be informative in species and population studies and for estimating genetic diversity of rare and endangered plant species. Ten primers were used for 36 individuals representing *I. corei* and *I. remota*. For *I. remota*, four Virginia, one Indiana, and four Illinois populations were sampled. *Iliamna corei* representatives were obtained from the natural population on Peters Mountain and the research garden at Virginia Tech. The data

were analyzed cladistically using parsimony and by UPGMA and neighbor-joining analysis. The results correlate with the geological distribution of the species and suggest multiple introduction events of *I. remota* to Virginia.

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Morphological and genetic variation in Hibiscus sect. Muenchhusia (Malvaceae)

The Rose Mallows (*Hibiscus* sect. *Muenchhusia*, Malvaceae) as currently circumscribed include five species: *Hibiscus coccineus*, *H. dasycalyx*, *H. grandiflorus*, *H. laevis*, and *H. moscheutos*. Further, *H. moscheutos* includes up to four subspecies, although the most recent taxonomic treatment recognizes only two (*H. moscheutos* subsp. *moscheutos* and *H. moscheutos* subsp. *lasiocarpus*). Previously published experimental hybridization studies as well as morphological data suggest that these species are divided into two natural groups: (1) *H. grandiflorus* and *H. moscheutos*; and (2) *H. coccineus*, *H. dasycalyx*, and *H. laevis*. Beyond these inferences, however, phylogenetic relationships among these species and their relationship to other *Hibiscus* species are unknown. Further, the number of subspecies of *H. moscheutos* that are recognized varies in different treatments and the suite of morphological characters that distinguish them is highly variable. Phylogenetic analyses of molecular data (both chloroplast and nuclear DNA sequences) are being conducted to elucidate relationships among the species of *Hibiscus* sect. *Muenchhusia*, and to discover their relationship to other *Hibiscus* species. Additionally, analyses of morphological and genetic variation within and among populations of those taxa referred to *H. moscheutos* are being conducted to determine how many unique biological entities exist within this taxon.

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Evolution and phylogenetic analysis of Gcyc (a Gesneriaceae cycloidea homolog) in subfamily Gesnerioideae (Gesneriaceae)

The gene *cycloidea* (*cyc*) has been documented in its control of bilateral floral symmetry in *Antirrhinum* and *Linaria*. The role of *cyc* in the control of floral symmetry in other genera and its phylogenetic potential have not been widely explored. Recent work on subfamily Cyrtandroideae of Gesneriaceae has revealed a *cyc* homolog named *Gcyc*. At least two duplicates of this gene are known from Cyrtandroideae. Phylogenetic analyses using these sequences at the intra- and intergeneric levels have shown that *Gcyc* can provide data of phylogenetic utility. Using primers designed to amplify *Gcyc* from diverse Gesneriaceae, one copy of *Gcyc* from most taxa was isolated. In order to amplify *Gcyc* from additional (problematic) taxa, a new, internal 5' primer was designed. Sequences were obtained from all tribes and many genera of Gesnerioideae (including genera with non-bilateral floral symmetry). In only two genera (*Fielidia* and *Negria*) have duplications of *Gcyc* been found. Sequences are readily alignable and show less variability than found in subfamily Cyrtandroideae on the basis of indels. There is no evidence for frame shift or stop codon mutations, implying that gene function is maintained across all taxa. Parsimony and maximum likelihood are congruent with previous analyses of relationships among tribes and genera in Gesnerioideae.

567 SOROS, CONNIE L.* AND DONALD H. LES

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Phylogenetic relationships in the Alismataceae

A phylogenetic analysis of Alismataceae was conducted using data from the internal transcribed spacers (ITS-1;2) of the nuclear ribosomal genes, the chloroplast gene *rbcl*, the flanking introns and coding region of the chloroplast *matK* gene and morphology. The aquatic, monocotyledonous Alismataceae consists of 13 genera which are similar in habitat, pollination and morphology. Numerous convergences and reduced vegetative and reproductive structures make it difficult to interpret morphological characters for phylogenetic analysis. Our combined data set showed high congruency with results published previously using *rbcl* data alone. The combined molecular data consistently show a monophyletic origin for the family. Other results include a sister group relationship of Limncharitaceae and Alismataceae, a polyphyletic origin for the genus *Echinodorus* and several well-supported monophyletic clades within the family.

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A phylogeny of Costaceae: implications concerning floral morphology

The phylogenetic relationships of Costaceae, a tropical monocotyledonous family sister to the ginger (Zingiberaceae), were investigated with a combination of two chloroplast loci (*trnLF* and *trnK*) and one nuclear locus (ITS15.8s ITS2). The resulting parsimony analysis of selected taxa which demonstrate the range of floral morphological variation in the family shows that the *Caldavena*-type floral morphology is ancestral to the group and that both *Tapeinochilus* species and a *Monocostus* + *Dimerocostus* clade represent recent divergences. The genus *Costus* is broadly paraphyletic but *Costus* subgenus *Costus* represents a large monophyletic radiation with low robustness at the species level. Within this clade, secondary analyses suggest that pollination syndrome, traditionally used for taxonomic and classification purposes within the genus *Costus*, is a relatively plastic trait of limited phylogenetic utility. This represents the first detailed investigation into intra-generic and intra-specific evolutionary relationships within the family Costaceae and presents some novel evolutionary trends with respect to floral morphology and biogeography.

569 STEFANOVIC, SASA* AND RICHARD G OLMSTEAD

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Molecular systematics of Convolvulaceae inferred from multiple chloroplast loci

Convolvulaceae are a large family, traditionally comprising 55 genera with some 1600-1700 species, the members of which present a rich diversity of morphological characteristics and ecological habitats. Previous efforts to systematize this diversity without a cladistic phylogenetic framework have disagreed on the circumscription of the family as well as tribal composition and relationship. In order to circumscribe the family and assess the relationships among its major lineages, a broad data set was constructed, containing representatives of all ten recognized tribes of Convolvulaceae plus representatives of putatively related families within Asteridae. This is done by using four chloroplast regions: *rbcl*, *atpB*, *psbE-J* operon, and *trnL-F* intron/spacer. The

results indicate that Convolvulaceae are sister to Solanaceae, with 100% bootstrap support for each family and the clade comprising both families. Two of the three groups that have been proposed previously as segregate families, *Cuscuta* and *Dichondrea*, are nested within the Convolvulaceae in this analysis, and the third, *Humbertia*, is the sister to all other members of the family. The exact position of *Cuscuta* could not be ascertained, but some alternatives were rejected with confidence. The study identified several distinct monophyletic groups, some of which correspond to earlier ideas. Close relationships of tribes Hildebrandtieae with *Cresseae* and *Ipomoeae* with *Argyreieae* (forming *Echinoconieae*) were confirmed. The polyphyly of *Poraneae* and *Erycibeae* is first reported in this study.

570 STEVENS, PETER F.

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Angiosperm phylogeny and morphology: characterizations of "all" clades of subfamilies and above

The tree on which the Angiosperm Phylogeny group based orders, etc., together with elaborations since, allow morphological (inc. chemical, anatomical) characters to be optimized (but *cautiously*) on the tree. Characterizations of well-supported lineages from genera groups upwards, and for all lineages at the family level and above, can be provided. These characterizations are part of a web-based resource that also includes literature, character definitions, synonymies, and photographs. Although only an interim solution to our changing understanding of phylogenetic relationships and to the absence of an archived database in which individual observations are linked to literature records (databases of character states would be inadequate), it provides a heuristic resource for both research and teaching that is archived and updated every six months. Characters and states can be considered in a local context, so allowing a more sensitive treatment of variation. Thus fruits need not be considered as "types", but as morphologies whose elements can be teased apart and treated independently. Interesting perspectives on the evolution of trimerous, pentamerous and bisymmetrical flowers, and of floral evolution in general, quickly become apparent for instance, the plesiomorphic monocot flower differs in basic construction from that of both many Commelinid and core Eudicot flowers as do differences in variation patterns within the units that we conventionally discuss as families. The questionable nature of the idea of "family variation" promulgated in ordinary texts becomes inescapable. Family characterizations become ever shorter as data are added and character states are removed to appropriate hierarchical levels, our knowledge of evolution thereby simultaneously increasing, and the many gaps in our basic morphological knowledge also become glaringly evident.

571 STONE, R. DOUGLAS

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Southern hemisphere biogeography: phylogenetic evidence from angiosperms and other groups

Cladistic methods were used to infer the Mesozoic and Cenozoic history of the major southern hemisphere land areas. The study included reduced area cladograms for ten putative "Gondwanan" groups, including the angiosperm taxa *Winteraceae* and *Proteaceae: Macadamieae*. Brooks parsimony analysis produced a single most parsimonious tree that resolves the area relationships (southeastern Asia (India (Africa, Madagascar) (South America, Australia))). A proposed Tertiary land connection between Africa and Madagascar may help to explain their inferred

sister relationship. Coding of Madagascar as a composite area also yielded a single tree differing only by the addition of Madagascar 2 as sister to India. Hovenkamp's (1997) vicariance analysis failed to resolve a general area cladogram because of conflicting area relationships and occurrence of sympatric (redundant) or widespread taxa in the source cladograms. The area relationships inferred using Brooks parsimony are more-or-less congruent with a model of Gondwanaland fragmentation derived from independent geological evidence. Brooks parsimony under a topological constraint corresponding to a hierarchical earth history model yielded a tree five steps longer than in the unconstrained analysis. Similarly constrained analyses of multiple randomizations of the source data failed to produce any trees as short as the "real" one, which evidently lies on the tail of a null distribution of tree lengths. The biogeographic pattern in the phylogenetic data examined is thus consistent with a vicariance hypothesis.

572 TANK, DAVID C.^{1,2*}, XIAO-QUAN WANG³, AND TAO SANG²

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Recent transfers of cinnamyl alcohol dehydrogenase genes between conifers diverged 200 million years ago

The nuclear genome of conifers is large and organized in complex gene families, and due primarily to a lack of comparative studies of protein coding nuclear genes across conifer families, very little is known about its evolutionary dynamics. In this study, we investigated the evolution of a low-copy nuclear gene encoding cinnamyl alcohol dehydrogenase (CAD), a key enzyme in the lignin biosynthetic pathway, in Pinaceae and Taxodiaceae. A portion of the CAD gene, including three exons and four introns, was PCR-amplified, cloned, and sequenced from all eleven genera of Pinaceae and five sampled genera from Taxodiaceae. Sequences of 627 nucleotides of the three exons were aligned among the sampled conifer species, as well as angiosperm species used as outgroups. Phylogenetic analysis of the aligned exon sequences yielded 862 most parsimonious trees, of which the strict consensus topology of the ingroup taxa is identical to that of the maximum likelihood tree. Surprisingly, a clade, which contains members of Taxodiaceae and species of *Abies* (Pinaceae), is nested within Pinaceae and has extremely short internal branches. The average synonymous and nonsynonymous divergences within this clade are 0.0149 + 0.0058 and 0.0074 + 0.0019, respectively. Given that Pinaceae and Taxodiaceae diverged as early as the Triassic Era, it is striking that such similar CAD sequences were found. Herein, three hypotheses explaining the remarkably similar CAD sequences are examined, DNA contamination, extremely slow rates of sequence divergence, and recent lateral gene transfer. Ultimately, we conclude that it is most likely that the CAD genes were recently transferred from *Abies* to members of Taxodiaceae. The lateral transfer of functionally important structural genes between reproductively isolated plants opens a new avenue for the exchange of genetic material, and may provide new insights into conifer evolution.

573 TATE, JENNIFER A.* AND BERYL B. SIMPSON

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Double trouble: multiple origins of polyploidy in Tarasa (Malvaceae)

A molecular phylogenetic analysis of the Andean genus *Tarasa* (Malvaceae) and related genera has yielded unexpected results regarding generic boundaries, the origins of polyploidy within the genus, and the morphological attributes of the polyploid taxa. As currently circumscribed, the 30 species of *Tarasa* are morphologically characterized by their blue or purple flowers (but sometimes white) displayed in axillary scorpioid cymes, with apically aristate, completely dehiscent mericarps, and a base chromosome number of $x=5$. Most species are found at high elevations (2000-4200 m) from central Peru to southern Chile and adjacent Argentina, with two species disjunct in central Mexico. Interestingly, the polyploid species (all tetraploid) of *Tarasa* occupy the highest elevation habitats in the Andes. Further, the tetraploids are unusual in that they are all annuals and have reduced floral morphologies as compared to the diploid species. We used nuclear (ITS) and chloroplast (*psbA-trnH* and *trnT-trnL* spacers, *matK-3'trnK* intron) sequence data to reconstruct independent phylogenies to test monophyly of the genus, determine its sister taxon, and investigate the origin of the polyploid species. Both the nuclear and chloroplast phylogenies do not support monophyly of *Tarasa* as currently circumscribed. The high Andean genus *Nototriche* and the North/South American disjunct genus *Sphaeralcea* are placed within the *Tarasa* clade. The sister taxon to this clade is equivocal. Lastly, the polyploid species of *Tarasa* do not form a monophyletic clade and thus have been generated multiple times. This finding is quite intriguing and suggests that there has been morphological convergence toward reduced floral features (including smaller pollen) of the high altitude polyploid taxa.

574 TAYLOR, DAVID WILLIAM

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Systematics and phylogeny of Chione DC (Rubiaceae)

Chione DC. is a genus of rare trees and shrubs native to neotropical wet forests. The definition of this genus was previously unclear, it never having been the subject of taxonomic revision. A clear definition of *Chione* is necessary in order for it to be properly represented in phylogenetic analyses at the level of tribe, subfamily, and family. For this reason, and to improve understanding of neotropical flora taxonomy, a monographic treatment and phylogenetic reconstruction of *Chione* was undertaken. Results from morphological and DNA sequence (ITS 1&2 region of nuclear ribosomal DNA) data have shown *Chione* s.l. to be composed of two divergent lineages. The definitions of *Chione* s.s. and the new segregate genus *Colleteria* D. W. Taylor (unpublished) will be discussed. In addition, a phylogenetic reconstruction of *Chione* s.s. (based on data from the 5S NTS region of nuclear ribosomal DNA) will be presented.

575 TAYLOR, DAVID WINSHIP^{1*}, GILBERT J. BRENNER², SA'D H. S. BASHA³, AND ALI H. AL-HAMMAD³

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Lower Cretaceous evidence for the Cabombaceae water lily lineage and implications for molecular divergence in ancient monophyletic clades

Most molecular phylogenies suggest that there are two well supported clades in the Nymphaeales: the Cabombaceae clade and the Nymphaeaceae-Barclayaceae clade. Recently flowers of the Nymphaeaceae-Barclayaceae clade have been described from the Lower Cretaceous of South America and Europe, whereas we describe vegetative evidence of the Cabombaceae clade. The *Brasenia*-like fossils have leaves with long petioles which are attached to slender shoots in an alternate arrangement. The leaves are orbicular, simple with entire margins, and peltate with the petiole attached at the center. The venation is palmate with four, sometimes five, primary veins. One primary has pinnate secondaries while the others, grouped proximally, branch dichotomously. The primaries and secondaries curve to form brochidodromous loops. The tertiaries are variable and intergrade with the quaternaries in a reticulate to random reticulate manner. The affinities to the nymphaeoids is based on the peltate attachment, leaf shape, leaf architectural characters, and the apparent aquatic nature of the leaves and stems. The shape of the leaf and the aquatic shoots, as opposed to rhizomes, are restricted to the Cabombaceae clade. The minimum ages for both groups of fossils are Albian. Yet molecular phylogenetic analyses of living members suggest that the two clades diverged within the Nymphaeales after a long period of shared ancestry. This is in contrast to the ITA clade and the Chloranthaceae, both which have shorter stems of molecular divergence and greater divergence of the individual end members. This may have importance implications for reconciling molecular clock results and the differences among molecular and morphological phylogenies.

576 TEPE, ERIC J.*, MICHAEL A. VINCENT, AND LINDA E. WATSON

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Evolution of ant mutualisms in Piper subg. Macrostachys (Piperaceae): variation in ant-associated characters

Several Central American species of *Piper* have developed obligate mutualisms with ants, in which plant partners provide nesting sites and food for ant partners. In turn, the plants receive some protection from herbivores and fungal infection. In addition to these obligate ant-plants, some species of *Piper* are found that have resident ants only sometimes (facultative), and still other *Piper* species are never found with ants. This continuum is found in *Piper* subg. *Macrostachys*, and the degree of ant association is closely correlated with plant morphology. This variation in morphology and ant presence has contributed to confounding evolutionary relationships. In obligate ant-plants, the sheathing petioles that are typical of some *Piper* become tightly rolled into a tube. The ants, *Pheidole bicornis* in most cases, move into this cavity, and in general, the stems become hollow as the plant increases in size with the colony eventually occupying the entire plant. The food bodies that the ants subsist on are produced on the adaxial surface of the petioles (i.e. inside the tube), thus available exclusively to the ants; furthermore they are only produced in the presence of the

ants. While food bodies and hollow stems are only found in the obligate ant plants, variously closed petiole domatia are found in other *Piper* species; an increased degree of closure corresponds with increased density of ant residents. In these facultative ant plants, the association between ant and plant is less specific, and a number of ant species inhabit these plants. This continuum of ant mutualisms and plant adaptations is being examined in the context of an independently derived molecular phylogeny of *Piper* subg. *Macrostachys*, with the ultimate goal of understanding the evolutionary sequence of events and the key adaptations that resulted in obligate associations between ants and plants.

577 TIMME, RUTH E.* AND ISABELLE DE GEOFROY

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A molecular phylogeny of the genus Polemonium (Polemoniaceae) using ITS sequence

Polemonium consists of an estimated 28 species. Its distribution is almost entirely Northern Hemisphere, with a single species also occurring in Chile. The majority of recent phylogenetic studies of this genus have focused on the seven alpine species, and have neglected the remainder of the genus. Despite recent allegations that the alpine members constitute a monophyletic group that may have evolved from the subalpine *P. pulcherrimum*, ITS sequence data provide a phylogeny where the alpine species are not monophyletic. It is apparent that rather than undertaking further investigations of relationships of subsets of Polemonium, it is more important at present to explore the phylogeny of the entire genus. Results of this study show several patterns: 1) Polemonium is a strongly supported monophyletic genus; 2) the annual *P. micranthum* is sister to the rest of the genus (all perennials); 3) the Mexican-southwestern *P. pauciflorum* and *P. mexicanum* form a monophyletic group; 4) at least two species, *P. caeruleum* and the western North American *P. pulcherrimum*, are not monophyletic. Ultimately these results will allow a determination of the actual number of lineages within Polemonium.

