# STUDIES IN HAWAIIAN POLLEN STATISTICS

## Part I

## THE SPORES OF THE HAWAIIAN PTERIDOPHYTES

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### PREFACE.

Seven years have gone by since I left Hawaii after a summer with Prof. Dr. C. Skottsberg's »Hawaiian Bog Survey 1938». The object of my work — to attempt to discover by pollen statistics something of the history of Late Quaternary vegetation in the islands — proved a more protracted task than was originally anticipated. To speak only of the internal aspects of the investigation, it soon became evident that a monographic study of the spores and pollens of the native vascular plants was a *sine qua non* for any scientific evaluation of the motley flora of the samples taken from the bog deposits. I therefore began to work on that line, hoping to provide an illustrated survey to diminish to some extent the many obstacles to a thorough use of pollen statistics in the islands and to facilitate the discovery of other fossil species, if any, than the *Schizaea* recently found which are unknown in the living flora. Such a survey of a flora of great age might also be expected to be of some value to the study of microfossils in Tertiary deposits in any part of the world.

In completing this first part of my work, which will be followed by another paper dealing with the pollens and a third on the history of the vegetation, I am well aware of the many gaps it has left. The lack of own observations in the field, and the impossibility of consulting the herbarium of the Bishop Museum in Honolulu and other collections during the war, have in many instances had a restrictive effect not to be avoided.

The following principles are common to parts I and II.

Previous morphological data in literature (available up to 1943, when the manuscript was completed) are recorded. In several cases I also include statements likely to broaden the view taken of the observations on the different species or genera. In the literature dealing with pollens and spores a tendency to disregard earlier data is undoubtedly much too common. This

is quite understandable, because such data are not easily found, being scattered in studies of widely different character and met with in papers on both morphology and anatomy (incl. embryology and cytology), taxonomy, flower biology, palaeobotany, geology (particularly Quaternary geology), and medicine (hay fever), etc. They are nevertheless more frequent than is generally supposed. Above all, the lack of knowledge of previous observations, however scanty, makes for a random progress also in this field. Numerous recent papers of apparent pioneering character give evidence of this. A summary of morphological observations as detailed as the one I have attempted has been considered all the more justified as European literature containing early statements in this field is rather inaccessible in the countries in and round the Pacific, where it is expected that this paper may be to some extent consulted.

The morphological survey of each species at present considered to deserve one is followed by an account of certain data as to recent occurrences compiled from a pollen statistical point of view. Such accounts, however defective, are necessary in dealing with the fossil finds, since no modern Hawaiian flora gives a survey of all the so far known native species. Degener's valuable Flora Hawaiiensis (1932 onwards) has so far given only glimpses of the native flora, and the only complete work, Hillebrand's Flora of the Hawaiian Islands, is almost sixty years old.

Finally, a summary is published of the fossil occurrences of each recognizable spore and pollen type. This cannot be fully understood until the third part of this work (dealing with the pollen diagrams and the history of the vegetation) has appeared, as it is largely based on the results that will be published there. In several cases of which no fossils were found, I have discussed what might be expected of that particular species or group of species, emphasizing especially the spores and pollen types that appear to be of a certain interest to future studies.

For herbarium material and financial support I am indebted to institutions and private persons to be mentioned in parts II and III.

Palaeobotanical Department, Swedish Museum
of Natural History, Stockholm, September, 1945.

## KEY TO THE SPORES OF THE HAWAIIAN PTERIDOPHYTES.

(Referring to their appearance as acetolysed fossils, see p. 10.)

I. Spores bilateral, monolete (with an undivided tetrad scar).

A. Exospore without sculpture.

a. Thick-walled (about 4—5 $\mu$); largest equatorial diameter about 90-100 $\mu$ ..... *Schizaea robusta*

b. D:o; largest equatorial diameter about 70 $\mu$ ..... *Polypodium spectrum*

c. Walls about 3 $\mu$, devoid of texture (when observed with ordinary magnification); largest equatorial diameter about 30 × 43 $\mu$ ..... *Hypolepis*

d. Walls about 2 $\mu$, of prominent granular texture; largest equatorial diameter about 42 × 69 $\mu$ ..... *Coniogramme* (aberrant)

e. Walls about 1.5 $\mu$ or less; granular texture little prominent or absent; largest equatorial diameter about 24—75 $\mu$ ..... *Asplenium*
*Athyrium* (exospore minutely punctulate)
*Cyrtomium*
*Cystopteris*
*Diellia*
*Diplazium*
*Doodia*
*Dryopteris* (p. p.)
*Elaphoglossum*
*Loxoscaphe*
*Polystichum*
*Sadleria*
*Stenoloma*
*Tectaria*
*Vittaria*
*Gleichenia owhyhensis* (ridges bordering the tetrad scar very prominent)

B. Exospore with minute granules or very low projections.

a. Spores dark-coloured; largest equatorial diameter about 90-100 $\mu$ ..... *Schizaea robusta*

b. Spores light-coloured; largest equatorial diameter about 25 $\mu$ (cf. also *Astelia*, in part II) ..... *Marattia*

C. Surface (exospore or fairly resistant perispore) with spines.

a. Spines about 6 $\mu$ long (in fossil material generally much corroded) ..... *Hypolepis*

b. Spines about 2—3 $\mu$ long.

1. Average largest equatorial diameter of the spores over 75 $\mu$ ..... *Dryopteris latifrons*

2. D:o about 66 $\mu$; the ratio P:E about 0.8 ..... *D. honolulensis*

3. D:o about 55 $\mu$; the ratio P:E about 0.65 ..... *D. goggilodus*

D. Exospore with a well-developed reticulate or distinctly pitted sculpture (see also under E).

a. Exospore about 4—4.5 $\mu$ thick; reticulum well-developed, fairly regular; spores as a rule over 90 $\mu$ in largest equatorial diameter ..... *Schizaea Skottsbergii*

b. Exospore about 3 $\mu$; sculpture coarsely pitted, its surface fairly even; spores about 70 $\mu$ in largest equatorial diameter ..... *Ophioglossum falcatum* (aberrant)

c. Exospore of about the same thickness as stated under b (or even thicker); sculpture of the pitted type but somewhat less clearly defined, its surface very irregular; spores about 60 $\mu$ in largest equatorial diameter ..... *O. concinnum* (aberrant)

d. Exospore about 2.5 (—3) $\mu$; sculpture of the pitted type, its surface fairly even; spores about 42—58 $\mu$ in largest equatorial diameter ..... *Lycopodium spp.* (aberrant)

e. Exospore about 2.5 $\mu$; sculpture of the truly reticulate type, with fairly irregular lumina into which occasional ridges send free ends; spores about 35 $\mu$ in largest equatorial diameter ..... *Botrychium* (aberrant)

E. Exospore at least partly shallowly pitted.

a. Exospore 3—4 $\mu$ thick; spores 60—80 $\mu$ in largest equatorial diameter, the ratio P:E about 0.55 ..... *Psilotum*

b. Exospore about 2 $\mu$ or less thick, regularly pitted; spores as a rule over 80 $\mu$ in largest equatorial diameter, the ratio P:E about 0.70 ..... *Schizaea Skottsbergii* (immature specimens)

F. Exospore (> 3 $\mu$ thick) with $\pm$ indistinct, minute, and irregular projections.

a. Spores about 50—80 $\mu$ in largest equatorial diameter.

1. Projections irregularly arranged on a fairly smooth surface ..... *Adiantum* (aberrant)

2. A smooth surface under the projections not discernible; sculpture often transitional to shallow pitting *Psilotum*

b. Spores about 90 $\mu$ or over in largest equatorial diameter ..... *Schizaea robusta*

G. Exospore with coarse, $\pm$ irregular projections.

a. Largest equatorial diameter about 90 $\mu$; projections angular and very irregular in both surface and side views ..... *Polypodium atropunctatum*

b. D:o about 85 $\mu$; projections $\pm$ rounded ..... *Schizostege* (aberrant)

c. D:o about 57 $\mu$; projections rounded ..... *Polypodium pellucidum* (cf. occasional, aberrant spores of *Pteris cretica*)

d. D:o about 50 $\mu$; projections in the shape of warts and ridges of different appearance and arrangement, somewhat angular, at least in surface view ..... *Nephrolepis exaltata*

[e. D:o about 43 $\mu$; projections very irregular, recalling corroded spines ..... *Hypolepis* (specimens with corroded perispore)]

F. Exospore with coarse ($\pm$ longitudinal) ridges; spores large (no strictly monolete spore so far known; cf. p. 40) *Cibotium* (aberrant)

II. Spores tetrahedral, trilete (with a triradiate tetrad scar).

A. Largest equatorial diameter over 75 $\mu$.

a. Thick-walled, dark-coloured, with warts or granules — *Schizostege*
b. D:o, with coarse ridges — *Cibotium* (p. p.)
c. Thin-walled, light-coloured, with minute spines or d:o granules — *Hymenophyllum* (p. p.) *Trichomanes* (p. p.)

B. Largest equatorial diameter under 75 $\mu$.

a. Exospore devoid of sculpture and of prominent secondary thickening.

1. Equatorial diameter about 30 $\mu$.

§ Exospore about 2 $\mu$ thick, devoid of texture; ridges of the tetrad scar not as stated under §§; spores often subtriangular in polar view, ± ellipsoidal in equatorial view, about 26 × 31 $\mu$ — *Microlepia speluncae*

§§ Exospore about 1.5 $\mu$, of indistinct granular texture; branches of the tetrad scar reaching the equator and followed all along their length by markedly raised portions of the exospore, very prominent in both polar and equatorial views; spores about 23 (22, raised portions excluded) × 28 $\mu$ — *Lindsaya*

§§§ Exospore about 1—1.5 $\mu$, indistinctly textured; branches of the tetrad scar bordered by well-developed ridges (not raised as in *Lindsaya*), which reach the equator; spores (viewed from the poles) with somewhat acuminate angles and straight or somewhat retracted sides (in the latter case not evenly concave but often with slight bends near the angles); about 22 × 30 $\mu$ — *Gleichenia glauca*

§§§§ Exospore about 1 $\mu$, of granular texture; branches of the tetrad scar often not reaching the equator, bordered by ridges less distinct towards the periphery of the spores (viewed from the poles; often the ridges ± disappear about half-way between the proximal pole and the equator); spores triangular with rounded angles to subtriangular; sides straight or often slightly and evenly concave (together with adjoining parts of the proximal wall; about 25 × 31 $\mu$ — *Pteridium*

2. Equatorial diameter about 35—43 $\mu$.

§ Contours of the tetrad scar ± irregular; equatorial diameter about 36 $\mu$ — *Selaginella arbuscula*

§§ Contours of the tetrad scar regular; spores distinctly triangular in polar view, though not rarely with somewhat rounded angles.

† Ridges bordering the tetrad scar ± prominent along the greater part of its branches; scar as a rule reaching the equator of the spore — *Gleichenia emarginata* *G. linearis*

†† Ridges bordering the tetrad scar diminishing in width half-way between the proximal pole and the equator of the spores; scars, seen in polar view, often not reaching the rounded angles of the spores — *Microlepia setosa*

§§§ Contours of the tetrad scar regular; spores almost globular (rounded to subtriangular in polar view), about 35 × 40 $\mu$ — *Doryopteris* *Pellaea*

3. Equatorial diameter about 51 $\mu$; exospore of distinctly granular texture ..... *Coniogramme*

b. Exospore with sculpture or at least with ± thick secondary thickening (perispore *not* included).

1. Surface only rough; spores ± triangular in polar view.

§ Surface minutely rough; thickening of medium thickness and distinctly granular; equatorial diameter about 51 $\mu$ ..... *Coniogramme*

§§ Surface coarsely rough; exospore ± thick; equatorial diameter 40—50 $\mu$ ..... *Adiantum*

2. Surface with (minute) granules or tubercles, which are not combined with pitting; no spines.

§ Spores triangular with rounded angles; equatorial diameter about 40—50 $\mu$; exospore fairly thick, brown, with minute tubercles ..... *Adiantum*

§§ Spores triangular to subtriangular in polar view; exospore thick; equatorial diameter rarely under 75 $\mu$ (cf. above, II:A:a) ..... *Schizostege*

§§§ Spores subtriangular to rounded in polar view; equatorial diameter 40—75 (—80; cf. II:A:c) $\mu$; exospore ± thin, light-coloured, with minute, rounded or ± spiny projections ..... *Hymenophyllum* (p. p). *Trichomanes* (p. p.)

§§§§ Spores globular or nearly so; equatorial diameter about 25—50 $\mu$; exospore of medium thickness, dark brown or brown, provided with warts or granules of varying sizes ..... *Polypodium* (p. p., sect. *Eupolypodium* with the exception of *P. pellucidum*)

§§§§§ Spores globular or at least rounded in polar view; equatorial diameter about 25 $\mu$; exospore light-coloured, with very low projections ..... *Marattia* (aberrant)

3. Surface with spines.

§ Spines 7—9 $\mu$ long ..... *Selaginella deflexa*

§§ Spines about 1 $\mu$ long ..... *Hymenophyllum* (p. p.) *Trichomanes* (p. p.)

4. Surface with irregular, coarse warts and ridges.

§ Spores with a ± complete equatorial ring.

† Distal wall provided with fairly long, distinct ridges; equatorial diameter about 50—75 (—80; cf. II:A:b) $\mu$ ..... *Cibotium* (p. p.)

†† Distal wall with irregular, short ridges or wart-like projections; equatorial diameter 50—60 $\mu$ ... *Pteris cretica* *P. irregularis*

††† Distal wall with a few polygonal, just a little elevated portions; equatorial ring thick; equatorial diameter about 44 $\mu$ ..... *Pteris excelsa*

§§ Equatorial ring lacking or little prominent.

† Distal wall with irregular and coarse warts; equatorial diameter rarely under 75 $\mu$ (cf. above, II:A:a) ..... *Schizostege*

†† Distal wall with wavy, irregular ridges; equatorial diameter about 30—50 $\mu$ ..... *Lycopodium* (p. p., key to the spores belonging here p. 11)

5. Surface with distinct, regularly distributed pitting, sometimes combined with irregular projections (cf. under II:B:a:2).
   - § Spores rounded to subtriangular in polar view.
     - † Equatorial diameter about 55 $\mu$; pits coarse; surface contour fairly even ..... *Ophioglossum falcatum*
     - †† Equatorial diameter about 48 $\mu$; pits dense and small; surface contour very rough ..... *O. concinnum*
   - §§ Spores distinctly triangular in polar view, with straight, convex or concave sides ..... *Lycopodium* (p. p., key to the spores belonging here p. 11)

6. Surface with indistinct (coarse and shallow) or irregularly distributed pitting (cf. under 7).
   - § »Pitting» indistinct; exospore ± thick; equatorial diameter about 40—50 $\mu$ ..... *Adiantum*
   - §§ Pitting irregularly distributed, also over the distal parts of the spores ..... *Psilotum* (occasional spores)

7. Surface with a reticulum rather than pitting.
   - § Reticulate sculpture high (about 3 $\mu$ or more) ..... *Lycopodium* (p. p., key to the spores belonging here p. 11)
   - §§ Reticulate sculpture low (less than 2 $\mu$).
     - † Angles of the spores rounded in polar view; reticulum of medium coarseness with irregular lumina, into which occasional ridges send free ends; equatorial diameter about 34 $\mu$ ..... *Botrychium*
     - †† Angles of the spores somewhat pointed in polar view; lumina fairly regular at the distal pole, irregularly elongate towards the equator; equatorial diameter about 39 $\mu$ ..... *Lycopodium polytrichoides* (cf. p. 11)

III. Spores globular, alete (devoid of tetrad scar) ..... Occasional, aberrant spores of various species (see the text)

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Note. — *Marsilia:* excluded (cf. p. 73).
*Selaginella:* megaspores excluded (cf. p. 19, 20—22).
Undescribed fern: spores unknown (cf. p. 62).

