

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/225511978>

# Molecular biogeography and origins of the Hawaiian fern flora

Article in *Brittonia* · April 2007

DOI: 10.1663/0007-196X(2007)59[142:MBAOOT]2.0.CO;2

CITATIONS

51

READS

144

4 authors, including:



Jennifer M O Glowienka

Carroll College

9 PUBLICATIONS 422 CITATIONS

[SEE PROFILE](#)



Tom A. Ranker

University of Hawai'i at Mānoa

103 PUBLICATIONS 2,944 CITATIONS

[SEE PROFILE](#)



Jennifer M. Ramp Neale

Denver Botanic Gardens

20 PUBLICATIONS 129 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Evolution of the Hawaiian Flora [View project](#)



Hybridization status of the Genus *Sclerocactus* [View project](#)

# Molecular biogeography and origins of the Hawaiian fern flora

JENNIFER M. O. GEIGER<sup>1</sup>, TOM A. RANKER<sup>2</sup>, JENNIFER M. RAMP NEALE<sup>3, 4</sup>,  
AND SUSAN T. KLIMAS<sup>3, 5</sup>

<sup>1</sup>Carroll College, 1601 N. Benton Ave., Helena, MT, 59625, U.S.A.; e-mail: jgeiger@carroll.edu

<sup>2</sup>University Museum and Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, 80309, U.S.A.; e-mail: ranker@colorado.edu

<sup>3</sup>Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, 80309, U.S.A.; e-mail: <sup>4</sup>rampj@colorado.edu, <sup>5</sup>sklimas@colorado.edu

---

**Abstract.** Located approximately 4000 km from the nearest continent, the Hawaiian Islands comprise the most isolated archipelago on Earth. This isolation has resulted in a unique flora that includes nearly 200 native ferns and lycophytes, 77% of which are endemic to the islands. Because the Hawaiian Islands are volcanic in origin, all abiotically dispersed organisms must have arrived there via the wind or the water. Fern spores are most likely dispersed through the air, and thus patterns of air movement have undoubtedly played a significant role in determining the geographic origins of the ancestors of the Hawaiian ferns. We have identified four possible climate-based or weather-based spore dispersal hypotheses that could have resulted in the movement of ancestral spores to the Hawaiian Islands: (1) the northern subtropical jetstream, moving spores from Indo-Pacific regions; (2) the trade winds, dispersing spores from Central and North America; (3) storms carrying spores from southern Mexico and/or Central America; and (4) a dispersal mechanism carrying spores from the South Pacific across the equator resulting from the combined influence of a seasonal southern shift of the Intertropical Convergence Zone (ITCZ), Hadley Cell air movement, and the trade winds. Utilizing recently published molecular phylogenetic studies of three fern genera (*Dryopteris*, *Polystichum*, and *Hymenophyllum*) and new analyses of three additional genera (*Adenophorus*, *Grammitis*, and *Lellingeria*), each of which is represented in the Hawaiian Islands by at least one endemic lineage, we reviewed the biogeographical implications for the Hawaiian taxa in light of the possible common dispersal patterns and pathways. We hypothesize that three of the five endemic *Dryopteris* lineages, both of the endemic *Polystichum* lineages, at least one endemic *Hymenophyllum* lineage in the Hawaiian Islands, and, perhaps, one endemic *Grammitis* lineage resulted from ancestral spores of each lineage dispersing to the Hawaiian Islands via the northern subtropical jetstream. *Adenophorus* is sister to a mostly neotropical clade, therefore, it is likely that the ancestor of the Hawaiian clade dispersed to the Hawaiian Islands via the trade winds or a storm system. The ancestor of the endemic *Lellingeria* lineage may have dispersed to the Hawaiian Islands from the neotropics via the trade winds or a storm system, or from the South Pacific across the equator through the combination of a seasonal southern shift of the ITCZ, Hadley Cells, and the trade winds.

**Key words:** Biogeography, dispersal, ferns, Hawaiian Islands, spores.

---

The study of the biogeographical relationships of Hawaiian lineages is intriguing because of the extreme isolation of the Hawaiian Islands. All geological evidence suggests

that the Hawaiian Islands have always been well separated from continental regions and from other large archipelagoes, because of the mid-oceanic location of the tectonic

hotspot from which they arose (e.g., Clague & Dalrymple, 1987; Carson & Clague, 1995). Thus, all abiotically dispersed species migrating to the Hawaiian Islands must have arrived via long-distance dispersal either through the air or on/in the water. The current high islands of the archipelago are approximately 4000 km from the nearest continent (North America) and other archipelagoes. Such isolation has fostered high levels of species endemism in all native groups of organisms. For example, of the ~1000 species of flowering plants and of the 188 species of ferns and lycophytes native to the Hawaiian Islands, 90% and 77%, respectively, are endemic to the archipelago (Wagner, 1988; Palmer, 2003). These are the highest levels of species endemism of any regional flora in the world (Smith, 1972; Wagner et al., 1999).

Due to reproduction through small, wind-blown spores, ferns and lycophytes are generally thought to be easily dispersed long distances through the air (Tyron, 1970; Smith, 1972; Carlquist, 1980; Ranker et al., 1994). In this paper, we examine four climate- or weather-based phenomena that might provide common paths of airborne dispersal of fern spores to the Hawaiian Islands and we examine data from molecular phylogenetic studies of the Polypodiaceae (Grammitidoideae), the genus *Hymenophyllum* Sm. (Hymenophyllaceae), and the genera *Dryopteris* Adans. and *Polystichum* Roth (Dryopteridaceae) reviewed in light of these putatively common pathways of dispersal. Our goal is to evaluate molecular phylogenetic and resulting biogeographical analyses (i.e., molecular biogeography; see Moore, 2001) in a comparative context to assess whether long-distance dispersal to the archipelago has been essentially random across groups or if there are common patterns across groups due to the influence of shared historical processes. Over the past 20 years, molecular phylogenetic analyses have increased our abilities to develop more robust, testable historical biogeographical hypotheses for Hawaiian plants utilizing the estimated evolutionary relationships among taxa of interest. Based on the relationships of Hawaiian taxa and their non-Hawaiian relatives, we can estimate the number of inferred colonizing ancestors (for multi-species Hawaiian groups) and the most likely geo-

graphic region of origin of each ancestor. Thus, we can then infer which of the possible shared climate-based or weather-based phenomena is likely responsible for delivering particular ancestral propagules to the Hawaiian Islands.

Although several phylogenetic and biogeographical studies have been published in recent years on various groups of Hawaiian flowering plants (and other organisms) (e.g., Wagner & Funk, 1995, and references therein; Gemmill et al., 2002; Howarth et al., 2003; Wanntorp & Wanntorp, 2003; Wright et al., 2001; summary in Price & Wagner, 2004), few studies have sampled widely enough outside of the Hawaiian Islands to elucidate the biogeographical origins of Hawaiian taxa. Examples of studies that have provided strong evidence for extra-Hawaiian biogeographical relationships of Hawaiian plants include: the silversword alliance (Asteraceae), with a putative ancestor from North America (e.g., Baldwin & Sanderson, 1998); *Sanicula* L. (Apiaceae), with closest relatives in North America (Vargas et al., 1998); *Schiedea* (Caryophyllaceae) with closest relative in temperate/boreal North America (Wagner et al., 2005); *Bidens* L. (Asteraceae), with closest relatives in the South Pacific and Mexico (Ganders et al., 2000); *Metrosideros* Banks ex Gaertn. (Myrtaceae), with closest relatives on the Marquesas Islands (Wright et al., 2001); and *Pittosporum* Banks ex Gaertn. (Pittosporaceae), with closest relatives in Fiji and Tonga (Gemmill et al., 2002).

Ferns and lycophytes comprise about 15% of the approximately 1,200 native vascular-plant species of the Hawaiian Islands, whereas worldwide, they comprise only about 3% of the vascular plant flora. Despite their abundance, relatively few phylogenetic studies have been published to date that focus exclusively on Hawaiian ferns or lycophytes (Ranker et al., 2003, 2004; Geiger & Ranker, 2005; Schneider et al., 2005; Driscoll & Barrington, in press), and very few that include Hawaiian ferns or lycophytes at all (but see Haufler & Ranker, 1995; Pryer et al., 2001; Hennequin et al., 2003, 2006; Ebihara et al., 2004; Schneider et al., 2004). Few of these studies have sampled widely enough outside of the Hawaiian Islands to resolve the biogeographical origins of native Hawaiian fern lineages examined.

Fosberg (1948) hypothesized the following

geographic origins for the original colonizing ancestors of native Hawaiian ferns and lycophytes: Indo-Pacific(48%); Pantropical (20.8%); American(11.9%); obscure(11.1%); Boreal(4.4%); and Austral(3.7%). For each genus, he indicated a probable number of colonizing ancestral species and a putative geographical region of origin for each, although he did not specify which ancestor came from which region in the case of multi-species groups. Fosberg's general hypotheses remain largely untested to this day.

