Evolution of Hawaiian Ferns and Fern Allies in Relation to Their Conservation Status[1]

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ABSTRACT: Evolutionary and conservational differences between Hawaiian pteridophytes and angiosperms involve differences in life histories (free-living generations, fertilization, and spore dispersal). Very high base chromosome numbers characterize the homosporous pteridophytes. Long-distance spore dispersal took place mainly from Old World and pantropical ancestors, accounting for some 80% of the taxa. The ratio of native pteridophyte to angiosperm taxa in Hawai'i averages roughly 1:6, much higher than in continental floras with 1:14. Two hundred twenty-four pteridophyte taxa, including hybrids and naturalizations, are known in Hawai'i. The 170 native orthospecies include endemics (highly variable taxa with polymorphies involving one or more characters, monophyletic species swarms, and solitary endemics) as well as nonendemics. Hybrid nothospecies compose an important additional component, as do naturalized orthospecies. Most of the hybrids are sterile intermediates that propagate by vegetative means; sexual hybrids are rare. The percentage of naturalized species is only one-fourth that of angiosperms. Hawaiian pteridophytes have evolved much more slowly than the angiosperms, as shown by lower endemism (75% versus 91% overall and relatively fewer one- or two-island endemics) and much smaller species swarms (average 1.5 versus 16.0 descendants from each introduction in the 20 most species-rich genera, respectively). Anticipated listing of Hawaiian rare and endangered fern species will probably comprise ca. 17% of the natives, including four believed to be extinct. Naturalized species compose only one-fourth of the percentage in angiosperms, and very few are pests. Habitat destruction by humans and feral mammals is the major conservation problem. Although artificial spore banks and whole-plant culture may help save some rare pteridophytes, the most promising procedure is establishment of natural preserves.

COMPARING THE PATTERNS of Hawaiian pteridophytes with their flowering plant counterparts reveals numerous differences, especially in their relative numbers, their endemism (both overall and island-by-island), the number and size of monophyletic species swarms, incidence of polyploidy, and extent of hybridization, all of which bear upon our understanding of their evolutionary processes.

In this essay I have tried to establish a broad view as a framework for more detailed investigations. Most of the observations reported here are based on intensive studies by the author with the help of Florence S. Wagner over the past 8 yr, together with a number of other individuals. We have also relied heavily on substantive contributions in particular groups, such as *Elaphoglossum* (Anderson and Crosby 1966), *Cystopteris* (Blasdell 1963), *Ophioglossum* (Clausen 1954), Thelypteridaceae (Holttum 1977), *Marsilea* (Johnson 1985), *Deparia* (Kato 1984), *Pteris* (W. H. Wagner 1949, 1968), and *Diellia* (W. H. Wagner 1952, 1953) My

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Hawaiian research was actually begun in 1947, with the help of Lincoln Constance, Annie M. Alexander, and Harold St. John.

The ferns and fern allies differ radically from seed plants in their life history biology. It is not surprising, therefore, that there are strong differences in their evolutionary patterns, and this is well illustrated by their differences in evolution on oceanic islands, such as those of Hawai'i. Pteridophytes have a distinctive alternation of independent free-living generations: the familiar spore-producing plants that are dominant and long-lived, and the tiny gamete-producing plants that are inconspicuous and short-lived. In flowering plants, the gamete-producing generation has become parasitic on the sporophyte and only the diploid stage is free. Ferns and fern allies reproduce simply by wind-blown spores, but flowering plants require transfer by pollen grains to the ovaries where the embryonic seed or ovules occur and where fertilization takes place on the plant. In pteridophytes, fertilization requires merely layers of water on the substrate in or through which the ciliated sperm can swim from the male sex organs to the female organs. In flowering plants the process is much more complicated and specialized: the sperm must be transferred by pollen tubes. The whole process of pollination in flowering plants is mediated mainly by the behavior of volant animals, especially insects (primarily Lepidoptera and Hymenoptera) and birds, the latter especially in the Tropics. Thus there are profound differences in the life cycles of pteridophytes and angiosperms, and these no doubt bear upon the differences in their island evolution.

Most pteridophytes are homosporous, but several groups are heterosporous and have male and female spores, which store food implanted in them by the parent plants. The native heterosporous orders represented in the Hawaiian flora are Selaginellales (spikemosses, two species), Isoetales (quillworts, one species), and Marsileales (water clovers, one species). Why these heterosporous pteridophytes are so few and have evolved so little in Hawai'i is unexplained. Only one of the heterosporous species is widespread and

common in the Islands, viz. *Selaginella arbuscula* (Kaulf.) Spring; this is also the only one that is polymorphic with many variations, some of which have been named. In North America, the percentage of heterosporous pteridophytes is more than eight times as great. Because of the low incidence of heterospory, the following discussion deals only with homosporous pteridophytes, and the major basis for comparison will be the indigenous species.