578 TRUSTY, JENNIFER L.*¹, ARNOLDO SANTOS-GUERRA², AND JAVIER FRANCISCO-ORTEGA¹

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Interspecific relationships and morphological adaptation within the Macaronesian endemic genus Bystropogon (Lamiaceae): evidence from the Internal Transcribed Spacer

The Canary Islands consist of seven islands forming a volcanic archipelago off the northwest coast of Africa. The location and relative isolation of these islands has made them a rich source of endemic plants. The unique flora of the Canary Islands includes approximately 600 endemic species with at least 23 endemic genera that represent 40% of the native plant species of these islands. The genus *Bystropogon* (Lamiaceae) is endemic to the Macaronesian region and is represented by 11 species in the Canary Islands and one species in Madeira. These taxa are distinguished by both morphological and ecological differentiation in addition to geographic distribution. The incredible morphological flexibility of island plants that allows them to adapt to new and diverse environments has made the study of the systematic relationships of island endemics a challenging endeavor. The recent use of molecular tools has allowed for new insights in understanding the systematic and biogeographic relationships of island taxa.

An ITS phylogeny of all the species of *Bystropogon* has resolved the relationships of these taxa in Macaronesia and offers insight into the plasticity of morphological adaptation in this group.

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Molecular systematics of the Eriocaulaceae: evidence from chloroplast sequence data

The Eriocaulaceae is a pantropical family comprised of ten genera and approximately 1100 species. Members of the family are typically small annual or perennial, basally rosulate herbs. Flowers occur in compact involucrate capitula that superficially resemble inflorescences found within the Asteraceae, hence the description "Composites of the monocots." The Eriocaulaceae has traditionally been considered a natural group and allied with the Commelinales. The monophyly of the family has been supported by recent studies utilizing molecular data such as *rbcl*, although the close relationship to the Commelinales has been discarded and a closer relationship to the Poales proposed. In contrast to strong familial support, relationships within the family have proven difficult to determine. This is in part due to an overall lack of morphological variation and a reliance on minute floral characters. The majority of species are found within three large core genera, *Eriocaulon* (400 species), *Paepalanthus* (485 species) and *Syngonanthus* (200 species). Recent cladistic analyses of the family based on morphological and chemical characters have supported the monophyly of *Eriocaulon* and *Syngonanthus*, however *Paepalanthus* appears to be polyphyletic. To utilize a data set independent of morphology, we are sequencing the chloroplast *trnT/L* and *trnL/F* intergenic spacers as well as the 3' end of the *ndhF* gene. The trees generated from our data sets so far also support the monophyly of *Eriocaulon* and *Syngonanthus* and concur with the polyphyly of *Paepalanthus*. However, the molecular data differs from the morphological data for the placement of the smaller genera, and for the circumscription of the subgenera of *Paepalanthus*. For example, *Lachnocaulon* and *Tonina* have a sister group relationship and *Blastocaulon* appears to be polyphyletic. As more representative taxa are examined, a clearer picture of relationships within the family should emerge.

580 URBATSCH, LOWELL^{1*}, PATRICIA COX², AND RICHARD RUTH¹

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Is Rudbeckia heterophylla (Asteraceae, Heliantheae) a central Florida endemic of "ancient" hybrid origin?

Rudbeckia heterophylla, a species in the southeastern clade of subgenus Macrocline, is restricted to Levy County Florida where it is locally abundant. Although originally described as a distinct species, it has been treated for the past 50 or more years as a variety of the widespread, common *R. laciniata* based largely on their sharing deeply lobed to pinnately compound cauline leaves. Spontaneous garden hybrids between *R. auriculata*, a species restricted to Alabama and the panhandle of Florida, and *R. laciniata* resemble *R. heterophylla* in having simple basal and upper cauline leaves - characters used to separate this taxon from other entities of *R. laciniata*. ETS sequences of *R. auriculata* and *R. laciniata* are complemented in the garden hybrid and clearly show at least 12 polymorphic sites. ETS sequences for several individuals of *R. heterophylla* from Levy County show a similar degree of polymorphism indicating their possible hybrid nature. The polymorphisms, however, are not the same as seen in the garden samples.

In order to determine more precisely the origin and nature of *R. heterophylla*, ETS sequence variation is being explored further in *R. mohrii* and *R. nitida* which are also members to the southeastern Macrocline clade. The fact that *R. heterophylla* is completely allopatric from its sister taxa suggests that the probable hybridization event had taken place in the distant past, and that geographic distributions for these taxa or their ancestors differ dramatically from the present.

581 VANDERPOOL, STARIA S.* AND LINH V. HOANG

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Genetic variation among populations of Solidago riddellii (Asteraceae): an uncommon species with a wide range

Solidago riddellii Frank is an outcrossing, clonal, herbaceous perennial species with a localized but widespread distribution. It occurs in fens and wet meadows with a global range from northern Arkansas through the upper Midwest with eastern extensions into Ontario and western populations known from southern Manitoba. Genetic variation within and among populations of *Solidago riddellii* was assessed using allozyme polymorphism to investigate the consequences of rapid migration of plant species on population genetic structure. Modern distribution is inferred as the result of colonization northward following retreat of glaciers in the upper Midwest and the fragmentation of wetland habitat by modern land use patterns. A total of 416 individuals from 30 populations collected from 10 states and 2 Canadian provinces was characterized using enzyme electrophoresis. Estimation of population level genetic variation was accomplished using standard methods. Total genetic variability is consistent with that of other species with similar life history characteristics. Mean identity was 0.93, with identity values for regions ranging from 0.97 to 0.91 (south, including Arkansas and Missouri populations). UPGMA cluster analysis using genetic identity revealed 5 clusters. Cluster 1 includes 2 eastern populations (Ohio, Illinois), Missouri and Arkansas populations. Cluster 2 includes 9 eastern populations, 1 western population (Wisconsin) and 1 Missouri population. Cluster 3 includes 3 eastern populations, 8 western populations, and 1 Arkansas population. Cluster 4 consisted of a single, anomalous population in Missouri, and Cluster 5 a single Minnesota population. No strong pattern of genetic differentiation between geographic regions, or distribution of genetic variability was seen although weak regional patterns could be developed.

582 VERA-CALETTI, PATRICIA¹* AND TOM WENDT²

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A revision of the genus Calatola (Icacinaceae) in Mexico

The family Icacinaceae is represented in Mexico by four genera of trees (*Calatola*, *Oecopetalum*, *Mappia*, and *Ottoschulzia*), of which only *Calatola* is dioecious. *Calatola* is a Neotropical genus previously considered to consist of about six species, of which two (*C. mollis* Standl. and *C. laevigata* Standl.) were reported for Mexico, where the genus occurs in lowland rain forest and middle elevation cloud forest. A unique feature of *Calatola* is the presence in all parts of the plant of a compound, identified as a flavonoid in the present study, that oxidizes to a blue-violet color upon exposure to air. The present revision, which incorporates data from traditional morphology, field characters, chromosome numbers, pollen, germination and seedling morphology,

recognizes five species for Mexico, adding *C. costaricensis* Standl. and two undescribed taxa to those previously known. *C. laevigata* is shown to be a rare species of the Pacific slope, while populations of the Mexican Gulf slope, Guatemala, and Belice previously referred to this taxon represent an undescribed species. *C. costaricensis* displays geographic variation and possible intergradation with *C. mollis* and thus requires further study. The chromosome counts of $n = 14$ from two species (and $n = ca. 14$ from two others) represent the first counts for the genus, first counts for the family in the New World, and a new number for the family. Seed germination occurs in ca. 7-9 month in situ and over 12 months ex situ. All species in Mexico are represented by either small or very dispersed populations and are thus of conservation concern.

583 VERBOOM, G. ANTHONY*, SIMON T. MALCOMBER, ANDREW N. DOUST, AND ELIZABETH A. KELLOGG

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Sequence variation in the KNOTTED1 gene family across the grass family (Poaceae): implications for protein primary and secondary structure

KNOTTED-like homeobox genes are thought to be critical in plant morphogenesis, apparently being involved in meristem initiation and/ or maintenance. Sequence variation in this potentially important gene family is, however, poorly documented. In grasses, for example, published knowledge of sequence variation among *Kn1* homologues is based on data from as few as three species (barley, maize and rice). In order to gain a broader understanding of variation among *Kn1* homologues in grasses, we designed primers to amplify an 800bp portion of this gene family across a phylogenetically-diverse array of grasses. This sequence excludes the homeodomain and spans two introns that have a total length of about 300bp. In this paper we compare levels of sequence variation between coding and non-coding regions and evaluate how changes in the former influence protein primary and secondary structure. Finally, using the GPWG phylogeny of the grass family as a baseline, we use character optimization methods to identify in which lineages major levels of change have taken place.

584 WAGSTAFF, STEVEN J* AND ILSE BREITWIESER

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Phylogenetic relationships of New Zealand Asteraceae inferred from ITS sequences

Thirty-six new sequences including members of all New Zealand genera of Asteraceae and 60 published sequences representing the tribal diversity in the family were analyzed to assess the utility of ITS sequences to resolve phylogenetic relationships. Sequence divergence and length variation make the alignment challenging, nevertheless the utility of ITS sequences to resolve relationships within and among tribes of Asteraceae has been demonstrated in several recent publications. The ITS sequences comprised conservative regions at the 3' end of the 18S gene, the entire 5.8S gene, and the 5' end of the 26S gene along with the intervening internal transcribed spacers. The ITS region varied between 648 and 717 bp with a mean of 707 bp. Most insertions or deletions were only 1-3 bp with one large deletion of 58 bp identified in the ITS-1 spacer of *Brachyscome*. Independent analyses of the ITS spacer regions were largely congruent. The presence or absence of indels gave little resolution and exhibited high levels of homoplasy. Previous studies using chloroplast DNA sequences and morphology provided support for several clades, yet the relationships among some of these clades were uncertain.

The combined analysis of the entire ITS region yielded results that were largely consistent with these earlier studies. The New Zealand species are included in at least six clades corresponding to recognized tribes. Our results have also clarified the tribal affinities of a few genera. *Haastia*, previously aligned with the Gnaphalieae or the Astereae, is nested in the Senecioneae. *Centipeda*, previously included in the Astereae or Anthemideae, emerges near the Inuleae. *Abrotanella* emerges near the base of the Senecioneae confirming previous findings.

585 WALLACE, ROBERT S.

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Phylogenetic relationships among North American columnar cacti revisited

The evolutionary diversification of columnar cacti in North America has resulted in a range of morphologies from large trees, shrubs, and epiphytes, to geophytes, and single-stemmed dwarf forms. This group of cacti include members of the tribes Pachycereae, Leptocereae, which are predominantly large to moderately-sized trees and shrubs, and the Hylocereae which are primarily epiphytes. The South American genus *Corryocactus* (formerly placed in tribe Notocacteae) also has been allied to this clade. Comparative sequencing evidence from variation in plastid markers supports an origin for these North American cacti from within a sub-clade of the presently circumscribed tribe Brownieae of the central Andean region. The present study examined the primary patterns of phylogenetic divergence in this North American clade and reviews the systematic relationships between these tribes. Additionally, the phylogeny within each of the represented tribes was examined in the context of understanding the evolution of systematically useful morphological characters (vegetative and floral), and to evaluate present geographic distribution as related to phylogenetic divergence. Sequences of plastid non-coding regions of the *psbA-trnH* intergenic spacer and the *rp16* intron were used in concert with maximum parsimony techniques to develop a phylogenetic assessment of the various groups. It was discovered that the two subtribes of the Pachycereae, Pachycerinae and Stenocerinae, were strongly supported, the latter containing the genus *Echinocereus*. The relationship between the tribes Leptocereae and Hylocereae was found to be closer than previously hypothesized. Bat pollination is prevalent throughout these clades, however multiple shifts to entomophily were also suggested.

586 WALLICK, KYLE¹, WAYNE ELISENS^{1*}, PAUL KORES², AND MIA MOLVRAY³

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Phylogenetic analysis of trnL-F sequence variation indicates a monophyletic Buddlejaceae and a paraphyletic Buddleia

Recent molecular investigations of Buddlejaceae s. str. confirmed close phylogenetic relationships among *Buddleia*, *Emorya*, *Nicodemia*, and *Gomphostigma* and to certain groups within Scrophulariaceae and Lamiales. *Buddleia* is the largest genus within Buddlejaceae. Although *Buddleia* has over 90 species distributed in Africa, Asia, and the Americas, only two species have been examined using molecular data. To further test the monophyly of Buddlejaceae and to elucidate phylogenetic relationships among species of *Buddleia* and segregate genera, we examined nucleotide variation from the *trnL-F* region of the plastid

genome among 23 species of *Buddleia*, two species of *Nicodemia*, one species each from *Emorya* and *Gomphostigma*, and eight outgroup taxa. From an aligned length of 1029 bp, exclusion of gaps resulted in 778 sites and 79 informative characters. Seven indels were identified as parsimony informative when treated as binary characters. Maximum parsimony analyses of the combined data yielded 12 most parsimonious trees (length 419, CI = 0.969) after successive weighting. Our results indicated strong support for: 1) a monophyletic Buddlejaceae s. str. (bootstrap = 100, d = 8) comprising species placed in *Buddleia*, *Emorya*, *Nicodemia*, and *Gomphostigma*; 2) a paraphyletic *Buddleia*; 3) exclusion of *Nuxia* from Buddlejaceae; and 4) sister group status for the South African genus *Teedia* to Buddlejaceae (bootstrap = 100, d = 7). Within *Buddleia* and segregates, there was strong support for a clade made up of Asiatic species of *Buddleia* + *Nicodemia* + *Gomphostigma* + *Emorya*. African and most New World species were less resolved but formed a weakly supported clade. Within the *trnL-F* region, there were higher substitution rates in the IGS region compared to the *trnL* intron. Comparisons among five ingroup species with sequence data from nrDNA ITS and cpDNA *trnL-F* indicated that the *trnL-F* region had higher proportions of informative nucleotide substitutions and informative indels.

587 WANNTORP, LIVIA

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Phylogeny of Gunnera

Gunnera is a genus of angiosperms with 30-40 species occurring in America, from Southern Patagonia to Mexico, in New Zealand, Tasmania, the Malayan Archipelago, Hawaii, from South Africa to Ethiopia and on Madagascar. Many studies have recently been conducted in order to identify the systematic position of *Gunnera*. In contrast, the phylogeny within *Gunnera* has never been studied before. Consequently, no cladistic studies intended to explain the biogeographic antarctic pattern of *Gunnera* have been presented so far. The phylogeny of *Gunnera* investigated here for the first time by using three different gene regions, *rbcl* and the *rps16* intron of the chloroplast genome, and the nuclear ribosomal transcribed internal spacer (ITS) region. Analyses based on single gene regions, as well as the combined analysis of the three gene regions, all confirmed the same general phylogenetic pattern: the rare *G. herterifrom* Uruguay, which is also the only annual in the genus, is sister to all other species. Furthermore, the African *G. perpensis* sister to two well-supported monophyletic clades, one including all the South American and the Hawaiian species, and the other comprising all the species from New Zealand, Tasmania and the Malayan area. The phylogeny of *Gunnera* discussed and in the light of the new results, the evolution of some morphological characters, as well as biogeographical patterns of *Gunnera* are addressed.

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Intergeneric hybrids in New Zealand Gnaphalieae (Compositae)

Gnaphalieae in New Zealand comprises an estimated 70 to 80 species in ten genera. Most species, and three of the genera, are endemic. All genera were earlier included, at least in part, in *Gnaphalium* or *Helichrysum* with the exceptions of *Rachelia*, which is newly described, and *Craspedia*, which belongs to a quite different alliance. Interspecific hybrids are not infrequent in the New Zealand flora, but reports of intergeneric hybrids are

rare except in Gnaphalieae, for which a surprising number of anecdotal reports exist, many of them supported by herbarium material. We report here on the first rigorous testing of these hybrid hypotheses. Putative intergeneric hybrids were located in the wild. Four alternative hypotheses were tested for each specimen: that it was (a) within the range of variation of an existing species, (b) a mutant form of an existing species, (d) a hybrid, but of different parentage to that postulated. Specimens shown to fit none of these hypotheses were analyzed for intermediacy between the putative parent species, proximity to one or both parents, and fertility. Artificial resynthesis was attempted. Results of the analyses of two putative hybrids are presented. The existence of such putative intergeneric hybrid links led us to hypothesize that most New Zealand species evolved very recently within New Zealand rather than arriving separately by long distance dispersal from several sources. These would include the species of *Anaphalioides*, *Leucogenes*, *Rachelia*, *Raoulia*, those currently retained in *Ewartia* and *Helichrysum*, and possibly *Euchiton*, but not *Ozothamnus* or *Pseudognaphalium*. Independent support for this hypothesis has come from a recent analysis of ITS sequences which showed the group of all hybridising genera except *Euchiton* to be monophyletic.

589 WATSON, LINDA E.^{1*}, TIMOTHY M. EVANS², MATTHEW M. UNWIN¹, AND AMY B. KORKVEN

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Origin and diversification of Tribe Anthemideae (Asteraceae), based on molecular phylogenies of ndhF and ITS

The Anthemideae is primarily an Old World tribe that occurs mostly in north temperate regions, with centers of endemism in Mediterranean climates including the Iberian Peninsula of Europe and North Africa, as well in as the Cape Province of South Africa. It contains numerous cultivars, such as daisies and chrysanthemums, and also includes ecologically-important and widespread species such as sagebrush. The tribe is composed of 109 genera and 1700 species, however, the majority of species comprise five large core genera of 100+ species each, including *Artemisia*/*Seriphidium*, *Tanacetum*, *Achillea* and *Anthemis*. Molecular phylogenies based on chloroplast gene *ndhF* and the internal transcribed spacers (ITS) of nrDNA place several South African genera in a basal grade. The phylogenies also support an early divergence between members that occur in Far East Asia and the western Eurasian region. These two major clades are sister to clades that are also centered in South Africa. A South African origin for the Anthemideae is in contrast to previous hypotheses that the tribe originated in Eurasia, with an early vicariant event resulting in relictual members occurring in South Africa. In addition, derived placements of all five core genera indicate that these large and geographically-widespread genera are recent. There is little congruence with taxonomy and morphologically-based phylogenies, with considerable homoplasy in the morphological characters.

590 WEBSTER, GRADY L.^{*} AND KEVIN J. CARPENTER

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Pollen morphological characters as phylogenetic markers in neotropical taxa of Phyllanthus (Euphorbiaceae)

Pollen morphological characters as phylogenetic markers in neotropical taxa of *Phyllanthus* (Euphorbiaceae). Over 800 species of *Phyllanthus* have been classified into 10 subgenera with over 30 sections, but the broad scope of variation has

made it difficult to define monophyletic groups. Pollen morphological studies have provided clues to phylogenetic relationships, but have dealt mainly with Old World taxa. In the present study, pollen morphology has been illustrated (using SEM) of 22 American species in 11 sections. Pollen in subgenus *Conami* is of special interest because of reductions of apertures and exine ornamentation (pilae in most species). In subgenus *Xylophylla*, the spectacular development of clypeate grains (with exine shields defined by distinct muri) provides the most useful synapomorphy for defining this group of 80 species. An even more remarkable occurrence of clypeate pollen, with very small exine shields, occurs in section *Cyclanthera*; it remains unclear whether this indicates a common origin with subgenus *Xylophylla*.