### **Impact of paleoclimates on Hawaiian biogeography**

Several important aspects of the geological history of the Hawaiian archipelago determine the extent to which paleoclimate models must be considered in assessing the historical biogeography of any group of Hawaiian organisms. These islands have been produced in a conveyor-belt-like fashion by a stationary volcanic hotspot in the earth's mantle subtending the Pacific tectonic plate (e.g., Clague & Dalrymple, 1987). As the islands ride the Pacific plate to the northwest away from the hotspot, the volcanoes become extinct and the islands eventually subside and erode to sea level or below. Terrestrial species colonizing or evolving *in situ* from earlier colonizers on any particular island, thus, may further disperse to newly produced islands as they arise in the growing chain of islands. Because the oldest part of the Hawaiian-Emperor island chain was produced approximately 85 million years ago (Ma), inter-island colonizations theoretically could have been occurring since at least the late Cretaceous. Such island-hopping colonization is contingent upon adjacent or nearby islands having suitable habitats for colonists to survive. Clague (1996) and Price and Clague (2002) conducted detailed, quantitative analyses of the long-term landscape changes in the Hawaiian archipelago and their potential impact on dispersal, speciation, and extinction of the biota. They provide compelling evidence that the ancestors of extant Hawaiian, terrestrial biota could certainly not have colonized the Hawaiian chain prior to about 23 Ma (early Miocene) and that mid- and high-elevation montane taxa (i.e., most ferns), could not have colonized the islands

prior to the formation of the oldest, current high islands ~5.2 Ma (early Pliocene). Pertinent results of the works of Clague (1996) and Price and Clague (2002) are: (1) There was a ~10 million-year period from ~33 Ma to ~23 Ma in which new island formation slowed such that most terrestrial species on the Hawaiian archipelago would have gone extinct because of island subsidence and erosion to sea level before new high islands were produced to receive colonists; thus, colonization and evolution began anew at ~23 Ma; (2) “[P]rior to the formation of the modern principal Hawaiian Islands starting about 5.2 Ma, there was once again a period of about 5–6 million years when no new islands formed that grew taller than 1 km” (Clague, 1996, p. 48); (3) “Contemporary species living in montane habitats probably arrived from outside the Hawaiian archipelago or evolved after the formation of Kauai” (i.e., 5.2 Ma; Price & Clague, 2002, p. 2432), because appropriate montane habitats simply did not exist on islands older than Kauai by the time Kauai was high enough to support such habitats. Thus, in considering the geographical origins of the present-day Hawaiian flora, patterns of dispersal, and the potential impact of paleoclimates, the geological evidence suggests that we primarily need to be concerned with the last ~5 million years (early Pliocene to present).

Geological, paleoclimatic, and oceanographic evidence suggests that the broad-scale patterns of both air and water movement in the Pacific Basin were already established by the early Mesozoic (~245 to 208 Ma), when water circulation became dominated by two gyres: the clockwise northern gyre and the counter-clockwise southern gyre (see the extensive reviews by Nunn, 1999, and Metcalfe et al., 2001, and references cited therein). Air and water circulatory patterns that were essentially identical to those of the modern Pacific Basin were developed by (1) the opening of the gaps between Antarctica and Australia and between Antarctica and South America during the Palaeocene and Eocene (66–36 Ma; see also Figs. 4–11 of Kroenke, 1996), and (2) the effective or actual closing of the gaps between Australia and Southeast Asia and between North and South America by the start of the Neogene (~24 Ma). Thus, modern patterns of

air and water movement in the Pacific region have been in existence since long before the putative origins of even the oldest colonizing ancestors of the modern Hawaiian montane flora.

Climatic changes over the last 5.2 million years have been too numerous and complex, and are too poorly understood, especially during the glacial times of the Pleistocene (Nunn, 1999; Metcalfe, 2001), to allow us to make specific predictions about their impact on dispersal patterns to the Hawaiian Islands. Because we are focusing on relatively large geographic units (e.g., Indo-Pacific, America, etc.), however, this does not hamper our ability to assess broad-scale patterns. That is, elevational and latitudinal migrations of species and species assemblages due to glacial activity generally occurred within each of Fosberg's (1948) biogeographical units (e.g., Morley, 2001; Wilf et al., 2003).

### **Patterns and Mechanisms of Airborne Dispersal to the Hawaiian Islands**

Numerous studies have documented the occurrence of airborne fern and other spores at various altitudes in the atmosphere (e.g., McDonald, 1962; Hirst et al., 1967). Gressitt et al. (1961) captured a whole fern sporangium at an altitude of 2400 m in the air above Oahu. Gradstein and van Zanten (2001) experimentally tested the ability of fern and bryophyte spores to survive exposure to high levels of UV radiation at high altitudes (9000 to 12,000 m), by flying spores across the Atlantic Ocean on the wings of a commercial jetliner. They discovered that the spores of widespread species generally survived and were able to germinate subsequent to their travels. Thus, spores are not only regularly transported by the wind, but those of some species can survive limited exposure to high altitudes and UV radiation.

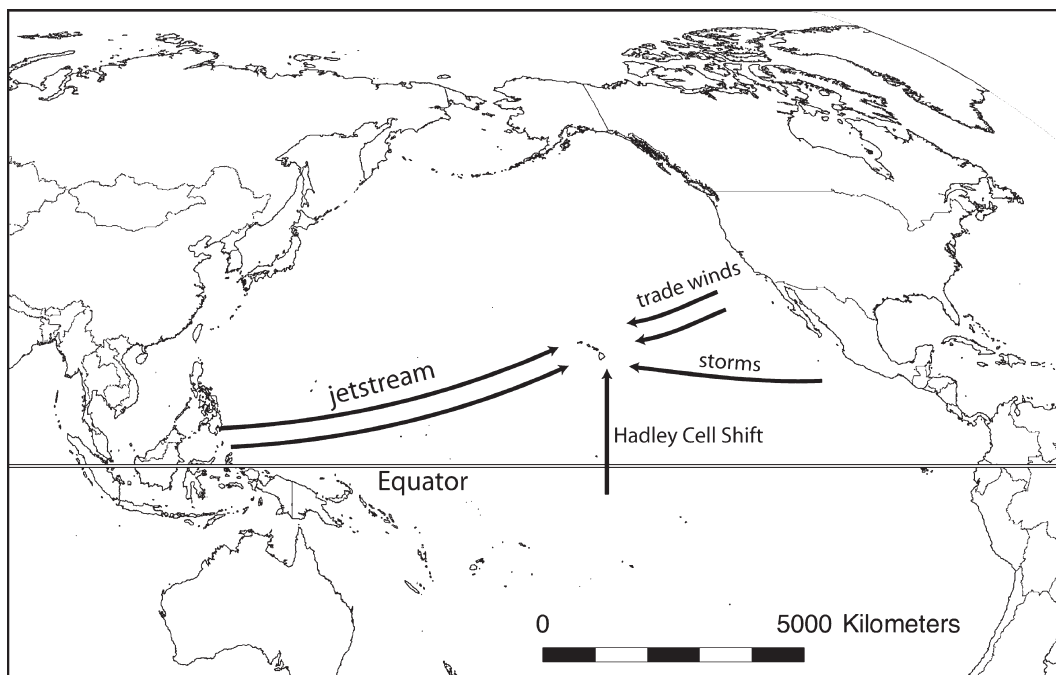
There are four climate- or weather-based phenomena that might lead to common means of airborne dispersal of fern spores to the Hawaiian Islands (see Fig. 1). First is the jetstream. The northern subtropical jetstream occurs as a wave-like band of fast-moving air (up to 485 kph), ~5500 to ~17,000 m in altitude, flowing from west to east (Ratner, 1955). The jetstream accelerates as it moves

eastward from SE Asia (~195 kph) and decelerates as it moves over the Hawaiian Islands (down to ~115 kph; Fosberg, 1963; Carlquist, 1980). Spores could be moved up into the jetstream by storms and transported from SE Asia/Malaysia to the Hawaiian Islands in two to four days. Thus, the combined activity of storms and the jetstream could account for colonizing species arriving from the direction of SE Asia/Indo-Malaysia to the Hawaiian Islands. In fact, the ancestors of the majority of Hawaiian taxa (plants and animals) are thought to be of Indo-Malaysian/Pacific origins (e.g., Fosberg, 1948; Zimmerman, 1948; Carlquist, 1980).

The second possible common means of spore dispersal to the Hawaiian archipelago is via the trade winds. The southernmost extent of the Hawaiian Islands is defined by the location of the volcanic hot spot that produces them, at approximately 19° N latitude. The present-day high islands extend from that point to about 640 kilometers NW, ~22° N. Thus, they are within the northern trade wind belt (which occurs from 25–30°N to the equator), wherein for much of the year, but especially the summer, these low elevation and surface winds are from the north-northeast to east 90% of the time. The clockwise-rotating North Pacific anticyclone feeds into the trade wind belt, drawing northerly air masses towards the equator (Fig. 1). Thus, the trade winds could account for the dispersal of spores from America.

The third possible common spore dispersal pathway is via regular, tropical storm and hurricane tracks from the vicinity of southern Mexico and Central America moving to the Hawaiian Islands. For example, see the track of hurricane Daniel from the year 2000 at <http://www.nhc.noaa.gov/prelims/2000daniel1.gif> and that of hurricane Dora from 1999 at <http://www.nhc.noaa.gov/prelims/1999dora1b.gif>. Storms that make it to the Hawaiian Islands from the Mexican/Central American region can do so in 7–10 days. Thus, spores could be transported to the Hawaiian Islands from America via storms if they are lifted high enough into the air column.

The fourth possible common spore dispersal pathway is through the trade winds in combination with the effects of Hadley Cells and a seasonal shift southward of the inter-



**FIG. 1.** Map of the Pacific Basin illustrating the possible climate- or weather-based phenomena that might lead to common paths of airborne dispersal of fern spores to Hawai'i.

tropical convergence zone (ITCZ; see Wright et al., 2001). The ITCZ (or doldrums) marks an atmospheric discontinuity between the northern and the southern hemispheres, which tends to limit the movement of low altitude air masses across the equator (Fig. 1). Thus, the existence of the ITCZ would also tend to limit dispersal of wind-blown organisms between the two hemispheres. The ITCZ essentially tracks the relative position of the sun to the earth, thus at each equinox the ITCZ hovers around the equator. In the austral late summer/early fall, the ITCZ forms south of the equator to 5–10° S (see Wright et al., 2001, and references therein). The Marquesas Islands lie at approximately 9° S latitude and are 3000 km SSW of the Hawaiian Islands. The seasonal more southerly positioning of the ITCZ therefore includes the Marquesas Islands in a northern hemisphere atmospheric circulation. At the same time, the mostly northern hemisphere Hadley Cell moves, rising from its southern boundary at the ITCZ initially North-Pole-ward to later descend at about 25° N, northeast of the Hawaiian Is-

lands. Spores or other propagules of southern hemisphere origin being carried by this mass of air could then be transported to the Hawaiian Islands via the northeasterly/easterly trade winds. This mechanism of trans-equatorial dispersal was proposed by Wright et al. (2001) to account for dispersal from the Marquesas Islands to the Hawaiian Islands of wind-blown seeds of *Metrosideros* Gaudich. (Myrtaceae).