## SYSTEMATIC ACCOUNT.

Unless otherwise stated, all the spore slides referred to were prepared uniformly by the acetolysis method (see Erdtman 1943, with bibliography), which was used throughout the investigation of the peat samples. «KOH» indicates that the spores referred to were boiled in a solution of KOH (10 %) in water for two minutes, and then immersed in glycerin before being measured.

P and E (polar and largest equatorial diameters) were measured in, as a rule, 10 spores of each individual. Exceptions are specified in the text. Though not considered sufficient for closer comparisons, the values thus obtained give a preliminary idea of size conditions.

Abbreviations:

G — Botaniska Trädgården, Göteborg;
H — Bishop Museum, Honolulu;
SP — Riksmuseets Paleobotaniska Avdelning, Stockholm (the designation SP used to avoid confusion with Riksmuseets Botaniska Avdelning, SB, as cited in part II of this paper);
U — Botaniska Museet, Uppsala.

### Fam. LYCOPODIACEAE.

#### **Lycopodium** L.

The species of this genus have long been known to be characterized by trilete, tetrahedral spores (see Kaulfuss 1827 and the literature cited there). As regards exospore (cf. Hannig 1911 b, p. 365) morphology, Mohl (1833, 1845) noted two types, one with and the other without a distinct reticulum. Pritzel (1900) emphasized that the spores of the subgenus *Rhopalostachya* are characterized by reticulate or occasionally spiny sculpture, those of the other subgenus, *Urostachya*, by pitted, and this was confirmed by Miss Knox (1938). With some justification both types may of course be called »netzartige Verdickungen» (Herter 1908, 1909, p. 13), but this does not emphasize the differences sufficiently. That the differences between the spores of different species are but slight, as stated by Herter (l. c.) and after him by Nessel (1939), is but half a truth, for in several cases they are considerable. This has been made clear by, for instance, Potonié (1934 b) and Wilson (1934), and also applies to the Hawaiian species studied by me, though some species may be difficult to distinguish from one another by single spores. In the Hawaiian species *L. nutans* a type of sculpture (reticulate flanges) was found which was previously considered peculiar for *Rhopalostachya*. The said spe-

cies belongs to the more primitive subgenus *Urostachya*, in which we thus find the ornamentation of the more advanced types already present. As regards size, at least one Hawaiian species extends the variation limits (»from 23 μ or less. . . . . to about 45 μ«) given by Erdtman (1943) after Wilson and Miss Knox. Potonié (1934 b, p. 44) has, besides, published the average 51 μ for *L. inundatum*, and Erdtman himself mentions a specimen of the same species measuring 55 μ. The spores of *L. phyllanthum* measure up to 62 μ (cf. below), and even that is certainly not the extreme value.

Key to the spores of the Hawaiian species of *Lycopodium*.

I. Exospore with shallow sculpture, pitted or irregularly reticulate (»wavy«).
  A. Regular pits.
    1. Walls concave or straight in polar view.
      a. Shape of the spore mainly triangular, walls but slightly concave (or not at all), pits scattered, coarse ..... 1. *L. erubescens*
      b. Shape of the spore ± hexangular, angles broad, walls pronouncedly concave, pits less sharply defined ..... 2. *L. Haleakalae*
      and 3. *L. serratum*
    2. Walls convex in polar view.
      a. Equatorial diameter about 55 μ ..... 5. *L. phyllanthum*
      b. Equatorial diameter about 39 μ ..... 7. *L. Mannii*
  B. Ridges fairly regular, distinct, lumina often transitional to pits, equatorial diameter about 39 μ ... 4. *L. polytrichoides*
  C. Wavy, irregular ridges.
    1. Ridges very irregular, often not quite distinct, angles (slightly) protruding, equatorial diameter about 50 μ ..... 6. *L. nutans*
    2. Ridges irregular, distinct, separated by ± long, sharply bent furrows, angles well rounded, equatorial diameter about 30 μ ..... 8. *L. cernuum*

II. Exospore with high, reticulate sculpture.
  A. Sculpture about 3 μ high, equator bordered by a well-developed, light-coloured, only slightly serrate wing, proximal facets devoid of sculpture ..... 9. *L. volubile*
  B. Sculpture about 5 μ high, no wing of the kind mentioned under A, proximal facets with fragmentary sculpture ..... 10. *L. venustulum*

Subgen. *Urostachya* Pritzel.

Sect. I. *Selago*.

§ 1. Euselago.

1. **L. erubescens** Brack. — Pl. 1, Fig. 1.

There seems to be no description of the spores and only one figure, a contour sketch, showing their trilete type but not giving any scale (Brackenridge 1855, Pl. 45, fig. 1 c).

Tetrahedral, trilete, 24×37 (22—25×33—40) μ, rarely bilateral, monolete, c. 29×46 μ. Distal wall comparatively little arched. Seen in polar view, the sides of the spores are but indistinctly retracted, and the peculiar contours of the *L. serratum* spores do not seem to occur in this species. Tetrad scar not reaching quite to the angles. Exospore brown, with scattered coarse pits chiefly on the distal wall, 3—4 μ apart. This coarseness of the pitting is not found in the closely related *L. Haleakalae*. The suspicion put forward by Christensen (1925, p. 20) that this could be a variety of the following species does not seem wellfounded. — Specimen studied: Kauai: summit of Waialeale, 23/8 1938; O. H. Selling (spore sample only).

Recent: A rare endemic species, recorded from Kauai, E. Maui and Hawaii (Nessel 1939, p. 62, credits it also to Tasmania!). Robinson (1914, p. 52) says: »This very compact form is well suited to the xerophytic conditions of the high altitudes where it is found» — it is, however, peculiar to wet regions, in one case to the second rainiest spot in the world. Moreover, Brackenridge's description of the type locality runs: »on Mouna Haleakala, East Maui, in wet lands, at the altitude of 6000 feet» (1854, p. 320). Hillebrand (1888 b, p. 643) also lists: »high plateau of Kauai; (Mr. Johnson). *Waialeale*, Kauai, on rocks (Wawra)». The latter locality had earlier been published by Luerssen (1875 b, p. 438) and was there specified »Bei 4000' auf Felsen mitten im Walde». Rock, who had found it also among *Panicum* in the swamps of Kauai (1913, p. 59; 1915, p. 299) published the first locality from Hawaii, Kohala, »on rocks in streambeds» (1913, p. 66; 1915, p. 302; cf. also Skottsberg 1942, p. 130). Hence, the data in MacCaughey (1918 a, p. 203 and 210), »Kauai and East Maui, 5000—6000 ft», are, as usual, unreliable. The altitudinal range known at present is about 4000—6000 ft.

Fossil: Not found.

2. **L. Haleakalae** Brack. — Pl. 1, Figs, 2, 3.

The literature on the spores of this species is just as comprehensive as is that of *L. erubescens*. Brackenridge (1855, Pl. 45, fig. 2 c) gave the same kind of picture as of *L. erubescens* here, too, saying nothing in the text.

Tetrahedral, trilete, rarely bilateral and monolete, or alete; regular spores: 24×41 (20—27×36—45) μ, occasionally considerably larger and more rounded with a largest diameter of 57 (44—75) μ, as ascertained in 10 specimens. Spores on the whole very irregular, and not of the pronouncedly hexangular outline of those of *L. serratum*, to which they are similar in many other respects. Distal wall and tetrad scar as in *L. erubescens*, but pitting less coarse and the sides on the whole more concave than in this species. — Specimen studied: W. Maui: Puu Kukui, summit bog, 9/10 1922; C. Skottsberg 1094 (U).

Recent: A rare species, found in bogs and on wet rock slopes of both W. and E. Maui. Miss Robinson (1914, p. 53), who seems under the impression that this was an alpine species, states that it is peculiar to »Eeka, West Maui», which is listed as the type locality. The species is neither alpine nor peculiar to W. Maui, however, nor is this the type locality. It was discovered »on Mouna Haleakala, East Maui: in wet land, at the altitude of 7000 feet» (Brackenridge 1854, p. 321). Hillebrand later found it also in W. Maui, on »the top of *Eeka*» (1888 b, p. 643) — which does not mean Mt Eke but Puu Kukui — »an wenig bewachsenen Hängen» (label cited by Nessel 1939, p. 31). From the latter locality it was reported also by Rock (1913, p. 79; 1915, p. 308) and Skottsberg (1926, p. 200). In 1927, Degener found it also on the summit of Mt

Eke (Nessel l. c. p.). Eke is 4480 ft high. Hence the altitudinal distribution of the species, stated by MacCaughey (1918 a, p. 218) to be about 5000 ft, should rather be given as 4500—7000 ft.

Fossil: Not identified with certainty, though a few of the spores from W. Maui referred to *L. serratum* might possibly have belonged to this species.

3. **L. serratum** Thunb. — Pl. 1, Fig. 4.

Neither the figures nor the text published by Hooker and Greville (1831, I, Tab. XXXVII, fig. 5) give any idea of the true appearance of the spores. Spring (1842, p. 39) says nothing of his *L. serratum*, and under »*L. sulcinervium*» only: »*farina* sulfureo-albida repleta». Hillebrand (1888 b, p. 642) called them pale whitish, but noted no sculpture (cf. his notes on *L. venustulum* cited on p. 19 below).

Tetrahedral, trilete (rarely bilateral and monolete), 26×39 (21—30×33—43) $\mu$ (30 spores from the three collections cited below), bilateral spores (Degener 12030) 25×42 $\mu$ in polar view. Distal wall comparatively little arched. Tetrad scar often not reaching the angles, sometimes indistinct in the outer parts. Seen in polar view the sides are distinctly retracted, making a hexagonal figure. The same thing could be traced in *L. Haleakalae* and *L. erubescens*, though gradually less marked in the said order. Exospore brown, with shallow, distinct pits of about the same size as in the preceding scattered all over the distal surface, to a less degree also on the proximal facets. Irregular specimens may be hard to distinguish from the spores of these species, particularly *L. Haleakalae*. — Specimens studied: W. Maui: summit bog of Puu Kukui, 23/7 1938; HBS 2649 (SP): 24×36 (21—26×33—40) $\mu$; W. Maui: N slope of Puu Kukui, at Nakalalua, 28/7 1938; O. H. Selling (spore sample only): 28×41 (24—30×39—42) $\mu$; Oahu: Aiea, summit, 6/12 1937; O. Degener, C. Salucop and V. Arlantico 12030 (SP): 24×40 (21—28×36—43) $\mu$.

Recent: Recorded from all the islands, from rain-forests and bogs, rather common and locally abundant. Not only epiphytic as stated by Robinson (1914, p. 52) and MacCaughey (1918 a, p. 218), but also terrestrial. Robinson (l. c.) says 700—2200 m, but this cannot refer to these islands alone. MacCaughey copied these data, saying »2400—7500 ft» (p. 218; on p. 203: »2500»). I know of records from c. 700 m (Skottsberg 1936, p. 101) to c. 1750 m (Puu Kukui, Skottsberg 1926, p. 200; also seen by myself).

Fossil: Spores, of the type apparently belonging to this species (though I must leave open the question whether a few of them may not be fairly regular spores of the preceding) have been found in almost all the series, though as a rule occasionally or rarely. The species has not been found in BP 10, in 57, 71 and 87 it occurs in most samples. The records comprise just over 1/4 of the analysed samples. On Molokai the occurrences are half as common as on the other islands.

The values vary from traces to 18%, as a rule from traces to 3 %. Traces and 1 % are the commonest (about 90 %), the average is slightly over 1 %. The highest values were found in 358 (81): 18 %; 357 (81): 7 %; 339 (81): 6 %; in 226 (57) and 482 (87): 5 % each.

§ 2. Subselago.

4. **L. polytrichoides** Kaulf. — Pl. 1, Figs. 5—7.

These were the first spores of Hawaiian lycopods described in literature. Kaulfuss (1824, p. 6) says: ». . . semina albida pyramidalia, quaternatim conglutinata». Spring (1842, p. 73; 1849, p. 33) is silent on this point. Hillebrand (1888 b, p. 644) described them as »whitish, smooth», a statement repeated by Degener (Fl. Haw., Fam., 19, 4/20/'34). No other notes on the spores of this species have been found. As seen below, the spores are not devoid of sculpture. They belong to the so-called »Tüpfelsporen» found by Lüstner (1898, p. 11) to characterize the closely related *L. verticillatum*.

Tetrahedral, trilete (rarely bilateral and monolete), 23×39 (20—26×36—44) $\mu$ (20 spores from the two collections cited below); a monolete spore measuring 43×43 $\mu$ in polar view. The normal spores are also fairly rounded in this view, though the angles are somewhat pointed. The tetrad scar reaches the angles. Exospore brown. Sculpture recalling the irregular reticulum in *L. cernuum* (there are thus as a rule no rounded pits making the contour rough). The sculpture occurs only on the distal wall. The spores are easily distinguished from those of *L. cernuum* by their shape. — Specimens studied: W. Maui: N slope of Puu Kukui at Nakalalua, 28/7 1938; HBS 2715 (SP): 23×40 (21—26×27—44) $\mu$, and W. Maui: Puu Kukui, c. 1600—1700 m, 9/10 1922; C. Skottsberg 777 (SP): 23×38 (20—24×36—40) $\mu$.

Recent: Reported from all the islands, generally epiphytic in forests of varying types, also in those bordering the bog areas. Brackenridge (1854, p. 324) and Degener (l. c.) found it also on lava blocks. Hillebrand (1888 b, p. 644) says »not frequent», and in this he is followed by MacCaughey (1918, p. 218). From their excursions Wawra (see Luerssen 1875 b, p. 438) and Heller (1897, p. 729) characterized it as rare, and Degener finds it so in all the islands (l. c.; cf. 1930, p. 24). This author also says: »It can grow in drier forests and on smaller trees than can the more common *L. phyllanthum* Hook. & Arn.» He also reports it from sea level up to 5000 ft elev., while Robinson (1914, p. 56) gave only 600—1000 m and MacCaughey (l. c. p.) 2000—4000 ft. The records of 3000 and 2800 m elev. in Nessel (1939, p. 130) are evidently misprints for ft.

Fossil: Not seen. Occasional occurrences may be expected in future research.

Sect. II. *Phlegmaria*.

5. **L. phyllanthum** Hook. et Arn. — Pl. 1, Figs. 8—9.

Spring (1842, p. 66, under *L. pachystachyon* Spr., nothing under the valid name, p. 73), Hillebrand (1888 b, p. 644) and Degener (Fl. Haw., Fam. 19,

8/22/'34) state that the spores are pale yellow, but give no other description. Pritzel (1900, p. 587, Fig. 371 C, D) gave two pictures of them showing their general appearance, exaggerating the pitting slightly. I can add the following description to the pictures published here:

Tetrahedral, trilete (rarely bilateral and monolote), 30×55 (27—33×48—62) $\mu$ (20 spores from the two collections cited below), a bilateral spore: 38×58 $\mu$ in polar view. Distal wall but little arched. Angles somewhat rounded in polar view, reached by the tetrad scar. Exospore brown, with numerous, comparatively crowded pits on the distal wall, none on the proximal facets. — Specimens studied: Oahu: Honolulu, 1852, N. J. Andersson (SP): 20×55 (27—32×50—62) $\mu$ and W. Maui: N slope of Puu Kukui, between Haelaau and Nakalalua, 1/8 1938; HBS 2761 (SP): 30×54 (28—33×48—60) $\mu$.