A poorly understood feature of all homosporous pteridophytes is the number of chromosomes (Wagner and Wagner 1980). The base numbers range mainly from 20 to 70, much higher than those in flowering plants. Some of the largest genera in Hawai'i display such numbers (e.g., *Asplenium* with $x = 36$, and *Dryopteris* with $x = 41$). Polyploid species are frequent, as in the dryopteroid ferns, with n numbers of 41, 82, 123, and 164. The importance of these high numbers is still not fully understood. It has been suggested that the polyploid base numbers arose in antiquity and gene-silencing effectively diploidized the genome, so that the paleopolyploids are genetically no more heterozygous than typical flowering plants (Haufler 1987). Neopolyploids may occur within species or be derived from sterile hybrids between species. The latter situation involving hybridization between two known parental species producing allopolyploids seems to be rare among Hawaiian pteridophytes, unlike those of North America and temperate Asia, where such allopolyploids are frequent to common, at least in certain genera.

The immigration of pteridophytes to Hawai'i has been primarily due to the long-distance dispersal of spores. The majority of native Hawaiian pteridophytes, estimated to be over half of the taxa, appear to have their closest affinities in the Old World. Of the remainder, some 60% are pantropical, and less than 20% are New World in their relationships. Even though some spores could be carried among the feathers of migrating birds, the overwhelming pattern has surely been by wind because spores are readily airborne. Presumably, a majority of spores have the ability to produce gametophytes that can

become under certain conditions bisexual, thus making it possible to have intra-gametophytic mating. Many spores germinate and form female gametophytes, which, if not fertilized for a long period, may produce male organs and male gametes capable of fertilizing eggs on the same gametophytes. Thus a single spore from thousands of kilometers away could start a whole colony. The ages of the current high islands (i.e., those with well-developed rain forest) range from ca. 5.7 to 0.5 million yr old. Most native species occur on all the major islands, with only a minority of approximately one in six species one- or two-island endemics. The latter more localized species are probably either relicts of once widespread species, species of highly specialized habitats, or species of recent arrival.

The mode of long-distance dispersal by spores together with the ability for a single spore to become established and form a population, plus the nondependency of pteridophytes on animals for fertilization, probably explain in large part the high percentage of ferns versus flowering plants in floras of oceanic islands. Hawai'i is no exception; 17% of the species in the indigenous vascular flora are pteridophytes, approximately one-sixth. According to preliminary data on oceanic floras, provided to me by Robbin Moran of the Missouri Botanical Garden, the average percentage of pteridophytes of nine oceanic island groups is 23 (range, 14–34) %. For six continental floras, preliminary data indicate an average of only 7 (range, 3–9) %.

The data on the composition of the pteridophyte component of the Hawaiian flora are still somewhat in a state of flux as a result of new findings in connection with an intensive research program that started in 1987. Any of the numbers given below are still subject to modification as the investigation proceeds. A distinction is made between orthospecies (species that according to our current evidence are the result of cladogeny or divergent evolution), and nothospecies (those resulting from hybridization or reticulation). All of the orthospecies listed below are separated into endemic and nonendemic. Species swarms are presumed to be

derived from single original introductions that diverged into two or more monophyletic species; solitaries are single isolated species presumably resulting by direct descent from original ancestors or surviving branches of ancient swarms. The native nothospecies include taxa that originated by local hybridization involving native and (or) recently introduced species. Only one nothospecies is thus far demonstrated to have resulted from hybridization that took place outside of Hawai'i. Naturalized describes those species known to have been introduced into the archipelago and established mainly in the last century by Western commerce. Numbers of each of these groups are shown in Table 1.

Patterns of biodiversity in Hawaiian pteridophytes in many respects suggest various underlying evolutionary processes. These patterns assume several different forms: (a) Within endemic species variation—monotypes to polytypes, taxa with a high level of genetically controlled variation in one or more characters. (b) Within endemic clade speciation—the presence of two or more related sister-species obviously derived from a single progenitor. (c) Solitary endemics—isolated taxa with no near Hawaiian relatives, probably mostly evolved locally without species splitting. (d) Indigenous non-endemics, essentially lacking evolutionary change—local taxa that appear to be identical or nearly identical to counterparts in other geographical areas. (e) Nothospecies—sexually sterile or fertile derivatives of two

TABLE 1

TYPES AND NUMBERS OF PTERIDOPHYTE SPECIES IN HAWAI'I

HAWAIIAN FLORA	NO. OF TAXA
I. Native	197
A. Orthospecies	170
1. Edemics	127
a. Swarms	48
b. Solitaries	79
2. Nonendemics	43
B. Nothospecies	27
II. Nonnative naturalized	27
Total taxa	224

separate evolutionary lines that reticulate. (f) Recent naturalizations with no known local evolution—usually more or less weedy cultivars that escape and spread spontaneously, either locally or widely.