591 WHITE, PAMELA J.^{1,2*} AND DENNIS W. STEVENSON²

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An emerging analysis of the evolution of fruit and seed features in the Menispermaceae

Fruits and seeds of the dioecious family Menispermaceae are notable for their remarkable variation as well as for the excellent details preserved in the fossil record. Endocarps can range in shape from erect to reniform to circinnate and are frequently ornamented with unique wings and protrusions. Seeds are sometimes observed cupping a ventral intrusion known as the "condyle" and can vary with regard to embryo shape, presence of endosperm, and orientation of the cotyledons. Although features such as these have traditionally provided many important taxonomic characters, they have never been tested objectively for their ability to distinguish natural groups. Classifications within the Menispermaceae have historically been unstable at the tribal as well as generic level. A preliminary combined analysis using morphological and molecular sequence data from the chloroplast *trnL* intron refutes the monophyly of at least some menisperm tribes and suggests novel relationships at the generic level.

592 WHITLOCK, BARBARA A.^{1*}, JUNGHOO LEE^{1,2},

OLENA DOMBROVSKA^{1,2}, FABIANA BERNASCONI-QUADRONI², AND YIN-LONG QIU^{1,2}

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Dating the age of angiosperms with DNA sequences of seven mitochondrial, plastid, and nuclear genes

There has been remarkable progress recently in clarifying phylogenetic relationships among basal angiosperm lineages using DNA sequences from multiple sources. Two major questions, however, have not been addressed using this massive amount of data: substitution rates of these genes in all lineages of basal angiosperms and use of these data to date major divergences within angiosperms. Here, we use a data set of seven genes, from the chloroplast (*atpB*, *rbcl*), mitochondrial (*atp1*, *matR*, and *SSU* and *LSU rDNA*), and nuclear genomes (*18S rDNA*), to examine patterns of substitution rates of these genes and to estimate the age of angiosperms. A global molecular clock can be rejected for all genes, and all combinations of genes, under all models of evolution explored. This is due in part to an apparent increase in substitution rate in 3-4 lineages, including monocots, Piperales, *Ceratophyllum*, and perhaps Ranunculales in the eudicots. This increase in rate is found in all three plant genomes. Nevertheless, by excluding these clades, it is possible to find local rate constancy among the remaining lineages. Using this pruned phylogeny, we attempt to estimate the age of angiosperms and divergence times of some basal

angiosperm clades. We compare these estimates to those derived from an alternative approach of using models that allow for heterogeneous rates of evolution.

593 WHITSON, MARY KATHRYN

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Untangling Physalis (Solanaceae) from the physaloids: two-gene phylogeny vindicates the splitters

In *Physalis*, yellow flowers with darkly spotted throats give rise to berries which are completely enveloped by inflated, lantern-like calyces. Despite this distinctive morphology, taxonomists have had difficulty delimiting the genus, and little is known about the phylogenetic relationships of the 75+ species of *Physalis*. DNA sequence data from a segment of the nuclear gene *waxy* (600 bp) and the ITS region of the nrDNA (800 bp) was used to generate a phylogeny of *Physalis*. Taxon sampling included 30 species of *Physalis* plus related physaloid genera. The data sets were analyzed simultaneously using maximum parsimony as the optimality criterion. All characters had equal weights and gaps were treated as missing data. Trees were rooted using the outgroup *Witheringia*. As currently defined, *Physalis* is polyphyletic. While the morphologically typical species form a strongly supported clade, *P. alkekengi* (white flowers), *P. carpenteri* (clustered flowers) and *P. microphysa* (deeply lobed calyx) are separated from this clade by a grade of physaloid genera including *Quincula*, *Physalis* subgenus *Physalodendron* (*P. melanocystis* and *P. arborescens*), *Oryctes* and *Chamaesaracha*. *P. alkekengi*, the type of *Physalis* and its only Eurasian member, is not included in the main *Physalis* clade. That clade consists of *Margaranthus* (in fruit, indistinguishable from *Physalis*) and *Physalis* species with solitary yellow flowers and highly inflated calyces. Other than section *Viscosa* (predominantly North American), the sections of *Physalis* do not appear to be monophyletic, though a rhizomatous perennial clade is formed by section *Viscosa* and the U.S. species of section *Lanceolatae*. In general, the phylogeny supports the physaloid genera as being distinct from *Physalis*, but does not support the monophyly of sections within the genus. However, further sampling within *Physalis* may suggest ways in which the infrageneric classification can be adjusted to recognize both monophyletic and morphologically distinctive units.

594 WHITTON, JEANNETTE*, STACEY THOMPSON, KATRINA DLUGOSCH, AND LINDA P. JENNINGS

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Phylogenetic relationships in the genus Townsendia (Asteraceae: Astereae) based on nuclear ribosomal DNA variation in ITS and ETS regions

The North American genus *Townsendia* comprises approximately 25-30 taxa that occur predominantly at mid to high elevations in the Rocky Mountains. Most species have narrow distributions: some are restricted to specific edaphic conditions, and species of *Townsendia* are assigned conservation status in both Canada and the United States. The genus includes annual, biennial and perennial taxa. In addition, diploid sexual and polyploid asexual populations occur in a number of species, and the genus has been considered a single agamic complex. We have sequenced the nuclear ribosomal spacers ETS and ITS for representatives of most taxa. Phylogenetic trees obtained from separate and combined analyses are all essentially congruent and reveal strong support for the monophyly of the genus, and the presence of a number of well-supported groupings. The deepest divergence within *Townsendia* separates the only annual species, *T. annua*, from the remainder of the genus. This findings contradicts the hypothesis proposed in Beaman's 1957 monograph of the genus.

In addition, our analysis reveals that apomixis and polyploidy are scattered among groups that include species known only as diploid sexuals. One well-supported clade includes a number of taxa known to have apomixis, but three additional groupings include both sexual and apomictic species. Thus, the genus provides an ideal study system in which to examine the evolution and spread of apomixis.

595 WIESE, ANNA K.* AND L. ALAN PRATHER

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Phylogenetic relationships in Cantua (Polemoniaceae): inferences from cpDNA sequences, nrDNA ITS sequences, and pollen morphology

Cantua is a small but complex genus in the Polemoniaceae subfamily Cobaeoideae. The species have Andean distributions, and are characterized by their shrubby or diminutively arborescent habits, dimorphic shoots, and pantoporate pollen. Comparative gene sequencing of the species has been undertaken for three regions of the chloroplast genome (*trnT trnL* 5' and *trnL* 3' *trnF* spacer regions, and partial *ndhF* coding region) and the inter-nal transcribed spacer region of nuclear ribosomal DNA to help elucidate relationships within the genus and among members of the subfamily Cobaeoideae. In a recent classification, the genus *Huthia* was subsumed in *Cantua*, but no phylogenetic data have been applied to this problem. Our phylogeny suggests that *Cantua* is paraphyletic to the former genus *Huthia*, and that *C. (Huthia) coerulea* is sister to *C. quercifolia*. This result is consistent with the recent nomenclatural changes. A preliminary study of the pollen morphology using scanning electron and light microscopy corroborate the molecular results. Among *Cantua* species, *C. quercifolia* and *C. coerulea* share the pollen synapomorphy of irregularly spaced verrucae on their areolate semitectate sexine.

596 WILLIAMS, RACHEL A.* AND L. ALAN PRATHER

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Evolutionary relationships of the Clinopodioid complex and allied genera (Lamiaceae: Nepetoideae) based on ITS sequence data

Subfamily Nepetoideae is the largest and most economically important subfamily of the Lamiaceae. Prior studies have supported the monophyly of the subfamily and a study based on cpDNA restriction site data identified a clade of several genera in tribe Menthaeae, including *Blephilia*, *Calamintha*, *Clinopodium*, *Monarda*, and *Hedeoma*, that have apparently undergone a rapid diversification. This clade of 11 genera includes some that have been collectively referred to as the 'Clinopodioid complex'. The cpDNA restriction site study provided very little resolution of the relationships between these taxa. Here we use ITS sequence data to study the relationships of these eleven genera plus several additional ones that we have identified as belonging to this clade. The ITS data provided variation that yielded substantial resolution among these taxa. Preliminary results from the phylogenetic analysis indicate that several genera are non-monophyletic. Furthermore, many of the characters that are used to circumscribe genera in this complex, such as stamen number and calyx shape, are highly homoplasious. Our data suggest that *Clinopodium*, *Hedeoma*, and *Monardella* are non-monophyletic, and that *Blephilia*, *Monarda*, and *Pycnanthemum* are monophyletic. Major clades in this group are biogeographically cohesive.

597 WILSON, CAROL A.

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A phylogenetic study of Iris subgenus Iris utilizing matK sequence and morphological data

The genus *Iris* has more than 250 species in six subgenera. Subgenus *Iris* is the largest subgenus with approximately 90 species that are especially well represented in Caucasia and the Middle East. The most recent revision of *Iris* subgenus *Iris* (Taylor, 1976) segregated taxa into five sections based on presence or absence of an aril, nature of beard, number of inflorescence bracts and rhizome characters. I have undertaken a phylogenetic study of *Iris* subgenus *Iris* using *matK* sequence and morphological data. Preliminary data does not support current sectional divisions within the subgenus. Preliminary evidence based on the inclusion of species from *Iris* subgenera *Limniris*, *Scoparis* and *Hermodactylodes* also indicates that *Iris* subgenus *Iris* may not be monophyletic.

598 WOLFE, ANDREA D.^{1*}, CHRISTOPHER P. RANDLE¹, AND KIM E. STEINER²¹Dept. of EEOB, The Ohio State University; ²Dept. of Botany California Academy of Sciences*Phylogeny and biogeography of Orobanchaceae reconstructed from nuclear rDNA 5.8s and ITS sequence data*

Orobanchaceae, as recently redefined, has 88 genera and ca. 1530 species. Most taxa are distributed in temperate regions of the world with the highest density of genera and species in the northern hemisphere and in Old World floristic regions. We sequenced the nuclear rDNA 5.8s and ITS regions from 29 parasitic and six nonparasitic genera from Lamiales to reconstruct the phylogeny of Orobanchaceae. Our sampling included all of the major parasitic genera and several of the smaller genera from throughout the range of distribution. The ITS phylogeny supports the monophyly of Orobanchaceae with *Lindenbergia* as the basal lineage. Genera with distributions in southern and eastern Africa are located in the most derived position of the tree. The topology of the ITS tree suggests an origin of Orobanchaceae in Asia with subsequent migration of elements to North America and the Mediterranean region via the Tethyan seaway, followed by dispersal to northeastern Africa and a secondary diversification of genera throughout the southern hemisphere.

599 WOLFE, ANDREA D.^{1*}, REBECCA REILAND¹, CHRISTOPHER P. RANDLE¹, FRANK J. SMITH², AND PAUL G. WOLF³¹Dept. of EEOB, The Ohio State University; ²Western Ecological Services, Inc.; ³Dept. of Biology, Utah State University*Conservation genetics of Penstemon bicolor ssp. bicolor*

Penstemon bicolor ssp. *bicolor* is endemic to the Spring Mountains of Clark County, Nevada. It has been designated a sensitive species threatened by urban growth in the Las Vegas Valley, which is resulting in habitat degradation and loss. We used ISSR markers to assess the amount of genetic diversity present in populations of *P. bicolor* ssp. *bicolor*, and we compared the genetic diversity of ssp. *bicolor* to the widely distributed ssp. *roseus*. Two hundred ninety five individuals from seven populations of *P. bicolor* ssp. *bicolor*, six populations of *P. bicolor* ssp. *roseus*, and several populations of *P. palmeri* were used in the survey. Our results suggest that the amount of genetic divergence between the two subspecies of *P. bicolor* is relatively low and that average similarity between subspecies is the same as within subspecies.

600 WURDACK, KENNETH J.^{1*} AND JAMES W. HORN²¹The Lewis B. and Dorothy Cullman Program for Molecular Systematics, The New York Botanical Garden, Bronx, NY 10458; ²Dept. of Biology, Duke University, Box 90338, Durham, NC 27708*A reevaluation of the affinities of the Tepuianthaceae: molecular and morphological evidence for placement in the Malvales*

The Tepuianthaceae consists of the genus *Tepuianthus*, containing 7 taxa that are narrow endemics within the Guayana Highlands region of Venezuela and adjacent Colombia and Brazil. Hypotheses of the systematic affinities of this family have suggested relationships with the Celastrales (Cronquist) and Rutales (Takhtajan, Thorne), though the Tepuianthaceae is unplaced in the APG system. Parsimony analysis of sequence data from 18S rDNA, *atpB*, and *rbcl* places *Tepuianthus* within the Malvales, sister to the Thymelaeaceae, *sensu lato* (including Gonystylaceae). The secondary phloem of *Tepuianthus* is characteristic of Malvales in that it is tangentially stratified into fibrous and nonfibrous layers, with radially dilated phloem rays. Potential morphological synapomorphies with Thymelaeaceae include the absence of stipules, unilacunar nodes, a single ovule per locule with apical-axile placentation, ovules with a ventral raphe, and ovules with the micropyle formed exclusively from the inner integument. We propose to taxonomically accommodate *Tepuianthus* in a new Thymelaeaceae subfamily. The unusual pollen of *Tepuianthus* may represent an intermediate state between a tricolporate type—ubiquitous in early-branching lineages of major clades within Malvales—and the highly derived crotonoid exines found in Thymelaeaceae. The presence of a well-formed, 5-merous corolla in addition to a series of extrastaminal, glandular scales in *Tepuianthus* leads to the reinterpretation of similar scales in *Gonystylus* as not representing a vestigial corolla as previously thought. The phylogenetic position of *Tepuianthus* is biogeographically significant in that, like the malvlean dipterocarps *Pakaraimaea* and *Pseudomonotes*, it represents an early-branching, presumably relictual, Guayana Shield-centered lineage of an otherwise mostly paleotropical clade.

601 YANG, L.^{1*}, K. STEELE¹, AND M. LAVIN²¹California State University, Hayward; ²Montana State University, Bozeman*Phylogenetic analyses of selected genera of subfamily Papilionoideae, using nucleotide sequence data of the nuclear-encoded gibberellic acid 20-oxidase genes*

The gibberellic 20-oxidases are important enzymes that catalyze some of the later steps in the gibberellic acid biosynthetic pathway. The GA 20-oxidases are encoded by three nuclear of a gene family that encodes other enzymes active in the gibberellic acid biosynthetic pathway, such as 3b-hydroxylase encoded by Mendel's stem length gene *Le*. The GA 20-oxidases are members of the 2-oxoglutarate dependent dioxygenase group of enzymes. The genes encoding the three GA 20-oxidases have diverged sufficiently so as to make it possible to design ortholog specific primers for each paralog using published sequence data from *Pisum*, *Phaseolus*, and *Glycine*. We are using these sequence data to test or provide additional support for selected phylogenetic relationships among genera in subfamily Papilionoideae that have been hypothesized on the basis of morphological data and/or phylogenetic analyses of the family based on chloroplast gene sequences. Two examples are as follows. Phylogenetic analyses of *matK* data indicate that *Trifolium* is basal to a clade composed of genera in the Viciaeae, *Vicia*, *Lens*, *Pisum*, and *Lathyrus* rather than being in a clade with other genera in the Trifolieae, the tribe in which *Trifolium* is placed. The relationship suggested by *matK* data is supported by phylogenetic analyses of genes encoding GA 20-

oxidases. Within the Millettieae/Phaseoleae clade analyses of matK data indicate that Dalbergiella is sister to a clade consisting of core Millettieae, Phaseoleae and related genera, but this relationship is weakly supported; however analyses of genes encoding GA 20-oxidases provide strong support for this relationship. Genes encoding GA 20-oxidases provide phylogenetically informative characters that support a number of hypothesized relationships within subfamily Papilionoideae.

602 YELTON, SHARON¹* AND ROBERT F. NACZI²

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Sectional circumscription and relationships of gynecandrous Carex subgenus Vignea (Cyperaceae) based on morphology

Carex is one of the ten largest genera of flowering plants in the world, containing about 2500 species. Despite its great size and ecological importance, there has been little phylogenetic analysis within the genus. Nearly all of the classifications that do exist are strictly phenetic and, therefore, probably not natural. One probable clade within subgenus *Vignea* contains eight sections (about 165 species) and can be recognized by the presence of gynecandrous spikes. The clade is wide-ranging in occurrence and especially diverse in Eastern North America. We used micromorphological and anatomical data to reconstruct the phylogeny of sections within this clade. Characters include: macromorphology (especially reproductive features), culm anatomy using light microscopy, perigynia anatomy using light microscopy, and achene surface morphology using scanning electron microscopy. We polarized character states using a composite outgroup of nongynecandrous species within subgenus *Vignea*. Using parsimony methods, we conducted a phylogenetic analysis of these data. Our preliminary results of the sections we have studied indicate the following phylogenetic hypothesis: (*Stellulatae* + (*Carex seorsa* + ((*Glareosae* + *Deweyanae*) + (*Remotae* + (*Cyperoideae* + (*Ovales* + *Planatae*)))))). Our preliminary results also provide placement for two previously problematic species. We found that *Carex seorsa*, previously placed in section *Stellulatae*, belongs in a separate, apparently undescribed section. Our data also indicate a resolution of the controversial placement of *Carex laeviculmis*, placing the species in section *Glareosae*.

603 YIP, KWOK LEUNG¹* AND BRENT D. MISHLER²

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A reappraisal of the resorption pores of hyalocysts in the Calymperaceae and their phylogenetic significance

Despite difficulties in taxonomic circumscription and phylogenetic placement, the Calymperaceae, a diverse and ecologically important family of tropical mosses, exhibits an array of peculiar features. The 'leucobryoid' leaf architecture, found in some members of the family, features distinctive layers of chlorocysts and hyalocysts. Edwards (1980, J. Bryol. 11:49-93) previously studied layers of the resorption pores in the hyalocysts in the more "normal" leaves of *Calymperes*. As part of ongoing phylogenetic and monographic research in the Calymperaceae, we observed microscopically the variation of resorption pores among exemplar members of the family and its putative relatives, and evaluated their potential as taxonomic characters. Internal pores of hyalocysts are distributed on the lateral and transverse walls whereas pores on the adaxial and abaxial walls (when present) are open to the exterior.

This investigation supports recent phylogenetic analyses indicating an expanded concept of the Calymperaceae and helps to resolve relationships within the family. Acknowledgment: We are grateful to acknowledge the funding provided by the National Science Foundation (PEET: Partnerships for Enhancing Expertise in Taxonomy; DEB-9712347).