Recent: An epiphytic, pendulous rain-forest species, endemic to the islands. Brackenridge (1854, p. 327) called this »frequent on trees and decayed wood, on all the islands of this group visited by us» [Kauai, Oahu, Maui and Hawaii]. The species has also been reported from Lanai (Degener, l. c.) and Molokai (see, *e. g.*, Skottsberg 1942, p. 131). Hillebrand (l. c. p.) regarded it as »rather common», and MacCaughey (1918 a, p. 218) calls it common, but Heller does not go so far, saying only »occurring at intervals» (1897, p. 792). As Degener (l. c.) has pointed out, it is not uncommon in the Koolau Mountains of Oahu — the usual excursion ground — but is rare elsewhere. I know records from 480 m above the sea (Skottsberg 1926, p. 200) up to about 1100 m (Skottsberg 1942, p. 131). In all probability these are not limit values.

Fossil: Not seen. Whether this is due to its being comparatively rare in the islands concerned, or to the species possibly preferring less extreme rain forest types than those surrounding the bog areas, I do not know.

6. **L. nutans** Brack. — Pl. 1, Figs. 10—12.

The only author to communicate anything about the spores seems to be Brackenridge, who pictured them schematically (1855, pl. 46, fig. 1 e); his text says nothing about them.

Tetrahedral, trilete, 32×53 (24—37×46—60) $\mu$ (average of 25 measurements). Distal wall slightly arched, outline fairly rounded in polar view, angles a little protruding, obtusely pointed, reached by the tetrad scar. Sculpture only on the distal wall: the low, irregular ridges of an indistinct reticulum give the same wavy appearance as in *L. cernuum* (Pl. 1, Fig. 16). — Specimen studied: Oahu, Koolau, ridge above Kahana bay, c. 700 m, 17/9 1926; C. Skottsberg n. 1865 (G).

Recent: A very rare epiphytic species, recorded only from the Koolau Mts of Oahu (Brackenridge 1854, p. 327; Robinson 1914, p. 54; Degener, Fl. Haw., Fam. 19, 3/30/'34; Skottsberg 1936, p. 101; Hosaka 1937, p. 218; Nessel 1939, p. 208) and W. Maui: Wailua valley (found by Hillebrand, Robinson l. c. p. and Degener l. c.). MacCaughey (1918 a, p. 218) said all the islands, but I have found no basis for that statement. After Robinson, who says »600 m. — 1000 m.», the latter author gave the altitudinal range as »2000—3500 ft».

Fossil: Not seen.

7. **L. Mannii** (Hillebr.) Skottsb. — Pl. 1. Figs. 13—15.

The spores of this species, dealt with under *L. phlegmaria* (Robinson 1914, MacCaughey 1918 a), *L. phlegmaria* var. *Mannii* (Hillebrand 1888 b), and *Urostachys phlegmaria* var. *Mannii* (Nessel 1939 following Herter's ill-founded genus conception of 1922, p. 249) and recently instituted by Skottsberg (1942, p. 132), have apparently not been described before.

Tetrahedral, trilete, $28 \times 39$ (26—30 × 36—42) $\mu$ (13 spores boiled in KOH). In polar view the angles are somewhat pointed, the sides are not straight, but bulge and give the spore the rather rounded outline. The tetrad scar, bordered by well-developed ridges diminishing towards the periphery, reaches the angles. Exospore sculptured only on the distal wall, which has numerous pits of medium size. In polar view the optical section of the sculpture is of the same shape as in *L. cernuum*, the thickest part being about 2 $\mu$ across. Specimen studied: W. Maui: Haelaau, 18/12 1928; G. R. Ewart and O. H. Swezey 136 (G).

Recent: An extremely rare species, so far apparently represented by only two reliable records: one is Mann's from 1864—1865 on W. Maui: »On the mountain above Maalea bay» (Hillebrand 1888 b, p. 645), the other being the abovementioned, cited as »Maui: G. R. Ewart n. 136 (III, 1928)» by Nessel (1939, p. 222). The latter author also considers Heller 2904 from Oahu to belong here. The view that this probably is *L. phyllanthum* was held already by Skottsberg (l. c.). Rock (1913, p. 59; 1915, p. 298) used the name of *L. Mannii* for a plant found on mossy trunks on Kauai, but what that plant really is, I do not know.

Fossil: Not seen.

Remarks: A study of the spores supports the idea that this plant warrants specific rank. In *L. phlegmaria* the spores are smaller: $19 \times 34$ (17—20 × 32—36) $\mu$, as ascertained in acetolysed spores of a specimen from Samoa [Upolu, 1880, E. Besche (SP)], $35 \pm \mu$ as given by Brown and Brown (1931, p. 108). Other differences may be disclosed by further examinations. The spores of *L. phlegmaria* have been dealt with also by Lüstner (1898, p. 11), Bruchmann (1910, p. 225) and by Miss Knox (1938, p. 440, Fig. 4 on p. 441).

Subgen. II. *Rhopalostachya* Pritzel.
Sect IV. *Cernua*.

8. **L. cernuum** L. — Pl. 1, Fig. 16.

Spring (1842, p. 79—80), Müller (1861), and Krasser (1898) say nothing of the spores, but Hillebrand (1888 b, p. 645) calls them smooth. Lüstner, again, found them provided with »Leisten . . . fast verschwunden» (1898, p. 10—11) and this was reproduced by Bruchmann (1910, p. 225). Brown and Brown (1931, p. 106) described them as »small, spherical-tetrahedral, $28 \pm \mu$ in diameter, the surface minutely rugose, light yellow in color».

Wilson, who has given a good account of the lycopod spores in the U. S. A. and Canada (1934) has also given detailed information. On p. 18 he says: »Diameter of the spores 23 mu or less, reticulation on the basal surface wavy, apical surface unornamented»; the plate (275) shows them, but does not display their characteristic appearance well. The microphotograph of a spore of unknown taxonomic position from the Oligocene of Germany published by Thiergart (1940, Taf. VI, Fig. 30) gives a better impression of what they look like. Whether it belongs to a lycopod or not, it is rather similar to this species also in size: about 33 $\mu$.

Tetrahedral, trilete, 19×31 (17—21×30—34) $\mu$, with rounded angles not reached by the scars. Proximal facets devoid of sculpture. Distal wall with reticulate exospore thickenings, giving the impression of irregular waves; wall comparatively little arched. This type is unique in the Hawaiian flora. — Specimen studied: Oahu: Honolulu, 1852; N. J. Andersson (SP).

Recent: All the islands, common, especially in open places: dry treeless ridges in the lower regions as well as wet montane areas, both in bogs and in the outskirts of the forest. As emphasized by for instance Hillebrand (l. c. p.), Degener (1930, p. 20—22), and Fowler (1940, p. 16), it often forms thickets in the same manner as *Gleichenia linearis* (cf. p. 34) and *G. emarginata*. According to Degener (l. c.) it is the most common lycopod in the islands.

Fossil: The spores — more frequent than those of any other lycopod — have been recorded in 3/4 of the analyses, on Maui and Molokai in most of the samples (90 %), on Kauai in not quite half. The species is represented in all the series, though in widely varying percentages of the samples. In 37, 60, 71, and 78 it was found in every sample, in 1, 10, 35, and 57 in almost all, in 33, 34, 80, 81, and 87 in most samples. In BP 84 it is occasional and in BP 90 rare.

The frequencies in each sample are also very varying, from traces to 676 %, the highest being: 676 % in 429 (84), 315 % in 484 (87), 195 % in 336 (81), 164 % in 39 (1) and 140 % in 485 (78). All apparently indicate local thickets such as mentioned above. These cases have made the average comparatively high, 14 %. But the values exceed 4 % in only 1/3 of the samples. 1 and 2 % are the commonest (40 % of the occurrences), except in Kauai, where 1 % and traces predominate.

9. **L. volubile** Forst. — Pl. 1, Figs. 17—19.

The spores were first studied by Kaulfuss (1827, p. 22), who reported: »Die Haut . . . ist . . . netzartig . . .». Next they were dealt with by Hooker and Greville (1831, Tab. CLXX, fig. 4), but the pictures show no indications of sculpture, and the text says only: »granulis minutis plerumque globosis pallide flavis repletae». Spring (1842, p. 105) does not give any more details. Leitgeb included also this species in his developmental studies, and illustrated

part of its sculpture (1884, p. 71—72, Taf. III, Fig. 28—29). Later a description was published by Potonié (1934 b, p. 44): »etwa 32 $\mu$ r [with reticulum which is] etwa 4 $\mu$ [high] . . grobnetzigen Lycopodiaceentypus mit kräftiger Bastion» (cf. Potonié 1934 a, p. 6 and 11). My size values are different.

Tetrahedral, trilete, 35×44 (33—36×42—46) $\mu$. Tetrad scar reaching the angles, its contours somewhat wavy in polar view. Equator bordered by a light-coloured, almost smooth (only slightly serrate) and up to 6 $\mu$ wide wing, diminishing in width towards the somewhat rounded angles of the spore, and of a faint, radial texture. Distal wall heavily arched, covered all over by an irregular, brown reticulum, about 3 $\mu$ high. Besides the lists of the reticulum, which often send free ends into the lumina, there are also occasional rod-like projections; the designation »Bastion» (cf. above) is accordingly a little inadequate. Lumina about 4—5 $\mu$ wide, ridges 1 $\mu$. — Specimen studied: New Zealand: North Auckland bot. distr.: Tititikiora, 1/5 1927; G. Einar and Greta Du Rietz 2769 (SP).

Recent: In Herb. Kew there is a specimen collected by Menzies and credited to the islands without any further locality (Spring 1849, p. 49). Hillebrand (1888 b, p. 646) thought it must have been collected on Mauna Loa, Robinson, again, considered that it probably came from Mauna Kea (1914, p. 55). This is the only record, and it appears somewhat doubtful. The specimen has not been accessible to me.

Fossil: Not seen, though specially searched for.

Sect. V. *Clavata.*

10. **L. venustulum** Gaud. — Pl. 1, Figs. 20, 21.

Hooker and Greville (1831, Tab. CXIII, fig. 4) seem to have been the first to picture spores of this species; they used Menzies' specimen of »*L. heterophyllum*» from Hawaii. The picture is rather absurd, but the text indicates the nature of the sculpture: »*Semina* pallido-flava, minutissima, subreticulata». Spring (1842, p. 84) says merely: »farina pallide flava repleta». Hillebrand (1888 b, p. 645), again, states that they are not only reticulate, but also muricate (»Spores pale yellow, reticulate, muricate»). Robinson (1914) and Degener (Fl. Haw., Fam. 19, 10/14/'38) do not deal with the spores.

Tetrahedral, trilete, 30×46 (27—33×44—48) $\mu$, without projections, 22×35 (20—26×34—37) $\mu$. Distal wall heavily arched. Tetrad scar reaching the periphery of the spore. Exospore covered by a well developed reticulate sculpture, reduced only on the proximal facets. Reticulum about 5 $\mu$ high, lumina 6—8 $\mu$ wide, polygonal, irregular. The spores thus very much resemble those of the closely related *L. clavatum*, which have been described and pictured on numerous occasions (see the microphotograph in Rudolph 1935, Taf. V, Fig. 22, and others). They are unique in the Hawaiian flora.

— Specimen studied: W. Maui, Puu Kukui, in the more elevated regions, 9/10 1922; C. Skottsberg 775 (SP).

Recent: All the islands, in open places, in the bogs and in forests varying from the very wettest to the dry types, also in subalpine heaths; rather common locally. Hillebrand (l. c. p.) called it rare, MacCaughey (1918 a, p. 218) »not uncommon». Degener (Fl. Haw., Fam. 19, 10/14/'38; cf. 1930, p. 24, where it is called rather rare) gives more detailed information: rare in Oahu, occasional in Kauai and Molokai, common in Maui and Hawaii. The list of localities mentioned by Degener is not intended to be complete. As regards West Maui, his data agree with Skottsberg's (1926, p. 201): »common in the more elevated regions». Degener makes the remark: »It can grow in places too wet for *L. cernuum* L.» As to the latter species, see p. 17. The data on the altitudinal range of *L. venustulum* are much confused. Brackenridge (1854, p. 329) said 4000—8000 ft, and was cited by Nessel (1939, p. 307). Robinson (1914, p. 55) says 800—1200 m, which is repeated by MacCaughey (1918 a, p. 218), while Degener (l. c.) places the lower limit at 3500 ft (c. 1100 m). As to the upper limit of this species, Skottsberg (1926, p. 201) has published localities from Mauna Loa from 2500 to 2700 m above sea level.

Fossil: On all three islands, and in more than half the slides. Represented in all series: in 37, 57, and 87 the spores were not absent from any sample, in 60, 78, 80, 81, and 84 they are less frequent, in the remaining series they have been found in most of the samples. The values vary from traces to 149%. The highest are apparently due to local influences [149 % in 490 (90), 190 % in 242 (60), 80 % in 485 (87), 45 % in 491 (90)]. In the rest all integers up to 15 % may be found, though usually only up to 3 %. 1 % is the predominant value (40 % of the samples). The average is 4 %, or 2 % if the cited high values are excluded.

## Fam. SELAGINELLACEAE.

### **Selaginella** Spring.

Both the morphology and the development of the spores of this genus have often been studied. Unfortunately, it is out of the question to review here the comprehensive literature on the subject. Of recent papers on their development, with references to the most important older literature, may be mentioned Slagg 1932, and on the morphology, besides Hieronymus 1900, Reeve 1935 and Knox 1938. These latter share with most of the morphological papers the drawback of giving but few references to previous literature.

Two species occur in the Hawaiian Islands. Although the spores of neither have been described in any detail (those of *S. deflexa* are not even pictured), they have ever since the time of Hillebrand been known to differ widely in appearance. We will deal here primarily with the microspores, as the importance of the megaspores is rather insignificant to pollen-statistical purposes.

**S. arbuscula** Kaulf. — Pl. 1, Figs. 22, 23.

In his description of this species Kaulfuss asserted the trilete type of the spores: »semina miniata trigona pyramidalia» (1824, p. 20), which can also be seen in the first picture of them (Hooker and Greville 1831, Tab. CC). This also made it clear that there was no prominent sculpture. Spring (1849, p. 184—186), who included a note of the trilete type in his generic diagnosis, says of the spores only: »farina miniata repleta», and of *S. Menziesii*, which Skottsberg (1942) coupled with *S. Springii* as a variety of *arbuscula*, he remarks: »farina cinnabarina repleta»; nothing is said in this paper of the spores of *S. Springii*. Brackenridge (1854, p. 333) only mentions: »antheridia . . . filled with fine whitish powder». It was Hillebrand (1888 b, p. 648—650), who directly pointed out that the species which are now united under this name have smooth spores, which he called reddish. Hieronymus (1900, p. 678) described them as »mennigrot oder safrangelb, stets glatt», and pointed out the lack of distinguishing characters in the spores of the »species» belonging here. Robinson (1914) and Skottsberg (1942) speak of them as smooth. Brown and Brown (1931, p. 112) using material from the Marquesas credited to this species, have the most detailed description so far given: »triangular with rounded angles, 38 $\pm$ $\mu$ in diameter, smooth with a 3-branched ridge at the apex, yellowish-brown in color by transmitted light», and Miss Knox (1938) has published a picture of a spore of »*S. Menziesii*» — the only modern picture I know.