Hawaiian species that display extensive polymorphy in single characters are listed in Table 2. All of these have been treated in the past as two or more species. Only by comparative field studies of their morphology.has it been possible to show that they compose intergrading populations. The extreme forms have differences that equal or exceed those of many normal pairs or suites of sister-species. Perhaps some of these represent stages in di-

TABLE 2

POLYMORPHIES IN SINGLE CHARACTERS APPARENTLY NOT ACCOMPANIED BY SPECIATION

1. Sori at laminar level to stalked: *Dryopteris glabra* (Brack.) Kuntze
2. Sori dorsal to submarginal to marginal: *Deparia prolifera* (Kaulf.) Hook. & Grev., *Athyrium microphyllum* (Sm.) Alstor
3. Sori coenosoral to schizosoral: *Pteris lidgatii* (Hillebr.) Christ, *Diellia erecta* Brack.
4. Sori indusiate to exindusiate: *Ctenitis honolulensis* (Hook.) Copel.
5. Leaf blades glabrous to pubescent, or glandular: *Dicranopteris linearis* (N. L. Burm.) Underw., *Asplenium contiguum* Kaulf.
6. Leaf blades pinnate to tripinnate: *Asplenium macraei* Hook. & Grev., *Diellia erecta*
7. False veins absent to present: *Polypodium pellucidum* Kaulf.

vergent speciation, but they could represent rejoining segregates just as well. Much of the evolution of Hawaiian pteridophytes may have involved divergent disjunction, local differentiation, and subsequent rejunction, and both processes are occurring simultaneously in different taxa and on different islands. The polymorphies may involve incipient new speciation events caused by mutation, selection, and/or drift involving one or more characters of a single island population. Occasional island-to-island spore dispersal could allow the new genotype to infiltrate the old genotypes and thus produce mixtures and multiple variations.

One of the most striking examples of this phenomenon involves the O'ahu plant known as *Adenophorus hillebrandii* (Hook.) K. Wilson, morphologically a very distinct species in its genus, which seems to constitute one extreme and forms a series of introgressants with the other extreme, *A. tripinnatifidus* (Kaulf.) Hook. & Grev. (Figure 1). We regard them as separate species. However, so common are the intermediates that Bishop (1974) placed them all, including the *A. hillebrandii* extreme itself, in a single polymorphous species. He stated that "relatively uniform local populations may differ strikingly from one another."

The most typical *A. hillebrandii* extremes are on O'ahu. The islands of Kaua'i and Hawai'i show the least *hillebrandii* influences. The differences between the extremes are given in the key below.

Stipe and lower rachis 0.8–1.0 mm thick, blade outline lanceolate, blade base little to much reduced; blade division 3-pinnate, pinnule bases stalked; basal pinna shape lanceolate to ovate, median pinna length 3.0–4.5 cm; median pinna shape lanceolate, pinnae approximate to overlapping, ultimate segments 0.7–1.1 by 0.2–0.4 mm; lamina chartaceous, green to dark green (alive). All Islands .... *A. tripinnatifidus*

Stipe and lower rachis 1.0–1.3 mm thick, blade outline oblong, blade base not reduced to little reduced; blade division 2-pinnate; pinnule bases broadly adnate, basal pinna shape linear, median pinna length 4–6 mm, pinnae remote, separated by more than a pinna width; ultimate segments 1.2–2.0 by 0.4–0.7 mm; lamina coriaceous, light green to yellowish (alive). Mainly O'ahu .... *A. hillebrandii*

Forty-eight endemic Hawaiian species belong to monophyletic swarms of 12 genera and two to six species each (Tables 3, 4).