604 YOUNG, LAURA*, PAUL KORES, AND MIA MOLVRAY

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Phylogenetic analysis of Schoenoplectus (Cyperaceae) using ITS sequence data

Schoenoplectus is a morphologically diverse genus that contains 30-40 species that is found predominantly in wetland areas. The genus has a complex taxonomic history and was previously considered a segregate of *Scirpus*. Recent molecular analysis by Muasya et al. (2000) using *trnL-F* and *rbcl* has shown evidence of paraphyly in *Schoenoplectus*, but a comprehensive phylogenetic analysis of this genus has not been undertaken. This study attempts to clarify relationships within the North American species by using ITS DNA sequence data. Fourteen ingroup and two outgroup taxa were examined in this preliminary study using maximum parsimony. *Schoenoplectus*, as currently delimited, is paraphyletic. *Isolepis* is sister to the dwarf species of *Schoenoplectus*, and three sampled species that were formerly placed in *Bolboschoenus* are sister to the *Isolepis-Schoenoplectus* clade. In our preliminary analysis there are indications that the large-sized *Schoenoplectus* species form a monophyletic group. Expanded sampling within *Schoenoplectus* and related genera is in progress.

605 YOUNG, NELSON D.* AND JOHN HEALY

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Incorporating indels as characters in phylogeny and the search for the best multiple sequence alignment

One limitation to exploratory analyses of optimal DNA sequence alignment has been the lack of a computer program to code indels (gaps) as characters for phylogenetic analysis. We have produced a program, GapCoder, which does this. It can be used as part of an objective method to find the best multiple sequence alignment. The method involves four stages; (1) producing several alignments, either by eye or by using a program such as Clustal X. (2) coding indels as additional characters in the data matrix, using GapCoder. (3) doing a phylogenetic analysis based on each of the alignments, using PAUP or other phylogeny software. (4) choosing the best alignment according to the optimality-criterion, such as the following; the best alignment is the one that produces phylogenies with the least homoplasy. Examples from ITS and matK will be used to illustrate the method. Instructions on how to obtain a free copy of the program will be given during the talk.

606 ZEREGA, NYREE CONARD* AND TIMOTHY J. MOTLEY

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Artocarpus (Moraceae) molecular phylogeny and the systematics and origins of breadfruit, *Artocarpus altilis*

Artocarpus (Moraceae) is a paleotropical genus comprised of approximately 50 species native to the lowlands of Southeast Asia and Oceania. The species are primarily large monoecious, latex producing trees with a syncarpous fruit that may attain very large sizes in some of the species (i.e. *A. heterophyllus*, jackfruit and *A. altilis*, breadfruit). In the most recent revision of the genus Jarrett (1959) divided *Artocarpus* into two subgenera based on leaf arrangement and stipule attachment and further subdivisions were based on fruit and laminar characters. However, molecular and phylogenetic studies are still lacking for the genus. Additionally, Jarrett was unable to resolve the historically confused systematics of breadfruit, an important starch crop in Oceania. Three very closely related *Artocarpus* species must be considered in this matter. *Artocarpus altilis* is the cultivated primarily seedless breadfruit, *A. camansi* is a wild species native to New Guinea and possibly the Philippines and the Moluccas as well, and *A. mariannensis* is endemic to Micronesia. The great morphological variability and overlap of characters that exist within and among these taxa has made species delineation and breadfruit origins unclear leading Jarrett to lump all three taxa into one species called *A. communis*. Sequence data from both ITS (internal transcribed spacers) and the *trnL-F* region (intron plus spacer) for 25 ingroup and six outgroup taxa were analyzed using parsimony analysis. The results suggest that *Artocarpus* is monophyletic, but do not entirely support Jarrett's circumscription of the genus. As the sequence variation was not great enough to resolve issues concerning breadfruit systematics and origins, AFLP (amplified fragment length polymorphisms) analysis was employed at this level. The AFLP data set suggests that *Artocarpus camansi* and *A. mariannensis* are distinct species, which are both implicated in the origin of the cultivated *A. altilis*.

607 ZHANG, WEN-HENG, ZHI-DUAN CHEN*, HU-BIAO CHEN, AND YAN-CHENG TANG

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Phylogeny of the Dipsacales s.l. based on chloroplast trnL-F and ndhF sequences

The phylogeny of the order Dipsacales s.l. is still problematic. Prior molecular studies based on *rbcl* and *ndhF* genes discussed the phylogeny of Dipsacales s.l., but because of limited sampling the problems could not be resolved contently. In our research, the strategies of dense sampling and combined DNA sequence analysis (*trnL F* region and *ndhF* gene) are carried out within Dipsacales s.l. to elucidate the delimitation of families and the relationships among them. Sequence data for the *trnL-F* region of 26 taxa (25 ingroups and 1 outgroup) and *ndhF* gene of 28 taxa (25 ingroups and 3 outgroups) were used in the phylogenetic analyses. Parsimony analysis for the combined data sets for both genes resulted in only one most parsimonious tree. The results clearly demonstrate *Triplostegia* is extremely close to Dipsacaceae; *Morina*, which seems nearby Dipsacaceae, is possibly a separate family of its own. Both *Sambucus* and *Viburnum* have very close relationships with Adoxaceae, which implies they are two members of that family. Caprifoliaceae s.l. (excluding *Sambucus* and

Viburnum), which comprises the three clades Linnaeaceae (*Abelia*, *Dipelta*, *Kolkwitzia*, *Linnaea*), Diervillaceae (*Weigela*) and Caprifoliaceae s.str. (*Heptacodium*, *Leycesteria*, *Lonicera*, *Symphoricarpos*, *Triosteum*), is paraphyletic. The most parsimonious tree recognizes seven major clades of Dipsacales s.l. with the following relationships: (Apiales (Adoxaceae (Diervillaceae (Caprifoliaceae s.str. (Linnaeaceae (Morinaceae (Dipsacaceae, Valerianaceae).

608 ZJHRA, MICHELLE L.

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Cauliflory: seeing the flowers for the trees

Iam investigating the evolution of cauliflory (flowers/fruits woody stems or branches) within three plant families (Annonaceae, Bignoniaceae, Moraceae). Cauliflory is an important inflorescence architecture of the tropical rainforest understory and has evolved in parallel across many lineages. I will report on progress to date for phylogenetic, anatomical, and ecological aspects of cauliflory. Trends in evolutionary pathways will be discussed in the context of Malagasy Bignoniaceae (Coleae). The goal of this project is to tease apart the extent which phylogeny is involved in the multiple independent expression of inflorescences on wood, and in what way this trait evolved in association with other traits.

CONTRIBUTED POSTERS**609 ALEXANDER, J. ANDREW* AND AARON LISTON**

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Tests of recombinant speciation in Astragalus

Astragalus *mokiensis* Gray (Fabaceae), and *Astragalus preussii* Gray var. *laxiflorus* Gray are taxa endemic to the Mojave Desert that may be hybrids between two different sections of this genus. *A. mokiensis* is endemic to northeastern Clark County, Nevada and northwestern Mohave County, Arizona. *A. preussii* var. *laxiflorus* is endemic to the Lake Mead region of eastern Clark County, Nevada. These species are sympatric around Lake Mead, however, *A. preussii* var. *laxiflorus* is restricted to gypsum soils and *A. mokiensis* can be found on a variety of soil types. Two prevalent theories exist on the taxonomic relationships of *A. mokiensis* and *A. preussii* var. *laxiflorus*: either they are related to one of several varieties of *A. lentiginosus* (Section *Diphysi*) or they are related to *A. preussii* var. *preussii* (Section *Preussiani*). Alternatively, they could be recombinant hybrids between the two species. The relationships between *A. mokiensis*, *A. preussii* var. *laxiflorus*, *A. preussii* var. *preussii*, *A. lentiginosus* var. *ambiguus*, *A. lentiginosus* var. *palans*, *A. lentiginosus* var. *yucanus* will be investigated based on analyses of the internal transcribed spacer region (ITS) and morphological data.

610 ANDRUS, NICOLE

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Molecular evidence for a potential biogeographical connection between the Canary Islands and the Island of Socotra

Several genera exhibit biogeographical disjunctions between the Canary Islands-Morocco and East Africa-South Arabia [i.e. *Canarina* (Campanulaceae), *Campylanthus* (Scrophulariaceae), *Hemicrambe*, (Brassicaceae)]. These disjunctions represent

the remnants of a continuous vegetation that spread along North Africa before the formation of the Sahara Desert. The genus *Vieraea* (Asteraceae:Inuleae) is a monotypic genus restricted to ancient areas of the island of Tenerife (Canary Islands); based on morphological grounds this genus has been suggested to be closely related to one species of *Pulicaria* endemic to the island of Socotra south of Yemen (*P. vieraeoides*). A molecular systematic study based on ITS sequences of the nuclear ribosomal DNA was conducted to test the validity of this potential connection. This study includes a broad selection of genera of the tribe Inuleae.

611 ARIAS, SALVADOR^{1*}, TERESA TERRAZAS², AND KENNETH M. CAMERON³

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Phylogeny of Pachycereus (Cactaceae) based in molecular data

The phylogenetic relationships of *Pachycereus* species and subtribe Pachycereinae were studied using DNA sequence data. A parsimony analysis of chloroplast rpl-16 intron, trnL-F spacer, and internal transcribed spacer (ITS) region were sequenced for 29 species, representing the four genera of subtribe Pachycereinae (*Carnegiea*, *Cephalocereus*, *Neobuxbaumia* and *Pachycereus*), plus three additional genera of subtribe Stenocereinae, identified as closely related and used as outgroup. Phylogenetic analysis did not support the monophyly of *Pachycereus* with 12 species, including *Anisocereus*, *Backebergia*, *Lemaireocereus*, *Marginatocereus*, *Mitrocereus* and *Pterocereus* into its synonym. These results support three major clades into Pachycereinae, one defined to *Pachycereus hollianus* and *P. lepidanthus*, as the most basal lineage into Pachycereinae species. A second clade was resolved to *Cephalocereus* and *Neobuxbaumia*, with *Pachycereus fulviceps* as sister taxon. The tree topology suggested a third clade to *Carnegiea*, five *Pachycereus* species (here refer as *sensu stricto*), plus other five *Pachycereus* species as well as *Stenocereus aragonii* and *S. eichalmii*.

612 BECK, JAMES B.^{1*}, GUY L. NESOM², PATRICK J. CALIE³, GARY I. BAIRD⁴, RANDY L. SMALL⁵, AND EDWARD E. SCHILLING⁵

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Overview of Subtribe Solidagininae (Asteraceae: Astereae)

Subtribe Solidagininae O. Hoffm. is a generally accepted name referring to a portion of the tribe Astereae, but concepts of its morphological circumscription and constituent genera have varied widely. Sequences from the internal transcribed spacer (ITS) of nuclear rDNA were examined in an attempt to define Solidagininae and to test hypotheses regarding major lineages within this group. Parsimony analyses indicate that a monophyletic group can be identified that largely corresponds with Solidagininae as previously delimited by Nesom (1994)-characterized by glandular-punctate leaves, a corymboid capitulescence, yellow rays, disc style branches with papillate collecting appendages, and terete, multinerved achenes with a 1-seriate pappus, although exceptions abound. The group itself is less strongly supported than each of three constituent lineages. A "*Gutierrezia* lineage" composed of

genera producing small, turbinate achenes and basally indurate phyllaries occupies the basal position within the subtribe. An "*Ericameria* lineage"-an anomalous cluster of perennial shrubs (*Ericameria*) and annual herbs (*Pentachaeta*, *Rigiopappus*, *Tracyina*) is explicitly placed in the subtribe for the first time. The largest of the subgroups is the "*Solidago* lineage"-composed of a primarily herbaceous group (*Solidago* and close relatives) and a primarily woody one (*Chrysothamnus* and close relatives). The *Solidago* lineage exhibits low levels of sequence divergence within and between member genera, indicating a recent radiation, and the data are insufficient to draw conclusions regarding its internal phylogenetic structure. Solidagininae is almost an entirely North American group and apparently arose from near the very base of the "North American clade" of Astereae, although several of the genera have secondary radiations in South America.

613 BHARATHAN, G.^{1*}, L. RAZ², AND P. WILKIN³

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The true yams, Dioscorea (Dioscoreaceae): phylogenetic analysis of chloroplast nucleotide sequences

The origin and evolution of *Dioscorea*, the pantropical genus of true yams, are fascinating topics from historical, biogeographic, and morphological points of view. For instance, Burkill (1960) hypothesized an early split within the genus into New World and Old World lineages based on current non-overlap between species ranges in the two regions. However, a recent study of *Dioscorea*, based on rbcL sequences (Caddick et al. 2000), shows that some species in the New World are more closely related to those in the Old World. This suggests either that lineages with species in both regions have persisted, or, alternatively, that dispersal accounts for the appearance of Old World relatives in the New World. The present study extends sampling to other parts of the chloroplast genome (intergenic spacer between trnT and trnL genes, and ndhF gene) and other sections of the genus (in particular, the putative 'basal' section *Stenophora* and nested genus *Rajania*). Our findings are largely congruent with other results and are discussed in the context of the biogeographic hypotheses outlined above.

614 BLATTNER, FRANK R.

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Tracing allopolyploid speciation in Hordeum

The genus *Hordeum* L. occurs with about 32 species in temperate climates mostly in Eurasia and the Americas. Four basic genomes were described within *Hordeum*: 'I' in barley and the closely related *H. bulbosum*, 'Y' in *H. murinum*, 'X' in *H. marinum*, and 'H' in all other species of the genus. The latter group contains several (tetra- and hexa-) polyploids. To reveal species history the nrDNA ITS region of all *Hordeum* species was PCR amplified, cloned, and several clones of each species were sequenced. The analysis of the resulting sequences allowed in many cases the reconstruction of the parental ancestors (or ancestor groups) of allopolyploids and a distinction between putative auto- and allopolyploid species. Phylogenetic analysis clusters 'I' and 'Y' genomes and 'X' and 'H' genomes, respectively, and reveals a SW Asian origin of the genus. A relatively fast radiation occurred in C Asia and S America possibly due to the evolution of salt tolerance and/or small seeds in a basal taxon of the X/H subgroup of the genus.

615 BOGLER, DAVID J.^{1,2*}, ALEXANDRA MARRACCINI¹, AND JAVIER FRANCISCO-ORTEGA^{1,2}

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Molecular systematic studies of cycads (Cycadales): initial results based on chloroplast DNA gene spacers, ITS rDNA sequences, and DNA fingerprinting

Cycads are an ancient group of gymnosperms that were abundant and widely distributed during the Mesozoic, but are now largely confined to isolated tropical and subtropical regions. Many cycads are currently threatened with extinction and there is an urgent need for more information about their taxonomy and genetics. Extensive molecular studies of cycads were initiated at the molecular systematics laboratory set up in collaboration with Florida International University, utilizing the world renowned cycad collections at Fairchild Tropical Garden and the Montgomery Botanical Center. The 11-12 genera of cycads currently recognized are thought to comprise a monophyletic group, classified as a single order, the Cycadales, which is divided up into three or four families. Analysis of morphological characters could not fully resolve all the genera. We studied cycad phylogeny using a variety chloroplast genes and spacers (trnI intron, trnS-trnG, psbB-psbF, atpB-rbcL) and nuclear regions (ITS). The results of this study are presented and assessed with reference to previous phylogenetic analyses and classification schemes based on morphology and anatomy. *Cycas* is the most divergent genus, followed by *Dioon*, which is also isolated from the other genera and contains two major clades. *Stangeria* appears to be related to *Ceratozamia*, *Zamia*, and *Microcycas*. *Lepidozamia* appears to be more closely related to *Encephalartos* in Africa than to *Macrozamia*. Sequence variation among the species of *Ceratozamia* is especially low. DNA fingerprinting studies were also initiated with *Microcycas* to try and find molecular markers for sex determination of seedlings and markers for future conservation genetics projects.

616 BROWN, GREGORY K.* AND DOROTHY E. TUTHILL

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Inter-simple sequence repeat (ISSR) variation in three populations of Gaura neomexicana ssp. coloradensis (Onagraceae)

Gaura neomexicana ssp. coloradensis, commonly known as the Colorado butterfly plant, is a regional endemic restricted to approximately 1700 acres of habitat in Laramie County, Wyoming, western Kimball County Nebraska, and Weld County, Colorado. The taxon was recently listed as Threatened under the Endangered Species Act (U.S. Fish and Wildlife Service, October 2000). The three largest populations of *G. neomexicana ssp. coloradensis* are confined to F.E. Warren Air Force Base, Cheyenne, Wyoming, and are known in the literature as the Crow Creek, Diamond Creek, and "unnamed drainage" populations. For each population, DNA samples were obtained from 50 different randomly selected individuals. An initial survey of ISSR locus variation, using three primers on the entire sample of 150, revealed very low levels of variation, both within and between populations. In an effort to reveal additional ISSR locus variation, subsets of eight individuals were randomly chosen from each population sample of 50. The reduction of sample size from 150 to 24 permitted examination with more ISSR primers. A total of 12 ISSR primers were applied to the sample of 24, revealing 88 loci. A sample-by-locus matrix was constructed, and loci were scored as present or absent (or as missing data if PCR failed). The matrix contained 3.4% miss-

ing data, with most coming from one individual. Results from cluster analysis revealed a high level of genetic similarity (0.88) across the entire sample, and no similarity clustering by population. The apparent ISSR locus homogeneity across these three populations was not unexpected. Prior to the establishment (1867), and subsequent expansion of the military base, these three populations were very likely lobes of a larger, contiguous population.

617 BUNSAWAT, JIRANAN* AND LAWRENCE A. ALICE

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Molecular characterization and phylogenetic utility of nrDNA ETS Sequences in Rubus (Rosaceae)

In a continuing effort to gain insight into the systematics of *Rubus* (Rosaceae), we examined the external transcribed spacer (ETS) of nuclear ribosomal DNA (nrDNA) to assess its suitability for phylogenetic analysis. We sampled four *Rubus* species (*R. arcticus*, *R. idaeus*, *R. odoratus*, and *R. trivialis*) representing four subgenera and corresponding to distinct clades based on previous analysis of ITS region sequences. We PCR amplified the entire nrDNA intergenic spacer (IGS) using universal primers (18S-IGS and 26S-IGS). The size of IGS in *Rubus* is approximately 2.5 kb. We sequenced the 3' end of ETS using primer 18S-E. ETS sequences of these species can be readily aligned by eye. Pairwise divergences among the four species noted from the ETS data range from 4.0 to 5.9% with a mean of 4.5%, whereas data from the ITS region for these same species range from 4.4 to 9.3% with a mean of 6.8%. Percent variable/parsimony-informative sites for ETS and ITS 1 + ITS 2 are 10.2/0.7% and 12.8/1.0% respectively. In contrast to published studies of ETS sequences in other plant taxa, variation in ETS is somewhat lower than for ITS in these four *Rubus* species. However, we have only sequenced the 3' portion of ETS, which is expected to be conserved.