Tetrahedral, trilete, 27 × 36 (25—30 × 33—40 $\mu$) (average of 20 spores from two collections cited below). Distal pole rounded, proximal pole flattened pyramidal, angles rounded. Inner contours of the tetrad scar slightly irregular (in both polar and equatorial views), a distinguishing feature from certain spores of *Gleichenia*, to which there is a certain resemblance in other respects. Lists bordering the scar less prominent than in these, and the exospore on closer examination of minutely rough contour. Colour after acetolysis a more or less turbid gray. Specimens examined: Oahu: Koolau, Manoa valley, rocky embankment, 1/5 1926; O. Degener 5663 (SP): 27 × 36 (26—30 × 33—40) $\mu$; and Hawaii: S slope of Manua Loa, wet forest above Pahala, c. 1050 m, 19/9 1922; C. Skottsberg 582 (SP): 27 × 36 (25—29 × 34—40) $\mu$.

Recent: A common to occasional species in damp forests (epiphytic as well as terrestrial) and on moist rocks in all the large islands, possibly less frequent in the wettest parts.

Fossil: Occasional occurrences noted in W. Maui, but none of any particular interest.

MEGASPORES: Of the early literature I mention only Hillebrand (1888 b)

who called them smooth in his *arbuscula* and *parvula*, but verruculose in *Springii*. Skottsberg (1942, p. 136) describes them thus: »The rounded side is more or less distinctly reticulate-pitted, but it happens that this sculptured coating does not extend all over this side, but leaves an area, which is evenly and finely punctulate, free (distinct under high power only). Figs. 689 and 690 give an idea of what the macrospores look like, and there is no difference between »*Menziesii*» and »*Springii*» in this respect. The diameter across the equator is 250—280 $\mu$.»

**S. deflexa** Brack. — Pl. 1, Figs. 24, 25.

In describing this species, Brackenridge (1854, 1855) did not mention or picture the microspores; he confined himself to remarking (p. 332) that he had found the »antheridia filled with a yellowish powder». Hillebrand (1888 b, p. 648) discovered that the spores were »muricate». Hieronymus (1900, p. 669) is somewhat more detailed: »Mikrosporen schwefelgelb an der abgerundeten Seite mit zerstreuten, dünn kegelförmigen Höckern besetzt». Robinson (1914, p. 57) said »spores rough» in her key to bring out the difference between this and the other species; Skottsberg (1942, p. 143) considers this statement incorrect, but as a matter of fact it is not, if we were allowed to refer it to the microspores only. But Miss Robinson does not state to what kind of spores her statement refers. The microspore characters of this species, which comes close to the boreal *S. selaginoides*, are also highly reminiscent of those of the latter (cf. Link 1842, p. 5 and Tab. IV, Fig. 16: B; Milde 1859, p. 411; Braun 1860, p. 57; Luerssen 1889, p. 869; Hieronymus 1900, p. 669 and Fig. 401: N; Hegi 1906, p. 70, Taf. I, Fig. 51; 1936, p. 96, Taf. 1, Fig. 51; Beijerinck 1933, p. 275, Fig. 1; Firbas 1934, p. 156, Taf. XVI, Fig. 5; Reeve 1935, p. 343, Pl. 380; Erdtman 1943, p. 150, Pl. XXVIII, Figs. 487 and 488).

Spores tetrahedral, trilete, 45×62 (39—50×56—68) $\mu$, spines excluded: 37×50 (34—41×44—56) $\mu$, united in tetrads about 90 $\mu$ in diam. (about 76 $\mu$ excluding spines). Distal side heavily arched, the proximal flattened pyramidal, lacking the spiny sculpture characterizing the former. Exospore covering of granular texture. Spines scattered all over the said surface, about 7—9 $\mu$ long, and about 2 $\mu$ wide at the bases, rapidly narrowing to about 1 $\mu$ in width. Colour yellowish brown. In the fossil state the spores generally occur separated. — Specimen studied: W. Maui: summit of Puu Kukui, 22/7 1938; O. H. Selling (spore sample only).

Recent: Not uncommon in the bogs and swampy forests of all the large islands. Both epiphytic and terrestrial.

Fossil: The spores (both tetrads and monads) of this species occur in more than 90 % of all analysed samples from all the islands. In Molokai

they occur in every sample, in Maui in all of the series 33, 34, 35, 37, and 78, and in most samples of 57, 60, 71, and 80. On Kauai they have been found in all samples of 87 and 90 and in most of those of the series 81 and 84.

The values vary greatly, traces to 328 %. No reaction to climate during the periods involved could be detected. In this respect, too, the species is thus similar to *S. selaginoides* (cf. Faegri 1944, p. 83). 1—2 % are the commonest values, but these samples do not cover quite 20 % of the occurrences. A third of them are over 20 %, and among the rest almost all integers up to 60 % are represented. This is reflected also in the average, which is a trifle over 20 % (all the islands included). On Kauai it is 30 %, Molokai, 20 %, and on Maui, 17 %. The highest frequencies are 328 % in 225 (37), 227 % in 404 (84), 174 % in 230 (57), 165 % in 491 (90) and 158 % in 227 (57), all from Maui or Kauai; on Molokai 93 % were recorded in 5 (1).

MEGASPORES: In describing the species Brackenridge (1854, p. 332) paid attention to these, stating them to be »nearly round, echinate yellowish grains». They were figured in his atlas (1855, Pl. 45, fig. 3 e). Hillebrand (1888 b, p. 648) gave them the better designation »papillate» and called the colour white. Hieronymus (1900, p. 669) took the middle way: »Makrosporen gelblich weiss, an der Scheitelseite mit hohen, an der abgerundeten Seite mit viel kleineren, oft etwas gekrümmten kegelförmigen Erhöhungen dicht bedeckt; . . .». Robinson (1914) says »spores rough» but it is not known whether this refers to the megaspores or not (cf. above). Skottsberg (1942) made no comments on them. A number of these megaspores were found in the fossil state but none of them permitted any conclusions of particular interest.

## Fam. PSILOTACEAE.

### **Psilotum** Sw.

Spores bilateral and monolete, but tetrahedral, trilete spores may also occasionally occur with them in the same sporangium (Goebel 1918, p. 1162; 1930, p. 1332; Tammes 1930, p. 17, Fig. 5 c—e on p. 18). Still, the genus is not — as stated by the last named author — the only one among the pteridophytes in which this has been observed; I have published a list of similar cases elsewhere (1944, p. 7—8), and the present paper gives further examples. No perispore has been observed in the family (cf. Hannig 1911 a, p. 344). The exospore is sculptured. Miss Knox, who examined both the species mentioned below, writes (1938, p. 439): »In *Psilotum* the spore surface is rough, and in both species short spicules appear irregularly. . . . .». At least

in *P. complanatum* it is, however, better characterized as irregularly pitted (cf. below). Without success I have been looking for any occurrences of the said spicules. In the fairly extensive literature on *Psilotum* spores they seem to be mentioned only by Miss Knox. Whether they really occur or not should be thoroughly investigated. It is at any rate worth noting that in the picture of *P. complanatum* (l. c. p. 441, Fig. 1) they appear only inside the contours of the spore, where they occur here and there like foreign bodies. Some of them might be expected to occur also along the contours.

There are two species in the Hawaiian Islands:

**P. complanatum** Sw. — Pl. 2, Fig. 26, 27.

Pictures of these spores: see above, and also Bischoff 1828.

Generally bilateral, monolete, acetolysed: $40 \times 75$ ($37—44 \times 71—80$) $\mu$; boiled in KOH: $38 \times 73$ ($32—46 \times 66—79$) $\mu$ (of the latter, 25 spores were measured). Tetrad scar bordered on each side by a list about three quarters of the length of the spore. In both the examined numbers the exospore was about 4 $\mu$ thick and provided with a distinct though rather irregular pitting, which at once distinguished these spores from aberrant, bilateral, monolete specimens of *Adiantum capillus veneris* (cf. p. 52). In this distinct pitting, as well as in the somewhat greater average size, the Hawaiian populations of this species seem to differ from those of *P. nudum*. Still, the characters may of course sometimes overlap. — In HBS 3446 a few irregular trilete spores were found and also one where the spore mother cells had evidently failed to divide and a globular, alete spore had been formed, which measured $70 \times 79$ $\mu$ and was sculptured like the normal spores. — Specimens studied: Hawaii: Kohala, Kehena trail, 1938; HBS 3446 (acetolysed); and W. Maui: between Haelaau and Nakalalua, in rain-forest, 1938; HBS 2753 (SP) (boiled in KOH).

Recent: Epiphytic, occurring in the rain forests of all the big islands, also in the wet forests near the bogs. In the dry outskirts of these forests it grows with *P. nudum*. Rather rare, decidedly more so than *P. nudum*. Reported also from some other Polynesian groups and Malaya, as well as from the West Indies.

Fossil: The rarity of the spores in the fossil state indicates that the species used not to be much commoner than it is now. I have not seen more than 11 spores among about a quarter of a million microfossils so far examined: two in Molokai, two in Kauai, and the rest in Maui. Except in 229 (57), where two spores were found, there are always solitary occurrences. Hence the finds are of rather limited value to other questions. The oldest was found in 57: 239.

**P. nudum** (L.) Griseb. — Pl. 2, Fig. 28.

Spores dealt with by numerous authors, generally under the synonym *P.*

*triquetrum* Sw.: Brown 1810, Palisot 1811 (ill.), Kaulfuss 1824, 1827, Purkinje 1830 (ill.), Hooker and Bauer 1838—1842 (ill.), Spring 1840, 1849, Link 1842 (ill.), Mettenius 1856, Hooker 1859 (ill.), Kickx 1870 (ill.), Pritzel 1902 (ill., reproduced in, *e. g.*, Lotsy 1909), Darnell-Smith 1917 (ill.), Goebel 1918, 1930, Wettstein [1923—]1924 (ill.), 1935 (ill.), Tammes 1930 (ill.), Brown and Brown 1931, Knox 1938, to which still more could be added; there are also cytological papers from Hofmeister's days onwards, all cited by Manton 1942. The statements cited above by Goebel and Tammes regarding occasional trilete spores refer to this species. Judging by the words »alia vero graniformia ut in plurimis Lycopodiis nuspiam inveni» Kaulfuss (1824, p. 22) had already noted the same thing when he determined the collection made in Oahu by Chamisso. I have seen no such cases.

Bilateral, monolete, acetolysed: $36 \times 67$ (33—$39 \times 63$—74) $\mu$; boiled in KOH: $37 \times 65$ (28—$41 \times 60$—71) $\mu$ (25 specimens). Irrespective of the method employed, we thus find slightly lower averages and limits than in the preceding species, but whether this holds good everywhere in the islands cannot yet be stated. One need but compare the data available in literature to find a certain variation in the species. In Australian material from the vicinity of Sydney, Darnell-Smith (l. c. p. 83) found an average of $32.4 \times 64.8$ $\mu$, *i. e.* about the same as I have done. From SE Polynesia Brown and Brown (1931, p. 110) recorded an average of $29 \times 54$ $\mu$, however, which corresponds to that given in Knox 1938 for both species: $30 \times 55$ $\mu$. These might possibly be different geographical races, and we cannot tell whether the Hawaiian populations ever reach the latter averages. The differences may, at least to some extent, be due to cytological conditions. Okabe (1929) found tetraploid plants in cultivated material, and Manton (1942) later showed that wild populations also contain both diploid and tetraploid races. Nobody has yet studied the variations in spore size, however, in relation to chromosome numbers in this species.

The exospore sculpture is not as distinctly pitted as in *P. complanatum*. At first one is inclined to designate the surface as merely rough, as did Knox (see p. 22), but on closer examination of mature spores lumina of the same general nature as in the former species are found, though much narrower. This was also observed both by Darnell-Smith (»delicate reticulate epispore structures») and Brown and Brown (»the surface minutely pitted»). — Specimens studied: Oahu: Ewa coral plain, 11/8 1922; C. Skottsberg 134 (acetolysed); and Kauai: Kokee-Milolii trail, 14/8 1938; HBS 2921 (boiled in KOH). Both in SP.

Recent: A common species of comparatively dry districts, occurring in all the islands: according to MacCaughey (1918 a, p. 201, 203, and 218) from sea-level up to 3000 ft, but also higher, in certain localities up to 4000 ft (Hillebrand 1888 b, p. 647;

Skottsberg 1926, p. 201). Fowler, referring to the Kilauea-Mauna Loa section of Hawaii National Park, says »common on trees and rocks in the drier regions of the Park below 4,500 feet.» More xerophytic than the preceding, together with which it occurs only in the outskirts of the rain forest (see above). The species is both terrestrial and epiphytic.

Fossil: Not seen.

## Fam. OPHIOGLOSSACEAE.

As pointed out by Bitter (1900, p. 464) and others, the family is with but few exceptions (aberrant cases in some species) characterized by tetrahedral, trilete spores. All the Hawaiian species are of this type. Two genera are represented.

### **Botrychium** Sw.

Spores of several species have been dealt with by a number of authors. Those of the Hawaiian species were pictured by Brackenridge (1855, Pl. 44, fig. 2 c) in a contour drawing suggesting their trilete type. Milde (1869, p. 157) does not mention them, but Hillebrand (1888 b, p. 641) says: »Spores whitish subglobose, finely granular». The appearance of the sculpture was correctly described by Prantl (1883, p. 349; 1884, p. 337): »sporae reticulatae areolis rotundis clausis». Clausen (1938, p. 59) says nothing of sculpture.

**B. subbifoliatum** Brack. — Pl. 2, Figs. 29, 30.

Tetrahedral, trilete, only rarely bilateral and monolete, with distal wall heavily arched, 26×34 (24—29×30—37) $\mu$; specimens devoid of sculpture about 24×32 $\mu$. Often somewhat irregular in shape, with transitions to the monolete specimens, which measure 25×35 (24—26×32—38) $\mu$. Tetrad scar generally reaching the rounded angles of the spore, though not always clearly defined all along its length. Sculpture in the shape of a reticulum of medium coarseness with irregular lumina, into which occasional ridges send free ends. — Specimen studied: D. D. Baldwin: Hawaiian Ferns, no locality (SP).

Recent: Evidently a rare species preferring, according to Hillebrand, the »deep forests» of Kauai, Oahu, Molokai, and W. Maui. Brackenridge (1854), who says »shady places», lists it also for Hawaii. Wawra found it on Kauai in »Wälder der Niederungen, an schattigen, humusreichen Stellen in kleinen Gruppen vorkommend» (Luerssen 1875 b, p. 440). Robinson (1912 a, p. 234) says: »On the ground in wet forests».

Fossil: Especially looked for, but not seen.

### **Ophioglossum** L.

Two species are at present recognized to occur in the islands:

**O. concinnum** Brack. — Pl. 2, Figs. 33—35.

The spores of the closely related *O. vulgatum* have been studied by a great

many authors (Hooker and Bauer 1838—1842, Moore 1859, 1860, Russow 1872, Prantl 1883, 1884, Reinsch 1884, Rostowzew 1891, Lüstner 1898, Karpowicz 1927, McVaugh 1935, Rudolph 1935, Bertsch 1942, and others), and those of *O. nudicaule* by, for instance, Bitter (1900) and Miss Knox (1938, p. 444—445, fig. 27), but the spores of the Hawaiian species do not seem to have been described.

