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THE GENUS *GLEICHENIA* (*DICRANOPTERIS*) IN THE HAWAIIAN ISLANDS

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The pteridophyte flora of the Hawaiian Archipelago comprises 43 genera and 185 or more known species; of these 2 genera and 118 species are endemic. There are 18 genera with 75 per cent. or over of endemic species; 18 genera either possess no endemic species, or have 75 per cent. or over of non-endemic species.* In this rich and extremely interesting fern flora the genus *Gleichenia* (*Dicranopteris*) holds a unique position with reference to range and ecology. Whereas the great majority of the Hawaiian ferns are of small stature and of scattering occurrence, the *Gleichenias* form solid and extensive thickets and jungles, almost impenetrable (owing to the peculiar growth-habits of these plants), and occupying hundreds of acres. There are four species in the Hawaiian flora, of which two are endemic, and two are found in other countries. The ubiquitous and dominant character of *Gleichenia dichotoma*, for example, has made it a serious pest in the montane forests. The *Gleichenias*, in terms of both bulk and area, are at the present time the most abundant ferns in the Hawaiian forests, not even excepting the tree-ferns,† which were formerly much more plentiful than at present.

It is the purpose of the present paper to give a succinct account of this remarkable fern genus, with descriptions of the Hawaiian

* For further data see MacCaughey, Ecological Survey of the Hawaiian Pteridophytes, *Journal of Ecology*; in course of publication.

† MacCaughey, The Tree Ferns of Hawaii, *American Botanist* 22: 1-9, 1916, 2 figs.

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species, and with special emphasis upon the ecological features of these plants. There is nowhere in the literature a comprehensive account of this group in Hawaii. The present material is based upon field studies throughout the Islands during the past nine years.

The genus *Gleichenia* J. Sm. was named in honor of Friedrich W. Gleichen, a German botanist, 1717–1783. It comprises 25 or more species, which are abundant in many tropical countries, in subtropical eastern Asia, and also in moist situations in the southern hemisphere. The taxonomic status of many of the species and varieties is still unsettled, and it is entirely probable that the genus is much larger than is commonly stated. One species, *flexuosa*, has been recorded from Louisiana. The writer has retained the old name *Gleichenia*, in preference to the modern *Dicranopteris*, because the former is so thoroughly incorporated into the literature, and because it is used in the standard flora of the Hawaiian Islands, that of Hillebrand.

The *Gleichenias* are all characterized by their habit of growing in dense thickets. The development of the leaves is very distinctive. The foliage is woody and perennial, and growth is indeterminate. The dichotomously branching apical regions resume growth season after season, so that in some species the long, trailing, vine-like leaves attain lengths of *over 100 feet*. The pinnae are pinnatifid, with segments either small and concave-orbicular, or pectinate and elongate. The *Gleichenias* are noteworthy in possessing two leaf-characters which indicate a very primitive condition—the striking and unparalleled dichotomous branching of the frond, and the frequent development of subsidiary pinnae between the ordinary ones. The leaves of most species are repeatedly dichotomous; the ultimate branches bear pinnately arranged pinnules.

All four species are known to the native Hawaiians by the name of *Uluhe*; *Unuhe* and *Enuhe*, sometimes used, are variants of this. The English name is “Staghorn Fern,” referring to the branched leaves, or “Wire Fern,” referring to the wiry petioles.

In *Gleichenia* the sori are subglobose, and comprise 2–6 nearly sessile sporangia, seated on the apex or back of a vein. Each

sporangium is surrounded by a broad, transverse, equatorial annulus, and opens vertically.* The spores are ovoid or tetrahedral, without chlorophyll and with a single dorsal line.

1. GLEICHENIA HAWAIIENSIS Hook.

Dicranopteris Hawaiiensis (Hook.) Robins.; *Mertensia Hawaiiensis* Brack.