Several of the swarms, namely *Adenophorus*, *Oligadenus*, *Diellia*, and *Sadleria*, are generally considered to be endemic genera: the
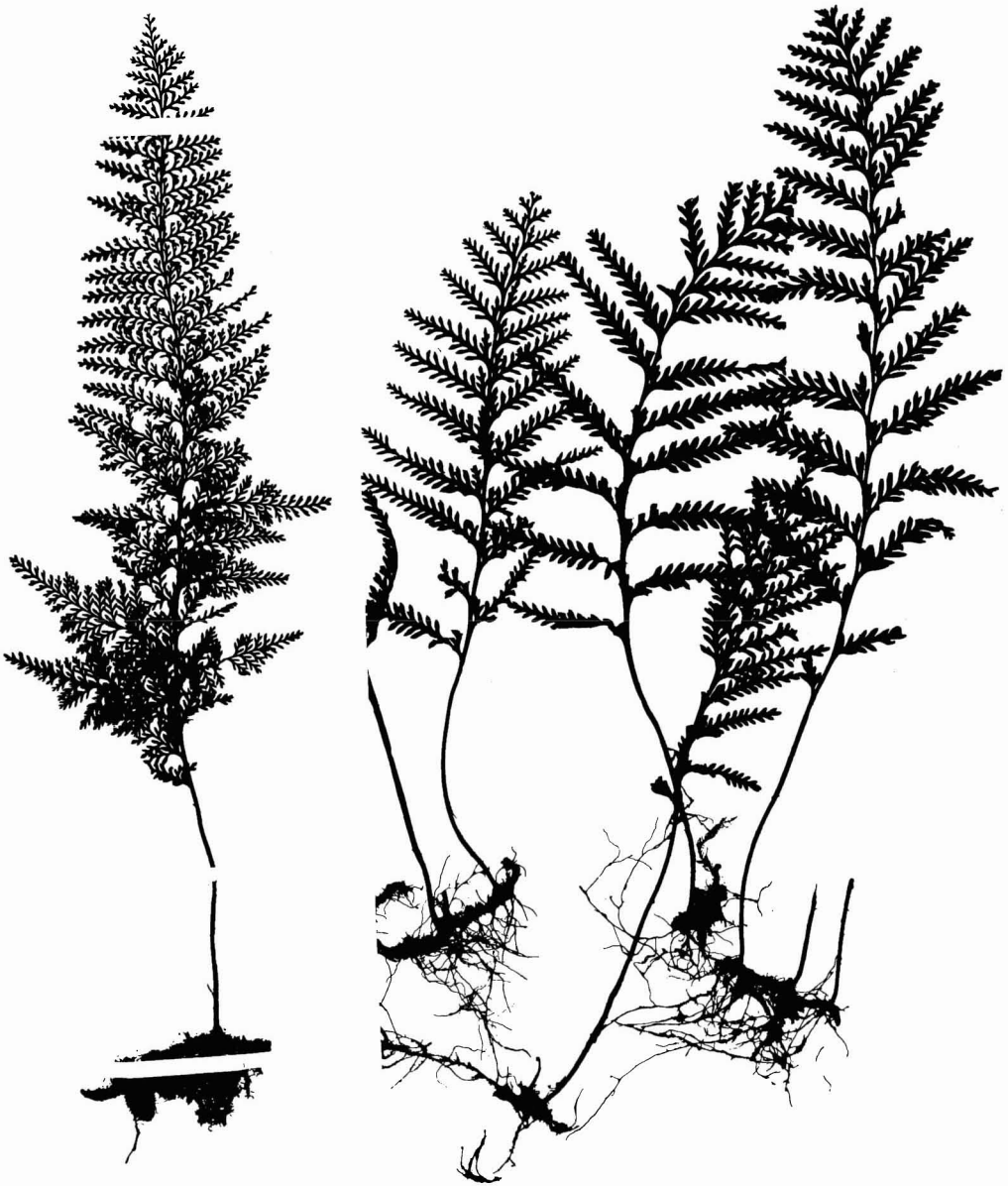
FIGURE 1. Single frond on left: *Adenophorus tripinnatifidus*, Kahokuamanui, Kaua'i, *Rock 5572* (MICH). Cluster of fronds on right: *A. hillebrandii*, Kawailoa, O'ahu, *Topping 3785* (MICH).

first two related to *Grammitis*, the third to *Asplenium*, and the fourth to *Blechnum*. Table 4 compares the Hawaiian species-rich clusters of the angiosperms and the pteridophytes. According to these data, the former show an average increase of 16 (± 2) for each colonist, and the latter only 1.5 (± 0.1). Nearly 80 species are solitary endemics, all of them belonging to genera known outside of Hawai'i. These may be relics of species now extinct in their original homes or derivatives of past introductions that have undergone all

TABLE 3

ENDEMIC ORTHOSPECIES SWARMS IN HAWAIIAN FERNS
(CLOSELY RELATED CLUSTERS OF SPECIES HAVING
A SINGLE ANCESTOR)