Tetrahedral, trilete, 34×48 (31—37×45—52) $\mu$, occasionally bilateral and monolete (one spore 50×58 $\mu$ in polar view), or alete, rounded to subtriangular in polar view, distal wall well arched, proximal pole a little protruding. Tetrad scar generally reaching the equator, bordered by distinct lists which ± disappear, however, a short distance from the end of the scar branches. Distal wall, to some extent also the proximal facets, covered by a fairly thick, dark brown sculpture with dense, small pits and very rough surface contour. Abnormal local thickenings in this sculpture have been observed (cf. Fig. 35). — Specimen studied: D. D. Baldwin: Haw. Ferns, s. l. (SP).

Recent: Hillebrand (l. c. p. 640) listed *O. nudicaule* L. fil. and *O. vulgatum* L. from the islands, but in both cases the specimens represent this species. It has been reported from Kauai, Oahu, Maui, and Hawaii. Robinson (1912 a, p. 235) says »On ground, appearing after rains; often near the sea-shore or in soil that has been taken from the shore». Hillebrand mentions his *vulgatum* also from 6000 ft altitude on Haleakala, a locality to which shore soil appears hardly to have been transported. Fowler (1940, p. 10) lists the species from earthquake cracks of Kilauea, Hawaii.

Fossil: As the preceding.

**O. falcatum** (Presl) Fowler — Pl. 2, Figs. 31, 32.

The spores of *O. pendulum*, with which this species was united until recently, were figured by Hooker and Greville (1831). They show their trilete type, but the text says only: »Semina parva, sphaerica fusco-lutea». Presl (1845) characterized them as »albido-flavescentem exhibentes» (p. 55); in dealing with the family as a unit (p. 41) he called the spores small and smooth, tetrahedral. In his paper of 1883 Prantl says nothing, but he gives a detailed description in 1884 (p. 332): »Sporae 50 $\mu$ latae, areolis 15 $\mu$ ad diam., rotundis, striis non elevatis». Lüstner (1898, p. 11), too, emphazised that the spores have no high reticulum like some other species of this genus, but »stimmen mit den Tüpfelsporen der Lycopodeen vollkommen überein». Such a sculpture is indicated by a picture in Campbell 1911, p. 7, Fig. 1. Brown and Brown (1931, p. 105) give a good description: »spores spherical-tetrahedral with a prominent 3-parted ridge, 55 ± $\mu$ in diameter, the surface minutely pitted, light yellow in color». Clausen (1938), finally, who calls the spores of the genus »yellowish» and »thick-walled» (p. 111), says no more about the species (p. 116). Material referable to the Hawaiian species does not seem to have been described before.

Tetrahedral, trilete, 38×55 (36—41×50—59) μ, occasional larger spores, *e. g.*, 41×65 μ. A few bilateral and monolete (40×68 μ) as well as alete spores observed (mentioned under *O. pendulum* in Selling 1944, p. 7—8). Outline of the trilete specimens rounded in polar view. Tetrad scar not reaching the periphery, bordered by ridges diminishing towards the points of the branches. Exospore brown, with coarsely pitted sculpture, rather shallow and of fairly even surface contour. The slightly raised proximal facets less sculptured. — Specimen studied: Hawaii: Hilo, May, 1909; U. Faurie 182 (SP).

Recent: Hillebrand says only »Common on trees» (1888 b, p. 641). Degener (Fl. Haw., Fam. 1, 9/10'32) and St. John (1940, p. 354) are more detailed and credit it to moss-covered trunks and branches in the rain forests of middle elevations. Degener calls it »Comparatively rare excepting on Tantalus Mountain near Honolulu», St. John says »abundant». Whether Robinson's figure (1912 a, p. 235) »600—1500 m.» refers only to the islands is not certain. Reported from Kauai, Oahu, Maui and Hawaii (Degener l. c.), also from Molokai (Clausen 1938, p. 118).

Fossil: Not observed.

## Fam. MARATTIACEAE.

### **Marattia** Sm.

The spores of this genus are among the smallest of all pteridophyte spores. Both monolete and trilete spores may occur together in the same species, as was first pointed out by Mettenius (1856, p. 118) after studies on cultivated material, and by Luerssen (1872, 1874, 1875 a), who also examined wild species. The former type seems, however, to be predominating. It has been observed exclusively or in most cases in *M. alata* (Hooker and Bauer 1838), *M. cicutaefolia* (Luerssen 1872, 1874, 1875 a, b and c; Knox 1938), *M. fraxinea* (Kaulfuss 1827, Jonkman 1878, 1880; cf., however, Brown and Brown 1931, p. 103, who in Marquesan forms — as in the closely related species of Rapa, *M. Stokesii* — found only »3-parted ridge»), *M. laevis* (Kaulfuss 1827), *M. laxa* (Luerssen ll. c.), *M. raddiana* (»*M. Raddii*»; Schott 1834), *M. sambucina* (Knox 1938), and *M. verschaffeltiana* (Sturm 1859). To this list can now be added the Hawaiian species, the spores of which have apparently not been described before. Fragments of their characteristic sculpture can, however, be seen in the picture published by Campbell (1911, p. 121, Fig. 88) of the prothallium of this species.

The spore sculptures range from granular to minutely spinose. Presl (1845, p. 7) called them »nudae aut granulato-tuberculatae», and in the figure published by Schott to illustrate »*M. Raddii*» (1834) there is no sculpture, but too much should not be made of these data in this connexion. For the development of the spores, see papers by Tschistiakoff (1871, 1874 a and b, 1875),

Luerssen (1872, 1874), Jonkman (1878, 1879, 1880), and Leitgeb (1884), as well as the excellent survey in Campbell 1911 (p. 119).

Only one species found in Hawaii:

**M. Douglasii** (Presl) Bak. — Pl. 2, Figs. 36, 37.

Bilateral, monolete (rarely tetrahedral, trilete), 18×25 (16—20×21—30) μ. Tetrad scar somewhat shorter than the largest diameter of the spore. Exospore minutely papillate and light gray in colour, *viz.* after acetolysis. Recent spores have occasionally an outer coating, possibly a perispore (cf. Leitgeb l. c. p. 6—7). At first Luerssen was inclined to regard the trilete spores of this genus as »die normale, allein fortbildungsfähige Entwicklungsform» (1872, p. 19; 1874, p. 331; 1875 a, p. 38), but later (1875 c, p. 47) he abandoned this view which is not applicable to this species either, as the trilete type occurs only as a rare anomaly.

This spore type is quite distinctive. Some specimens of the pollen of, for instance, *Astelia menziesiana* (Liliaceae) are sometimes similar to it, but are not so pronouncedly bean-shaped as this. On closer examination all risks of error in the determination disappear. — Specimens studied: W. Maui: above Haelaau, in wet forest, c. 1000 m alt., 1/8 1938; O. H. Selling (spore sample only): 18×25 (16—20×21—30) μ; Hawaii: S slope of Mauna Loa, wet forest, c. 1100 m, 19/9 1922; C. Skottsberg 579 (SP): 17×25 (16—19×23—28) μ.

Recent: Brackenridge, who called the species *M. alata*, says only »frequent in humid forests» (1854, p. 311), a statement which may not give quite the correct impression, however. At any rate, the species is fairly local, and hardly more than rather common at present, if we consider its whole area of distribution. It prefers the damp, shady habitats under the canopy of the rain forest, as pictured in some detail by Wawra (1872, p. 300) and Hosaka (1937, p. 204) from Oahu. Rock also considered it »a typical fern of the middle forest zone» (1913, p. 65; 1915, p. 301); Hosaka (l. c. p. 218) records it from both his Koa and Ohia zones. Its altitudinal range depends, of course, upon the occurrence of the humid vegetation types. Hence the statements vary a great deal. MacCaughey's summary (1918 a, p. 203 and 204) is hardly reliable; he gives »1500—3000 ft». Bailey (1882, p. 58) says »3—5000 feet», Heller (1897, p. 791) found it on Kauai at 4000 ft, as did Skottsberg (1926, p. 186) and our party during the HBS in 1938. Heller also considered it »a plant of high elevations, at least on Kauai and Oahu», but he also pointed out that »it may be found at much lower elevations on the windward sides of the islands». In fact, Campbell, who had seen the plant on Kauai, had earlier reported it to be »common in the damp forests at an elevation of 300—400 metres» (1892, p. 2). To sum up, the species has been recorded from rain forests 300 to 1500 m above sea level.

Fossil: 90 % of the samples and all the boring series contain these spores. The values vary from traces to 31 %; 1 % is the most frequent, then 2, 3, 4 %, and traces. The average is between 3 and 4 %. The highest values are: 31 % in 330 (81), 22 % in 404 (84), and 20 % in 339 (91), all from Kauai, 19 % in 225 (37) and 16 % in 242 (60) from W. Maui, and 8 % in 6 (1) from Molokai.

In Kauai the spores occur more frequently and show higher average values than in the other islands. They are not absent in any sample and show all integers between 1 and 17 % besides those already mentioned, 3 % being the commonest (average about 7 %).

In Molokai only five samples »lack» the species; the values vary generally from traces to 5 %. 1 % is predominant (average about 2 %).

In W. Maui only three series, 34, 35 and 37, contain these spores in all analyses. In the other series they were found in most (BP 71) or almost all analyses (remaining series). In one sixth of all samples they are »absent». The values lie between traces and 6 %, 1 and 2 % being the commonest (average 2 %).

The occurrences will be further dealt with in part III.

## Fam. SCHIZAEACEAE.

### **Schizaea** Sm.

The spores of this genus, the only one represented in the Hawaiian Islands, are all bilateral and monolete. As I have once before (1944) dealt in detail with the spore characters of this genus, including literature references, I need only be brief here, and refer for all details to the said paper.

Two species belong to the native flora, but only one of them is known in the living state. Of the other, all that is known are its peculiar spores, which occur very sparsely in the island peat deposits.

#### Recent species.

**S. robusta** Bak. — Pl. 2, Figs. 38, 39.

Bilateral, monolete, 67×88 (48—88×80—110) $\mu$, as ascertained in seven specimens (175 spores) from four islands (particulars in Selling 1944, p. 26; preparations boiled in KOH); 10 acetolyzed spores from Puu Kukui, W. Maui: 75×99 (64—81×88—120) $\mu$. Exospore brown, 4 $\mu$ thick, provided with distinct lists on both sides of the tetrad scar, which takes about 3/4 of the largest equatorial diameter of the spores. In occasional aberrant spores an additional (triradiate) scar has been found on the distal side, and sometimes only one spore of the tetrad is fully developed, and even larger than the normal spores, while the three others form a small structure adhering to its tetrad scar. A spore with the latter feature has been found also in the fossil material (cf. l. c. p. 8, 9 and 24). Exospore surface generally covered by exceedingly small and dense projections, but not unfrequently quite smooth. Illustrations of the spores in surface view, and full reference to the literature dealing with them, are given in my 1944 paper.

Recent: A species sometimes more than 40 cm high (Richter 1915, p. 382; 1916 a, p. 19; 1916 b, p. 17), endemic to Kauai, Oahu, Molokai, W. Maui and Hawaii. MacCaughey (1918 a, p. 217) says »probably also in . . . Kohala, Hawaii», which misled me to exclude Hawaii from its area of distribution (1944, p. 69), all the more as not even Degener (Fl. Haw., Fam. 7, 10/12/'34) lists it. The species had, however, been reported from the said mountains as early as by Rock (1913, p. 73; 1915, p. 304). MacCaughey's data on altitudinal range, »3000—5000 ft.» (l. c., p. 203), are also unsatisfactory. They were apparently copied from Hillebrand (1888 b, p. 543), from whom also Guppy (1906, p. 593) got the firstnamed value. But in 1897 Heller (p. 789) reported the species from »perhaps 2500 feet» in Oahu, and about 2000 ft in Kauai (Wahiawa bog). As regards the highest value, Guppy's »6000 ft.» would be better, for Puu Kukui, from where Hillebrand had listed the species, is 5788 ft. Luerssen (1875 b, p. 419) says 8000', but this is a mistake for 5000', the height of Waialeale. The species occurs in bogs or bog forests, preferably the former and on the ground in the open forests, but is also epiphytic, as stated already by Hillebrand. This author considered the species rare, and MacCaughey copied him without additions. Heller suggested that »Diligent search in situations favourable to its growth, would probably prove it to be much less rare than it is supposed to be» on account of its being easily overlooked (1897, p. 790). Degener (l. c.) found it in large quantities in some bogs, *e. g.*, N of Mt Eeke, W. Maui, and E of Hanalilolilo (= Pepeopae bog), Molokai. On Puu Kukui as well as at Kilohana, Kauai, it is also rather often seen in the bogs.

Fossil: In all series of samples, and in a little over half of all samples examined. These spores occur throughout two series (10 and 87), in half or more of seven series (1, 33, 37, 78, 81, 84, 90) but in others they occur rarely (34, 35, 57) or sparsely (60, 71). Frequencies vary from traces to 18 %, 1 % being the commonest, and next traces, 2, 3, and 4 %. The highest values were found in 31 (1): 18 %; 3 (1) and 153 (10): 13 %; 273 (80): 12 %; and 485 (87): 10 %; all of them probably due to local overrepresentation, possibly from particularly rich stands. The average for all the islands is just over 2 %. The frequency distribution in the islands shows no marked differences that might conceivably be of a general nature.

## Fossil species.

**S. Skottsbergii** Selling — Pl. 2, Figs. 40, 41 (—44; cf. below).

Bilateral, monolete, 78×114 (70—91×96—132) $\mu$, as ascertained in 25 spores boiled in KOH (Selling 1944, p. 71). Exospore 4—4,5 $\mu$ thick, brown, with a ridge 2/3 to 3/4 of the length of the greatest equatorial spore diameter on each side of the dehiscence mark, and provided with an alveolate sculpture as described in l. c. p. Next to the primary exospore membrane is a solid part of the secondary thickening, which is of minutely granular or radial structure. The alveoles correspond to a rounded pore in the outermost part of the exospore; the pores measure about 2.5 (1—5) $\mu$ in diameter and are bordered on the exospore surface by well developed ridges with transverse furrows half-way between the points of convergence. The ridges constitute a reticulum of hexagonal or pentagonal lumina with rounded angles (sometimes with four or seven sides). The membrane between the pores about

1 $\mu$ across. The spore characters of this species (incl. its variety) are unique in the Hawaiian flora.

Occurrence: In Molokai and Kauai, rather locally; one variety (see below) in W. Maui. The main species has been observed in eight samples: BP 1: 57 (3 %), 59 (3 %), 84 and 135 (no other microfossils counted); BP 10: 157 (traces), 158 (3 %), all six from Molokai, and from Kauai in BP 81: 373 (traces) and 374 (2 %). These spores were thus found only in the earliest part of the Post-Glacial. The variety has also been found in considerably younger deposits.

**S. Skottsbergii** var. **mauiensis** Selling — Pl. 2, Figs. 42—44.

Differing in size and sculpture: 72×103 (58—82×88—116) $\mu$, measured in the same way as before. Alveoles and pores in the outermost wall larger and less numerous; sometimes only half the number per surface unit. Pores more frequently fused, and also wider, about 4 (2—7) $\mu$ in diameter. Width of the intervening part of the outermost wall about 2 $\mu$.