Petiole rough, compressed, and margined with two lines of small scales. The leafy portion is 3 or 4 times dichotomous at somewhat acute angles. All of the divisions are pectinately pinnatifid down to the rachis. There is a bud in each fork, covered with small ($1\frac{1}{2}$ –2 lines), falcate, acute, dark, ciliate scales. Ultimate divisions of the leaf-blade are linear-lanceolate, 6–12 inches long; their segments are linear, rather acute, subcoriaceous, dark-green, $\frac{1}{2}$ – $1\frac{1}{2}$ inches long, their under side, and more so the rachis, chaffy with lacinate ferruginous scalelets. The veins are vertical, with 2 or 3 branches. The sori are on raised punctiform receptacles, copious and close, with 3–6 sporangia in each sorus; often the sporangia are irregularly scattered. Annulus indistinct; spores compressed.

This species occurs on all the islands, at elevations of 3,000–6,000 ft., but is rare. Typical stations are: Halemanu, Kauai; Ka-ala and Kona-hua-nui, Oahu; Pele-kunu, Molokai; Eeke, West Maui; and Mauna Kea, Hawaii. It is distinctly a plant of the montane rain-forests, and does not descend to the lower levels or give any evidence of xerophytic tendencies. It is endemic, but according to Hillebrand is closely related to *G. flagellaria* Spring., which extends from Madagascar and Malaysia up through southern Polynesia. It is notably shade-tolerant, and does not form large thickets, but grows in isolated clumps here and there in the forest. Its distinctive feature is that all or most of the petiole branches are foliose.

2. GLEICHENIA LONGISSIMA Blume

Dicranopteris glauca (Thunb.) Underw.; *Gleichenia glauca* Hook.; *Mertensia glauca* Brack.; *Mertensia pinnata* Kze.

*F. O. Bower, Studies in the Morphology of Spore producing Members. IV, The Leptosporangiate Ferns, Phil. Trans. Roy. Soc., Series B, Vol. 192: 29–138. 1899.

Petioles repeatedly dichotomous, the last branches bearing a pair of bipinnate pinnae. The bud in the axil between these pinnae is densely covered with stiff, black, ovate pubescent scales, which are about 1 line long and cordate. The rachides are plano-convex and sparingly clad with scales like those of the bud. The tender tips of the pinnae are tomentose with light-brown cobwebby wool. The pinnae are subcoriaceous, glaucous beneath, oblong, 2-4 ft. long, and broadest about the middle. The pinnules are 40-50 on a side, linear, 6-9 inches by $\frac{1}{2}$ -2 inches, subsessile or shortly stipitate, with an even-sided truncate base, acuminate, deeply pinnatifid to the rachis near the base. The ultimate segments are linear, $1-1\frac{1}{2}$ lines broad, obtuse; the lowest pair longest and often reflexed over the rachis. Veins distinct, almost vertical, simple, or forking near the base. The sori are dorsal on the anterior branch or at the fork, frequently one to each vein, each comprising 3 or 4 sporangia.

This species, although nowhere abundant, occurs on all the large islands of the group, in the rain-forests, at elevations of 2,000-4,000 ft. It is also native to Japan, China, Malaysia, tropical Australia, and Polynesia. The Hawaiian Islands represent its northernmost geographic limit in the Polynesian area. It is often found in the same habitats as *G. Hawaiiensis*, but does not mingle with the latter, and is readily recognized by its bipinnate frondose portions. On the island of Oahu it is not uncommon along the summit ridges of the main ranges, Ko'olau and Waianae, and appears to maintain itself successfully along the wind-swept crests and windward precipices. It forms much larger clumps or thickets than does *G. Hawaiiensis*, but never makes the extensive jungles on the lower skirts of the forests, as does *G. dichotoma*.

✓ 3. GLEICHENIA EMARGINATA (Brack.) Hbd.

Dicranopteris emarginata (Brack.) Robins.; *Gleichenia dichotoma* Hook. var. *emarginata* Hbd.; *Mertensia emarginata* Brack.