SPECIES SWARMS	NO. OF SPECIES
Doryopteris decipiens (Sm.) Hook.	3
Adenophorus tamariscinus (Kaulf.) Hook. & Grev.	6
Oligadenus periens (L. E. Bishop) W. H. Wagner ined.	3
Cibotium menziesii Hook.	4
Thelypteris cyatheoides (Kaulf.) Fosberg	2
Sadleria cyatheoides Kaulf.	5
Doodia kunthiana Gaud.	2
Diellia falcata Brack.	5
Deparia prolifera (Kaulf.) Hook. & Grev.	4
Dryopteris glabra (Brack.) Kuntze	3
Dryopteris unidentata (Hook. & Arn.) Copel.	3
Elaphoglossum alatum Gaud.	4

or most of their evolution in the Islands. It is particularly interesting to compare the incidence of polyploidy in the divergent species of monophyletic swarms with the solitary endemics. Only 2% of the species of swarms are polyploid, but 58% of the solitary species so far counted are polyploid (Table 5). Thus, there appears to be good evidence that the presence of polyploidy has had a dampening effect on the evolution of pteridophytes. Many of those taxa that are polyploid apparently lack the ability to form local derivatives.

A survey of island polyploidy that includes the Canaries, Madeira, Trinidad, New Zealand, Ceylon [Sri Lanka], Jamaica, and Tristan da Cunha gives a range from 25 to 65% (Walker 1984). On the basis of current knowledge, Hawai'i appears to be squarely in the middle with 45%.

TABLE 4

TWENTY MOST SPECIES-RICH GENERA AND PRESUMED NUMBER OF ORIGINAL COLONISTS

FLOWERING PLANTS (W. L. Wagner et al. 1990)			PTERIDOPHYTES		
GENUS	NO. OF SPECIES	PRESUMED NO. OF COLONISTS	GENUS	NO. OF SPECIES	PRESUMED NO. OF COLONISTS
Cyrtandra	53	4–6	*Asplenium*	19	19
Cyanea	52	1	*Dryopteris*	15	8–11
Pelea	47	1	*Thelypteris*	13	7–11
Phyllostegia	27	1	*Elaphoglossum*	9	9
Peperomia	25	3–4	*Adenophorus*	9	1
Clermontia	22	—	*Sadleria*	6	1
Schiedea	22	1	*Diellia*	6	1
Dubautia	21	1	*Huperzia*	5	5
Lipochaeta	20	2 (polyphyletic)	*Cibotium*	5	1
Stenogyne	20	—	*Deparia*	5	1
Myrsine	20	1–2	*Phlegmariurus*	4	4
Hedyotis	20	1–2	*Pteris*	4	4
Bidens	19	1	*Cheilanthes*	4	1
Pritchardia	19	1	*Oligadenus*	4	1
Chamaesyce	15	1–2	*Vandenboschia*	4	3–4
Labordia	15	1	*Grammitis*	3	2–3
Sicyos	14	1	*Ophioglossum*	3	3
Coprosma	13	2	*Microlepia*	3	2
Lobelia	13	2	*Diplazium*	3	3
Wikstroemia	12	1	*Polystichum*	3	3
Totals	469	26–32		125	79–88

TABLE 5

ENDEMIC FERN ORTHOSPECIES
(WITH KNOWN CHROMOSOME NUMBERS)

No. of species in the 12 species swarms	44	
No. that are diploid	43	98%
No. that are polyploid	1	2%
No. of solitary species	43	
No. that are diploid	18	42%
No. that are polyploid	25	58%
Of the 25 polyploid species:		
17 (68%) are tetraploid		
4 (16%) are hexaploid		
4 (16%) are octoploid		

Some 43 of the indigenous Hawaiian taxa are nonendemics, known from outside Hawai'i. Most likely these are more recent arrivals than the endemics and have had little time to evolve locally. To be sure, it will probably be shown that at least some of these nonendemic natives have minute technical differences from their counterparts elsewhere, but in terms of ordinary taxonomic practice, all of these can be interpreted as conspecific with taxa known elsewhere. A small number of them are New World species, some of which tend to occur in drier, higher altitude situations (e.g., East Maui and the volcano regions of the island of Hawai'i), such as *Pellaea ternifolia* (Car.) Link, *Asplenium monanthes* L., *Tectaria cicutaria* (L.) Copel., and *Nephrolepis exaltata* (L.) Schott. *Marsilea villosa* and *Asplenium rhomboideum* Brack. are but little differentiated from *M. vestita* Hook. & Grev. and *A. fragile* Presl, respectively. However, as noted above, the majority of nonendemic indigens appear to be Old World in affinities.