Occurrence: Hitherto found only in W. Maui, in several samples: BP 33: 163 (tr.), 173 (tr.), 176 (tr.), 177 (1 %), and 181 (no other microfossils counted); BP 34: all samples except 196—202, mostly 1 %; 2 % in 191, and traces in 195; BP 57: 239 (3 %). The variety is thus found all through the Post-Glacial warm period.

The ecology and history of this species are discussed in Selling 1944, p. 73—86.

## Fam. GLEICHENIACEAE.

### **Gleichenia** Sm. (sens. lat.)

A certain confusion regarding the spore type of this genus reigned in literature up to the end of the 19th century, and Hillebrand (1888 b, p. 543) — like Endlicher (1836—1840, 1841), Mettenius (1856) and Sturm (1859) — were among those who were incorrectly informed. These authors stated the spores to be monolete. But if Hillebrand had studied the Hawaiian species, he would have found the trilete type in all but one of them. That both types are found in the genus (incl. *Mertensia*) was expressly stated by Mohl (1833, 1845). His statements do not seem to have been generally known, however, though they were later cited by Russow (1872), Rauwenhoff (see below), and others. The same was in fact indicated already by Kaulfuss (1827, p. 36 and 39) and Martius (1828—1834). The best known early picture of a trilete spore (*G. polypodioides:* Hooker and Bauer 1838, Tab. XLI A: 7) left much to be desired, while good pictures of monolete spores were published in

Hooker and Greville 1831 and Hooker and Bauer 1838; this may have added to the confusion.

Be that as it may, the occurrence of both types in the genus became known especially by the investigations of Rauwenhoff (1877, 1879 a, b, c, 1890). As to their distribution in the genus, Miss Knox (1938, p. 449) found that of the species studied by her, those of subgen. *Eugleichenia* had trilete, those of subgen. *Dicranopteris* mainly monolete spores. In the same year Christensen (1938, p. 530) suggested a splitting up of the genus (as it had been interpreted by, *e. g.*, Diels 1902 a) into four, leaving *Gleichenia* to comprise only about 10 species of the southern hemisphere. One of these genera, *Dicranopteris* Bernh., was divided into two sections, *Heteropterygium*, to which two of the Hawaiian species would belong, with tetrahedral (trilete) spores and *Acropterygium* with bilateral (monolete). *Sticherus* Presl, in which he included Diels' sections *Holopterygium* and *Diplopterygium* and to which the two other Hawaiian species would belong, is stated to have only bilateral spores. Chrysler (1943, p. 488), who kept *Hicriopteris* Presl (= *Diplopterygium* Diels) distinct from *Sticherus* — as did St. John in a paper of 1942, which I know from Chrysler's quotation only — tabulated also spore characters and found them distributed in the same way as indicated by Christensen. Still, one of the Hawaiian species shows a discrepancy from this scheme. To use the old nomenclature provisionally preferred below, *G. glauca* (= *Hicriopteris pinnata* (Kze) Ching) turned out to have trilete, tetrahedral spores. Only *G. owhyhensis* is provided with the monolete, bilateral type.

Miss Knox states that the trilete spores of this genus vary between 25 and 50 $\mu$ in equatorial diameter. The Hawaiian species seem to keep inside these limits, which, however, do not give the full range: in *G. rupestris*, for instance, they measure 53 $\mu$ (Rauwenhoff 1890, p. 13).

Rauwenhoff was also the principal contributor to a detailed knowledge of the appearance and construction of the spores. His pictures from 1879 and 1890 are even superior to those published much later. For the details of the spore membrane construction, reference is made to his papers cited above. The occurrence of a true perispore hardly appears likely (cf. Hannig 1911 a, p. 242). At any rate I have not seen anything like it in my slides.

The genus is represented by four indigenous species, at present — as pointed out by MacCaughey (1918 b, p. 41) — the most abundant ferns of the Hawaiian forests.

**G. emarginata** (Brack.) Moore (*G. sandwicensis* Degener) — Pl. 3, Figs. 45, 46.

Tetrahedral, trilete, 29×40 (27—32×35—44) $\mu$, average of the two col-

lections cited below. Triangular in polar view, with straight or somewhat concave sides with slight bends near the angles, and rounded to slightly acuminate angles. Proximal pole often not protruding at all, distal wall strongly arched though not quite rounded, the pole being somewhat »drawn-out». Branches of the tetrad scar, which reaches the equator, bordered by well-developed lists in the exospore along their full length. These lists seem to be of general occurrence in the genus. Rauwenhoff also pictures them (1879 b, 1890), but they are not correctly reproduced by Miss Knox (1938, Fig. 49). They afford a possibility of distinguishing the spores of this genus from those of *Microlepia* (see p. 44—45 below). Wall generally somewhat less than 2 $\mu$ thick, light brown, smooth, and of indistinct texture giving it a turbid appearance, but the contours are occasionally very minutely rough. Specimens studied: Oahu: Waianae, Mt Kaala, c. 3000 ft, 25/9 1938; O. H. Selling (spore sample only; HBS 3674 collected in the same spot): 29×39 (27—31×35—41) $\mu$. Hawaii: Hiulani forest SW of Olaa, c. 500 m, 8/9 1922; C. Skottsberg 418 (SP): 30×40 (27—32×37—44) $\mu$.

Recent: Endemic, reported from all the islands by MacCaughey (1918 b, p. 45), only from Oahu and Hawaii by Hillebrand (1888 b, p. 545), Skottsberg (1926, p. 200; 1936, p. 101; 1942, p. 127), Degener (1930, p. 24), and others, but later stated by Degener (Fl. Haw., Fam. 5, March 15, 1940) to occur also in Kauai (Alakai swamp), Maui (near Olowalu), and Lanai. In the area studied by Hosaka (1937, p. 218) it is a rare component of the Cluod zone rain forest. In other localities it is commoner, much less so than *G. linearis*, but at the same time much commoner than the other two species. To quote MacCaughey (l. c. p.), who ascribes it to elevations from 1000 to 3000 ft, it »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.» Fowler (1940, p. 10) records it as »common in open places throughout the eastern half of the Kilauea-Mauna Loa section of Hawaii National Park to an elevation of about 4000 feet, frequently forming dense thickets» (cf. Degener l. c.). Degener states it to be found fertile more often than *G. linearis* and that it seems at times to hybridize with this closely related species.

Fossil: see below.

**G. glauca** (Thunb.) Hook. — Pl. 3, Figs. 47—49.

Tetrahedral, trilete, 22×30 (19—24×27—34) $\mu$. Essentially like the preceding, differing mainly in size. In certain specimens lists occur only along one of the three branches. The membrane appears somewhat thinner, about 1.5 $\mu$, but may vary in different individuals. Still, the spores appear to be distinct from those of *Lindsaya*, *Microlepia speluncae*, and *Pteridium*, which are of the same general size (equatorial diameters): see the key p. 7 as well as text and figures referring to these species. *G. glauca* belongs to *Sticherus* (*Hicriopteris*), stated by Christensen and Chrysler to have bilateral (monolete) spores (see above; papers by Ching, Copeland, and St. John cited by Chrysler not seen by me). — Specimen studied: W. Maui: N slope of Puu Kukui, Haelaau-Nakalalua ridge, 1/8 1938; HBS 2740 (SP).

Recent: Reported by Hillebrand from all the islands, here and there at elevations of 2000—4000 ft (1888 b, p. 544); MacCaughey (1918 a, p. 216; 1918 b, p. 44) copied him, adding »nowhere abundant». Robinson (1912 a, p. 240) found it »in fruit somewhat rarely». It occurs in the rain forest and in very wet districts. MacCaughey (1918 b, p. 44) says: »It is often found in the same habitats as *G. Hawaiiensis* [= *G. owhyhensis*] but does not mingle with the latter . . .». He adds that it »appears to maintain itself successfully along the windswept 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* [= *G. linearis*]». A typical occurrence will be pictured in part III.

Fossil: See below.

**G. linearis** (Burm.) Cl. — Pl. 3, Figs. 50, 51.

Tetrahedral, trilete, $27 \times 38$ ($25—30 \times 35—42$) $\mu$. Like the preceding, but in polar view the angles are more acuminate than in those species; the sides still straight, or sometimes slightly concave. Tetrad scar very pronounced, with distinct lists. Wall thickness apparently about the average of that found in the preceding species. The spores have been previously dealt with by Brown and Brown (1931, p. 97) on material from SE Polynesia: »spores tetrahedral, $35 \pm \mu$ in average diameter, the surface smooth, light yellow in color» After acetolysis they become $\pm$ light brown. — Specimen studied: Oahu: Nuuanu-Kalihi ridge, lower slopes, 13/8 1922; C. Skottsberg 154 (SP).

Recent: Nowadays the commonest *Gleichenia*, occurring in all the islands in humid and semi-humid regions. Hillebrand (1888 b, p. 545) reported it »from 600 ft. above the sea (*Hilo* district) to 3000 ft.», MacCaughey (1918 b, p. 46) says »from 500 to about 3000 feet» but it is found above 4000 ft elev. on some of the bog hills visited in 1938. Besides, I have seen fronds of it buried in the peat just below the surface in one of those localities (Molokai: Pepeopae). On the other hand it does not, according to MacCaughey (l. c.), grow well in the lowlands below 500 ft, and never appears in the littoral, nor does it ascend into the higher regions, being most abundant from 800 to 2200 ft. »It is not found in 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 rainforest. It is hygrophytic, but not strongly so, and will maintain itself successfully on semi-xerophytic slopes and ledges.» Whether it has any special objections to »flat land», as suggested by this author, I do not know. Climbing in trees and shrubs, it forms thick tangles also on plateaux. In decadent forests, and in clearings made by cattle and man, it rapidly spreads (cf. the detailed study by Hosaka 1937, p. 209—210), forming vast troublesome thickets (cf. ill. in part. III). MacEldowney (1930, p. 273), for instance, states that it occurs in an almost unbroken blanket throughout the length of the Koolau Range in the makai portions of the forest reserves», constituting a serious menace in case of fire.

Fossil: Trilete spores of *Gleichenia* occur in 95 % of the samples from each of the three islands. They are found in all samples of the series 33, 35, 37, 60 and 78 from Maui, and in 84 and 87 from Kauai. In the other series they are found in most samples. The values vary from traces to 20 %, generally (more than 9/10 of the cases) from traces to 8 %. 1—3 % are the commonest (half of the occurrences). The highest values were found in 242 (60) and 404 (84); both 20 %; in 1 (1): 17 %; in 429 (84): 16 %; in 5 (1), 7 (1) and 21 (1): all 14 %; in 11 (1): 13 %. The average of all occurrences is 4 %.

The task of recognizing different species in the fossil finds is at present very hazardous, and I have refrained from attempting it. It seems likely, however, that the bulk of the spores come from *G. linearis* and *G. emarginata*. On the other hand, these spores are distinct from all other Hawaiian spores. The features distinguishing them from those of *Microlepia* were dealt with above (p. 7, 33). They might also be confused with spores of *Selaginella arbuscula* (p. 7, 20), though the latter often seem to have a more elevated proximal pole. In *Selaginella arbuscula* the spores have indications of lists bordering the tetrad scar, but these are rather indistinct, and the scar itself is not straight but slightly undulating and sometimes even more irregular. This feature can be observed also in equatorial view.

As regards *G. linearis*, considerable stands of it might well have existed earlier, especially during periods of relative drought in one or more regions. It is interesting to note that the two highest frequencies of fossil spores seem to reflect recent conditions, and that almost as high values were found in sample 429 from the beginning of the Post-Glacial. These finds may, however, also include *G. emarginata* (cf. above).

**G. owhyhensis** Hook. — Pl. 3, Figs. 52, 53.

Bilateral, monolete, $23 \times 43$ ($19—26 \times 39—46$) $\mu$. Scar straight, bordered by well developed lists, which do not occupy the whole diameter of the spore. The lists makes it possible — at least in many cases — to distinguish this species from the common polypodiaceous type, to which the spores bear a close resemblance in other respects. — Specimen studied: Kauai: vicinity of Kokee, Aug. 1938; J. Wichmann (HBS distrib. nr) 2939 (SP).

Recent: A rare endemic, belonging to *Sticherus* (see above, p. 32), not xerophytic, reported by Hillebrand (1888 b, p. 544; cf. also MacCaughey 1918 b, p. 43) from all the large islands at elevations from 3000—6000 ft. Robinson (1912 a, p. 241) says 1,500—2,000 m. It has been found in the vicinity of the boggy districts of Kauai as well as of Molokai and Maui.

Fossil: I have no record of this species, but it may have been overlooked. Still, as pointed out also by MacCaughey (1918 b, p. 43), the species does not form large thickets but occurs in isolated clumps here and there in the rain-forests.

## Fam. HYMENOPHYLLACEAE.

The whole family is characterized by trilete, $\pm$ light-coloured, spiny or papillose spores, rounded or slightly triangular in polar view. Only three divergencies in type are known to me. Hooker (1846, p. 86) found the spores »oval», not »3-angular or 3-lobed» in *Trichomanes elegans* Rudge = *T. diversifrons* (Bory) Mett., Mettenius (1864, p. 489), again, of the usual type, and he was

unable to verify the former statement. Recently, Miss Knox (1938, p. 489 and fig. 52) stated that *Hymenophyllum tunbridgense* has bilateral spores, but generally they are trilete (Hooker and Bauer 1838, Moore 1859—1860, Milde 1865, Luerssen 1889, Hegi 1906, and others). Provided that the determination is correct, we are thus here faced with another example of such deviations in type as I have tabulated elsewhere (1944, p. 7—8). To these the case noted below under *H. lanceolatum* may be added (still more additions are noted under their respective genera).

So far, it has not been possible to show any spore characters distinguishing, generally speaking, the species of one of the said genera from those of the others.

**Hymenophyllum** J. Sm.

Miss Knox, who examined 58 species of the genus, found that the spores vary from 25 to 90 $\mu$ in diameter. With the exception of the case referred to above, which seems to be from an aberrant individual, all of them had relatively delicately sculptured, thin and transparent membranes. The spores of the Hawaiian species fall within the limits of this description. It may be added that distinct lists bordering the tetrad scar are common to them all. There are three species:

**H. lanceolatum** Hook. et Arn. — Pl. 3, Figs. 54, 55.

Tetrahedral, trilete, $46 \times 57$ $(43—51 \times 52—60)$ $\mu$, rarely monolete (one specimen, $52 \times 69$ $\mu$ in polar view). Subtriangular to rounded, distal wall evenly arched. Scar $\pm$ reaching the periphery. Exospore thin, covered on both distal and proximal sides with small, crowded, rounded projections. — Specimen studied: Kauai: Kohua ridge, Kawaia trail, 19/8 1938; HBS 3001 (SP).

Recent: A rare species, reported from the rain forest of all the islands. Fowler (1940, p. 11) found it common in the Kilauea-Mauna Loa section of Hawaii National Park, however.

Fossil: See below, as to the family.

**H. obtusum** Hook. et Arn. — Pl. 3, Fig. 56.

As the preceding, $E = 63$ $(58—68)$ $\mu$. Projections possibly somewhat shorter than in *lanceolatum*. — Specimen studied: Oahu: Palolo, Kaau crater, 23/10 1922; C. Skottsberg 921 (SP).

Recent: Apparently a rather rare species, reported from rain forests of at least Oahu, Molokai, W. Maui, and Hawaii. Fowler (l. c. p.) calls it occasional.