This species closely resembles *G. dichotoma*, but is a much larger and stouter plant. The petioles are muricate at the base, and are scantily villous. The leaf-blades are thick coriaceous,

and conspicuously tomentose underneath with a brown wool composed of branching hairlets. The last branches are 9–12 inches by 3–4 inches; segments emarginate or bifid, the outer one (basal) pectinate or pinnatifid. The veins are prominent above, sometimes uniting to form a costal areole. A distinctive feature of this species is that all of the buds are enclosed between 2 small but leafy, ovate, crenate bracteal leaflets. Most of the leaves are spore-bearing, whereas *G. dichotoma* is rarely found so.

This easily recognized species is endemic. It occurs on all the islands, on open mountain ridges and in clearings in the forests, at elevations of 1,000–3,000 ft. Although it is much more abundant than the two preceding species, it is much less plentiful than is *G. dichotoma* which is the dominant species in the Islands.

G. emarginata shows a slight tendency toward semi-xerophytic habitats, often growing in clearings and on dry ridges that are much more xerophytic than the forest-lands immediately adjacent to them. It often forms very dense and impenetrable tangles, which may cover areas of many square rods.

✓ 4. GLEICHENIA DICHOTOMA Hook.

Dicranopteris linearis (Burm.) Underw.; *Mertensia dichotoma* Willd., Gaud., Brack.; *Polypodium dichotomum* Thunb. and Forster.

This species, which occurs in many of the islands of the Pacific, and in tropical countries throughout the world, has become such a pest in the Hawaiian forests that a detailed description seems pertinent. Many of the features enumerated below are also applicable, in greater or less degree, to the other Hawaiian species of *Gleichenia*.

The rhizome either runs along the surface of the ground, or is wholly subterranean. On rocky or impervious material the rhizome is aerial, but closely appressed to the substratum and affixed thereto by numerous short, tough roots. In earth or mud it penetrates to a depth of from 4 to 15 inches, running horizontally and showing only the leaves above the surface of the soil.

The rhizome is $\frac{1}{8}$ to $\frac{1}{4}$ inch in diameter, terete, and of indefinite length. Its appearance has been aptly compared with stout

copper wire. Rhizomes 10 to 15 feet long are not uncommon, and under favorable conditions may become very much longer. The rhizome is more or less highly ramified—when soil conditions are favorable the branches form an intricate, tough, close-meshed network below the soil. The color is glossy dark chestnut brown; the extreme terminal portions are tender and pale green. The surface of the rhizome, although apparently smooth, upon close examination is found to be sparsely clad with short, brown, shining, appressed hairs. On the younger portions these hairs are arranged in star-like tufts. In texture all portions of the rhizome except the growing tips are very tough, wiry, and bamboo-like; this is due to the abundant deposition of sclerenchymous material in the cortical regions. *Add long discussion*

In cross-section the rhizome shows a heavy, woody cortex, surrounding a soft, pale green stele. A single axial bundle traverses the rhizome, and is separated from the cortex by a distinct endodermis. Within the latter is a pericycle of several layers of cells, within which is a continuous zone of phloem, containing large and small sieve-tubes and phloem parenchyma.*

On the rhizome are four kinds of structures, in various stages of development—branches of the rhizome; leaf-buds; leaves, and roots. The roots are numerous and arise irregularly along the rhizome, chiefly along its lower surface. They are short (1–6 inches), sparingly branched, woody, and brown. The tips of the larger roots are greenish or pale.

The leaf-buds are also scattered irregularly along the rhizome; on the average they are not more than 3 inches apart. The buds are $\frac{1}{4}$ – $\frac{1}{2}$ inch long, slender, obtusely pointed, soft, tender, and densely clad with brown hairs similar to those on the rhizome.

The rhizome-branch buds are similar in appearance and distribution to the leaf-buds; they are not as numerous, however, as the latter, and give rise to the branches of the rhizome. Their growth plane is horizontal, while that of the leaf-buds is vertical.