Among the taxa of hybrid origin (i.e., nothospecies), roughly 75% are sterile primary crosses. However, many of these plants, although sexually sterile, are capable of forming vast populations. Some, such as sterile hybrids of *Huperzia* and *Psilotum*, can reproduce by specialized gemmae, on either aerial or subterranean parts. A few hybrids apparently propagate by root proliferation, but more commonly they reproduce by rhizomes that grow and branch extensively. Among the root-reproduced sterile hybrids are *Pityrogramma* × *mckenneyi* W. H. Wagner (*P. austroamericana* Domin × *P. calomelanos* [L.] Link), and the stem-reproduced, *Microlepia* × *adulterinum* W. H. Wagner (*M. speluncae* [L.] T. Moore × *M. strigosa* [Thunb.] Presl), *Thelypteris* × *palmeri* W. H. Wagner (*T. cyatheoides* × *T. dentata* [Forsk.] E. St. John, *Asplenium* × *kokeensis* W. H. Wagner (*A. cookii* Copel. × *A. aethiopicum* [N. L. Burm.] Becherer), and *Nephrolepis* × *medlerae* W. H. Wagner (*N. exaltata* × *N. multiflora* [Roxb.] Jarrett ex Morton). In contrast, some hybrids apparently are unable to reproduce in any way, such as × *Lindsaeosoria flynnii* W. H. Wagner (*Lindsaea ensifolia* Sw. × *Odontosoria chinensis* [L.] J. Sm.), and hybrids among the tree ferns *Cibotium* and *Sadleria*. Each individual results from a separate fertilization.

In addition to sexually sterile hybrids, there are a few allohomoploids (e.g., *Diellia falcata* × *unisora* W. H. Wagner), allopolyploids (e.g., *Asplenium adiantum-nigrum* L.), and apogamous × sexual hybrids (e.g., *Pteris cretica* L. × *P. irregularis* Kaulf.). In terms of the provenance of the parents, the largest number of nothospecies is endemic × endemic. But there are also other combinations (Table 6). Most noteworthy is the black spleenwort, *Asplenium adiantum-nigrum*, which arose as an ancient allopolyploid of two European species and has now become widespread in the Northern Hemisphere, a remarkable example of a nothospecies the

TABLE 6

PROVENANCE OF NOTHOSPECIES PARENTS

Endemic × Endemic	12
Endemic × Indigenous	5
Indigenous × Indigenous	5
Endemic × Naturalized	1
Indigenous × Naturalized	1
Naturalized × Naturalized	2
Foreign × Foreign	1
Total	27

parents of which now occur thousands of kilometers away. (On the basis of isozyme electrophoresis, Ranker et al. [1992] suggested that this species was introduced in Hawai'i at least several different times. An alternative explanation is that the descendants of a single founder have undergone isozyme mutations.) The paucity of known allopolyploids in Hawai'i is unusual in comparison with Asia and North America. Current numbers of the cytogenetic categories of hybrid taxa now known in Hawai'i are as follows: sexually sterile, 19; allohomoploid, 4; allopolyploid, 3; sexual × apogamous, 1, for a total of 27.

PROBLEMS IN CONSERVATION

The conservation status of Hawaiian pteridophytes is considerably more favorable than that of the angiosperms, in terms of survival of species. It will be relatively easier, therefore, to save pteridophyte species if the proper precautions are adopted. Only about 12% of Hawaiian ferns and fern allies of all categories have been naturalized successfully in the Islands, compared with ca. 45% of angiosperms (W. L. Wagner et al. 1990). The overall rate of endemism among native angiosperms is considerably higher than among pteridophytes, 91% versus 75%, respectively. The majority of angiosperms are animal-pollinated and have, therefore, greater vulnerability to habitat changes. Unlike the angiosperms, the pteridophytes have relatively few

single-island and two-island endemics. There is a general correlation between endemism and the age of the island, as shown in Table 7. This must be taken into consideration in conservation efforts. Unquestionably, Kaua'i is the most vulnerable island because of its numerous single-island endemics.

A preliminary summary of presumed extinct, endangered, and threatened to very rare Hawaiian pteridophytes is given in Table 8. It will be noted that surprisingly few

TABLE 7

ONE- AND TWO-ISLAND ENDEMICS (FIVE MAJOR ISLANDS)

Single island:	
Kaua'i	15 (5.7)[a]
O'ahu	3 (3.6–2.6)
Moloka'i	1 (1.8)
Maui	7 (1.6–0.8)
Hawai'i	0 (0.5–0.6)
Two islands:	
Kaua'i-O'ahu	4 (5.7–2.6)
Maui-Hawai'i	6 (1.6–0.5)

[a] Parentheses: estimated ages of islands in millions of years.