### Biogeographical Patterns of Hawaiian Ferns

#### EVALUATION OF HAWAIIAN *DRYOPTERIS* (DRYOPTERIDACEAE)

Geiger and Ranker (2005) presented a molecular phylogeny for approximately 25% of the species of *Dryopteris* (Dryopteridaceae) based on the chloroplast DNA (cpDNA) regions *rbcL* and the *trnL-F* intergenic spacer (IGS). They sampled the chloroplast genomic regions for 18 Hawaiian *Dryopteris* taxa, 45 non-Hawaiian *Dryopteris* taxa, and two non-



*Dryopteris* outgroup species, one of which was the Hawaiian endemic *Nothoperanema rubiginosum* (Brack.) A. R. Sm. & D. D. Palmer. Utilizing the results from the phylogenetic analysis, they inferred the minimum number of dispersal and colonization events of dryopteroid ferns to the Hawaiian Islands and inferred from where they dispersed given the native range of each Hawaiian clade's closest living relative.

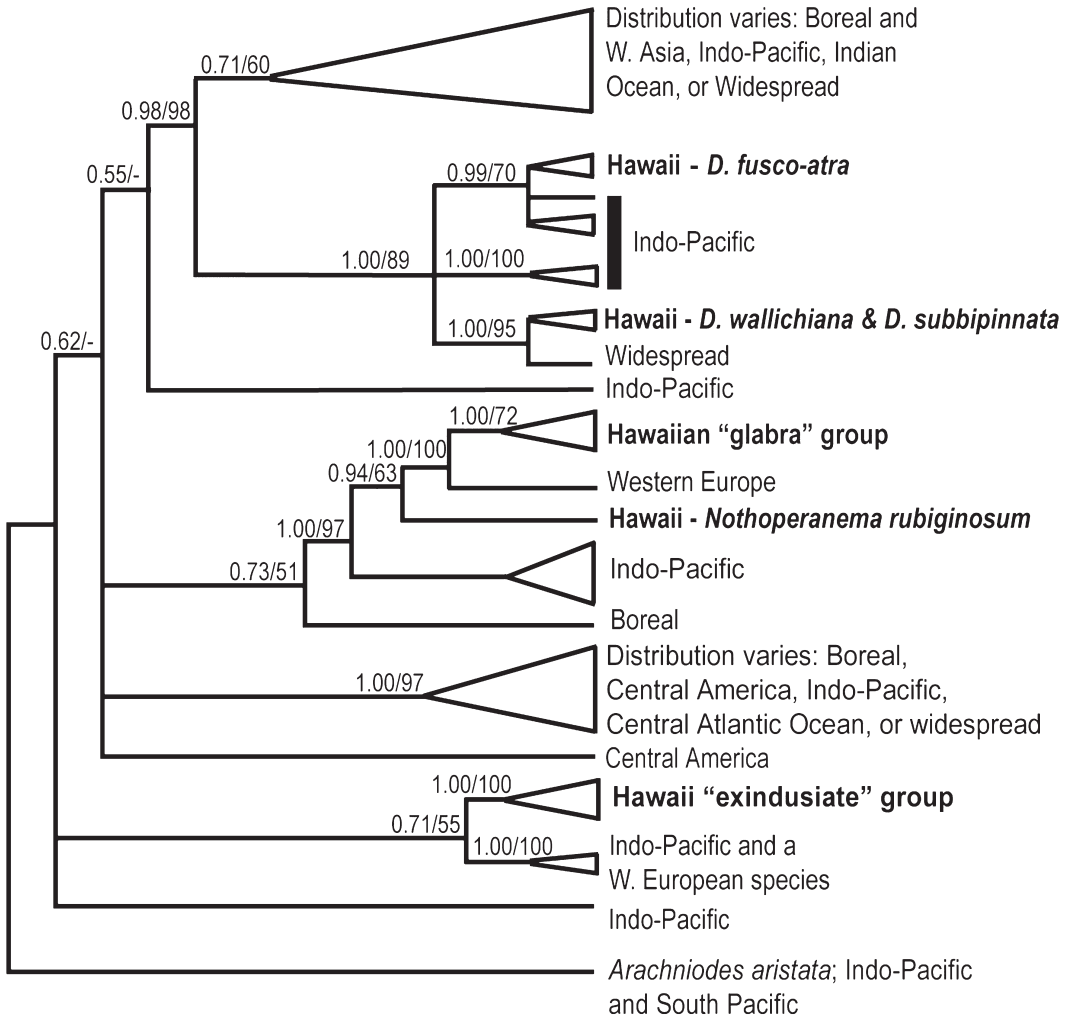
In the Hawaiian Islands, the genus *Dryopteris* is represented by 18 endemic taxa and one pantropical, native species. Based on previous taxonomic treatments and morphological analyses it had been hypothesized that there were anywhere from 25 separate dispersal and colonization events of *Dryopteris* to the Hawaiian Islands (Fosberg, 1948) to as few as three (Fraser-Jenkins, 1994). Fosberg's (1948) high number of colonization events may reflect different generic circumscriptions than those of Palmer (2003), but since Fosberg did not provide a species list, we cannot discern this. The phylogenies presented in Geiger and Ranker (2005) indicate that the Hawaiian *Dryopteris* species do not comprise a monophyletic group and therefore support that the diversity of the genus observed in the Hawaiian Islands is indeed the result of multiple introductions. The Hawaiian *Dryopteris* taxa were resolved in four different clades, while the non-*Dryopteris* endemic *Nothoperanema rubiginosum*, included in the analyses as an outgroup, was resolved among the *Dryopteris* taxa and represents an additional Hawaiian endemic dryopteroid lineage. These analyses indicated that there have been three to five dispersal and colonization events of dryopteroid ferns to the Hawaiian Islands (Fig. 2).

Of the five clades in the Hawaiian Islands, three, possibly four, have closest relatives in the Indo-Pacific. The basal-most Hawaiian group, the *Dryopteris* "exindusiate" clade, shares a common ancestor with a clade comprised of two species with an E Asian distribution and one species that occurs in W Europe. Geiger and Ranker (2005) suggested that it is possible that an ancestral Asian species dispersed to the Hawaiian Islands and that there was a separate dispersal event of a close relative to W Europe. They noted that the relationship between the two clades did

not have strong support (Bayesian analysis posterior probability (PP)=0.71, and maximum parsimony bootstrap (BS) support=55; Fig. 2) and that it is likely with increased sampling, better hypotheses for the relationships of the Hawaiian exindusiate clade to other non-Hawaiian clades would be developed. Their results do, nonetheless, provide some support for one dispersal event to the Hawaiian Islands via the northern subtropical jetstream.

*Nothoperanema rubiginosum* was strongly supported (PP 0.94, BS 64) in the analyses of Geiger and Ranker (2005) as sister to a clade comprised of two W. European species and the Hawaiian endemic *Dryopteris glabra* (Brack.) Kuntze clade. The W. European species were strongly supported as sister to the Hawaiian endemic *D. glabra* clade (PP 1.00, BS 100). The entire clade was sister to a clade in which all of the species have an Indo-Pacific distribution (PP 1.00, BS=97). Geiger and Ranker (2005) hypothesized that one dispersal event of a dryopteroid ancestor to the Hawaiian Islands via the northern subtropical jetstream resulted in the *N. rubiginosum* lineage, while a second dispersal of a close relative dispersed to the Hawaiian Islands, also via the northern subtropical jetstream, gave rise to the *D. glabra* clade. In a recent study of Chinese *Dryopteris* based on chloroplast *rps4-trnS* sequence data in which three different *Nothoperanema* (Taq.) Ching species were included, Li and Lu (2006) found that the three *Nothoperanema* species were nested among the *Dryopteris* species. In their study, the *Nothoperanema* species were closely related to *D. erythrosora* (Eat.) Kuntze, which in the Geiger and Ranker (2005) analyses was resolved as part of the above mentioned sister Indo-Pacific clade.

The results of Geiger and Ranker (2005) did not allow for the development of any well-supported biogeographical hypotheses for the origins of the fourth Hawaiian clade, comprised of the pantropical *Dryopteris wallichiana* (Spreng.) Hyl. and *D. subbipinnata* W. H. Wagner & R. W. Hobdy, due to the widespread distribution of its sister species, *D. affinis* (Lowe) Fraser-Jenk. subsp. *borreri* (Newman) Fraser-Jenk. However, the fifth Hawaiian lineage, *D. fusco-atra* Robinson, was strongly supported as a member of a



**FIG. 2.** Summary phylogeny of a combined Bayesian analysis of *rbcL* and the *trnL-F* IGS for *Dryopteris* (Dryopteridaceae) modified from Geiger and Ranker (2005). Hawaiian clades are named and geographic distributions are indicated for each non-Hawaiian clade or taxon. Posterior probabilities are the first number above each branch and were obtained from running 1,000,000 generations of which one tree was sampled per 100 trees generated. The second number above each branch (when present) represents maximum parsimony bootstrap values from 1303 repetitions and 10 random stepwise addition replicates each.

clade (PP 0.99, BS 70) in which all of the other members have an Indo-Pacific distribution. Thus, these results suggest another ancestral *Dryopteris* dispersal to the Hawaiian Islands via the northern subtropical jet-stream. Although sampling across the genus *Dryopteris* was fairly broad, only about 25% of the genus was sampled, therefore further sampling may allow us to make stronger inferences in the future.