* See further G. Poirault, *Recherches d'histogénie végétale. Développement des tissus dans les organes végétifs des cryptogames vasculaires. Mém. de L'Acad. imp. des sciences de St. Pétersbourg, ser. 7, t. 37, 1890.*

L. A. Boodle, On the Anatomy of the Gleicheniaceae, *Annals of Botany* 15: 703–747, 1901.

Although the characteristics of the rhizomes contribute in no small degree to the success of this domineering plant, the leaves are the main visible feature. The petiole closely resembles the rhizome in size, color, and texture. It is slender, $\frac{1}{8}$ – $\frac{1}{4}$ inch in diameter, and of variable height depending upon ecologic conditions. The height varies from a few inches to 10 or 15 feet; plants clambering up into trees and bushes often have petioles much longer than this. The petiole is terete, not sulcate, flexuose below, and notably erect and rigid. It is smooth, hard, tough, and brittle. Its texture and surface is much like that of bamboo; at the forks and buds it is wooly-tomentose. In cross-section the petiole much resembles the rhizome.

The young petiole looks like an erect piece of heavy green wire, 10–30 inches high, and rolled at the apex into a tight spiral about 1 inch in diameter. The petiole-base is brown and hard, the upper portion and spiral are quite soft and green. All parts are glabrous except the spiral, which is sparingly clad with appressed brown hairs. The spiral unrolls and bifurcates, repeatedly forking in the upper portion at open angles, the ultimate pair of branches frondose.

On the summit of the petiole is the leaf-blade or frondose portion. This comprises a series of dichotomously branching ramifications. The lower are the largest and most mature, the upper tiers or strata of pinnae are progressively younger. In the axil of each bifurcation is a small bud, covered with brown wool; by means of these buds the growth may continue more or less indefinitely. Usually the bud in the first or lowest fork develops into a strong rachis, also dichotomously branching, and giving the leaf a loosely pinnate appearance. The leaf may thus have three or more tiers of pinnae, with a total of several hundred pinnae.

Each pinna or frondose branch is rigid, chartaceous, glaucous underneath, glabrous, elliptico-oblong, 6–9 inches long and $2\frac{1}{2}$ –4 inches wide, broadest about the middle. The pinna is divided down to the rachis into closely set, blunt pinnules; these are at right angles to the strong midrib, and are linear, $1\frac{1}{2}$ –3 lines broad, entire, obtuse or emarginate. The inner or upper pin-

nules shorten toward the base; the lowest one on the outside is deflexed and generally larger, crenate or pinnatifid. At the base of each bare forking or bifurcation there is a pair of smaller lateral pinnules. The lateral pinnules are of varying sizes, the lower ones often equal to the frondose branches; the upper reduced, crenate, or even subentire. The veins have 3-5 parallel branches.

The pinnules unroll as they mature, the young leaves or leaflets being readily recognized by the rolled tips of the pinnules, and by their pale green color. The maturing leaflets are strongly and rigidly deflexed, so that usually the center of the leaf is noticeably higher than the peripheral parts. This doming of the leaf give the *Gleichenia* thicket a characteristic scalloped or hummocky appearance.*

The sori are of 10-12 sporangia, and are seated on the middle of the anterior veinlet. The sporangia are sessile, with a very wide complete ring, which opens by the separation of two joints.†

The petioles of *uluhi* (to use the convenient Hawaiian name) are so woody and elastic and the blades so coriaceous that the dead leaves form a massive, resistant part of the thicket. Upon death the leaves do not fall or break, except through mechanical injury, but remain erect, their blades interlocked with the living fronds. Gradually the latter rise above the dead leaves, so that a vertical section of an *uluhi* thicket shows a canopy of living leaves surmounting and masking a woody jungle of dead foliage.

The general color effect of *uluhi* is a clear, bright, yellow-green. The yellowish constituent is conspicuous, particularly in the young foliage. An *uluhi* thicket contrasts strikingly with the heavy green of the *lehua* (*Metrosideros polymorpha*), the gray green of the *koa* (*Acacia koa*), or the silver green of the *kukui* (*Aleurites Moluccana*), common trees with which it is often asso-

* Hillebrand suggests that whenever the lateral pinnules are large and deeply divided the lowest outer segments of the frondose pinnae are likewise, only in a less degree, suggesting the idea that the former are in reality only the lowest segments of an otherwise aborted frond or pinna.