TABLE 8

HAWAIIAN PTERIDOPHYTE SPECIES OF SPECIAL CONSERVATION CONCERN

Extinct
  Botrychium subbifoliatum Brack.
  Deparia kaalaana (Copel.) M. Kato
  Diellia leucostegioides (Baker) W. H. Wagner ined.
  Diellia mannii (D. C. Eaton) W. Robinson

Endangered
  Doryopteris takeuchii W. H. Wagner
  Ctenitis squamigera (Hook. & Arn.) Copel.
  Cystopteris douglasii Hook.
  Diellia pallida W. H. Wagner
  Diplazium molokaiense W. Robinson
  Dryopteris podosora W. H. Wagner & Flynn
  D. tenebrosa W. H. Wagner
  Huperzia haleakalae (Brack.) Holub
  Isoetes hawaiiensis W. C. Taylor & W. H. Wagner
  Marsilea villosa Kaulf.
  Phlegmariurus mannii (Hillebr.) W. H. Wagner ined.
  P. nutans (Brack.) W. H. Wagner ined.
  Pteris (Schizostege) lidgatii (Hillebr.) Christ
  Thelypteris boydiae (D. C. Eaton) Iwats.

Threatened to very rare
  Adenophorus abietinus (D. C. Eaton) K. A. Wilson
  Adiantum capillus-veneris L.
  Asplenium hobdyi W. H. Wagner
  A. rhomboideum Brack.
  A. schizophyllum C. Chr.
  Cystopteris sandwicensis Brack.
  Diellia erecta Brack.
  D. unisora W. H. Wagner
  Doodia lyonii Degener
  Dryopteris parvula W. Robinson
  D. tetrapinnata W. H. Wagner & Hobdy
  Gonocormus prolifer (Blume) Prantl
  Lindsaea repens (Bory) Thwaites var. *macraeana* (Hook. & Arn.) Mett. ex Kuhn
  Microlepia mauiensis W. H. Wagner
  Oligadenus periens (L. E. Bishop) W. H. Wagner ined.
  Sadleria unisora (Baker) W. Robinson

taxa are listed as extinct. It is conceivable that one or more of these will be rediscovered, in view of the recent upswing of interest in and exploration of Hawaiian flora. (Two of the taxa previously listed as "extinct" were rediscovered in 1992–1993.) Among those listed as endangered, most are known from only one or two locations; others occur in habitats especially liable to destruction.

Many of the Hawaiian ferns and fern allies have probably always been more or less rare and local, especially those confined to distinctive habitats such as rocky streambeds; steep, dark, mossy banks; very wet rain forest; and bogs. Although some species (e.g., of *Diellia*) occurred primarily in (now mainly destroyed) dry forest, the number is not large. The bulk of Hawaiian rare pteridophyte species tends to occur in the middle- and high-elevation rain forests at 450–1830 m, and most of them are apparently intolerant of very warm ambient temperatures and drought. Some seem to require nearly incessant mist and rain. Many are very delicate and sensitive, such as some of the grammitids and filmy ferns. There is preliminary evidence that the montane pteridophytes have larger spores than those of low altitudes and dry forests (Carlquist 1966).

The disappearance of Hawaiian pteridophytes has been caused mainly by habitat destruction, at first by Polynesians and later and much more extensively by Western world commerce. Invasive species of large herbivorous mammals, especially feral sheep, cattle, goats, and pigs, are demonstrably among the primary factors that have led to reduction of the pteridophyte populations. Also, invasive plants, such as ginger, lantana, guava, eucalyptus, Christmas berry, various members of the Melastomaceae, and many other flowering plant species, enter disturbed areas and often take over completely.

The first analysis of naturalized ferns in Hawai'i was published over 40 yr ago (Wagner 1950). Since then, many introduced species reported there have expanded their ranges and numbers considerably, and other new arrivals have appeared. There are various reasons why there are relatively few invasive pteridophytes and even fewer that are serious pests in Hawaiian ecosystems. Ferns and other pteridophytes are less popular than flowering plants for horticulture, and there are far fewer of them transferred to Hawai'i. Pteridophytes are nonwoody and only a few of them reach any stature, most being less than 1 m tall, except for the vining and tree-fern species. The most abundant naturalized ferns currently are *Adiantum raddianum* Presl. (rocky, shaded, moist banks), *Pityrogramma austroamericana* (dry open fields and exposed lava surfaces), *Phlebodium aureum* (L.) J. Sm. (lianas in second-growth forests), *Phymatosorus scolopendria* (N. L. Burm.) Pichi. Serm. (abundant ground cover and climber in many disturbed habitats), *Thelypteris dentata* and *T. parasitica* (L.) Fosberg (abundant along roadsides and paths), *Blechnum occidentale* L. (with the foregoing), *Deparia petersenii* (Kunze) M. Kato (with *Thelypteris*), and *Nephrolepis multiflora* (many habitats, especially abundant as a ruderal, also forms enormous populations on exposed lava fields). Currently, we are witnessing a dramatic spread of the tree fern *Cyathea cooperi* (Hook. ex F. Muell.) Domin on several islands. In truly pristine forests, except along pathways and waterways, there still remain a number of localities where practically all of the pteridophytes are natives.