618 CANNON, CHARLES^{1,2*} AND PAUL MANOS¹

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The use of morphometric shape descriptors in relation to an independent molecular phylogeny: the case of fruit type evolution in Bornean Lithocarpus (Fagaceae)

The Bornean assemblage of the genus *Lithocarpus* (Fagaceae) contains several novel modifications of the classic oak-acorn fruit type, which encompasses much of the generic level morphological variation. The shape variation in fruit type was adequately captured by continuous morphometric descriptors of radial outlines of fruit exocarp and receptacle. Both a principal components analysis of elliptic Fourier coefficients (EF-PCA) and eigen-shape analysis (EGS) provided informative descriptors of shape variation. A neutral evolutionary model and restricted maximum likelihood was used to create a morphometric transformation series. Several important taxonomic and phylogenetic aspects were captured by these analyses. An independent molecular phylogeny of the ITS regions of the nuclear ribosomal DNA for the same exemplar species supported parallel derivations of a specialized fruit type, not apparent in the morphometric transformation series. This incongruence suggests convergent evolution of a complex fruit morphology between independent lineages. Conversion of morphometric series into matrix representations weighted by standardized branch lengths allowed a combined phylogenetic analysis with the molecular data which produced a single most parsimonious tree and supported two independent derivations of the specialized fruit type. The relative rates of change between morphology and molecules is not correlated between well-supported nodes and do

not consistently deviate in one direction or the other. The molecular change from outgroup to ingroup is much greater than the morphometric change while transitions to the specialized fruit type involved large morphometric changes with little corresponding molecular change. The use of continuous morphometric shape descriptors significantly contributed to our understanding of fruit evolution in a morphologically difficult group.

619 CARLSWARD, BARBARA S.^{1*} AND W. MARK WHITTEN²

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Molecular systematics of leafless Vandaeae (Orchidaceae): an example from tropical America

Leafless members of tribe Vandaeae (Orchidaceae) have undergone extreme reduction in habit and represent a novel adaptation to the canopy environment. In these leafless orchids, photosynthetic leaves are absent or reduced and deciduous. Instead, green roots have assumed the role of food-assimilation. Many also possess an extremely condensed stem, making the plant appear "shootless." Vandaeae form a large, pantropical group of orchids traditionally divided into three subtribes: Aeridinae, Aerangidinae, and Angraecinae. Leafless taxa occur throughout Vandaeae and are geographically distributed in Africa, Asia, and tropical America. While the most widely accepted classification system is based solely on floral morphology, our study was based upon sequence data primarily from ITS nrDNA. Preliminary results from this nuclear data set indicate the African Aerangidinae form a paraphyletic grade from which the African and Madagascan Angraecinae are derived. The Asian Aeridinae, however, do form a well-supported clade. Phylogenetic relationships of leafless neotropical Angraecinae (*Dendrophylax*, *Harrisella*, *Polyradicion*, and *Campylocentrum*) were estimated using combined nuclear (ITS) and plastid (*trnL-F*) data sets, with African *Angraecum* species as outgroups. Our molecular analyses support only two monophyletic genera, *Campylocentrum* and a broad *Dendrophylax*, which seem to indicate that traditional approaches of classification, based primarily on floral morphology, are not predictive of phylogenetic relationships.

620 CARPENTER, K. J.^{*} AND G. L. WEBSTER

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Evolution of pollen diversity in neotropical Phyllanthus (Euphorbiaceae)

The genus *Phyllanthus* (Euphorbiaceae), with over 800 described species of trees, shrubs, and herbs, has a pantropical distribution. To better understand the range of pollen morphology and its evolution in the neotropical taxa, and to elucidate their relationships, 22 species from 11 sections have been examined with scanning electron microscopy. Special attention has been paid to the subgenus *Conami* because of its apparent close affinity to the African subgenus *Kirganelia*, and the variation in apertures and exine sculpturing among closely related species. Of particular interest are clypeate pollen grains, in which the exine is differentiated into polygonal shields. These are best known in the large subgenus *Xylophylla*, with over 80 species; however, a unique type of clypeate grain has evolved, apparently independently, in section *Cyclanthera*. Indeed, the extraordinary grains of *P. lindeni* appear to be unique in the Euphorbiaceae and in all seed plants. Phylloclade-bearing species of section *Xylophylla* in the West Indies have clypeate pollen grains, while phylloclade-bearing Brazilian species (section *Phyllanthus*) have 3-colporate pollen

grains with reticulate exine; the pollen evidence suggests the convergent evolution of similar vegetative morphologies in neotropical *Phyllanthus*.

621 CLEMENT, WENDY L.^{1*}, LAURA L. FORREST², AND SUSAN M. SWENSEN¹

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Phylogenetic placement of Hillebrandia sandwichensis (Begoniaceae)

Members of the angiosperm family Begoniaceae are spread globally throughout the tropics and collectively comprise three genera: *Begonia* with approximately 1400 species, *Symbegonia* with 12 species endemic to New Guinea, and *Hillebrandia* which is monotypic and endemic to Hawaii. *Begonia* is currently divided among 63 sections with most sections being restricted to particular continents. Recent phylogenetic reconstructions have revealed distinct clades of American, Asian, and African species. Cladistic analyses using sequence data from ITS, *rbcl* and 18S indicate that African species of *Begonia* are basal and that *Hillebrandia* is the most ancestral member of the family. A broader phylogenetic analysis that includes representatives from the order Cucurbitales (Cucurbitaceae, Datisceae, Tetramelaceae, Begoniaceae, Coriariaceae, and Anisophylleaceae) provides an expanded view of *Hillebrandia's* position within the order. The ancestral placement of *Hillebrandia* within Begoniaceae combined with its endemism to Hawaii poses an interesting biogeographic question.

622 CORTES, ROCIO^{1*}, PIERO G. DELPRETE¹, AND TIMOTHY J. MOTLEY²

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Systematics of Retiniphyllum (Rubiaceae)

The neotropical genus *Retiniphyllum* consists of approximately 23 species of shrubs and small trees, most of them occurring in the Guayana region, and with a few species reaching the Amazon basin, Central, and Eastern Brazil. This genus is characterized by having stipules producing copious resinous secretion, inflorescences racemose, spicate or fasciculate, flowers subtended by bracteoles and involucels, corollas white, pink or red, anthers with apical and basal appendages and 5-locular ovary with two collateral ovules per locule. Because of its peculiar morphological features, the taxonomic position of *Retiniphyllum* has been debated among botanists. Robbrecht placed it in the monotypic tribe Retiniphyllae. Recent phylogenies using molecular data support Robbrecht's placement in this tribe, and indicate that this tribe should be included in the Ixoroideae sensu lato. A phylogenetic analysis using morphological characters was performed analyzing a data matrix with 23 taxa and 42 characters. *Sipanea* and *Sipaneopsis* were selected as outgroup. The analysis produced four shortest trees of 169 steps each, where *Retiniphyllum* appeared to be monophyletic. The morphological cladogram showed that white flowers were derived once in *Retiniphyllum*. A preliminary phylogenetic analysis using ITS sequences was performed including the nine *Retiniphyllum* species of which fresh material was available. In the phylogeny obtained, two major clades were formed, which seemed to correspond to Müller's sections *Euretiniophyllum* (with racemose inflorescences) and *Commianthus* (with spicate inflorescences). According to the results obtained, there was conflict between the morphological and molecular data. For example, *Retiniphyllum speciosum*, a species with red flowers, was nested

within the white flower species in the molecular cladogram. Because the molecular analyses was performed with only a few species, at this point it is difficult to determine the significance of the incongruence between the molecular and morphological phylogenies.

623 GONZALEZ, DOLORES* AND ANDREW P. VOVIDES

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Low interspecific divergence in the genus Ceratozamia (Zamiaceae) detected with nuclear ribosomal DNA ITS, and chloroplast DNA trnL-F non-coding region as indication of recent speciation

The cycads are generally perceived as a very ancient lineage. In addition, high extinction rates and very long generation times may preclude the dynamics of genetic variation. More than 20 of the known and putative species of the Mexican cycad genus *Ceratozamia* were examined for variation at the molecular level in non-coding regions from the chloroplast and nuclear genomes. Cladistic analyses of single and combined sequences of ITS and *trnL-F* non-coding region supported three main clades within *Ceratozamia*. The rate of change of these genomes is considered fast and appropriate to recover variation at the level of genera. However, only 33 nucleotide positions were informative out of 2184, among the species. Such low level of variation suggests that, despite the genus being considered very old, the species appear very young as inferred by the amount of sequence divergence. The three clades, the pattern of low divergence, and restricted distribution of most species has biogeographic implications. First, it suggests a probable ancestral geographic area for *Ceratozamia* in Southeast Mexico, already known as a biodiversity "hot spot". Second, the time of speciation within the genus appears to be associated to the post-Pleistocene spread of floristic communities from proposed Pleistocene tropical refugia of S. E. Mexico that date back to or even beyond Miocene times.

624 GROSE, SUSAN O.* AND RICHARD G. OLMSTEAD

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Phylogenetic analysis of Crescentieae and Tabebuia s.l. (Bignoniaceae)

The Bignoniaceae tribe Crescentieae consists of 33 species in three genera. It belongs to a group of Mesoamerican plants putatively adapted for dispersal by the Pleistocene megafauna. Alwyn Gentry hypothesized that the common ancestor of this tribe was similar to the neotropical genus *Tabebuia*. Previous molecular studies have confirmed this relationship, and have shown that while Bignoniaceae are monophyletic, one tribe, the Tecomeae, is paraphyletic. One of these Tecomeae clades consists of *Tabebuia* s.l. and the three genera of Crescentieae. This supports a monophyletic Crescentieae but suggests that *Tabebuia* is paraphyletic unless it is expanded to include Crescentieae. The purpose of this research is to further resolve this relationship. Sequences of the chloroplast genes *ndhF*, *trnL/trnF* and the nuclear ribosomal ITS/ETS are being obtained to resolve the relationships within and between *Tabebuia* and the Crescentieae.

625 GROSS, BRIANA*, KARI ROLLENHAGEN, JAMIE MELLOR, AND SUSAN KEPHART

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Species boundaries in Camassia: analysis of a putative hybrid zone

In classic evolutionary models, species remain distinct when isolated by one or more extrinsic or intrinsic barriers to hybridization. If these barriers reduce or prevent genetic exchange, the morphological discontinuities among reproductively isolated species will provide an effective mechanism for their classification. We used morphological and molecular analyses, and data on flowering phenology, breeding systems, and pollination, to explore the taxonomic relationships between two camas lilies, *Camassia leichtlinii* and *C. quamash*, which occur sympatrically in Oregon. Differing classifications persist for these North American taxa: Gould treated the species as distinct in his monograph, noting the absence of hybrids, whereas a recent California flora relegates *C. leichtlinii* to a subspecies of *C. quamash*. Our surveys of single and mixed populations show extensive overlap in extrinsic factors such as flowering time and insect visitors. Morphological study confirms the presence of an intermediate form that differs significantly ($P < 0.05$) from one or more parental species in all but one of ten characters measured. Thus, pre-zygotic barriers appear weak, and inter-specific hybridization may occur in *Camassia*. Preliminary allozyme analysis of ten loci also revealed additive banding patterns and higher than average heterozygosities in putative hybrid zones. Of ISSR primers analyzed to date, two diagnostic bands of the parental species *C. leichtlinii* and *C. quamash* appear in 78% and 9% of the putative hybrids, respectively. Yet hybrid seeds produced from artificial pollen manipulations were inviable under glasshouse conditions, suggesting the presence of intrinsic, post-zygotic barriers to interbreeding. These data and multivariate numerical analyses imply that *C. leichtlinii* and *C. quamash* are best classified as separate species, but occasional hybridization and introgression may also play an important role in their evolution.

626 HALL, PAULA M.*, TIMOTHY K. LOWREY, AND DIANE L. MARSHALL

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Phylogenetic relationship and breeding system evolution in Callirhoe (Malvaceae)

Callirhoe comprises nine species and two varieties distributed from northeastern New Mexico through Florida including northeastern Mexico. The genus exhibits variation in sex expression possessing gynodioecy and dioecy. Gynodioecy is rare in the Malvaceae yet three of the nine species of *Callirhoe* are gynodioecious and a fourth exhibits functional gynodioecy. Preliminary results of morphology and sequence data derived from the nrDNA ITS region, will be presented to examine the phylogenetic relationships of the taxa. Breeding system data will be mapped onto the species phylogeny to estimate the pathway of breeding system evolution in the genus.

627 HEALY, JOHN* AND NELSON D. YOUNG

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A new computer program, GapCoder allows inclusion of indels as characters in phylogenetic analysis

The position of indels (gaps) in molecular data sets can be useful phylogenetic information, yet this information is rarely used, especially in large data sets with many indels. We have written a program that codes indels as characters for phylogenetic

analysis. This program is also useful for exploratory analyses of optimal DNA sequence alignment. The program, GapCode, parses aligned data sets, generates indel characters and produces a NEXUS-format output file, complete with a table of correspondences between the indels and their codes. We base our algorithm on the "simple gap coding" method of Simmons, M.P. and H. Ochoterena, 2000. *Systematic Biology* 49:369-381. In this method, indels are coded as the same if they start and end in the same place. Instructions on how to obtain a free copy of the program will be included in the poster.

628 HOLT, KATHERINE^{1*}, LEIGH A. JOHNSON¹, J. MARK PORTER², AND JOHN S. GARDNER¹

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External seed coat morphology of Gilia (Polemoniaceae) and segregate genera: comparison and correspondence with phylogenetic relationships

Pollen exine morphology has been widely surveyed in the phlox family with considerable discussion regarding its taxonomic utility. However, with the exception of thorough SEM sampling of *Collomia*, work in *Cobaea*, and description of general classes of mucilage production and cell-separation characteristics, seed coat micromorphology has been largely neglected in Polemoniaceae. A broad SEM survey of mature, dry seeds throughout this family reveals diversity in characteristics of cell wall boundaries, presence, absence, size, shape, and distribution of verrucae, and features of the hilum. Similar to the general uniformity in seed coats reported for *Collomia*, the seeds of *Gilia* sensu stricto show little variation: verrucae are either absent or minutely developed in the earliest branching species. Segregate genera *Lathrocasis* and *Saltugilia*, also members of Gilieae, are characterized by substantially larger verrucae and cell wall boundaries obscurely apparent as low ridges, but differ in finer levels of verrucae appearance. Two markedly different patterns distinguish the testa of former *Gilia* species removed to *Linanthus*, with both types represented in other members of Phlocideae. In Loeseliaceae, *Aliciella*, *Giliastrum*, *Bryantiella*, and *Dayia* possess distinctive testa and three readily distinguishable patterns are found in *Aliciella* alone. Although the several classes of external morphology noted in this study correspond well to lineages of Polemoniaceae identified in DNA-based phylogenetic analyses of this family, the greater value of this work is the description of characters for morphology-based phylogenetics and further investigation into seed evolution in this family.

629 HU, JER-MING*, NICOLE M. MATUREN, AND MICHAEL W. FROHLICH

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Studies of evolution and development of petaloid bracts in dogwoods (Cornus)

Transference of function, in which one organ takes over the function usually accomplished by another organ, is a very important phenomenon in plant evolution. Dogwoods provide an example, as some species have white, petaloid bracts that attract pollinators, a function normally done by petals and/or sepals. Dogwoods present an ideal system in which to study the evolution of transference of function, because: a) one entire clade in the genus (ca 10 species) has showy bracts, while the remaining ca 40 species lack showy bracts; and b) all species have flowers with true petals that typically become white, providing a morphological and developmental-genetic control for what constitute petal attributes. Development of petaloid bracts involves a suite of changes including size, pigment production, etc., as compared to

inflorescence bud bracts in the paraphyletic outgroup, the small-bracted and bractless dogwoods. A simple evolutionary-developmental explanation for acquisition of petaloidy would be the ectopic expression, in bracts, of genes specifying petal identity, i.e. A and B class, and *SEPALLATA*-like MADS-box genes. We have cloned cDNA sequences of B-class genes homologous to *AP3* and *PI* of *Arabidopsis* and to *TM6* of *Lycopersicon* from both a species with petaloid bracts, *C. florida*, and one without them, *C. alba*. RT-PCR results show that all three genes are expressed in flowers of both species, but we have not found expression of any of them in the mature petaloid bracts of *C. florida*. We are now testing expression by other methods and in earlier stages of bract expansion, and we are cloning other genes. If confirmed, absence of B-class gene expression would indicate that determination of petaloid bracts in dogwoods is due to elements other than B class genes.

630 HUYSMANS, SUZY^{1*}, STEVEN DESSEIN¹, STEVEN JANSEN¹, FREDERIC LENS¹, STEFAN VINCKIER¹, FREDERIC PIESCHAERT¹, PETRA DE BLOCK², KOEN ES², MARCEL VERHAEGEN², PIET STOFFELEN², ELMAR ROBBRECHT², AND ERIK SMETS¹

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Pollen morphological variation in Rubiaceae: a portrait

The predominantly tropical family Rubiaceae is with ca. 13,000 species one of the largest families of angiosperms. Contrary to some other huge families, the pollen morphological variation within the family is impressive. Although the tricolporate pollen type dominates by far, a number of tribes (e.g., Psychotriaceae, Spermaceae, Sabiceae) are highly eurypalynous. In many cases, the pollen morphological diversity observed has a high systematic value. Pollen grains are mostly dispersed as monads, but a small number of genera are characterized by permanent tetrads; polyads occur in a single genus, *Massularia*. Pollen size ranges from 6 to 120 µm; shape varies from oblate to prolate, but is most often subspheroidal. Number of apertures ranges from 0 to 30. They are generally compound, i.e. made up by different apertures one above the other. The sexine pattern is also variable, including psilate, perforate, microreticulate to reticulate, and rugulate patterns. Supratectal elements are mostly absent, but if present they show a wide array of morphological variation. Orbicules are often present and can be spherical, doughnut-shaped, irregularly folded or spinulate. The results presented are a summary of the pollen morphological observations achieved in the last 7 years at the Laboratory of Plant Systematics and the National Botanic Garden of Belgium. We aim to explore the pollen and orbicule morphological diversity of the Rubiaceae in order to assess the systematic value of the respective characters. The database of all genera investigated with reference to our papers will be available soon at <http://www.kuleuven.ac.be/bio/sys/pollen>.

631 KARAMAN, VESNA* AND LOWELL E. URBATSCH

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Phylogenetic analysis of Boltonia (Astereae, Asteraceae) based on nr ETS and ITS sequence data

The genus *Boltonia* mainly occurs in eastern North America. It comprises five species that grow in moist to wet habitats. The genus was previously suggested to be closely related to the Old World *Kalimeris*. However, morphological data by Gu and Hoch provided evidence that these two genera were not closely

allied. DNA sequence data by Noyes and Rieseberg supported *Boltonia*'s close affiliation with New World *Symphyotrichum*, *Batopilasia byei* (as *Erigeron byei*), and genera of Machaerantherinae. In our phylogeny based on ETS and ITS sequence data with *Aster amellus* as the outgroup *Kalimeris* appears basal, while *Boltonia* is the most derived lineage. *Batopilasia* and *Chloracantha* are sisters and this clade in turn is sister to *Boltonia*, thus supporting Nesom's most recent suggestion of relationship; *Symphyotrichum* in turn is sister to this clade. Furthermore, our sequence data resolves three lineages within *Boltonia* that conflict with current taxonomic hypotheses. *B. asteroides* var. *latisquama*, and *B. asteroides* var. *recognita* are separated from *B. asteroides* var. *asteroides* and are placed in a separate clade together with *B. decurrens* and *B. apalachicolensis*.