Fossil: See below, as to the family.

**H. recurvum** Hook et Arn. — Pl. 3, Fig. 57.

In shape like the preceding, but larger: $E = 72$ $(67—76)$ $\mu$, and spines replaced by a minute, granulated sculpture. Lists bordering the tetrad scar

prominent, not always reaching right to the periphery. — Specimen studied: W. Maui: rain forest patch on summit of Puu Kukui, 24/7 1938; O. H. Selling (spore sample only; specimens from the same place = HBS 2681).

Recent: A common species, reported from all the islands.

Fossil: Occasional spores on Maui and Kauai, permitting no conclusions of interest.

### Trichomanes L.

According to Miss Knox (1938) the spores of this genus are on the whole smaller than in *Hymenophyllum*, generally 20—35 $\mu$, though in *T. lucens* they were found to reach 65 $\mu$ in diameter. The same general feature holds of some Hawaiian species, while *T. Baldwinii* — earlier brought to *Hymenophyllum* — falls outside this range, being 76 (67—87) $\mu$ across. In the paper just referred to, the common type of ornamentation is stated to be spinose, and this is also the case in the five Hawaiian species. Hillebrand (1888 b, p. 634—635) mentions them only as »tetraedro-globose».

**T. Baldwinii** (Eaton) Copel. — Pl. 3, Fig. 58.

Tetrahedral, trilete, 48×76 (44—53×67—87) $\mu$ (as to composition of values, see below). Rounded or indistinctly subtriangular in polar view. Distal wall rounded in equatorial view. Exospore thin, covered all over with crowded, minute spines. Scar, seen in polar view, generally reaching the periphery. — Specimens studied: W. Maui: N slope of Puu Kukui, in very wet forest at Nakalalua, c. 1390 m, 28/7 1938; HBS 2676 [SP; P (1 spore) = 53 $\mu$; E (10) = 77 (73—84) $\mu$], and same locality and date, O. H. Selling [spore sample only; P (1 spore) = 44 $\mu$; E (10) = 75 (67—87) $\mu$].

Recent: A terrestrial species in wet woods of all the large islands. Hillebrand (1888 b, p. 637) says »not common», Robinson (1912 a), Copeland (1933, p. 231) and Degener (Fl. Haw., Fam. 10, 9/13/'35) are silent on that point. Local abundance has been noted, however, for instance in Kauai: Kaholuamano, by Heller (1897, p. 791).

Fossil: See below, as to the family.

**T. cyrtotheca** Hillebr. — Pl. 3, Figs. 59—61.

Tetrahedral, trilete, 40×46 (36—45×38—54) $\mu$. Distal wall strongly arched. Tetrad scar reaching the equator or nearly so. Sculpture in the shape of small and rounded projections densely covering the exospore also on the proximal side. It has not been possible to distinguish the spores of this species from those of the following, to which it is closely related (cf. also Christensen 1925, p. 7). — Specimen studied: Oahu; W. H[ille]b[ran]d (SP).

Recent: Endemic, recorded by MacCaughey (1918 a, p. 204) from Oahu and Maui, »above 1800 ft, in the rain-forests», known also from Hawaii (Skottsberg 1926, p. 188; Copeland 1933, p. 216). The lowest locality listed by the former author is at about 400 m alt.

Fossil: See below, as to the family.

**T. davallioides** Gaud. — Pl. 3, Figs. 62—64.

Shape, sculpture and tetrad scar as in the preceding, and also agreeing in size: 40×46 (36—44×39—52) μ. — Specimens studied: Hawaii: Glenwood, May, 1909; U. Faurie (SP): 40×47 (36—44×41—52) μ; and one without locality, leg. W. Hillebrand (SP): 39×44 (36—44×39—51) μ.

Recent: A very common species, reported from all the islands, also from W. and E. Maui (which is not mentioned in Copeland (1933, p. 214). Hillebrand (l. c. p. 636) says: »in damp forests of above 2000 ft. elevation festooning nearly every tree»; on Kauai and Oahu Heller (1897, p. 791) found it »climbing over tree trunks and rocks in the lower and middle woods».

Fossil: See below, as to the family.

**T. draytonianum** Brack. — Pl. 3, Fig. 65.

Perfectly round in polar view, 50 (44—54) μ across. Sculpture as in the preceding. Tetrad scar reaching but half-way to the periphery, at least in the specimen studied by me. — Specimen studied: Hawaii: Glenwood, May, 1909; U. Faurie 109 (SP).

Recent: Reported from all the large islands, generally rare, growing on rocks in moist woods. Heller (l. c. p. 790) has recorded local abundance also of this species (near Hanapepe falls, Kauai).

Fossil: Not seen.

**T. saxifragoides** Presl — Pl. 3, Figs. 66, 67.

In type and shape like *T. Baldwinii*, but smaller, 53×64 (50—57×59—68) μ. Sculpture with very low spines, transitional to granules. Tetrad scar reaching a little short of or almost to the periphery. — Specimen studied: Oahu: »covering side of large block near stream in Aiea gulch above Aiea», 9/4 1932; T. G. Yuncker 3026 (SP).

Recent: A rather rare species, reported at least from Oahu, Maui and Hawaii, creeping on trees and rocks. In some ravines of the Hilo district, Hawaii, Hillebrand (1888 b, p. 635) noted it covering entire rock-walls.

Fossil: See below.

Fossil spores of the Hymenophyllaceae. The easily distinguished types of Hawaiian spores are dealt with above. The others have been lumped as one unit in the records, even though it might have been possible to arrive at a somewhat closer classification, if a monographic study of the recent material had been possible before the peat samples were examined. Such hymenophyllaceous spores have been found in about 40 % of the examined slides and in all three islands. On Kauai they occur in almost half the number of samples, on Molokai in only 20 % of them. They are not absent from any series, though never found throughout them. In the series 35, 37, 71 and 78, 80, and 90 they were noted in half or most of the samples, in the others only occasionally.

The values are generally low, traces to 2 %, only exceptionally 5 %. 1 % is the commonest and at the same time the average. The highest values have been found in 362 (87) and 367 (87), both 5 %, in 5 (1), 206 (35) and 384 (87): 4 %, and 7 (1), 368 (81), 499 (90), and 505 (90): 3 %.

## Fam. DICKSONIACEAE.

The family is characterized by trilete spores and there are no exceptions in the single genus occurring in Hawaii (cf. p. 40).

### **Cibotium** Kaulf.

As far as I know, no spore pictures referring to Hawaiian species have been published and only very brief descriptions seem to be found in literature, as is also the case with non-Hawaiian species. Kaulfuss, in describing the genus (1824) does not say anything about them, nor does Hooker (1846). Hooker and Bauer (1838) described and figured those of *C. Schiedei* from Mexico, distinctly showing their trilete type, which was clearly noted also by, *e. g.*, Meisner (1836—1843, p. 434). Fée (1850—1852, p. 343) also characterized the genus with, among other words, »sporis trigonis, nudis, vitreis, episporio vestitis, fuscis». It was shown in Fischer von Waldheim's studies (1865 a and b) that the sculpture thus observed [cf. also Hasskarl's (1856) fairly detailed notes on the spores of *C. assamicum* and *C. djambianum*, both = *C. Barometz*, acc. to Christensen 1906, p. 183] was not made up of a perispore, a fact restated by Hannig (1911 a, p. 321 ff.)

Returning to the Hawaiian species, we only find the description »Spores tetraedrous» in Hillebrand 1888 b, p. 545. Miss Knox (1938, p. 450), when dealing with the genus, does not indicate the type of sculpture found in them. In the diagnoses of *C. hawaiiense* (Nakai and Ogura 1930, p. 468) and *C. St. Johnii* (Krajina 1938) they are mentioned as »tetraedrales fuscescentes». Miss Stokey (1930, p. 32 ff.), who studied the prothallia of three Hawaiian species, does not say anything about their spore morphology. Skottsberg (1942, p. 40 ff.) confined himself to notes on their sizes in some of the species. Whether Miss Knox' statement (l. c. p.) that the spores of the genus range from 50 to 75 $\mu$ was based on a study of the Hawaiian species also cannot be ascertained from her paper. The smallest that I have seen are 37 $\mu$, the largest 80 $\mu$.

There is considerable variation in both size and sculpture in the different species. With regard to size (cf. below), I find no possibility of distinguishing the commonest species on single spores, though it appears likely that the largest spores are produced by *C. Chamissoi*. The case of *C. St. Johnii*

(cf. p. 43 and Pl. 4) is somewhat doubtful; here we have to do with immature specimens. As regards morphology, individual spores of different species look rather different, and it does not appear impossible correctly to determine part of the spores of certain species. Still, my material is too limited to permit any positive statements on this point, and I have had to leave the question of distinguishing characters with the remark that the subject should be taken up again on a broader basis.

The spores of *Cibotium* are easily distinguished from other Hawaiian types. Small specimens should not be confused with certain spores of *Pteris*, however (cf. p. 8, 48 ff.). The following general description can be applied to the majority of species at least.

Tetrahedral, trilete, about 42×60 μ, very rarely almost monolete, bilateral, 39×85 μ (1 spore). Normal spores triangular, proximal wall flat, distal wall arched. Exine dark brown, about 8 μ thick including sculpture of the distal wall (sculpture absent or very slight on the proximal facets). The latter is made up of generally fairly thick, irregular ridges, sometimes fused so as to form a very irregular reticulum. Round the equator is a ring of about the same thickness, entire or interrupted at the angles in different ways, generally smooth but sometimes with rough contours, occasionally (cf. Pl. 4, Fig. 70) with depressions half-way between the angles of the spore, recalling conditions in spores of *Hemitelia* (Cyatheaceae), *e. g.*, *K. Karsteniana* (Knox 1938, fig. 79 on p. 453). The tetrad scar reaches the angles and is bordered by well-developed ridges with tapering ends, going almost to the angles. Their maximum width is about 6 μ and along their margins a minute perforation may be seen.

To the following survey of size values in each species (P×E in μ, 25 spores of each individual, unless otherwise stated) are added some notes on recent occurrences. They chiefly show the need of extensive, critical field studies along this line.

**C. Chamissoi** Kaulf. — Pl. 4, Fig. 68—72.

Syn. *C. Menziesii* Hook., non *C. Chamissoi* s. Hillebrand et auctt.

| | | |
|---|---|---|
| Kauai: Alakai, swampy forest near Kilohana, 15/8 1938; HBS 2958 | (SP) | 39×61<br>(36—41×53—65) |
| Oahu: »Konahu[a]nui Mountain east of Honolulu», 28/10 1907; P. Bartsch | (SP) | 46×69<br>(44—48×62—80) |
| Oahu: »Honolulu», 1852; N. J. Andersson | (SP) | 45×70<br>(43—48×60—76) |
| Oahu: Mt Kaala, 25/9 1938; HBS 3583 | (SP) | 46×64<br>(43—48×57—76) |
| E. Maui: Makawao, H. Beraz | (SP) | 48×70<br>(44—52×63—76) |
| Hawaii: Halawa, 800 m, June, 1909; U. Faurie s.n. | (SP) | 36×54<br>(32—38×50—58) |

| | | |
|---|---|---|
| Hawaii: Hiulani forest SW of Olaa, c. 500 m, 8/9 1922; C. Skottsberg 427 (60 spores from 2 pinnae) | (SP) | 40×57<br>(37—44×50—63) |
| Total (175 spores) | | 42×64<br>(32—48×50—80) |

Skottsberg (1942, p. 40) measured 10 spores (in water) and found the values 57.5 (54—60) $\mu$.

This species attains the greatest height among Hawaiian tree ferns: in the Island of Hawaii there are specimens up to 11 m high; of this figure the trunk, 1 m in diam., contributed 8 m [Hillebrand 1888 b, p. 546 (cf. also 1888 a, p. 312); Rock 1913, p. 91]. The species occurs in all the big islands. The data on altitudinal range vary: »2000—4000 ft.» (= 600—1200 m; Hillebrand l. c. p), »from 2000 to 6000 feet and perhaps higher» (= 600 — at least 1800 m; Rock l. c. p), »1000—5000 ft» (= 300—1500 m; MacCaughey 1918 a, p. 205); Skottsberg (1926, p. 188) published localities from 300—400 m to 1500—1600 m above sea level (cf. Skottsberg 1936, p. 98). It thus appears that the vertical range comprises a belt between about 300 and 1800 m alt. (rarely higher) As to the frequencies in different levels within this belt there are no data permitting positive conclusions. As to his *C. Menziesii* in Oahu, Luerssen (1875 b, p. 420 = p. 4 of the reprint) writes: »Nach den brieflichen Mittheilungen Wawra's kommt dieser prächtige Baumfarn an den freien, grasigen Lehnen in einer Höhe von 500—1000' vor, in lockeren, langgedehnten Beständen den Waldsaum (dessen Grenze bei 1000') einfassend. Sein Stamm wird hier bis 4 Fuss hoch, sein Blatt klafterlang.» Brackenridge states that what he calls *C. Chamissoi* (which may, however, be partly *C. splendens*) »principally inhabits the outskirts of forests» (1854, p. 280). MacCaughey (l. c. p.), on the other hand, calls his *C. Menziesii* more hygrophytic than *C. Chamissoi* (= *C. splendens*, at least partly), and Hosaka (1937, p. 217) reports it as common in his Ohia and Cloud Zones of Kipapa gulch, Oahu (cf. also the localities in Skottsberg 1926). — Hillebrand, on a label, stated *C. Chamissoi s. str.* to be the »Most common sp. of Cibot.» (cf. Skottsberg 1942, p. 40), whereas MacCaughey (1918 a, p. 205) does not find it as common as *C. splendens*. Degener (1930) and E. H. Bryan (1933, 1935) do not enter upon the question, nor does Rock (l. c.).

The Fern Weevil (*Syagirus fulvitarsis* Pascoe) now attacking the species is a recent arrival in the islands (Fullaway 1921).

On a label Hillebrand ascribed to this species the name of »Akoléa». It was published by Skottsberg 1942, p. 40: »Evidently a native name but not cited by Hillebrand and not found in either Degener's Hawaii National Park or Bryan's Hawaiian Nature Notes for either this or any other plant.» Hillebrand probably did not cite it, since it is the name of *Dryopteris honoluluensis* (*Phegopteris Hillebrandii*) in Hillebrand 1888 b, p. 567.

## **C. glaucum** (J. E. Sm.) Hook. et Arn. — Pl. 4, Figs. 73—76.

| | | |
|---|---|---|
| Molokai: Pukoo, May, 1910; U. Faurie 12 (aberrant form) | (SP) | —×53<br>(— —×50—57) |
| Molokai: Pukoo, 800 m, May, 1910; U. Faurie 16 (far from typical; 15 spores) | (SP) | [40]×60<br>(— —×52—70) |
| Molokai: head of Waikolu valley, between Upper Maunahui camp and Pepeopae, in wet forest, 11/7 1938; HBS 2563 | (SP) | 46×59<br>(40—54×53—67) |
| W. Maui: at Nakalalua, very wet forest, 28/7 1938; HBS 2714 | (SP) | —×64<br>(— —×58—68) |
| E. Maui: Haleakala; H. Beraz | (SP) | 41×64<br>(36—45×50—72) |
| Hawaii: Upper Hamakua ditch trail above Koiawe valley, plentiful in swampy country, 7/9 1938; HBS 3141 | (SP) | 40×56<br>(35—48×41—61) |
| Hawaii: Halawa, 800 m, June, 1909; U. Faurie 13 | (SP) | 43×58<br>(— —×53—64) |
| Total (165 spores) | | 42×59<br>(35—54×48—72) |

Skottsberg (1942, p. 41) examined 10 spores in water: »48—60 $\mu$, average of 10, 54.5 $\mu$.»