Some of the Hawaiian endemic pteridophytes can no doubt be maintained either as viable spores or as cultivated mature plants under suitable conditions, with a view to reintroduction as a part of habitat reclamation. However, many, if not the majority of pteridophytes, are difficult to maintain in botanical gardens. Some, such as grammitids and filmy ferns, have short-lived green photosynthetic spores. Others have highly specialized habitats and associations. Many of these cannot tolerate dry conditions or high greenhouse temperatures, and so must be placed in expensive controlled growth chambers. Very few botanical gardens have either the facilities, the personnel, or the funds to support such cultures in any major way in the framework of present-day economics.

My own conclusion, after years of study of

tropical ferns and of culturing ferns in green-houses, is that the surest way of saving the nearly 130 Hawaiian endemics is to find exactly where they live in their natural environment and to make definitive efforts to maintain those areas as strictly protected preserves. A number of such places still exist in Hawai'i and can be preserved starting now if the public and the politicians are willing to cooperate with the conservationists and the scientists. I am extremely impressed with the following general areas: the Kōke'e Alaka'i-Wai'ale'ale region in Kaua'i, parts of the still-remaining dry forest in the Wai'anae range of O'ahu, the Pu'u Kukui and Pu'u 'Eke slopes of West Maui, the Waikamoi and Palikū regions of Haleakalā of East Maui, and certain parts of the forests from Kīlauea to Glenwood on Hawai'i. Taken together, these and other still-surviving regions can probably continue to support all or most of the Hawaiian endemic pteridophytes in the natural living state.

LITERATURE CITED

ANDERSON, W. R., and M. R. CROSBY. 1966. A revision of the Hawaiian species of *Elaphoglossum*. Brittonia 18:380–397.

BISHOP, L. E. 1974. Revision of the genus *Adenophorus* (Grammitidaceae). Brittonia 26:217–240.

BLASDELL, R. F. 1963. A monographic study of the fern genus *Cystopteris*. Mem. Torrey Bot. Club 21:1–102.

CARLQUIST, C. 1966. The biota of long-distance dispersal. III. Loss of dispersibility in the Hawaiian flora. Brittonia 18(4): 310–335.

CLAUSEN, R. T. 1954. Ophioglossaceae of the Hawaiian Islands. Am. J. Bot. 41:493–500.

HAUFLER, C. H. 1987. Electrophoresis is modifying our concepts of evolution in homosporous pteridophytes. Am. J. Bot. 74:953–966.

HOLTTUM, R. E. 1977. The family Thelypteridaceae in the Pacific and Australasia. Allertonia 1(3): 169–234.

JOHNSON, D. M. 1985. Systematics of the New World species of *Marsilea* (Marsileaceae). Syst. Bot. Monogr. 11:1–87.

KATO, M. 1984. A taxonomic study of the athyrioid fern genus *Deparia* with main reference to the Pacific species. J. Fac. Sci. Univ. Tokyo 13:375–430.

RANKER, T. R., S. K. FLOYD, and P. G. TRAPP. 1992. Genetic evidence for multiple colonizations of *Asplenium adiantum-nigrum* onto the Hawaiian Archipelago. Am. J. Bot. 79 (no. 6, abstracts): 119.

WAGNER, W. H., JR. 1949. A reinterpretation of *Schizostege lidgatii* (Baker) Hillebr. Bull. Torrey Bot. Club 76:444–461.

———. 1950. Ferns naturalized in Hawaii. Occas. Pap. Bernice P. Bishop Mus. 20(8): 95–121.

———. 1952. The fern genus *Diellia*, its structure, affinities, and taxonomy. Univ. Calif. Publ. Bot. 26:1–212.

———. 1953. An *Asplenium* prototype of the genus *Diellia*. Bull. Torrey Bot. Club 80:76–94.

———. 1968. Hybridization, taxonomy, and evolution. Pages 113–138 *in* V. H. Heywood, ed. Modern methods in plant taxonomy. Academic Press, New York.

WAGNER, W. H., JR., and F. S. WAGNER. 1980. Polyploidy in pteridophytes. Pages 199–213 *in* W. H. Lewis, ed. Polyploidy: Biological relevance. Plenum, New York.

WAGNER, W. L., D. H. HERBST, and S. H. SOHMER. 1990. Manual of the flowering

plants of Hawai'i. University of Hawaii Press and Bishop Museum Press, Honolulu. 2 vols.

WALKER, T. G. 1984. Chromosomes and evolution in pteridophytes:. Pages 103–141 *in* A. K. Sharma and A. Sharma, eds. Chromosomes in evolution of eukaryotic groups. Vol. 2. CRC Press, Boca Raton, Florida.