#### HYMENOPHYLLUM IN THE HAWAIIAN ISLANDS

Worldwide, the filmy fern genus *Hymenophyllum* s.l. (Hymenophyllaceae) comprises over 300 mostly tropical species and in the Hawaiian Islands the genus is represented by three endemic species: *Hymenophyllum lanceolatum* Hook. & Arn., *H. obtusum* Hook. & Arn., and *H. recurvum* Gaudich. Four molecu-



lar studies of *Hymenophyllum* have recently been published, each of which included sequences from *H. lanceolatum* (Pryer et al., 2001; Hennequin et al., 2003, 2006; Ebihara et al., 2004). To our knowledge, the relationships of *H. recurvum* and *H. obtusum* to non-Hawaiian taxa have not yet been assessed. It was not the goal of any of these recent studies to investigate the origins of the Hawaiian species; however, we examine their results here, attempting to gain some insights into the biogeographical history of *H. lanceolatum*.

Studies based on *rbcL* sequences by Ebihara et al. (2004) and Hennequin et al. (2006), the two most recent that have included *Hymenophyllum lanceolatum*, allow for the development of biogeographical hypotheses regarding the geographic origin of the Hawaiian endemic. Ebihara et al. (2004) analyzed 60 *rbcL* sequences from members of Hymenophyllaceae and found weak evidence (bootstrap value < 50) for a sister relationship between *H. lanceolatum* and *H. pilosissimum* C. Chr., a species that occurs in Borneo and New Guinea (Fig. 3). Assuming this relationship is confirmed as more studies with additional taxa are conducted, we would have evidence that the Hawaiian colonizing ancestor was Indo-Pacific in distribution and that the vehicle for spore dispersal was the northern subtropical jetstream. Additionally, the analyses of Ebihara et al. (2004) placed *H. lanceolatum* and *H. pilosissimum* as unresolved among *H. frankliniae* Col., distributed in New Zealand and *H. subobtusum* Ros., a New Caledonian species. This unresolved group of four species was sister to a clade comprising species with Austral/South Pacific distributions and others that occur throughout the Indo-Pacific.

The analyses of Ebihara et al. (2004) included sequences from the two species supported as sister to *Hymenophyllum lanceolatum* in Hennequin et al. (2006), *Trichomanes digitatum* Sw. and *T. taeniatum* Copel. (Ebihara et al., 2004 used a different classification in which both of these species were treated in the genus *Microtrichomanes* (Mett.) Copel.). As described above, the results of Ebihara et al. (2004) did not support the sister relationship of *H. lanceolatum* to *T. digitatum* and *T. taeniatum*, likely due to the inclusion of more representatives from the

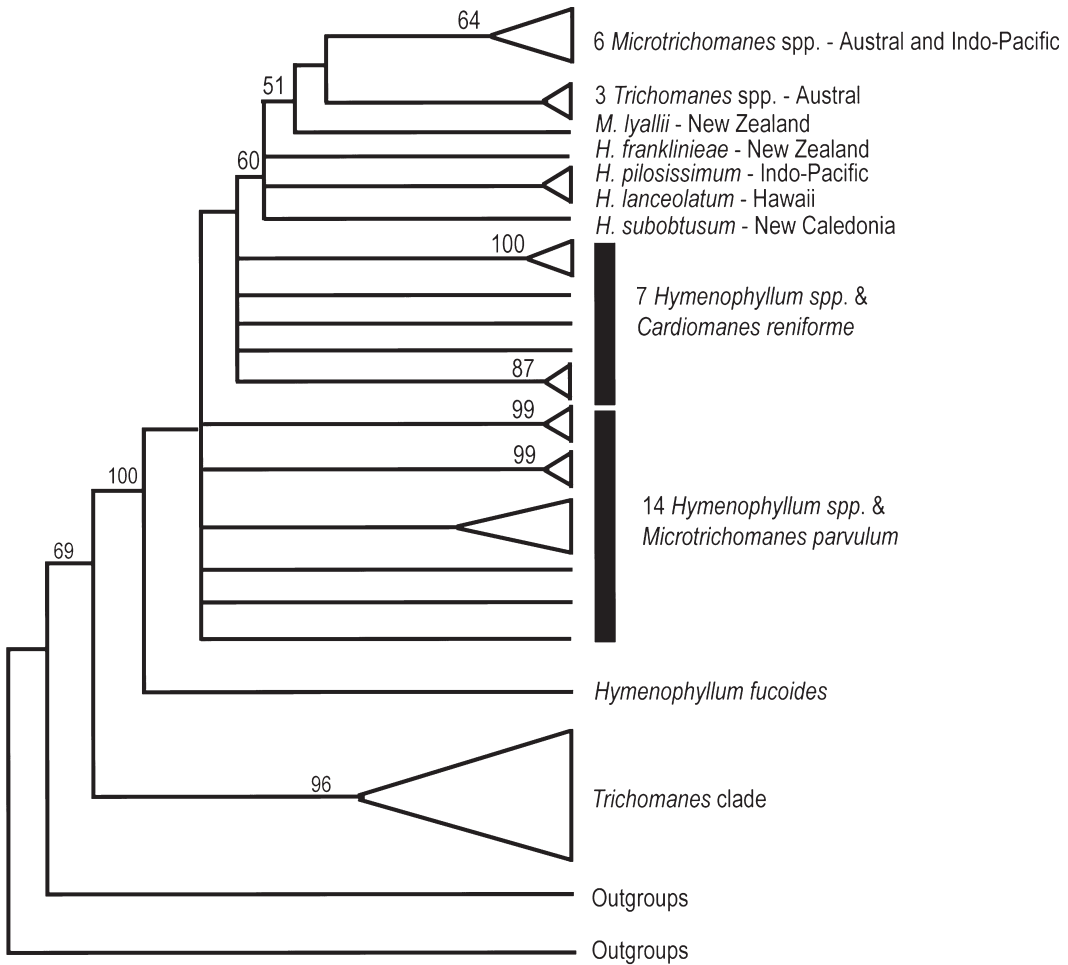
particular clade to which these species belong. The three species were resolved in one clade; however, within that clade, *H. lanceolatum* was supported among the basal-most taxa, while *T. digitatum* and *T. taeniatum* were among the most derived.

It is clear that further detailed studies are needed to fully resolve the biogeographical origins of *Hymenophyllum lanceolatum*; however, the current available evidence suggests that the northern subtropical jetstream was responsible for delivering colonizing spores to the Hawaiian Islands. Additionally, it is unknown whether two other Hawaiian endemics, *H. recurvum* and *H. obtusum*, share common ancestry with *H. lanceolatum*, and so the biogeographical story will not be complete with only investigations of the origin of *H. lanceolatum*.

#### HAWAIIAN *POLYSTICHUM* (DRYOPTERIDACEAE)

*Polystichum* (Dryopteridaceae) is represented worldwide by approximately 260 species and there are three endemic species in the Hawaiian Islands: *Polystichum haleakalense* Brack., *P. bonseyi* W. H. Wagner & R. W. Hobdy, and *P. hillebrandii* Carruth. Driscoll and Barrington (in press) recently conducted a molecular phylogenetic study of 50 *Polystichum* species, including the three Hawaiian endemics. They obtained sequences of the cpDNA regions *rbcL* and the *trnL-F* IGS to determine whether the three Hawaiian species comprise a monophyletic group and to infer their geographic region of origin by determining their closest living non-Hawaiian relatives.

Combined Bayesian analysis and maximum parsimony analysis of *rbcL* and the *trnL-F* IGS revealed that within the Hawaiian Islands there are at least two distinct *Polystichum* lineages (Fig. 4). *Polystichum haleakalense* and *P. bonseyi* comprise a derived clade with the Indo-China species *P. wilsonii* Christ (PP 1.00, BS 100). These three species were strongly supported as sister to a clade comprised of the Nepalese *P. yunnanense* Christ. and *P. piceopaleaceum* Tagawa (PP 1.00, BS 84), which is distributed in SE Asia. The sister species to these two clades was the SE Asian *P. tagawanum* Kurata (PP 0.92, BS 92). *Polystichum hillebrandii* comprises the second



**FIG. 3.** Summary phylogeny of the strict consensus tree of 4806 most parsimonious trees based on *rbcL* sequence data modified from Fig. 1 of Ebihara et al. (2004). Numbers above each branch represent maximum parsimony bootstrap values.