† For the development of the prothallium see N. W. P. Rauwenhoff, La génération sexuée des Gleicheniacées. Archives Néerlandaises des Sciences exactes et naturelles, t. 24: 157, 1891.

ciated. Dead *uluhi* is at first chocolate-brown, gradually bleaching to a peculiar dull gray-brown. These colors are so distinctive that a patch of living or dead *uluhi* may be easily recognized at a distance of several hundred yards.

A single *uluhi* thicket varies in depth from 2 to 8 ft., depending upon topography, and in area from a few square feet to several hundred square rods. The ticket comprises three strata or layers. Uppermost is the closely interlaced canopy of living leaves, beneath which is much dead material. This canopy is strongly supported by innumerable slender petioles, which are woody and elastic. The third stratum is the subterranean network of rhizomes.

The interlocking leaves and woody petioles render the *uluhi* thicket exceedingly difficult of penetration by the mountaineer. To break trail through this material is very arduous and fatiguing. The experienced mountaineer will always walk around, rather than attempt a way through. One is continually tripping over the unyielding petioles, and wounding oneself upon the sharp pseudo-spines. The ramifications of the older leaves often break off close to their points of origin. This produces short, sharp pseudo-spines, that are strong and rigid, and that often cause painful wounds. Mountaineers who have not examined the *uluhi* carefully are often under the impression that the plant is actually thorny or spiny. The silicious cortex of the petioles is so dense that the fragments wound like bamboo or glass.

In the forests, and along wooded ridges, the *uluhi* often assumes a climbing habit. The petioles and rachides become greatly elongate, so that a single leaf may attain the length of 20 or more feet. The ramifications continue indefinitely. The leaves clamber up over bushes and into the trees, but rarely rise over a height of 15 ft. There are no special climbing structures—the wiry petioles and rigid leaflets are well adapted to entangle and mount upon other vegetation. This leaning or semi-climbing habit is detrimental to the plants which are used for support, and distinctly assists the *uluhi* in smothering other vegetation and monopolizing new territory.

Uluhi is notably free from insect pests and fungus diseases.

It grows vigorously and without apparent intermission. There is no special evidence of a resting period; the production of new leaves and the extension of the rhizome is ceaseless.

Uluhi occurs throughout the humid and semi-humid regions of all the largest islands of the group, from 500 to about 3,000 feet above sea-level. It never appears upon the littoral, and does not grow well upon the lowlands below 500 feet. Neither does it ascend the higher mountains, but is most abundant between 800 and 2,200 feet. It is not found in the strictly arid regions. It reaches its optimum development in the clearings in the native forests—clearings that are sufficient to give it abundance of sunlight, but that leave enough forest to afford protection from the wind. It is partially shade tolerant, but does not grow well under the heavy canopy of the unbroken rain-forest. It is hygrophytic, but not strongly so, and will maintain itself successfully on semi-xerophytic slopes and ledges.

Uluhi is associated with the rugged topography of the montane forests, and is characteristic of steep declivities, ridge crests, valley walls, and similar situations. It is not prevailingly a plant of flat land and does not appear to seek such localities. The chief competitor of *uluhi* in the forest clearings is the pestiferous Hilo grass (*Paspalum conjugatum*), an introduced species that has become a serious menace in the forests. Hilo grass forms a very dense, impenetrable sod, which, like the *uluhi*, effectually prevents the growth of seedlings of the native trees or shrubs. *Uluhi* can and does drive out the Hilo grass.

The *uluhi* usurps the territory of the native undergrowth in two ways: root competition and smothering. By root competition is meant the slow, inexorable spread of the rhizomes into new territory. This takes place along the entire periphery of an *uluhi* thicket, and is irresistible by all other vegetation save large trees and bushes. The tough, woody branching rhizomes are able to literally oust all other roots. The mechanical occupation of the soil by the *uluhi* rhizomes is thorough and complete and results finally in an absolutely pure formation.