632 KIM, SANGTAE^{1,2*}, CHONG-WOOK PARK¹, AND YOUNGBAE SUH²

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Taxonomic revision of Magnolia section Maingola Dandy (Magnoliaceae) and the multivariate analysis of Magnolia macklottii complex

M*agnolia* section *Maingola* Dandy, distributed in tropical Southeast Asia from India (Assam) to Malay Archipelago extending Borneo, is distinguished from other taxa in Magnoliaceae by the combination of terminal brachyblast, cylindrical fruit, and free stipule. Morphological characters were re-examined for section *Maingola* and section *Alcimandra* which has been considered to be closely related to the former. Although section *Alcimandra* is distinguished from section *Maingola* in having long stamen to hide gynoecium, section *Alcimandra* was combined with section *Maingola* because this feature is frequently found in the various taxa of the family. Recent molecular phylogenetic studies have also demonstrated the close affinity between sections *Maingola* and *Alcimandra*. For the *Magnolia macklottii* complex which has been problematic due to the wide range of variation in taxonomically important characters, principal component analysis was carried out with the matrix of 52 OTUs X 28 characters. Two varieties, *M. macklottii* var. *macklottii* and *M. macklottii* var. *beccariana*, were recognized in the complex mainly by the presence/absence of hairs in fruits. Leaf shape and hairs in twig appeared to be variable. In result, seven species with five varieties were recognized within subsection *Maingola*.

633 KIM, SANGTAE^{1,2*}, DOUGLAS, E. SOLTIS³, PAMELA, S. SOLTIS⁴, YOUNGBAE SUH², AND MICHAEL ZANIS⁵

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Phylogeny of early-diverging eudicots based on multiple genes: rbcL, atpB, 18S and 26S rDNA sequences

Parsimony analyses were conducted using a four-gene data set (*rbcL*, *atpB*, 18S rDNA, and 26S rDNA; over 8000 bp/taxon) for genera of early-diverging eudicots and appropriate placeholders for core eudicots using basal angiosperms as outgroups (60 genera total). The strict consensus of two shortest trees reveals a well-supported Ranunculales as sister to the remainder of eudicots, followed by Proteales, Sabiaceae + Buxaceae +

Didymeliaceae + Trochodendraceae, and core eudicots. However, the clade of Sabiaceae + Buxaceae + Didymeliaceae + Trochodendraceae receives support < 50%. Within Ranunculales, most relationships receive support > 50%. Euptelea is sister to the remainder of the clade. Papaveraceae are the subsequent sister to the remaining Ranunculales. Lardizabalaceae and Circaeasteraceae form a clade that is sister to Menispermaceae and a clade of Ranunculaceae + Berberidaceae. Although our analyses provide additional support for relationships within Ranunculales, relationships among the groups of early-diverging eudicots are still unclear. Resolving these relationships will be a difficult task, requiring the sequences of still additional genes.

634 KOUKOL, SCOTT R.* AND CURTIS CLARK

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Comparative anatomy of the leaves and stems of Encelia (Asteraceae: Heliantheae)

E*ncelia* is a genus of mainly drought-tolerant shrubs found in arid to semi-arid areas of southwestern North America and western South America. Several species have well-characterized ecophysiological and morphological adaptations for dealing with drought. All but one species are currently assigned to one of two clades, based on morphological, phytochemical and preliminary genomic data. The purpose of this study was to determine whether the internal anatomy of leaves, stems, and peduncles reflects the adaptations and external morphology of individual species, or instead the basic phylogenetic patterns of the genus. The basic anatomy of stems and leaves is consistent with other xerophytic Asteraceae. Resin ducts are present in more species than indicated in earlier studies. The unique leaf shape of *Encelia ventorum* is reflected in its internal anatomy, but the similarities among the species are otherwise much greater than habitat, external morphology, or phylogeny might imply. This provides further evidence of the recent diversification of the group.

635 LEE, BYOUNG-YOON* AND CHONG-WOOK PARK

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A phylogeny of family Apiaceae genus Daucus derived from morphological characters: preliminary investigations

The umbelliferous genus *Daucus* consists of approximately 25 species (including carrots) which are characterized by the presence of spines and hairs on both primary and secondary ridges of dorsally compressed fruits. The genus is distributed primarily in Mediterranean areas, although it occurs also in South and North America, Australia, and Africa. Taxonomically, *Daucus* has been considered to be one of the most problematic genera in the Apiaceae due to the highly variable fruit morphology. Despite taxonomical controversy and economic importance of the genus, no rigorously constructed estimate of phylogenetic relationship exists. To examine generic limit and relationships among species of *Daucus* and relatives, phylogenetic analyses of characters derived from morphology and anatomy were conducted. The resulting consensus of parsimony trees showed that: (1) there was a dichotomy between European taxa and African, American taxa; (2) *Daucus* was not monophyletic with members of the genera *Agrocharis*, *Pachytenium*, and *Pseudorlaya* nested within the genus; (3) The African genus *Agrocharis* was incorporated within *Daucus* and showed close relationships with American taxa of *Daucus*; (4) *Daucus glochidiatus* with poorly understood relationships, restricted to Australia and Papua New Guinea, was closely related to African *D. hochstetteri*, and East Mediterranean *D. durieua*.

636 LEE, SANGTAE*, MEEKYOUNG KANG, AND CHUNGHEE LEE

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A palynotaxonomic study of the genus Filipendula Adans (Rosaceae)

Pollen from 19 taxa of the genus *Filipendula* Adans., were examined using light and scanning electron microscopy. The pollen morphology supported Shimizu's system (1961) in which the genus was classified into 3 subgenera and 4 sections. Subgen. *Hypogyna* is well distinguished from the other two subgenera by lacking a thick margined, protruded, vestibulate pore and an acutely tipped colpus with prominent costae colpi, and subgen. *Filipendula* by having large grain and pore size, and a longitudinally elliptical vestibulum. Within subgen. *Ulmaria*, sect. *Ulmaria* is distinguished from the other sections by having a scabrate-microechinate surface, sect. *Albicoma* by having a gradually thickened colpus margin, sect. *Sessilia* by having a relatively short colpus and sect. *Schalameya* by lacking all these characters.

637 LI, JIANHUA^{1,2,3*}, JOHN H. ALEXANDER III¹, TOM WARD¹, PETER DEL TREDICI¹, AND ROB NICHOLSON⁴¹Arnold Arboretum of Harvard University, 125 Arborway, Jamaica Plain, MA 02130; ²Dept. of Plant Biology, University of New Hampshire, Durham, NH 03824; ³University of Maine, Orono, ME 04469; ⁴Smith College Botanic Garden, 15 College Lane, Northampton, MA 01063*Phylogeny and biogeography of the Empetraceae based on sequences of nuclear and chloroplast genes*

The Empetraceae comprises three genera: *Empetrum* L., *Ceratiola* Michx., and *Corema* D. Don. *Empetrum* has an antitropical distribution; *Ceratiola* is endemic to southeastern US; and *Corema* is disjunctly distributed in northeastern North America (*C. conradii*), Portugal and Spain (*C. album*), and the Azores (*C. album* var. *azoricum*). A cladistic analysis of the Empetraceae using 28 morphological characters placed *Ceratiola* in alternate positions, with either *Empetrum* or *Corema*. This led to the hypothesis that *Ceratiola* might be a hybrid between ancestors of *Empetrum* and *Corema* (Anderberg 1994). In this study we used sequences of nrDNA ITS and chloroplast gene *matK* to evaluate the monophyly of *Empetrum* and *Corema*, and to examine phylogenetic relationships of the Empetraceae. Ten samples were used representing the monotypic *Ceratiola*, species and subspecies of *Corema*, and species of *Empetrum* from both Southern and Northern Hemispheres. Sequences of four species of *Rhododendron* were withdrawn from the GenBank and were used as outgroups. In both *matK* and ITS trees, species of *Empetrum* form a clade that is sister to the strongly supported clade containing both *Corema* and *Ceratiola*, suggesting that *Ceratiola* may not be of a hybrid origin between ancestors of *Corema* and *Empetrum*. In the *matK* tree, *Corema conradii* is more closely related to *Ceratiola* than to *Corema album* and *C. album* var. *azoricum*, whereas in the ITS tree, *Ceratiola* is weakly allied with *Corema album* and *C. album* var. *azoricum*. This suggests that *Ceratiola* might be a hybrid between ancestral populations of *Corema conradii*, as a maternal parent, and *C. album*, as a paternal parent.

638 LI, JIANHUA^{1,2,3*}, JOHN H. ALEXANDER III¹, AND DONGLIN ZHANG²¹Arnold Arboretum of Harvard University, 125 Arborway, Jamaica Plain, MA 02130; ²Dept. of Biosystems Science and Engineering, 5722 Deering Hall, Orono, ME 04469; ³Dept. of Plant Biology, University of New Hampshire, Durham, NH 03824*The genus Syringa (Oleaceae) is paraphyletic: evidence from sequences of nuclear ribosomal DNA ITS and ETS regions*

Sequences of nuclear ribosomal DNA ITS and ETS regions were used to examine phylogenetic relationships of *Syringa* and *Ligustrum*. Thirty samples were included in parsimony analyses, representing all major groups of these two genera. Two species of *Fraxinus* and one species of *Jasminum* were also included in analyses for rooting purposes. Species of series *Vulgares* (*Syringa*) and the monotypic series *Pinnatifoliae* (*Syringa*) are basal clades followed by a clade containing *Ligustrum* species and the remaining *Syringa* species. Species of *Ligustrum* form a well-supported clade, which is sister to a clade containing the rest of species of *Syringa*, including subgenus *Ligustrina*, and series *Pubescentes* and *Villosae*. All these groups are monophyletic. *Parasyringa sempervirens* is phylogenetically embedded within the *Ligustrum* clade, supporting its placement in *Ligustrum*. Our results indicate that *Ligustrum* is derived from within *Syringa*, suggesting that *Syringa* as traditionally circumscribed is paraphyletic. Berries are a synapomorphy of *Ligustrum* species, and the dehiscent berry of *Parasyringa sempervirens* is an evolutionary reversal to a capsule, which is characteristic of *Syringa*. The evolution of berries might have resulted in an accelerated speciation in *Ligustrum*.

639 LI, JIANHUA^{1,2,3*}, PETER DEL TREDICI¹, SHIXIONG YANG⁴, AND MICHAEL J. DONOGHUE⁵¹Arnold Arboretum of Harvard University, 125 Arborway, Jamaica Plain, MA 02130; ²Dept. of Plant Biology, University of New Hampshire, Durham, NH 03824; ³University of Maine, Orono, ME 04469; ⁴Institute of Botany, Academia Sinica, Kunming, Yunnan 650204, China; ⁵Dept. of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511*Phylogenetic relationships and biogeography of Stewartia (Camellioideae, Theaceae) inferred from nuclear ribosomal DNA ITS sequences*

Sequences of the internal transcribed spacers of nuclear ribosomal DNA were used to estimate phylogenetic relationships within *Stewartia*. Eighteen samples were included, representing two species of *Hartia*, seven species of *Stewartia*, and an outgroup, *Franklinia alatamaha*. Several different inference methods were used, including parsimony, neighbor-joining, and maximum likelihood. Parsimony analyses were conducted treating gaps as missing data or as a fifth character state. In all analyses *Hartia sinensis* and *H. villosa* form a clade that is the sister group of *Stewartia*. Within *Stewartia* the New World and the Old World species form well supported clades. The subgenera and sections of *Stewartia* proposed by previous authors are not supported by our ITS data. Two clades are recognized within the Old World lineage: *S. serrata*+*S. rostrata*; and *S. pseudocamellia*+*S. monadelphica*+*S. sinensis*. A comparison of levels of sequence divergence suggests that southeast Asia and China may be a recent center of diversification in *Stewartia*. Morphological disparity between the North American *Stewartia* species is much higher than it is among the larger number of Asian species.

640 LIM, CHAE EUN* AND CHONG-WOOK PARK

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Hybridization in Aconitum subgenus Aconitum (Ranunculaceae) at Mt. Sobaek in Korea inferred from morphology and flavonoid chemistry

Species of *Aconitum* subgn. *Aconitum* show very complicated patterns of morphological variation, resulting in confusion in delimiting species boundaries and in determining their relationships. Also, interspecific hybridization is relatively common in subgn. *Aconitum*, and many intermediated forms possibly derived from interspecific hybridization and introgressive hybridization have been reported. In the present study, we have examined the morphology and the flavonoid chemistry of putative hybrid populations of *Aconitum* subgn. *Aconitum* at Mt. Sobaek in southern Korea to understand the origin and structure of these populations. Five major morphological types were found among the individuals of these populations. Fourteen flavonoid compounds were isolated and identified from these populations at Mt. Sobaek representing these five morphological types. Characteristics of flavonoid profiles of the five morph types parallel the relationships suggested by the morphological evidence. In addition, the distribution pattern of flavonoid compounds among the individuals of the five morph types suggested that hybridization events involving at least three taxa probably occurred in these populations at Mt. Sobaek.

641 LINDEMUTH, RALF*, NORA WIRTZ, IMKE SCHMITT, AND H. THORSTEN LUMBSCH

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Evolution of filamentous Ascomycetes inferred from multiple-gene-analyses

The current classification of *Ascomycota* is mainly based on nuclear SSU rRNA data. Most classes circumscribed in the filamentous *Ascomycetes* are based on nu SSU rRNA characters and morphology, but some groups, such as *Lecanoromycetes* have only low bootstrap support and the relationships of the classes is currently unresolved. To improve this, we used a multi-gene-approach including nu SSU-, nu LSU- and mitochondrial SSU-rDNA sequences of all traditionally (morphologically) distinguished and most recently accepted classes of filamentous *Ascomycetes*. Combined data sets were analysed phylogenetically using maximum parsimony and minimum evolution, and constrained topologies were tested with parametric bootstrapping. Most of these classes were found to be monophyletic with high bootstrap support. *Lecanoromycetes* showed a well-supported monophyly for the first time. The classification based on SSU rDNA data and different morphological characters, is supported, while the traditional classification and classifications based on the ascus-type are rejected. In contrast to single-gene-analyses also the branching order and relationships among these classes could partly be well-resolved. Our results suggest a basal position of the *Dothideomycetes* in the *Leotiomyceta*. *Leotiomycetes* and *Sordariomycetes*, as well as, *Chaetothyriomycetes* and *Eurotiomycetes* form well-supported clades.

642 PARK, SEON-JOO AND KI-JOONG KIM*

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Sectional relationship Hypericum (Clusiaceae) based on the molecular data

Sectional relationship of *Hypericum* (Clusiaceae) based on the molecular data Seon-Joo Park and Ki-Joong Kim, Institute of Biotechnology and Department of Biology, Yeungnam University, Korea *Hypericum*, a large genus of Clusiaceae, consists of 30 sections and 450 species. The genus distribute worldwide. Considerable advances have been made in establishing phylogenetic hypothesis for the genus *Hypericum* using morphological data. However, the evolutionary directions of morphological characters are often limited to understanding the evolution of the genus. To examine the sectional phylogeny of *Hypericum*, we sequenced the ITS regions of nuclear rDNA and trnL-F and pasA-ycf3 regions of chloroplast genome. The data shows well-resolved phylogeny for the sectional relationships. The basal group in the genus is the section *Campylosporus* that mainly distributed in Tropical Africa and Mexico. The section *Brathys* derived from the section *Spachium*. The cosmopolitan section *Hypericum* was paraphyletic group. The geological isolation clearly has played a major role in the evolution of this genus.

643 POLANS, NEIL O.*, JEFFERY A. NELSON, DANA R. KURPIUS, AND DAYLE E. SAAR

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A phylogenetic study of pea

Sixteen pea taxa representing both wild populations and cultivated accessions of the genus *Pisum* are scored for morphological characters, allozymes, RAPDs, ISSRs and ITS sequences. Tests of skewness and partition homogeneity indicate that each of these individual data sets contains strong phylogenetic signal and sufficient congruence to support their combination in a single data set. Using both the maximum parsimony and bootstrap methods from PAUP, the small number of morphological characters precisely organizes the species into traditional taxonomic groupings, perhaps in part reflecting the role morphology plays historically in pea classification. Individual and combined molecular data sets support several of these same groupings. Decay indices and other branch values for the data-rich ISSR and RAPD trees reveal particularly strong support for three nodes that: 1) separate *P. fulvum* from the *P. humile*, *P. elatius* and *P. sativum* ingroup; 2) establish the northern *humile*, *elatius* and *sativum* clade; and 3) define *sativum* as a monophyletic group. The southern *humile* populations form a clade that is distinct from *elatius*, *sativum* and even northern *humile* in the combined molecular tree; although, this node is supported only tenuously by the individual molecular trees. The RAPD trees indicate that *elatius* is the sister taxon to the cultivated *sativum*, a relationship that is observed in the combined molecular tree. By comparison, the ISSR tree presents only modest support for northern *humile* as the single closest relative of the domesticated pea. A small number of polymorphic ITS sites actually places northern *humile* further from *sativum* and underscores the close affinity among all the non-*fulvum* peas. Species *fulvum* is clearly the most distinct of the pea taxa in every analysis.

644 PORTER-UTLEY, KRISTEN^{1*}, WALTER JUDD¹, JOHN MACDOUGAL², MARK WHITTEN³, AND NORRIS WILLIAMS³

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Phylogenetic relationships within Passiflora L. section Cieca Mast. (Passifloraceae) based on morphological and molecular evidence

As currently circumscribed, *Passiflora* section *Cieca* is characterized by its small, apetalous flowers with the filaments of the corona mostly in one or two series and by reticulate seed coats. The rapidly evolving species of the section are primarily distributed in the southern United States, Mexico, Central America, South America, and the Caribbean. One species is also found in the Old World (likely resulting from recent human introduction). Section *Cieca* contains two problematic species, *P. suberosa* and *P. coriacea*. Since Linnaeus first named *P. suberosa* in his *Species Plantarum*, taxonomists have disagreed about the circumscription of the species and, as a result, over 60 synonyms exist for it. Our preliminary analysis of the herbarium specimens of *P. suberosa* indicate that this variable species has likely served as a "taxonomic garbage can" for entities that cannot be assigned to any of the other members of the section. *Passiflora coriacea* is also a species that exhibits marked morphological variation over its distribution from eastern Mexico to northern South America, containing several distinct entities. Morphology along with nucleotide sequence data from GBSSI (*waxy*), ITS-1, ITS-2 and the intervening 5.8S region of the nuclear genome were used for the phylogenetic analysis of the species within *Passiflora* section *Cieca* (Passifloraceae). Preliminary morphological and molecular data indicate strong support for the monophyly of section *Cieca* and indicate that *P. suberosa* and *P. coriacea*, as currently circumscribed, are likely non-monophyletic groups of cryptic species. Morphological data suggest that the mainland entities of *P. suberosa* are more closely related to other mainland species in the section than to those entities of *P. suberosa* from the Greater Antilles and Galapagos. Furthermore, morphology indicates that hummingbird pollination has evolved twice within section *Cieca*.