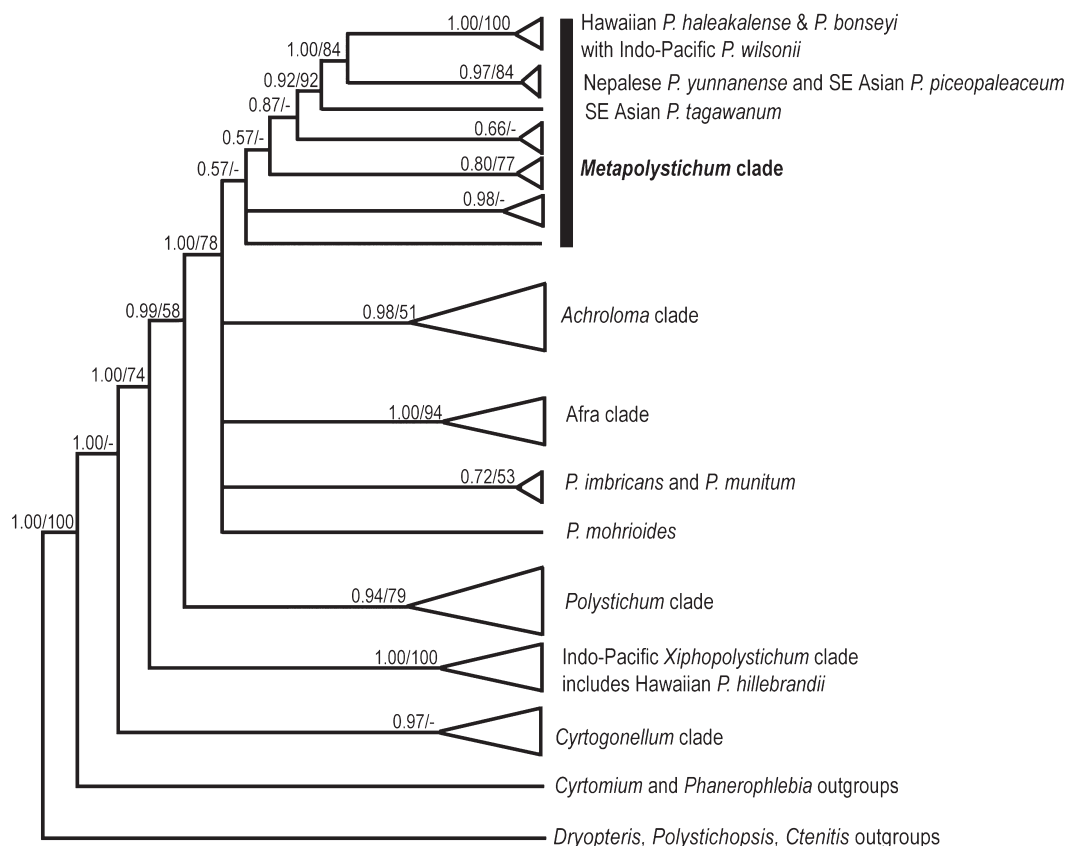
Hawaiian lineage and was resolved among a more basally positioned *Polystichum* clade as sister to the Himalayan/SE Asian species *P. neolobatum* Nakai. These two species were resolved within a strictly S/SE Asian clade (PP 1.00, BS 100).

Driscoll and Barrington's (in press) analyses support the hypothesis that the three Hawaiian *Polystichum* species have evolved from at least two colonizing ancestral *Polystichum* species. Both of the Hawaiian lineages were supported as belonging to clades in which the species are all distributed in the Himalayas and/or SE Asia. Thus, it is likely that the northern subtropical jetstream was

the mechanism of spore dispersal of two different lineages of ancestral *Polystichum* species to the Hawaiian Islands.

#### STUDIES OF HAWAIIAN GRAMMITID FERNS (POLYPODIACEAE: GRAMMITIDOIDEAE)

There are approximately 750 species of grammitid ferns occurring worldwide in mostly tropical and subtropical regions, and the majority of the species are epiphytes. In the Hawaiian Islands, the grammitid ferns are represented by three genera: *Adenophorus* Gaudich., *Grammitis* Sw., and *Lellingeria* A. R. Smith & R. C. Moran. Recent molecular



**FIG. 4.** Summary phylogeny of a combined Bayesian analysis of *rbcL* and the *trnL-F* IGS for *Polystichum* (Dryopteridaceae) modified from Driscoll and Barrington (in press). Posterior probabilities are the first number above each branch and were obtained from running 1,000,000 generations of which one tree was sampled per 100 trees generated. The second number (when present) represents maximum parsimony bootstrap values from 100 repetitions.

phylogenetic studies by Ranker et al. (2003, 2004) have helped elucidate the relationships among and within these taxa and have provided insights into the biogeographical origins of the Hawaiian taxa. We discuss their previous findings as they relate to our dispersal hypotheses and present new data from continued studies of this group. For the present analyses, we obtained *rbcL* and *atpβ* sequences for 17 grammitid species and *trnL-F* IGS sequences for 15 species that were not included in the analyses of Ranker et al. (2003, 2004) (see Table I) and added the new *rbcL* and *atpβ* data to the molecular dataset of Ranker et al. (2004) for a total of 106 in-group taxa, plus the same five polypod species used as outgroups in Ranker et al. (2004). We conducted a parsimony bootstrap

analysis of the combined dataset using the 'fast step-wise addition' algorithm of PAUP\* 4.0b10 (Swofford, 1998) with 10,000 replications to search for well-supported clades that included the Hawaiian taxa of interest. More intensive analyses were conducted of the smaller clades as described below for each group. In all analyses, uninformative and gapped (for *trnL-F* IGS sequences) characters were deleted and all character state transitions were unordered.

**Adenophorus.** The genus *Adenophorus* is endemic to the Hawaiian Islands. *Adenophorus*, as recently treated, comprises ten species, although Ranker et al. (2003, 2004) provided strong evidence, from molecular phylogenetic analyses of 79 grammitid species, that another Hawaiian endemic, *Grammitis tenella* Kaulf.,

TABLE I  
SPECIES, COLLECTION AND VOUCHER INFORMATION, AND GENBANK ACCESSION NUMBERS. DASHES INDICATE THAT  
GENBANK ACCESSION NUMBERS ARE CITED IN PUBLICATIONS CITED IN THE TEXT. ND=NO DATA

Species	Locality, collector & number (herbarium)	GenBank numbers new in this study		
		<i>rbcL</i>	<i>atpβ</i>	<i>trnL-F</i> IGS
<i>Cochlidium serrulatum</i> (Sw.)				
L. E. Bishop	Costa Rica, A. Rojas 3004 (UC)	EF178614	ND	ND
<i>Cochlidium serrulatum</i>	Dominica, S. R. Hill 29102 (UC)	EF178615	EF178632	ND
<i>Grammitis baldwinii</i> (Baker)	Hawaiian Islands, USA, K. Wood			
Copel.	10575 (PTBG)	EF178616	EF178633	EF178649
<i>Grammitis congener</i> Bl.	Sabah, Malaysia, Ranker 2126	EF178617	EF178634	EF178650
	(BORH, SAN, SNP, COLO)			
<i>Grammitis dolichosora</i>	Sabah, Malaysia, Ranker 2183			
(Copel.) Copel.	(BORH, SAN, SNP)	EF178618	EF178635	ND
<i>Grammitis forbesiana</i>	Hawaiian Islands, USA, Ranker			
W. H. Wagner	1321 (COLO)	–	–	EF178651
<i>Grammitis havilandii</i> (Baker)	Sabah, Malaysia, Ranker 2179			
Copel.	(BORH, SAN, SNP, COLO)	EF178619	EF178636	EF178652
<i>Grammitis holttumii</i> Copel.	Sabah, Malaysia, Ranker 2180			
	(BORH, SAN, SNP, COLO)	EF178620	EF178637	EF178653
<i>Grammitis</i> aff. <i>holttumii</i>	Sabah, Malaysia, Ranker 2175			
	(BORH, SAN, SNP, COLO)	EF178621	EF178638	EF178654
<i>Grammitis hookeri</i> (Brack.)	Hawaiian Islands, USA, Ranker			
Copel.	1116 (COLO)	–	–	EF178655
<i>Grammitis jagoriana</i> (Mett. ex.	Sabah, Malaysia, Ranker 2152			
Kuhn) Tagawa	(SNP)	EF178622	EF178639	EF178656
<i>Grammitis knutsfordiana</i>				
(Baker) Copel.	Fiji, J. Game 95-81 (UC)	–	–	EF178657
<i>Grammitis knutsfordiana</i>	Sabah, Malaysia, Ranker 2176			
	(BORH, SAN, SNP, COLO)	EF178623	EF178640	EF178658
<i>Grammitis kyimbilensis</i>				
(Brause ex. Brause & Hieron.)				
Copel.	Madagascar, Kessler 12773 (UC)	EF178624	EF178641	EF178659
<i>Grammitis padangensis</i>	Sabah, Malaysia, Ranker 2159a			
(Baker) Copel.	(BORH, SAN, SNP, COLO)	EF178625	EF178642	EF178660
<i>Grammitis reinwardtioides</i> Copel.	Sabah, Malaysia, Ranker 2160			
	(BORH, SAN, SNP, COLO)	EF178626	EF178643	EF178661
<i>Lellingeria major</i> (Copel.)				
A. R. Sm. & R. C. Moran	Ecuador, M. Lehnert 895 (GOET)	EF178627	EF178644	ND
<i>Lellingeria saffordii</i> (Maxon)	Hawaiian Islands, USA, Ranker			
A. R. Sm. & R. C. Moran	1892 (BISH, COLO)	EF178628	EF178645	EF178662
<i>Lellingeria subcoriacea</i> (Copel.)	Marquesas Islands, D. Lorence			
A. R. Sm. & R. C. Moran	8944 (PTBG)	EF178629	EF178646	ND
<i>Lellingeria subcoriacea</i> (Copel.)	Marquesas Islands, D. Lorence			
A. R. Sm. & R. C. Moran	8944 (PTBG)	EF178629	EF178646	ND
<i>Lellingeria</i> sp.	Ecuador, M. Lehnert 1232 (GOET)	EF178631	EF178647	ND
<i>Lellingeria</i> sp.	Bolivia, M. Lehnert 718 (GOET)	EF178630	EF178648	ND
<i>Prosaptia contigua</i> C. Presl	Taiwan, Chiou 97-09-12-05			
	(COLO, TAIF, UC)	–	–	EF178663
<i>Prosaptia pubipes</i> Copel.	Fiji, J. Game 95-65 (UC)	–	–	EF178664

is sister to *Adenophorus*. That *G. tenella* and the *Adenophorus* clade are resolved as sister taxa supports the hypothesis that they share a common ancestor that colonized the Hawaiian Islands. These analyses also supported the Hawaiian clade as sister to a mostly neotropical clade, including the monophyletic *Cochlidium* Kaulf., which was sister to two black-

margined *Grammitis* species. *Cochlidium* and *G. bryophila* (Maxon) F. Seym. are strictly neotropical, while *G. melanoloma* occurs in La Réunion.