Concomitant with the subterranean invasion is the smothering action of the masses of wiry, interlocking foliage. The erect

petioles form serried ranks of slender, durable columns; the tiers of tough foliage interlace into a dense canopy that excludes all direct sunlight from the ground below. It is practically impossible for any seed-plant to germinate and grow up through an *uluhi* thicket—the ground is wholly occupied by rhizomes, and the leaf-canopy means light starvation to any struggling seedling.

Uluhi usually begins its invasion of a new area from the upper portion of the slope, and gradually extends its range down the hillside and over the ridge, obliterating all other vegetation save trees and bushes. The damage which *uluhi* has done to the native forests is difficult to estimate. It may be safely stated that thousands of acres, once occupied by diversified indigenous and endemic flora, are now covered by practically pure stands of *uluhi*. From the standpoint of forest management *uluhi* is an undesirable intruder, as it thoroughly prevents the development of seedling trees in the regions which it has preëmpted. Furthermore, the large amount of dry woody material in *uluhi* thickets is much more dangerous from the standpoint of forest fires than is the sappy, non-combustible vegetation of the rain forests.

Gleichenia dichotoma has completely taken possession of a very considerable proportion of the Hawaiian trails. It should be noted that many of the Hawaiian mountains are deeply carved by valleys and gorges, which are separated from one another by narrow and precipitous forest-clad ridges. The old native trails ran along the crests of these ridges. When cattle, sheep, and goats were introduced, in the latter part of the eighteenth century, and permitted to roam and breed unchecked, these animals increased in prodigious numbers. They made serious inroads upon the native forests, following the ridge-crests and contour lines and destroying the underbrush. The *uluhi*, hitherto held in repression under the forest cover, rapidly invaded the clearings made by the cattle and goats, overran these places, and invaded the rapidly receding native forests.

It is difficult to give a quantitative idea of the present extent of *uluhi*. It forms more or less pure stands along scores of miles of native trail, and over thousands of square rods of valley wall and hillside. In many instances it has filled small valleys from side to side.

The *Gleichenias* are not utilized in Hawaii in any way. The *uluhi* is eaten by cattle and goats, in the absence of more desirable forage. The petioles, if properly gathered and prepared, would undoubtedly be excellent material for the manufacture of light basketry. At present *uluhi* is an undeveloped resource.

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BRYOLOGICAL NOTES

IV. A NEW HYBRID IN *PHYSCOMITRIUM*

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Begun in the fall of 1912 and resumed in the spring of 1913, a considerable reclamation project was carried out in Ithaca, N. Y., as a result of which a tract of cat-tail marsh at the head of Cayuga Lake was converted into something more nearly approaching *terra firma*. The new soil was a very fine silt pumped from the Inlet by suction-dredge. Among the bryophytes which immediately established themselves upon it, *Physcomitrium* species were especially well represented. Material collected in the autumn of 1913 shows abundance of *Physcomitrella patens* (Hedw.) Br. & Sch. together with some *Aphanorhegma serratum* Sull. and *Physcomitrium immersum* Sull. Occasionally also a strange emergent capsule was noted, not identifiable with any moss-species, but obviously a hybrid. These capsules were not well matured and were so sporadic in occurrence that it was difficult to collect satisfactory material for their study, but finally at a point where the more clayey soil of the hillside projected out into the new silt covering they were found in greater number. At this point were found the following spring (1914) capsules of *Physcomitrium turbinatum* (Michx.) Brid. together with those of *Physcomitrium Hookeri* Hampe.* The ♀ parent of the hybrid was clearly *Physcomitrella patens*, the ♂ parent was evidently *Physcomitrium turbinatum*. The description follows, the sporophyte alone partaking of the hybrid nature, the gametophyte

* The station for *P. Hookeri* is, so far as I know, the first east of Ohio.



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