645 PRINCE, LINDA M.* AND W. JOHN KRESS

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Species boundaries in Canna (Cannaceae): evidence from nuclear ITS DNA sequence data

Canna lilies (*Canna*: Cannaceae) are popular garden ornamentals throughout warm temperate regions, especially in the eastern US and Europe. Over 1000 named cultivars have been generated by hybridization and cultivation over the past 200 years. One species, *Canna edulis*, is grown in tropical regions around the world as an "arrowroot" starch source for both humans and as animal fodder. Many general plant books recognize approximately 50 species and new neotropical species continue to be described based on characters such as leaf, staminode, and rhizome size and shape. Morphological research suggests the number of species is grossly inflated. Nuclear ITS and chloroplast *rp16* intron DNA sequence data for 22 plants representing 7 broadly-defined species were collected. Molecular data confirm the recognition of a limited number of species including a broadly defined *Canna indica*. Morphological variation of the *C. indica* specimens sampled include leaf color (green versus purple) and surface (glabrous versus glaucous), flower color (all red, yellow with small

reddish spots, or a range of colors between these two extremes), and plant height. The important crop plant *C. edulis* falls within the broad morphological definition of *C. indica*. DNA data also group our sample of *C. edulis* with all other *C. indica* representatives. The closest relative of *C. indica* is the semi-aquatic species *C. glauca*. Other species which warrant specific recognition based on this study include: *C. tuerkheimii*, *C. jaegeriana*, *C. paniculata*, *C. iridiflora*, and *C. flaccida*.

646 PYCK, NANCY* AND ERIK SMETS

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Dipsacales phylogeny: combining chloroplast sequences with morphological evidence

The order Dipsacales is classified in Euasterids II and comprises six families following APG: Caprifoliaceae, Diervillaceae, Linnaeaceae, Dipsacaceae, Valerianaceae and Morinaceae. Despite its relatively small size, many phylogenetic questions on intergeneric and interfamilial relations still remain in this order. New sequences of both 5' and 3' region of the plastid *ndhF* gene are generated and combined with published *ndhF* sequence data; a combination with available *rbcl* sequences and a morphological data set is also performed. All major lineages within Dipsacales are represented. Parsimony analysis based on *ndhF* data shows *Heptacodium* as sister to all members of Caprifoliaceae; combined algorithms suggest an unresolved basal position in the Dipsacales. Trees inferred from all data sets indicate a paraphyletic nature of the tribe Patrinieae and suggest that *Nardostachys* can no longer be regarded as the basalmost member of Valerianaceae. Morinaceae are strongly monophyletic and behave as a basal clade to the Valerianaceae-Dipsacaceae clade. In classifications of Dipsacales the genus *Triplostegia* is treated as a member of Valerianaceae, Dipsacaceae, or even as a monogeneric family. The results presented, indicate that the position of *Triplostegia* remains equivocal: molecular data suggest a basal position in Dipsacaceae, while the morphological matrix and the total combined data set show *Triplostegia* as sister to all Valerianaceae.

647 RANDLE, CHRISTOPHER P.* AND ANDREA D. WOLFE

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Molecular evolution of photosynthetic genes in holoparasites Harveya Hook. and Hyobanche L. (Orobanchaceae)

Harveya Hook. (Orobanchaceae) is a genus of holoparasitic plants comprised of 25-40 species inhabiting southern Africa. Genes encoding photosynthetic proteins are expected to experience increased rates of mutation in holoparasites due to the relaxation of functional constraints on these genes. *Hyobanche* L., the sister genus of *Harveya*, has undergone *rbcl* pseudogene formation while species of *Harveya* have not. Two hypotheses may be invoked to explain the absence of an *rbcl* pseudogenes in *Harveya*. (a) The loss of Rubisco functionality has occurred via a different pathway in *Harveya* than *rbcl* pseudogene formation. (b) Rubisco retains function in *Harveya*, in facultative photosynthesis or an unknown, non-photosynthetic role. The gene encoding the small subunit of Rubisco, *rbcs*, has not been examined for loss of function in holoparasites. In this study, the evolution of Rubisco was examined by nucleotide sequencing of *rbcl* and *rbcs*, and detection of the RNA (RT-PCR) and protein products (by means of Western blot) of these genes in *Hyobanche* and *Harveya*. Structural motifs of the 3' and 5' untranslated regions (UTRs) of *rbcl*

may be important in promoting transcription. These were sequenced and analyzed for structural alterations which may prevent transcription of this gene.

648 RIGGS, ERIN L.* AND CAROL A. WILSON

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A phenetic study of the Iris hartwegii complex (Iridaceae) based on RAPD's and morphological data

The *Iris hartwegii* complex is within the genus *Iris*, series Californicae. The series Californicae has about 17 taxa and is restricted to the Pacific Coast of North America. In 1959 Lenz circumscribed the *I. hartwegii* complex suggesting new combinations and one new taxon. Problems persist regarding treatment of the *I. hartwegii* complex. Lenz speculated *I. h.* subsp. *australis* was sympatric with the progenitor *I. h.* subsp. *hartwegii*. These two species are currently separated by the Mojave Desert at a distance of 200 km. Lenz additionally questioned the phylogeny of *I. h.* subsp. *columbiana*, offering two explanations. He suggested *I. h.* subsp. *columbiana* may be ancestral to *I. munzii* and *I. h.* subsp. *hartwegii*, or alternatively that *I. h.* subsp. *columbiana* is a hybrid of *I. munzii* and *I. h.* subsp. *hartwegii*. Research by Young in the mid 1990's proposed that all members of the series Californicae be placed in one species complex. Recent work by Wilson suggests that the *I. hartwegii* complex may be polyphyletic. Preliminary evidence based on RAPD's and morphological data indicate that *I. h.* subsp. *pinetorum* may not be distinctly separate from *I. h.* subsp. *hartwegii*. However recognition of *I. h.* subsp. *australis* and *columbiana* are supported by RAPD's and phenetics data.

649 SLOTTA, TRACEY A. BODO* AND DUNCAN PORTER

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ITS phylogeny of Iliamna (Malvaceae) and related genera

Iliamna is a temperate North American mallow with eight species, seven of which are classified as rare or endangered. They occupy a range of habitats from streamsides at high elevations to arid hillsides. Cytological and morphological evidence has indicated a close relationship between *Iliamna* Greene, *Malacothamnus* Greene, and *Phymosia* Hamilton to form the Malacothamnus alliance. *Malacothamnus* is located in California and northern Baja California with an additional species in Chile. *Phymosia* is found in the Bahamas, southern Mexico, and Guatemala. In habit, species in *Iliamna* are herbaceous to small shrubs, *Malacothamnus* shrubs, and *Phymosia* small trees. All are distinctive in their non-reticulate dehiscent fruits and have showy flowers. Much hybridization has been reported within *Malacothamnus* and is suspected to occur in *Iliamna*. The internal transcribed spacer (ITS) of nuclear ribosomal DNA was used to develop a phylogeny for the Malacothamnus alliance. Parsimony was used to develop a phylogenetic tree by random stepwise addition with 100 replicates. Robustness of the phylogeny was tested using decay, bootstrap, and jackknife analyses. The results indicate that *Iliamna* is paraphyletic and closely allied to *Malacothamnus*. The phylogeny and biogeographic history of the Malacothamnus alliance will be discussed.

650 STANFORD, ALICE M.*, LAUREL ROYER, CHARMAINE BELLOT, LOI'Y MUSTAFA, AND NACHET WILLIAMS

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Genetic diversity of a rare Virgin Islands' endemic, Solanum conocarpum (Solanaceae)

During colonization (circa 1625), wide scale deforestation of the Virgin Islands devastated native plant populations. Some species have since begun to recover, while others have become extinct and still others remain rare. One such plant is *Solanum conocarpum* Dunal in Poir. (Solanaceae), an extremely rare shrub believed to be extant only on the island of Saint John in the United States Virgin Islands. In recent years, only four individuals (and no seedlings) have been found in the wild. As the first stage of a project analyzing the genetic diversity of rare Virgin Islands plants, we are using ten randomly selected 10-mer primers to perform RAPD analysis on *S. conocarpum*. We have detected a relatively high level diversity among the four extant individuals of the species. This diversity indicates that the existing plants may be the remnants of multiple populations of the species

651 TORRECILLA, PEDRO*, JOSE ANGEL LOPEZ-RODRIGUEZ, AND PILAR CATALAN

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Phylogenetic signal of structural characters on Festuca sensu lato (Poaceae, Poae)

Cladistic analysis of *Festuca* s. lat. representatives based on morphoanatomical characters separates major groups of taxa (Subgenera, Sections) that are consistent with those obtained from the analysis of nuclear and chloroplast molecules. Superimposed changes of structural characters on a combined ITS/trnL-F topology demonstrate the phylogenetic value of some sets of morphological characters for particular groups of taxa. Vegetative characters are similarly informative than floral characters on *Festuca* s. lat. and allied genera. Increased resolution is obtained in most cases when the total evidence principle is assumed under the simultaneous analysis of both molecular and structural data. A higher level of homoplasy is exhibited by the morphoanatomical traits when the evolutionary survey is extended to other Poae genera.

652 TRUSTY, JENNIFER L.1*, ARNOLDO SANTOS-GUERRA2, TORTSTEN ERIKSSON1, AND JAVIER FRANCISCO-ORTEGA1

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Biodiversity, conservation and molecular phylogenies in the laurel forest of the Canary Islands: the case of a critically endangered taxon of Sambucus

The laurel forests of the Canary Islands are a unique ecological zone created by the cool and humid northeastern trade winds on the islands' northern slopes. These evergreen forests have several monotypic endemic genera in addition to many endemic species which are restricted to this ecological zone in the Canaries. It has been suggested that most of the endemic plant species of the laurel forest represent relictual elements of the

flora which existed in the Mediterranean basin during the Tertiary. These isolated taxa that have not radiated into other ecological zones of the islands are considered as typical examples of ancient Mediterranean stocks from the Tertiary. *Sambucus* is an example of this kind of relictual taxa. This genus has only one endemic species (*S. nigra* subsp. *palmensis*) which is restricted to the laurel forests of the islands of Tenerife, La Gomera, Gran Canaria, and La Palma. *S. nigra* subsp. *palmensis* is considered as one of the most rare of the laurel forest and special funds from the European Union (Life Program) have been allocated for its conservation. A molecular phylogeny of nucleotide sequences of the Internal Transcribed Spacers of the nuclear ribosomal DNA of all the species of *Sambucus* reveals: (1) *S. nigra* subsp. *palmensis* has a derived position in the phylogeny which suggest that it colonized the laurel forest recently and, (2) the ITS sequences of *S. nigra*, *S. nigra* subsp. *palmensis* and *S. nigra* subsp. *maderensis* are nearly identical. Our results concord with previous morphological studies which suggested that *S. nigra* subsp. *palmensis* can be considered subspecies of *Sambucus nigra*. These results have conservation consequences, mostly concerning priorities for conservation of the unique plant biodiversity of the laurel forest of the Canary Islands.

653 VU, NINH VIET^{1*}, GREGORY MICHAEL PLUNKETT¹, AND PORTER P. II LOWRY²

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Phylogenetic study of Madagascan Polyscias and close relatives in the Ginseng family (Araliaceae)

Within the plant family Araliaceae, the genus *Polyscias* is thought to be closely related to *Gastonia* and *Cuphocarpus*, from which it may be distinguished morphologically by differences in carpel number, presence or absence of pedicel articulation, and leaf characteristics. Species of *Polyscias* from Madagascar and surrounding areas (Africa, the Comoro and Mascarene Islands) form a single clade within Araliaceae, and provide an ideal model to study evolution and biogeography. We present molecular evidence of relationships and compare the results with traditional taxonomic treatments, proposing a new biogeographic hypothesis to explain our results. Sequences from nuclear rDNA ITS and 5S, and from the cpDNA marker trnL-trnF were obtained from a highly representative sample of species (~40 spp.) found in this region. ITS, 5S, and trnL-trnF sequence lengths are 625, 320, and 850 base pairs, respectively; the 5S sequence has more variable and informative characters. Results of separate and combined analyses using parsimony methods suggest that *Polyscias* is paraphyletic, including within it *Cuphocarpus* and a polyphyletic *Gastonia*. Area cladograms based on the phylogenetic analysis show remarkable consistency with geographic distribution, which may have been the result of repeated and independent dispersal events from Madagascar to Africa, the Comoro and Mascarene Islands. An island stepping-stone model may explain the position of most African araliads, whose ancestors appear to have reached the continent relatively recently from the Comores via Madagascar. However, more detailed analysis of climate, geological history, ecological factors, and morphological studies are needed to assess these ideas further.

654 WEEKS, ANDREA*, LEAH LARKIN, AND BERYL B. SIMPSON

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A chloroplast DNA molecular study of the phylogenetic relationships of members of the Caesalpinia group (Caesalpinieae: Caesalpinioideae: Fabaceae)

Relationships within the tribe Caesalpinieae have proved problematic for over 200 years. The most recent treatment by Polhill placed the genera in this tribe in nine informal generic groups. Of these, the *Caesalpinia* group has proved to be particularly intractable because of the range of variation and apparent convergence in floral and fruit morphology. A morphological cladistic study by Lewis and Schrire indicated that the genus *Caesalpinia* was paraphyletic with all of the other genera currently placed in the *Caesalpinia* group included within *Caesalpinia*. We have used sequences from the trnL intron and trnL-trnF spacer regions to provide new insights into the phylogenetic relationships of these genera. Included in our study are representatives of most of the genera in the *Caesalpinia* group, numerous species of *Caesalpinia* itself, and various outgroups from Polhill's other informal Caesalpinieae groups. While our sampling is limited, our data indicate that Polhill's informal groups are monophyletic. Additionally, like Lewis and Schrire, we find that *Caesalpinia* is paraphyletic. However, our findings indicate very different relationships among the genera from those suggested using morphology. In particular, we find that *Pomaria* and *Hoffmannseggia* are not sister taxa and that South American genera such as *Zuccagnia* and *Balsamocarpon* are more closely related to *Hoffmannseggia* than *Hoffmannseggia* is to *Pomaria*.

655 WON, HYOSIG* AND SUSANNE S. RENNER

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Towards a phylogeny of Gnetum: first results from rbCL, Leafy, and ITS sequences

Gnetum has many unique features, such as bisexual strobili, net-veined leaves, lignin composition typical of angiosperms, and a climbing habit, that make it unusual among extant gymnosperms. Recent molecular phylogenies strongly suggest the inclusion of *Ephedra* (*Gnetum* + *Welwitschia*) in conifers as earlier suggested by morphologists. *Gnetum* has ca. 30 species of which 7 occur in the Neotropics, 2 in Africa, and ca. 21 in tropical Asia. All but two are canopy lianas. Previous classifications were based mostly on geography and variation in strobilus morphology. To assess the evolution of different strobilus types, growth forms, pollen morphology, and wood anatomy (studied in detail by S. Carlquist), we are constructing a molecular phylogeny for the genus. So far, we have sequenced the chloroplast gene *rbCL*, the second intron of the nuclear floral homeotic gene *Leafy*, and nuclear ribosomal ITS from 11 species (more will have been sequenced by the time this poster is presented). The species sampled represent the major groups recognized in the recentmost classification and the group's geographic distribution. The *rbCL* sequences show up to 2.6% sequence divergence, *Leafy* up to 5.8% divergence, and ITS shows such wide variation (with lengths varying from 410 to 986 bp) that it has not so far been alignable. However, the length variation in ITS is congruent with topologies resulting from parsimony analysis of *Leafy* and with geography. Combined *rbCL* and *Leafy* sequences yield highly resolved most parsimonious trees with bootstrap values between 83-100%. The topology suggests that, contrary to previous hypotheses, South American and Asian species are more closely related to each other than either is to the African species. Also, arborescent growth and

prominent sterile ovules on male inflorescences appear to have evolved recently within *Gnetum*.

656 WRIGHT, WESLEY A., MARGARET COX, AND CHRISTOPHER S. CAMPBELL*

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Internal transcribed spacer 1 (ITS1) in Picea (Pinaceae): structure and sequence divergence

Sequences of ITS1 of *Picea mariana* (black spruce) and *P. rubens* (red spruce) are at least 2750 base pairs long, longer than the longest previously known conifer ITS1 (*Pinus pinea*, 2631 bp). All studied Pinaceae ITS1 contain subrepeats, regions up to 265 bp in length, containing an embedded conserved motif (GGCCACCCTAGTC), and thought to be involved in secondary structure. In Pinaceae, there is a strong association between ITS1 length and number of subrepeats. *Pinus* has six subrepeats, but the two *Picea* species reported here are exceptional in having only three subrepeats with the conserved motif. Two of these subrepeats are 189 bp in length, and the third is roughly 50 bp long. *Picea* ITS1 also contains two regions about 480 bp long, with high sequence similarity, and lacking the conserved motif. Variation in *Picea* ITS1 appears to be complex in our sample, which includes multiple clones from four individuals, representing two populations from each species. We find variation between populations and within individuals, suggesting ineffectiveness of concerted evolution as in some other conifers. Black spruce and red spruce are considered sister species, hybridize frequently, and are sometimes difficult to distinguish morphologically. ITS1 sequence divergence between these two species is 2-4%, more than that between sister species in *Tsuga* (three pairs of sister species), *Larix* (two pairs), and *Pseudotsuga* (one pair), but similar to that between sister species in one other pair in *Pseudotsuga*.

657 YOO, MI-JEONG* AND CHONG-WOOK PARK

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Molecular phylogeny of Polygonum sect. Echinocaulon (Polygonaceae) based on chloroplast and nuclear DNA sequences

Polygonum sect. *Echinocaulon* (Polygonaceae) is a highly variable and taxonomically difficult taxon consisting of 21 species. The main objectives of this study were to infer phylogenetic relationships of the taxa within the section, and to provide a hypothesis on the origin of disjunct distribution pattern of the taxa based on molecular data. We have examined the ITS and *trnL-trnF* sequences from 18 taxa of sect. *Echinocaulon*. In all ITS and *trnL-trnF* trees, the taxa previously included in the section failed to form a monophyletic group: *P. bungeanum* was placed as sister to sect. *Persicaria*, suggesting that *P. bungeanum* should be transferred from sect. *Echinocaulon* to sect. *Persicaria*. The consensus tree obtained from the combined molecular data sets revealed the presence of five major lineages in the section; these include (1) *P. perfoliatum*-*P. senticosum* var. *senticosum* clade, (2) *P. dissitiflorum* clade, (3) *P. sagittatum* clade, (4) *P. dichotomum*-*P. muricatum* clade (seven taxa), and (5) *P. arifolium*-*P. biconvexum* clade (six taxa). Relationships of the taxa depicted in the consensus tree are, in general, in agreement with those previously suggested by the comparative flavonoid chemistry. In addition, the results strongly suggest that *P. sagittatum* may once have had a more continuous range in the northern Hemisphere and fragmented into two widely separated disjunct populations of eastern Asia and eastern North America during Pleistocene glaciation.