The fast step-wise addition bootstrap analysis of the large grammitid dataset supported the sister relationship between the *G. tenella* + *Adenophorus* clade and the *Cochlid-*

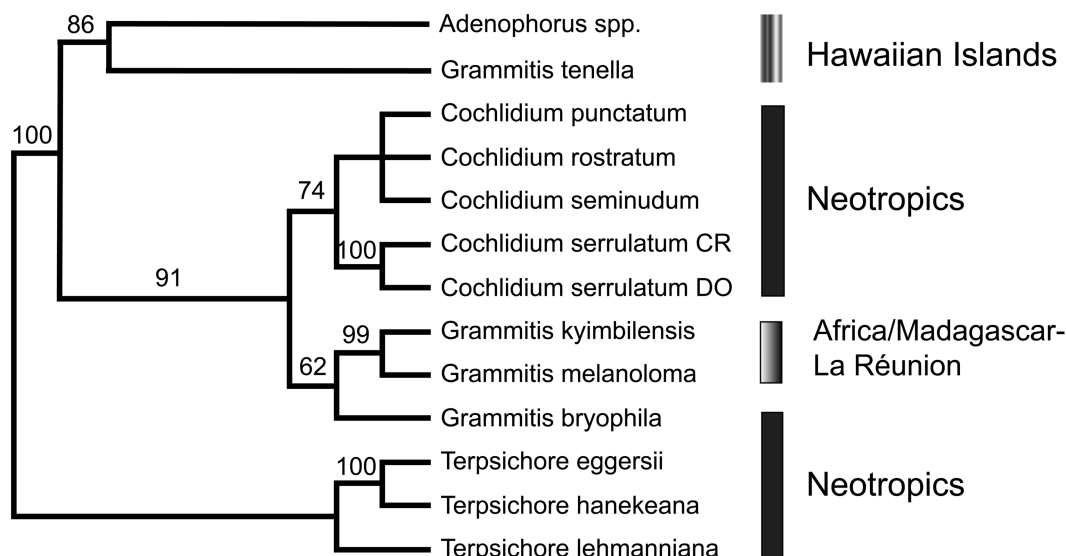


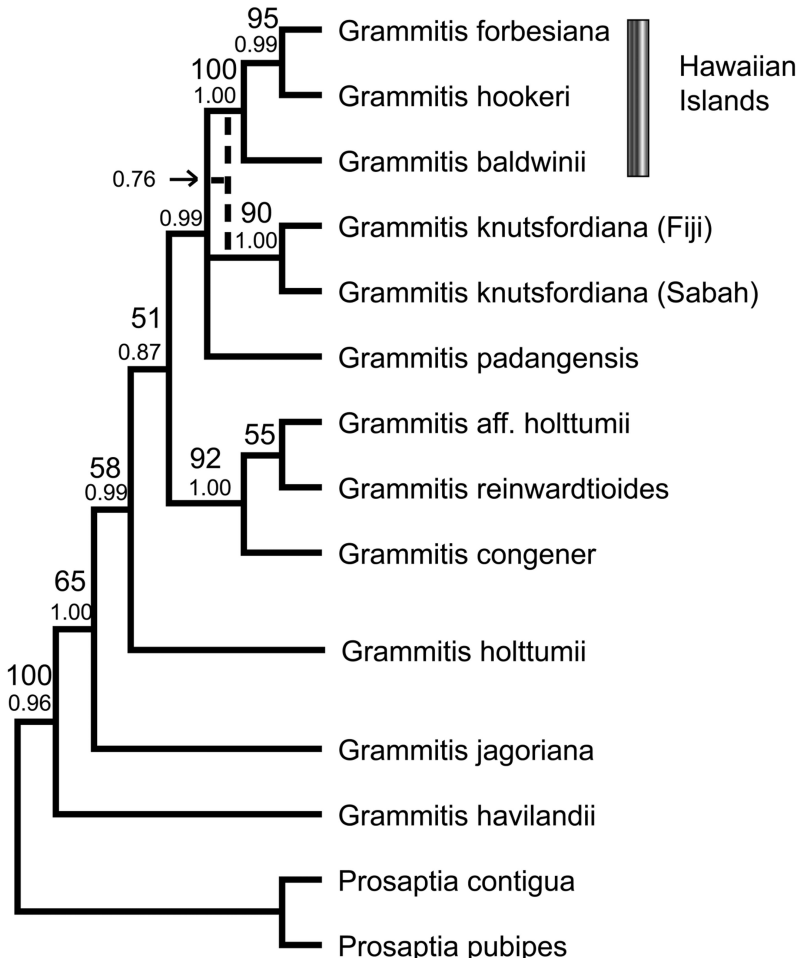
FIG. 5. Strict consensus tree of the three most parsimonious trees from branch-and-bound parsimony analysis of *rbcL* and *atpβ*, with bootstrap values reflecting 100 branch-and-bound bootstrap replicates for Hawaiian *Adenophorus* + *Grammitis tenella* and their non-Hawaiian relatives.

*ium* + black-margined *Grammitis* clade (results not shown; bootstrap [BS] support 97), as was found in Ranker et al. (2004). We conducted a branch-and-bound analysis in PAUP\* of a combined *rbcL* and *atpβ* dataset from all of the taxa shown in Fig. 5, using three species of *Terpsichore* A. R. Smith as functional outgroups. We also conducted a branch-and-bound bootstrap analysis with 100 replicates. The branch-and-bound analysis found three equally parsimonious trees, with consistency indices (CI) of 0.59 and retention indices (RI) of 0.75. The strict consensus tree, with bootstrap values, is shown in Fig. 5. The newly added black-margined *Grammitis kyimbilensis* was resolved as sister to *G. melanoloma* (BS 99) and occurs in Madagascar and Tanzania. The newly added *Cochlidium serrulatum* is neotropical and was resolved among the New World *Cochlidium* clade. Because the two Old World species were supported as derived within the neotropical clade that was sister to the *Adenophorus* + *G. tenella* clade, we hypothesize that the ancestor of the Hawaiian clade had a neotropical distribution and dispersed to the Hawaiian Islands either via the trade winds or a storm.

**Grammitis.** The biogeographical origins of a second grammitid clade endemic to the

Hawaiian Islands were assessed by Ranker et al. (2004). *Grammitis hookeri* and *G. forbesiana* are sister species and evolved from a second grammitid colonist to the Hawaiian Islands. Previous data resolved the two Hawaiian species as sister to *G. knutsfordiana*, and these three *Grammitis* species were sister to *Xiphopteris conjunctisora* (Baker) Copel. and *Themelium tenuisectum* (Blume) Parris. The latter two non-Hawaiian species occur in the SW Pacific or E. Asia.

The fast step-wise addition bootstrap analysis of the large grammitid dataset supported the three Hawaiian endemics, *G. hookeri*, *G. forbesiana*, and *G. baldwinii*, as part of a larger group of taxa primarily ranging from SE Asia to Indonesia, Malaysia, New Guinea, and the islands of the SW Pacific. We conducted several analyses of *rbcL*, *atpβ*, and *trnL-F* IGS sequences from the taxa shown in Fig. 6, employing two species of *Prosaptia* C. Presl as outgroups. A branch-and-bound parsimony analysis of a combined dataset found one shortest tree with CI=0.56 and RI=0.61. Bootstrap values were estimated with 100 branch-and-bound bootstrap replicates (Fig. 6). Among the three Hawaiian endemic species, *G. hookeri* and *G. forbesiana* were strongly supported as sister



**FIG. 6.** Strict consensus tree of the two most likely trees resulting from a GTR maximum likelihood analysis based on sequences of *rbcL*, *atpB*, and *trnL-F* for the *Grammitis hookeri* clade and relatives. The top numbers above branches are the parsimony bootstrap values, and the bottom numbers are posterior probabilities from Bayesian analysis. Dashed lines indicate the support for a sister relationship between the Hawaiian clade and *G. knutsfordiana* in the Bayesian analysis with a posterior probability of 0.76.

taxa (BS 95), and *G. baldwinii* was strongly supported as their sister (BS 100). Although the single branch-and-bound tree supported the Hawaiian clade as sister to a group of four Indo-Pacific/Austral species, bootstrap support for that relationship was less than 50% (Fig. 6).