658 ZOMLEFER, WENDY B.^{1*}, NORRIS H. WILLIAMS², W. MARK WHITTEN², AND WALTER S. JUDD³

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The genera of Melantheae (Liliales, Melanthiaceae): circumscription and relationships based on ITS and trnL-F sequence data

The little-studied tribe Melantheae is a group of temperate "petaloid lilioid monocots"—so named for their small lily-like flowers with petal-like tepals. Defining genera has been more problematic for these superficially similar plants than for most, if not all, other monocots. Until our current analyses, the circumscriptions of the constituent core genera of the Melantheae (*Amianthium*, *Schoenocaulon*, *Stenanthium*, *Veratrum*-*Melanthium*, *Zigadenus* s.l.) had not been the subjects of rigorous phylogenetic character analyses, and their intergeneric relationships were also unresolved. The circumscription and relationships of these genera (29 representative taxa) were evaluated using parsimony analyses of ITS (nuclear ribosomal) and *trnL-F* (plastid) DNA sequence data. Based on the molecular cladograms, *Stenanthium* is biphyletic, and the traditional *Zigadenus* s.l. is polyphyletic. *Amianthium* and *Schoenocaulon* are distinct entities; the *Veratrum* complex is conservatively treated as one large monophyletic genus (including *Melanthium*). Although some intergeneric relationships are not highly resolved, the analyses provide strong support for *Zigadenus glaberrimus* as sister to the rest of the tribe, and *Amianthium muscitoxicum* as closely related to *Veratrum* s.l. As a result of this study, seven genera (some with novel circumscription) are recognized within the tribe Melantheae: *Amianthium*, *Anticlea*, *Schoenocaulon*, *Stenanthium*, *Toxicoscordion*, *Veratrum*, and *Zigadenus*. These generic circumscriptions, strongly supported by the tree statistics and topologies in all analyses, are correlated with potential morphological synapomorphies (at the proper level of universality). The study includes practical recommendations, such as documentation of diagnostic characters to be ultimately used in keys and descriptions. Such features include rootstock type, bulb shape, inflorescence structure, indumentum type, tepal shape, nectary morphology, and ovary position.

TEACHING SECTION, BSA

SPECIAL PAPER

659 PATIL, M.S.^{1*} AND S.K. DESHPANDE²

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Agriculture education in India

Agriculture education system in India can be distinctly divided into two types (i) British system, (ii) American system. The British type followed annual education system, wherein regular lectures are being scheduled throughout the year. Annual exam carrying 100 marks in each subject would be conducted at the end of the year. Annual system faced the difficulties of compiling the whole portion taught in the final exams. Therefore an American type of Agriculture education was set up in India based on Land Grant College System. Here each academic year was subdivided into 3 trimesters of 14 weeks duration. In a trimester four exams viz., Announced quiz, Midterm, Unannounced and Final theory and Practical exams were conducted separately on every

subject. The degree program was extended to four academic years each of twelve months duration. The four points scale of evaluation based on Grade System was followed with minimum 60 for passing. Further, semester system gave birth. There were two semesters in an academic year. Each semester consisted of 21 weeks and only three examinations in a semester are conducted. Besides this an external examination for 50% marks has been introduced under this system. For a B.Sc. (Agri) degree programme under Botany, Genetics, Cytogenetics, Principles of Plant Breeding and Breeding field crops are being taught with 9 credit hours in all. 1. Director of Instruction (Agri) 2. Assistant Professor of and Sr. Sorghum Breeder Genetics and Plant Breeding College of Agriculture and College of Agriculture Research Institute Bijapur-586101, India Bijapur-586101, India.

CONTRIBUTED PAPERS

660 GERBER, D. TIMOTHY

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K-8 educational outreach: the TULIP project

In response to the BSA's call to action (Botany for the Next Millennium, 1995), the TULIP (Teachers Using Living Plants) Project was developed in 1997 to "enhance public awareness of the fundamental importance of plants to society" by promoting botanical education for K-8 teachers. To date, botanical education has been promoted via the TULIP Project by (1) sponsoring K-8 teacher retraining workshops, funded through a 3-year Eisenhower Professional Development Program grant; (2) interacting with science educators (University faculty in the Curriculum and Instruction Department and graduate students) to provide botanical expertise in teacher training; (3) working with pre-service teachers to improve their botanical knowledge; (4) promoting the use of plants for the teaching of Science Standards (American Association for the Advancement of Science at <http://www.project2061.org/> and National Research Council's National Education Science Standards at <http://stills.nap.edu/readingroom/books/nse/html/>) and (5) informing the general public about this project by providing information to local media outlets. This presentation is a report of the activities involved in setting up the TULIP Project to promote botanical education for K-8 teachers in the School District of Onalaska, Onalaska, WI.

661 NOYD, ROBERT K.

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Connecting classroom concepts to the local flora: the Plant Profile Project

Assessments show that students often fail to connect concepts and details presented in the classroom to specific plant species in nature. A semester-long project, called the plant profile, has students building a database of information concerning the biology of a single plant species from the local flora. Students use web-based and library resources, along with lecture material, to gather information or make predictions about the biology of the whole plant. The database is built through a series of assignments that coincide with topics addressed in class. Topics include plant classification, life history, photosynthesis (pathway, pigments, rate), anatomy (root and shoot structures), morphology, genetics (chromosome number, genome size), reproduction (floral formula, pollination syndrome, dispersal mechanisms), and ecology (habitat, relative resource requirements). A final profile serves as an organiza-

tional framework that reviews and anchors relevant details of the course. Through student surveys and feedback from the past eight semesters, the plant profile project was found to enhance many aspects of the teaching-learning process. Profiles enhanced learning by engaging students to actively reconstruct concepts and patterns in relation to a plant that they have experienced. From a teaching perspective, profile assignments served as an excellent assessment tool that readily exposed a student's lack of understanding or misconceptions. The project created a classroom of student "experts," which increased the quality and quantity of student to student, and student to teacher interactions. The project is "phenotypically plastic," or easily modified to match course content and meet teacher goals.

662 RICE, STANLEY A.

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South with the spring: teaching evolution through budburst times of deciduous trees

Organisms adjust to stress by tolerance or avoidance. Buds of deciduous trees that open early in the spring may be damaged by frost, but if they can tolerate frost, they have a longer growing season than deciduous trees that avoid frost by opening their buds later. Native tree species in a location have adapted to recent climatic conditions; however, tree species within families with a northern (Laurasian) origin have adapted more often by tolerance, and tree species within families with a southern (Gondwanan) origin have adapted more often by avoidance. A class project in which students monitor bud opening dates, then test the hypothesis that trees from northern families open their buds earlier, enhances student cooperative learning, awareness of biodiversity, and understanding of evolution. The project works best in temperate regions with high deciduous tree species diversity.

663 RICE, STEVEN K.*, GRANT E. BROWN, AND R. PAUL WILLING

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Computer modeling exercises enhance investigative laboratory experiences in plant biology

When combined with laboratory or field-based experiments, computer modeling exercises improve the ability of students to integrate biological content with experimental design and results. In our curriculum, undergraduate students design models that simulate leaf-level photosynthesis, plant growth, and nitrogen cycling processes and combine their modeling efforts with experimental investigations. Our students develop their own dynamic computer models using the STELLA programming environment. This software is simple enough for students to use without prior programming experience and powerful enough to simulate realistically complex biological processes. When developed prior to experiments, such modeling efforts reinforce biological content, assist with hypothesis generation, and guide the formulation of specific predictions that can be tested experimentally. Following experiments, simulation models can be parameterized with experimental data and the models used to explore the meaning and application of the students' results. By combining modeling experiences with investigative laboratories, students connect experiments with biological content more effectively. In addition, the learning process engaged in by students better reflects the scientific processes carried out by practicing biologists.

664 SCHERER, JACQUELYN*, GARLAND R. UPCHURCH, JR., AND MARGARET J. KNAUS

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A laboratory exercise for teaching plant-climate relationships

Students of Biology often ask questions such as, "How can anyone know what the vegetation and climate were like millions of years ago?" A related concept that many students find difficult is the role of modeling in science. Paleobotanists estimate temperature and precipitation for the distant geologic past through the functional morphology of fossil plants, and in particular features that correlate with modern climate, such as the shape and size of leaves. We demonstrate the basis for inferring past climates, plus the role of scientific modeling in paleobotany, through a laboratory exercise in which students use the leaf physiognomy of modern vegetation to estimate mean annual temperature and precipitation for their local region. Students divide into working groups, collect samples of leaves from a local forest, segregate their leaves into species, then calculate: 1) the percentage of species with toothed margins, and 2) average leaf size. Students then estimate local climate by fitting their data to graphs that relate the percentage of species with toothed margins to mean annual temperature (MAT), and the natural logarithm of average leaf size to the natural logarithm of mean annual precipitation (MAP). For San Antonio, Texas, students estimate a MAT of 16 °C and MAP of 77 cm (average of 25 working groups), close to average values of 20 °C and 76 cm derived from meteorological data. The laboratory exercise demonstrates the basis for estimating past climate from trends in living species and provides a venue for discussing issues of study design, sampling error, and biases caused by the misidentification of species. It is designed for the high-school classroom but is adaptable to the university and younger grade levels. Students develop an appreciation for how scientists reconstruct the past and for the breadth of information that can be inferred from fossil plants beyond simple identification.

665 THOMAS, MEGAN*, ROBERT REINSVOLD, AND GERRY SAUNDERS

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Interaction of self-efficacy and inquiry in an introductory biology laboratory

Due to the recent call for reform in science education, there has been a resurgence of interest in inquiry-based learning. Recent research has explored the idea of implementing and designing inquiry laboratories that are more effective in promoting students' understanding of complex topics (Sundberg & Moncada, 1994; Deckert et al., 1998; & Tamir et al., 1998). Other studies have looked at how students' prior knowledge effect or change their performance in biology and chemistry inquiry settings (Johnson & Lawson, 1998; Decker et al., 1998). Little research has been done on how self-efficacy effects students perform in an inquiry setting. In 1977, Bandura proposed that the beliefs a person has about whether they can perform a specific task would affect their effort in that given task or behavior (Bandura, 1977) this was termed self-efficacy. Since the original paper in 1977, research has focused on the theory of self-efficacy. Self-efficacy is hypothesized to have an effect on student performance and achievement in science and technical fields, as well as, playing a role in career selection in the above mentioned fields (Pajares, 1996; Betz & Hackett, 1981; & Lent et al., 1984 & 1986). However, the only known study on self-efficacy in a biology context was essentially the development of an assessment tool (Baldwin et al., 1999). We therefore, have looked at how self-efficacy is related to performance in inquiry laborato-

ries. More specifically, we have investigated the relationship of self-efficacy and inquiry in introductory biology laboratories across the Front Range at both four-year universities and community colleges.

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Plants that draw a crowd: an analysis of the visual characteristics of six unusual plants featured at botanic gardens

David Hershey (1999), a leading US authority on teaching about plants, noted that "Nonscientists are often fascinated by studies of unusual plants such as *Rafflesia [pricei]*, the world's largest flower, and carnivorous plants, or germination of thousand-year-old lotus seeds. The value of those [research] studies is not diminished because people make money writing about them in popular books or producing PBS shows about them. Rather, botany gets some much needed publicity." In a follow-up effort to explain scientifically what we have dubbed the 'marquee plant' phenomenon, and to derive some implications for improving public understanding of plants and botanical learning, we analyzed the visual characteristics of several unusual plants commonly found at botanic gardens, using selected vision science metrics. The six plants we studied were *Agave americana* (century plant), *Amorphophallus titanum* (titan arum), *Araucaria araucana* (monkey puzzle tree), *Musa sapientum* (grocer's banana), *Lithops lithops* (living stones), and *Victoria amazonica* (giant Amazon water lily). We also used Krippendorffian content analysis of written accounts of botanic garden visitors' responses to these plants as a cross-check when drawing our conclusions. Results of our study indicate, for example, that the public attention and curiosity aroused by these marquee plants may be explained, at least in part, by using marquee-plant-specific visiometric data and Solso's INFOPRO human visual information processing model. We then used our findings to propose a visual-cognition-based 'Limiting Cases learning strategy' which can be used to anticipate which plants may function as marquee plants, and to explain how they might serve as springboards for botanical learning about fundamental plant science concepts and principles—both in informal and academic botanical educational settings.

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Increasing biology undergraduates' mathematical proficiency through math/biology course using of the computer program MATLAB

Although various levels of mathematics are required of undergraduate biology majors, usually through calculus, students seem to rarely realize the importance of math for addressing biological problems. We, a mathematician and a botanist, developed a course, with NSF funding, for second year majors. The required prerequisite courses were introductory biology and college algebra. The purpose of the course was to introduce the students to a broad spectrum of mathematical concepts that have application to biological problems. Our goals were to 1) have students begin building a background of advanced mathematical concepts; 2) develop students' application skills so they can use these concepts; 3) increase the students' abilities to solve biological problems with mathematics and mathematical computer programs; 4)

improve the students' understanding of the limits of biological and mathematical models and 5) develop the students' appreciation of the importance of mathematics. The units in the course had the same structure: 1) introduction to the biological topic; 2) presentation of a problem; 3) group work to create a heuristic solution of the problem; 4) introduction of the mathematical concepts applicable to the topic; 5) solution of problem using the mathematical concepts through MATLAB; and 6) introduction of similar problems to be solved by the students. The use of examples, problem solving and take-home exam projects reinforced the use of the mathematical concepts. Assessment of the course revealed that students thought that they had a better understanding of the advance mathematical concepts they were introduced, were able functionally solve problems by using MATLAB, and had a strong appreciation for the advantages and disadvantages of models, than through traditional math courses.

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Creating a web based digital image database

The Internet and its concomitant technologies have led to a revolution in both the storage and distribution of scientific information. Research data, publications, teaching materials and digital images are now routinely made available via the web. However, as anyone who owns a large 35 mm slide collection knows, storing and retrieving images presents a special challenge. Few images fit into just one easily identifiable category, necessitating either an extensive cross referencing system or serious compromises. For example, it is unlikely that a taxonomist, ecologist and morphologist would file and/or search identical image collections in the same way. Making images available via the web further compounds the problem since it is impossible to "thumb through" large collections all at once. Therefore, most web based image collections are presented as a series of pages the user must drill down through. However, no matter how well these pages are organized, cross referenced and indexed, they may not meet the needs of every potential user. Web based digital image databases, which allow images to be retrieved via keywords, provide a more convenient and flexible way to serve up digital images. Such a database requires minimal maintenance and virtually no web authoring. The author need only add images and key words to the database as it grows. Each user is essentially a web author, generating their own personal web pages "on the fly". The construction of a web based digital image database, requiring absolutely no knowledge of programming, will be demonstrated. An example of such a database is available at: <http://amica.csustan.edu/photos>.

DISCUSSION SESSIONS

PRESIDENTS' FORUM

669 GENSEL, PATRICIA G.

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Federal funding for botanical research

The format of this Discussion Session will be a panel of program officers and society representatives who initially give a short presentation followed by a question session that involves the audience. Program officers present their perspectives on the current funding climate for plant biology as well as predictions for the future of funding for plant biology research, including

organismal level research. Society representatives will present a brief summary of what their society represents in terms of type of plant biology, constituency, programs, goals, significant achievements, etc.

CONTRIBUTED SESSIONS

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Scientific publishing in an electronic age

Scientific journals face any number of interesting challenges in this increasingly electronic age. How should journals manage their growth and development in both print and electronic media? How does the electronic availability of journal manuscripts affect continued interest in subscribership from scientific institutions as well as from individual scientists? For botanical and systematic journals, there are particular challenges to improve journal responsiveness to authors through both the peer review process and in manuscript publication times. Issues such as JSTOR, BioOne and copyright concerns will be explored.

671 KAPLAN, DONALD R.

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Why botany?

With the recent name change of the American Society of Plant Physiologists to the Society of Plant Biology, a significant challenge to the identity of the Botanical Society has been posed. Thus the time seems ripe for the BOT SOC to discuss, in an open forum, what the basic differences are between Botany and Plant Biology. In fact there are very basic differences and these will be aired in a brief introductory talk and the open discussion which follows. I consider it of the utmost importance for the Botanical Society at this juncture to reaffirm our common scientific and intellectual bonds as we develop for the future. There has been a long-standing but uncalled for lack of self-esteem on the part of many members of the Botanical Society and this has been exploited by other, more aggressive societies, such as ASPP, to their advantage. This forum can therefore represent the first step in the reassertion of our significance in the broader biological community. Hence this open discussion format is ideal.

672 KIRCHOFF, BRUCE

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A feeling for the organism

Many of us choose our profession because of our connection with and love of nature. We followed our hearts into a profession where we hoped to find a deepened connection with the natural world. As individuals, we may have found this, but as a community of scientists we rarely speak of it. This discussion section will give us a chance to talk about our relationship to nature; to explore, as scientists, what our love of nature means to us and to our science. E. O. Wilson has called for traditional religions to adopt more science, and for environmentalists to appeal more to humankind's spiritual impulses, but should not scientists also renew and reaffirm their love of nature? Do we not also contribute to the environmental crisis by portraying science as "value free?" If science is only about "facts," and has nothing to do with love, what prevents others from using the knowledge we generate to exploit nature? And if we allow this, are we not denying some-

thing essential, something that is at the basis of why we became scientist? These, and other issues, will be on the table during the discussion section.

673 UNO, GORDON E.

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The future of botany at the undergraduate level

BSA members report, with increasing frequency, attempts across the country to eliminate or reduce the number of botany courses taught at the undergraduate level, to reduce college/university resources directed toward plant science activities, to replace retiring botanists with scientists from other disciplines, as well as attempts to eliminate entire botany departments and programs. These events have had and will continue to have a major impact on graduate programs and the future of the botanical sciences at the undergraduate level. This roundtable discussion will include members of the Education Committee of BSA but is open to all interested members. We hope to hear from BSA members who may have experienced “assaults” on botany at their home institution or from members who have had success in convincing colleagues and administrators of the importance of botany to the life sciences and to their college or university. We will generate a “vision statement” in the defense of botanical sciences that focuses on the importance of keeping botany in the undergraduate curriculum. We also hope to develop a list of useful methods and strategies to include plants in the study of modern biology at the undergraduate level and a list of the best practices to attract and keep undergraduate majors and minors in botany. For those interested individuals who are unable to attend the discussion session, please send comments to Gordon Uno at guno@ou.edu.

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