An analysis of the combined dataset with Modeltest 3.6 (Posada & Crandall, 1998) revealed that the best model of sequence evolution was the GTR model selected by the AIC criterion. The GTR model was employed in a maximum likelihood phylogenetic analysis

that resulted in two equally likely trees (not shown), wherein the relationship of the Hawaiian clade was unresolved between *G. knutsfordiana* and *G. padangensis*. In an attempt to better resolve the relationships of the Hawaiian *Grammitis* clade, we conducted an analysis using Bayesian inference in MrBayes (Huelsenbeck & Bollback, 2001). Clade credibility values were estimated for the combined dataset by calculating the posterior probability for each node using Bayesian inference with a Markov-Chain Monte Carlo (MCMC) sampling method as



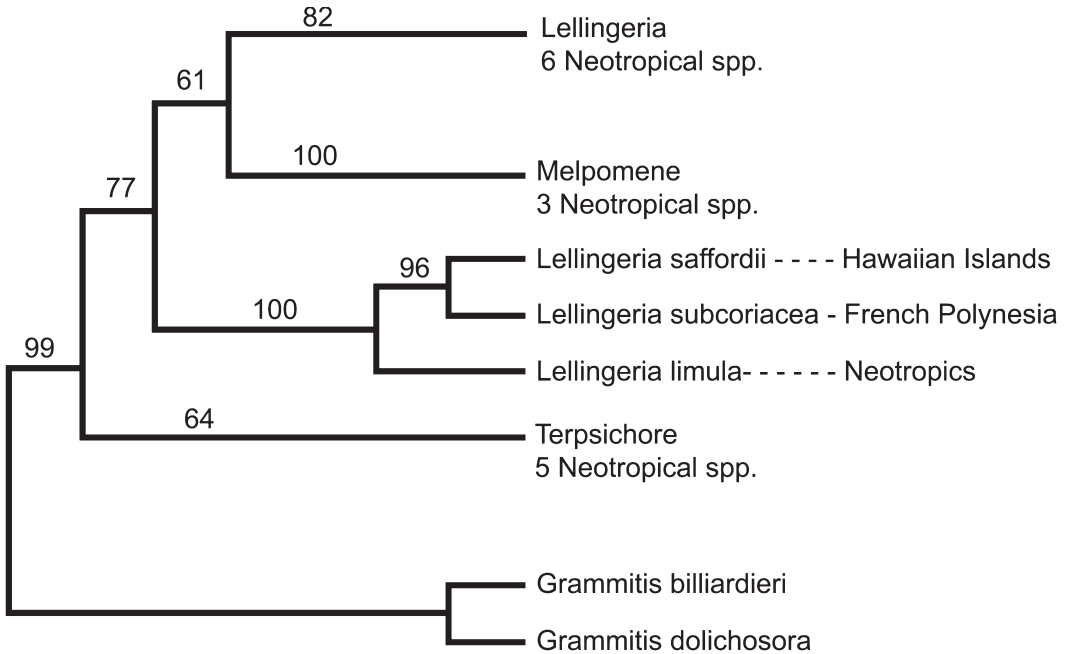
implemented in MrBayes 3.1.2 (Huelsenbeck & Bollback, 2001; Huelsenbeck & Ronquist, 2001) and employing the GTR model found by Modeltest. A tree was sampled every 100 generations for 1,000,000 generations and each analysis was run with four simultaneous MCMC chains. As per the MrBayes instruction manual, we specified a burn-in period that corresponded to ignoring the first 25% of the sampled trees. Clade credibility (or posterior probability, PP) values on the resulting tree are shown in Fig. 6. The resulting tree was similar to the maximum likelihood tree, except that a sister taxon relationship was supported between the Hawaiian clade and *G. knutsfordiana* (PP 0.76), as in the analysis of Ranker et al. (2004). Because the distribution of *G. knutsfordiana* straddles the equator in ranging from northern Borneo and the Philippines to Indonesia, New Guinea, the Solomon Islands, and Fiji, we cannot make a strong statement about the likely geographical origin of the ancestor of this Hawaiian clade of *Grammitis* species. Dispersal via the jetstream from the Indo-Pacific or dispersal via the Hadley Cell shift from the South Pacific seems equally likely. Further sampling of additional grammitid species may allow us to make stronger inferences in the future.

**Lellingeria.** *Lellingeria saffordii* is the third grammitid lineage endemic to the Hawaiian Islands. The genus *Lellingeria* has been shown, through molecular phylogenetic analyses, to be polyphyletic (Ranker et al., 2004), however, the phylogenetic placement of *L. saffordii* has not been assessed until now. The fast step-wise addition bootstrap analysis of the large grammitid *rbcL* and *atpB* dataset supported *L. saffordii* as part of a clade that included several other species of *Lellingeria*, *Melpomene* A. R. Sm. & R. C. Moran species, and several species of *Terpsichore* (BS 74). We employed two species of *Grammitis* as outgroups in a more detailed analysis of the *rbcL* and *atpB* sequences of this *Lellingeria* clade. We conducted a branch-and-bound analysis and a branch-and-bound bootstrap analysis with 100 replicates. *Lellingeria saffordii* was strongly supported as sister to *L. subcoriacea* (BS 96), which occurs in the Society Islands and the Marquesas Islands (Fig. 7). Sister to these two species is neotropical *L. limula* (H. Christ) A. R. Sm. &

R. C. Moran (BS 100). Based on these relationships, we hypothesize that the common ancestor of *L. saffordii* and *L. subcoriacea* is of neotropical origin and dispersed to Pacific islands via the trade winds or a storm. The common ancestor of the two Pacific island species could have had a broad latitudinal distribution similar to *L. limula* (i.e., ranging from Mexico to Brazil) and may have colonized the Hawaiian Islands and the French Polynesian islands independently via trade winds or storms. Alternatively, dispersal from the Americas to the Hawaiian Islands could have been direct, with subsequent dispersal across the equator to the South Pacific via the seasonal Hadley Cell shift accounting for the origin of *L. subcoriacea*. Conversely, dispersal from the neotropics could have first been to the South Pacific via the southerly trade winds or a storm, with subsequent dispersal northerly to the Hawaiian Islands via the seasonal Hadley Cell shift in that direction.

### Summary

We have reviewed molecular phylogenies for six fern genera, *Dryopteris*, *Hymenophyllum*, *Polystichum*, *Adenophorus*, *Grammitis*, and *Lellingeria*, each of which are represented in the Hawaiian Islands by at least one endemic species. From these studies, we found evidence for each of the four described weather-based spore dispersal mechanisms. The northern subtropical jetstream is implicated as the spore dispersal mechanism for several taxa. The following Hawaiian endemic lineages are strongly supported by molecular phylogenetic analyses as being of Indo-Pacific origin: the two endemic *Polystichum* lineages (Driscoll & Barrington, 2007), three of the five endemic *Dryopteris* lineages (Geiger & Ranker, 2005), and, perhaps, the endemic *Grammitis hookeri* clade. The Hadley Cell mechanism, however, cannot be ruled out for the *G. hookeri* clade. *Hymenophyllum lanceolatum* is supported as having close relatives with Indo-Pacific distributions at this time; however, the geographical affinities of this taxon have not been explicitly examined (Ebihara et al., 2004; Hennequin et al., 2006). *Adenophorus* + *G. tenella* are sister to a mostly neotropical clade, therefore, it is likely that the ancestor



**FIG. 7.** Strict consensus tree of the two most parsimonious trees from branch-and-bound parsimony analysis of *rbcL* and *atpβ*, with bootstrap values from 100 branch-and-bound bootstrap replicates for Hawaiian *Lellingeria saffordii* and close relatives.

of the Hawaiian clade traveled to the Hawaiian Islands via the trade winds or a storm. Lastly, we hypothesize that the Pacific species *Lellingeria saffordii* and *L. subcoriacea* share a common ancestor of neotropical origin that dispersed to Pacific islands via the trade winds or a storm. It is also possible that dispersal between the Hawaiian Islands and French Polynesia may have occurred via the Hadley Cell mechanism.

### Acknowledgments

We thank Robbin Moran for inviting us to present this paper at the Pteridophyte Biogeography Symposium at the 15<sup>th</sup> International Botanical Congress in Vienna, Austria. The authors thank Warren L. Wagner and David Lorence for their helpful suggestions and comments on a previous draft. Funding for this study was provided in part by a collaborative grant from the National Science Foundation to TAR (DEB-0344522) and JMOG (DEB-0343664), and the National Geographic Society. Laboratory assistance

was provided by, and training was provided to, Julie Fast ("Asparagus Queen of Colorado"), Olofron Plume, Margaret Wright, and Shannon Fehlberg. We thank Wen-Liang Chiou, John Game, Steven Hill, Michael Kessler, Marcus Lehnert, David Lorence, Alexander Rojas, and Ken Wood for generously providing specimens.

### Literature Cited

- Baldwin, B. G. & M. J. Sanderson. 1998. Age and rate of diversification of the Hawaiian silversword alliance (Compositae). *Proceedings of the National Academy of Science USA* 95: 9402–9406.
- Carlquist, S. 1980. Hawai'i, a natural history: geology, climate, native flora and fauna above the shoreline, 2<sup>nd</sup> ed. Pacific Tropical Botanical Garden, Lawai, Kauai.
- Carson, H. L. & D. A. Clague. 1995. Geology and biogeography of the Hawaiian Islands. Pp. 14–29. *In*: W. L. Wagner & V. A. Funk (eds.). *Hawaiian biogeography: evolution on a hot spot archipelago*. Smithsonian Institution Press, Washington and London.
- Clague, D. A. 1996. The growth and subsidence of the Hawaiian-Emperor volcanic chain. Pp. 35–50. *In*: A. Keast & S. E. Miller (eds.). *The origin and evolution of Pacific Island biotas, New Guinea to Eastern Poly-*

- nesia: patterns and processes. SPB Academic Publishing, Amsterdam.
- & **G. B. Dalrymple**. 1987. The Hawaiian-Emperor volcanic chain. Part I. Geologic evolution. U. S. Geological Survey Professional Paper 1350: 5–54.
- Driscoll, H. E. & D. S. Barrington**. In Press [2007]. Origin of Hawaiian *Polystichum* (Dryopteridaceae) in the context of a world phylogeny. *American Journal of Botany*.
- Ebihara, A., S. Hennequin, K. Iwatsuki, P. D. Bostock, S. Matsumoto, R. Jaman, J.-Y. Dubuisson & M. Ito**. 2004. Polyphyletic origin of *Microtrichomanes* (Prantl) Copel. (Hymenophyllaceae), with a revision of the species. *Taxon* 53: 935–948.
- Fosberg, F. R.** 1948. Derivation of the flora of the Hawaiian Islands. Pp. 107–119. In: E. C. Zimmerman (ed.). *Insects of Hawai'i*. University of Hawai'i Press, Honolulu.
- . 1963. Plant dispersal in the Pacific. Pp. 273–281. In: J. L. Gressitt (ed.), *Pacific basin biogeography, a symposium*. Bishop Museum Press, Honolulu.
- Fraser-Jenkins, C. R.** 1994. *Dryopteris* (Pteridophyta) of Hawai'i—a monographic study. *Thaiszia Journal of Botany* 4: 15–47.
- Ganders, F. R., M. Berbee & M. Pirseyedi**. 2000. ITS base sequence phylogeny in *Bidens* (Asteraceae): evidence for the continental relatives of Hawaiian and Marquesan *Bidens*. *Systematic Botany* 25: 122–133.
- Geiger, J. M. O. & T. A. Ranker**. 2005. Molecular phylogenetics and historical biogeography of Hawaiian *Dryopteris* (Dryopteridaceae). *Molecular Systematics and Evolution* 34: 392–407.
- Gemmill, C. E. C., G. J. Allan, W. L. Wagner & E. A. Zimmer**. 2002. Evolution of insular Pacific *Pittosporum* (Pittosporaceae): Origin of the Hawaiian radiation. *Molecular Phylogenetics and Evolution* 22: 31–42.
- Gradstein, R. & B. van Zanten**. 2001. High-altitude dispersal of spores: an experimental approach. XVI international Botanical Congress. Abstract no. 4439.
- Gressitt, J. L., J. Sedlacek, K. A. J. Wise & C. M. Yoshimoto**. 1961. A high speed airplane trap for airborne organisms. *Pacific Insects* 3: 549–555.
- Haufler, C. H. & T. A. Ranker**. 1995. *rbcL* sequences provide phylogenetic insights among sister species of the fern genus *Polypodium*. *American Fern Journal* 85: 361–374.
- Hennequin, S., A. Ebihara, M. Ito, K. Iwatsuki & J.-Y. Dubuisson**. 2003. Molecular systematics of the fern genus *Hymenophyllum* s.l. (Hymenophyllaceae) based on chloroplastic coding and noncoding regions. *Molecular Phylogenetics and Evolution* 27: 283–301.
- , ———, ———, ——— & ———. 2006. New insights into the phylogeny of the genus *Hymenophyllum* s.l. (Hymenophyllaceae): Revealing the polyphyly of *Mecodium*. *Systematic Botany* 31: 271–284.
- Hirst, J. M., O. J. Stedman & G. W. Hurst**. 1967. Long-distance spore transport: vertical section of spore clouds over the sea. *Journal of General Microbiology* 48: 357–377.
- Howarth, D. G., M. H. G. Gustafsson, D. A. Baum & T. J. Motley**. 2003. Phylogenetics of the genus *Scaevola* (Goodeniaceae): implication for the dispersal patterns across the Pacific Basin and colonization of the Hawaiian Islands. *American Journal of Botany* 90: 915–923.
- Huelsenbeck, J. P. & J. P. Bollback**. 2001. Application of the likelihood function in phylogenetic analysis. Pp. 415–443. In: D. J. Balding, M. Bishop & C. Cannings (eds.). *Handbook of statistical genetics*. John Wiley & Sons, Ltd., Chichester.
- Huelsenbeck, J. P. & F. Ronquist**. 2001. MrBayes: Bayesian inference of phylogeny. *Bioinformatics* 17: 754–755.
- Kroenke, L. W.** 1996. Plate tectonic development of the western and southwestern Pacific: mesozoic to the present. Pp. 19–34. In: A. Keast & S. E. Miller (eds.). *The origin and evolution of Pacific Island biotas, New Guinea to Eastern Polynesia: patterns and processes*. SPB Academic Publishing, Amsterdam.
- Li, C.-X. & S.-G. Lu**. 2006. Phylogenetics of Chinese *Dryopteris* (Dryopteridaceae) based on the chloroplast *rps4-trnS* sequence data. *Journal of Plant Research* 119: 589–598.
- McDonald, J. E.** 1962. Collection and washout of airborne pollens and spores by raindrops. *Science* 135: 435–436.
- Metcalf, L., J. M. B. Smith, M. Morwood & I. Davidson**. 2001. Faunal and floral migrations and evolution in SE Asia-Australasia. A. A. Balkema Publishers, Lisse.
- Moore, P. D.** 2001. Molecular biogeography. *Progress in Physical Geography* 24: 545–551.
- Morley, R. J.** 2001. Why are there so many primitive angiosperms in the rain forests of Asia-Australasia? Pp. 185–199. In: I. Metcalfe, J. M. B. Smith, M. Morwood & I. Davidson (eds.). *Faunal and floral migrations and evolution in SE Asia-Australasia*. A. A. Balkema Publishers, Lisse.
- Nunn, P. D.** 1999. *Environmental change in the Pacific Basin*. John Wiley & Sons, Chichester.
- Palmer, D. D.** 2003. *Hawai'i's ferns and fern allies*. University of Hawai'i Press, Honolulu.
- Posada, D. & K. A. Crandall**. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.
- Price, J. P. & D. A. Clague**. 2002. How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. *Proceedings of the Royal Society of London B* 269: 2429–2435.
- & **W. L. Wagner**. 2004. Speciation in Hawaiian angiosperm lineages: Cause, consequence, and mode. *Evolution* 58: 2185–2200.
- Pryer, K. M., A. R. Smith, J. S. Hunt & J.-Y. Dubuisson**. 2001. *rbcL* data reveal two monophyletic groups of filmy ferns (Filicopsida: Hymenophyllaceae). *American Journal of Botany* 88: 1118–1130.
- Ranker, T. A., S. K. Floyd & P. G. Trapp**. 1994. Multiple colonizations of *Asplenium adiantum-nigrum* onto the Hawaiian Archipelago. *Evolution* 48: 1364–1370.
- , **J. M. O. Geiger, S. C. Kennedy, A. R. Smith, C. H. Haufler & B. S. Parris**. 2003. Molecular phylogenetics and evolution of the endemic Hawaiian genus *Adenophorus* (Grammitidaceae). *Molecular Phylogenetics and Evolution* 26: 337–347.
- , **A. R. Smith, B. S. Parris, J. M. O. Geiger, C. H. Haufler, S. C. K. Straub & H. Schneider**. 2004.

- Phylogeny and evolution of grammitid ferns (Grammitidaceae): a case of rampant morphological homoplasy. *Taxon* 53: 415–428.
- Ratner, B.** 1955. Winds and fallout: a climatological appraisal. Washington, D. C.: U. S. Weather Bureau.
- Schneider, H., A. R. Smith, R. Cranfill, T. E. Hildebrand, C. H. Hafler & T. A. Ranker.** 2004. Unraveling the phylogeny of polygrammoid ferns (Polypodiaceae & Grammitidaceae): exploring aspects of the diversification of epiphytic plants. *Molecular Phylogenetics and Evolution* 31: 1041–1063.
- , **T. A. Ranker, S. J. Russell, R. Cranfill, J. M. O. Geiger, R. Agurauja, K. R. Wood, M. Grundmann, K. Klobardanz & J. C. Vogel.** 2005. Origin of the endemic fern genus *Diellia* coincides with the renewal of Hawaiian terrestrial life in the Miocene. *Proceedings of the Royal Society B* 272: 455–460.
- Smith, A. R.** 1972. Comparison of fern and flowering plant distributions with some evolutionary interpretations for ferns. *Biotropica* 4: 4–9.
- Swofford, D. L.** 1998. PAUP\*. Phylogenetic analysis using parsimony (\*and other methods). Version 4. Sinauer Associates, Sunderland, MA.
- Tryon, R. M.** 1970. Development and evolution of fern floras of oceanic islands. *Biotropica* 2: 76–84.
- Vargas, P., B. B. Baldwin & L. Constance.** 1998. Nuclear ribosomal DNA evidence for a western North American origin of Hawaiian and South American species of *Sanicula* (Apiaceae). *Proceedings of the National Academy of Science USA* 95: 235–240.
- Wagner, W. H., Jr.** 1988. Status of the Hawaiian fern flora. *Fiddlehead Forum*. 15: 11–14.
- Wagner, W. L. & V. A. Funk.** 1995. Hawaiian biogeography: evolution on a hot spot archipelago. Smithsonian Institution Press, Washington and London.
- , **D. R. Herbst & S. H. Sohmer.** 1999. Manual of the flowering plants of Hawai'i. Revised edition. University of Hawai'i Press/Bishop Museum Press, Honolulu.
- , **S. G. Weller & A. K. Sakai.** 2005. Monograph of *Schiedea* (Caryophyllaceae subfam. Alsinoideae). *Systematic Botany Monographs* 72: 1–169.
- Wanntorp, L. & H.-E. Wanntorp.** 2003. The biogeography of *Gunnera* L.: vicariance and dispersal. *Journal of Biogeography* 30: 979–987.
- Wilf, P., N. R. Cúneo, K. R. Johnson, J. F. Hicks, S. L. Wing & J. D. Obradovich.** 2003. High plant diversity in Eocene South America: evidence from Patagonia. *Science* 300: 122–125.
- Wright, S. D., C. G. Yong, S. R. Wichman, J. W. Dawson & R. C. Gardner.** 2001. Stepping stones to Hawai'i: a trans-equatorial dispersal pathway for *Metrosideros* (Myrtaceae) inferred from nrDNA (ITS+ETS). *Journal of Biogeography* 28: 269–774.
- Zimmerman, E. C.** 1948. *Insects of Hawai'i*. University of Hawai'i Press, Honolulu.