Reported by Hillebrand (l. c. p. 548) to occur »on most islands», and according to MacCaughey (1918 a, p. 205) it occurs on all the big islands. Skottsberg (1942, p. 41),

however, did not know of any specimens from Kauai and Oahu. During the U. S. E. E. it was met with only on the island of Hawaii, »in deep shady forests» (Brackenridge 1854, p. 279). Fowler (1940, p. 11) records it from »dry, open places» in Kipuka Puaulu (Bird Park), isl. of Hawaii. In other papers cited here, there are no notes on the subject. Nor has the altitudinal range been made the subject of particular study. MacCaughey (l. c. p.) says: »1000—3000 ft» (= 300—1000 m), but here, as is the case with other data in his paper, one does not know to what extent the statement is based on critical observation. Skottsberg collected the species in localities from 500 m (1926, p. 188) to 1300 m alt. (1936, p. 98), and from the excursions of the HBS there are several localities above 1000 m alt. (Skottsberg 1942, p. 41).

There is also great uncertainty with regard to frequency. Hillebrand (l. c. p.) and Rock (1913, p. 95) use the expression »rather rare», MacCaughey (l. c. p.) calls it »rare», E. H. Bryan (1935, p. 123) »quite rare». Besides, Brackenridge (l. c. p.) reports it as the rarest of the Hawaiian species of the genus. Locally it may however be abundant (cf. Skottsberg 1926, 1936, 1942).

**C. hawaiiense** Nakai et Ogura — Pl. 4, Figs. 77—79.

Hawaii: Hiulani forest SW of Olaa, c. 500 m, 8/9 1922; C. Skottsberg 428 (SP) — 41 × 59 (39—42 × 54—70)

Skottsberg (1942, p. 42) says: »spores 54—60 $\mu$, average of 10, 56 $\mu$, thus . . . . . as in *C. glaucum*.» As far as my experience goes, the exospore sculpture of this number appears to be more suggestive of *C. splendens*, however (cf. the figures).

The relations of this species and *C. glaucum*, which it resembles in many ways, need further study. It is only known to occur in the Hilo district of Hawaii (Ripperton 1924, Pl. I; Nakai and Ogura 1930, p. 468—469; Skottsberg 1936, p. 198; 1942, p. 42). In the bogs that I have studied, its spores cannot therefore be expected to occur among the microfossils. At any rate, I have never observed the type.

**C. splendens** (Gaud.) Krajina (in Skottsberg 1942, p. 40) — Pl. 4, Figs. 80—87.

(*C. Chamissoi* ap. Hillebrand 1888 b, p. 547, salt. p. p., non Kaulfuss 1824).

Oahu: Honolulu, 1852; N. J. Andersson (SP) — 44 × 63 (40—47 × 54—70)

Oahu: Mt Tantalus, c. 600 m, 7/8 1922; C. Skottsberg 70 (SP) — 42 × 59 (37—49 × 50—67)

Hawaii: Hilo, 500 m, May, 1909; U. Faurie 15 (SP) — 44 × 60 (— —× 56—64)

Total (75 spores) — 43 × 61 (37—49 × 54—70)

Skottsberg (1942, p. 41) found the spores slightly larger than in *C. Chamissoi*, 54—63 $\mu$; average of 10, 59.5 $\mu$» (in water).

This species like the preceding ones has its main distribution in the rain forest, but as pointed out by Rock (1913, p. 93) it occurs also as a straggler in xerophytic forests, though this is by no means common. It is stated to occur on all the big islands (Hillebrand 1888 b, p. 547; MacCaughey 1918 a, p. 205); the latter author gives the altitudinal limits as »1000—6000 ft» (= 300—1800 m). Hartt and Neal (1940, p. 263) found no earlier data for localities higher than 4300 ft (= 1300 m), and record that they collected the species on Mauna Kea, Hawaii, at an altitude of 6700 ft (= 2000 m). Skottsberg lists localities from 300—400 m (1926, p. 188; 1936, p. 98) up to 1600 m alt. (1926, p. 188). The vertical distribution thus seems to comprise the levels 300 to 2000 m above sea level, the highest limit probably as a rule situated somewhat lower. Hochreutiner (1912, p. 182) writes about »*C. Chamissoi*» on Kauai: »Commun au-dessus de 1400 m». Hosaka (1937, p. 217) notes it as abundant in his Koa, Ohia and Cloud zones of Kipapa gulch, Oahu; he also describes it (p. 205) as a second layer species in the four-layered Ohia zone. Gaudichaud (1829, p. 370) evidently did not state the entire truth when he said that it »croit au sem des forêts, dans les montagnes de l'ile Wahou»; cf. Wawra's notes above, under *C. Chamissoi*.

The data as to its absolute and relative frequency (in relation to other species of

*Cibotium* as well as trees of other genera) are also rare or vague. Some are quoted above. Rock (1913, p. 93) calls the species »one of the most common tree ferns of the group», but he possibly includes *C. glaucum* to some extent (he does not mention this species from near Kilauea, where it is common). MacCaughey (l. c. p.) says only »common in humid regions» (cf. also under *C. Chamissoi*). Baker (1886) is entirely silent as regards ecology.

The variety described by Hillebrand (l. c. p.) from Kauai is identical with the following species.

**C. St. Johnii** Krajina — Pl. 4, Fig. 88.

Kauai: Kaunupalanui, *Metrosideros*-forest 1500 m, 19/4 1905; B. P. G. Hochreutiner 3547 (SP) (var. *fallax* subvar. *integrilobatum*) [—×44 (— —×37—49) (immature specimens)]

A low species (trunk only up to 4 m high) peculiar to Kauai, where it has been collected in a number of localities in the rain-forests of the interior. Krajina (1938) describes the main species, one variety and three subvarieties from the same general region; the localities are situated between an altitude of 1050 and 1500 m. Nothing is definitely known as to its frequency. Hochreutiner (in Christ 1912, p. 182, under *C. Menziesii*; cf. also label in SP) calls it »commune au-dessus de 1400 m., alt. 1500 m.», thus the same data as he had given for his *C. Chamissoi* (see above, under *C. splendens*). It was not collected during the HBS.

Summary of recent occurrences: Of the five species of *Cibotium*, four are known from those islands, where the bogs that I have studied are located. *C. St. Johnii* is known only from Kauai, from whence, on the other hand, *C. glaucum* does not appear to have been reported. *C. Chamissoi* and *C. splendens* appear to be common on Kauai and Molokai as well as Maui. All the species are mainly found in the rain forest though they are not strictly confined to it. Ripperton (1924, p. 3) states that they occur in all parts of the group where the annual rainfall is 100 inches or more. They occur from 300 up to 1800 m, sometimes also at a height of 2000 m. Bailey (1882, p. 14) gave the general range as 1—3000 ft, Hillebrand (1888 a, p. 312) says: »Ihre höchste Entwicklung erhalten sie erst von 3500 Fuss aufwärts», and MacCaughey (1918 a, p. 205) states them to range »from 1000—6000 ft, sometimes lower». Ripperton (1924, p. 3) also points out that only on the island of Hawaii we find them in almost unbroken stretches from sea-level to an elevation of 6000 ft or more. The highest limit value »ten thousand feet or more», in Degener 1930, p. 27, appears to be exaggerated.

There are no definite data at hand permitting general conclusions as regards the relative and absolute frequency of the species on the different islands as well as different levels. Ripperton (l. c. p.) states that, taken as a unit, the species occur in dense forests only on the islands of Kauai and Hawaii. In the latter island the »windward slopes of Mauna Kea and Mauna Loa are one continuous tree-fern forest, the belt extending from the Puna district to the Hamakua district being about 10 miles wide and 40 miles long. It is estimated generally that there are 400,000 acres of tree-fern forests on the island of Hawaii alone». (l. c.). To this should be added that, as is well known, there are extensive areas of fern forest also in Kohala (see ill. in, *e. g.*, Rock 1913 and Campbell 1926, Pl. XXVII, as well as in part III of the present paper). The question arises as to what causes this extraordinarily rich development of the fern forests on this very island. It will be entered upon in connexion with a consideration of the fossil finds in part III of this paper.

Fossil: Spores of *Cibotium* are one of the main constituents of the pollen diagrams, where their curve is a rain-forest indicator. They occur in all samples so far studied, though in 155 (10) and 500 (90) they happened to be absent in the analysed part. The values vary between traces and 46 %, generally between traces and 8 % (80 % of all samples), in only 1/20 of the samples they exceed 15 %. The average (all islands) is slightly below 6 %.

Considering the different islands, we find Maui and Molokai similar to each other. For both the values generally vary between 1 and 5 %; for Molokai they reach 10 %, for Maui 18 %. The average for both islands is about 4 %. For Kauai, again, it is somewhat over 8 %. Here a long series of high values is found, the highest being 46 % in 353 (81) and 418 (84), 34 % in 340 (81), 33 % in 422 (84), 32 % in 409 (84) and 420 (84), finally 31 % in 369 (81). In series 81 it appears as if these values occurred at random, but they do not. This interesting feature is to be dealt with in connexion with the general discussion in part III, where due attention will be paid to the question of the fern forests in relation to secular changes of climate.

## Fam. POLYPODIACEAE

### I. Subfam. *Dennstaedtioideae.*

### Dennstaedtieae.

### **Microlepia** Presl.

Fée (1850—1852, p. 326), Mettenius (1856, p. 103—104), Prantl (1892, p. 16) and Miss Knox (1938, p. 452) have already pointed out that both monolete and trilete spores occur in the genus, while Keyserling (1873, p. 1) mentioned only the latter type. Hillebrand (1888 b, p. 626) reported one species to have alete spores, but the spores of both the Hawaiian species belong to the trilete type.

**M. setosa** (Sm.) Alston — Pl. 5, Figs. 89—91.

Tetrahedral, trilete, 36×44 (31—39×40—48) $\mu$. Triangular in polar view, with markedly rounded angles and often somewhat retraced sides. Distal wall heavily arched. Exine about 2 $\mu$ thick, brown, smooth, and of indistinct texture. Tetrad scar bordered by prominent ridges of characteristic appearance, generally $\pm$ disappearing about half-way between the proximal pole and the equator of the spore. These spores are distinct from other Hawaiian types. (The spores of the Hawaiian plant, at that time called *M. hirsuta*, were described by Hillebrand (l. c.) thus: »Spores smooth, tetraedrous, with convex back and grooved faces». The spores of *M. hirsuta*, however, were found by Knox (1938, p. 452) to be bilateral and monolete.) — Specimen studied: Oahu: Koolau, Kawaiiki, 15/8 1922; C. Skottsberg 200 (SP).

Recent: A common species in all the islands, preferring grassy slopes and outskirts of the lower forests; MacCaughey (1918 a, p. 209) says »800—18000» [1800] ft, but Skottsberg (1926, p. 191) lists the species from 1300 m altitude on Haleakala, and also records it from the forests near Kokee station, Kauai, not far from Alakai. Bailey (1882, p. 20) says »200—6000 feet».

Fossil: See below.

**M. speluncae** (L.) Moore — Pl. 5, Figs. 92, 93.

Tetrahedral, trilete, 26×31 (24—29×29—33) $\mu$ (aver. of 20 from the two coll. cited below). Irregularly rounded to subtriangular in polar view. In equatorial view almost ellipsoidal with proximal side but slightly pyramidal. Exine brown, about 2 $\mu$ thick, smooth, and also devoid of texture when observed with ordinary magnification. Tetrad scar reaching the equator and bordered by ridges of little peculiar appearance, all along the length of the branches. The exospore is covered by a spiny perispore. Hillebrand therefore called the spores »globose, without any lines, pale, minutely papillate (l. c. p. 626). To speak only of cases devoid of perispore, it appears possible to recognize this species on typical spores. — Specimens studied: 1. Oahu: Honolulu, 1852; N. J. Andersson (SP; = type of *Leptolepia Anderssonii* Mett. msc. in Kuhn 1882, p. 348; labelled *Microlepia Anderssonii* by Mettenius; cf. Christensen 1925, p. 12): 26×31 (24—28×29—33) $\mu$. 2. Kauai: ridge W of Hanapepe river, at 3000 ft, 1895; A. A. Heller 2650 (H): 26×31 (24—29×29—33) $\mu$.

Recent: Similar to the preceding, but less frequent. Hillebrand knew it only from Oahu and Hawaii, Heller (1897, p. 777) added Kauai, and Robinson (1912 b, p. 586) Maui. MacCaughey (1918 a, p. 209) says »apparently in all the islands».

Fossil: Some of the smooth trilete spores so far recorded do belong to this genus, but they are only occasional and say nothing.

Hypolepideae.

**Hypolepis** Bernh.

Fée's notes on the spores of this genus — »ovoideis, subreniformibus, fuscis» — give little information (1850—1852, p. 146). As interpreted by Mettenius (1859), all the species of this genus have bilateral spores, thus differing from those of the closely related *Cheilanthes*, and the same view was held by Keyserling (1873, p. VII, 1 and 2), Prantl (1892, p. 16, 17 and 20), Diels (1902 b, p. 277) and Brown and Brown (1931, p. 74). In some of the species examined by Miss Knox (1938, p. 452, Figs. 69—71: p. 453), however, the trilete type was found. Still, their generic status may be worth further study. The single Hawaiian species behaves like at least the majority of the genus. According to Hannig (1911 a, p. 340) some species have a perispore. The projections described below, though rather resistant, seem to belong to a perisporial covering.

**H. punctata** (Thunb.) Mett. — Pl. 5, Figs. 94, 95.

Hillebrand (1888 b, p. 562) described the spores briefly as »pale, ovoid-reniform» and this is the only description of spores from the Hawaiian plant

known to me. An examination shows that the spores come very close to those of the Marquesan *H. tenuifolia*, which are well described in Brown and Brown l. c. p. 76.

Bilateral, monolete, 41×53 (38—43×51—56) μ; spines excluded: 30×43 (27—32×41—46) μ (cf. p. 71). Exospore fairly thick-walled, smooth, perispore with about 6 μ long, densely packed spines. During acetolysis these spines are rather resistant, but sometimes they become corroded, giving the spores a peculiar appearance also observed in certain grains of the fossil material. — Specimen studied: W. Maui: summit bog of Puu Kukui, 23/8 1938; O. H. Selling (spore sample only).

Recent: Reported from the summit bogs and boggy forests of Kauai, Oahu, Molokai, Maui, and Hawaii. Hartt and Neal (1940, p. 263) state the altitudinal range to be 3,000—6,000 ft.

Fossil: Whether occasional grains found in all three islands with corroded spines very like those ocurring in the present species really belong to it, I do not know. Similar structures may appear from ± resistant perisporial spines such as in *Cystopteris* and *Loxoscaphe*, and they are besides found also in *Dryopteris*, in which genus there also remain a couple of species not seen by me. The exine thickness speaks in favour of the determination, however.

II. Subfam. *Lindsayoideae.*

**Stenoloma** Fée.

**S. chusanum** (L.) Ching — Bilateral, monolete spores. See p. 72.

**Lindsaya** Dry.

The spores of the single Hawaiian species were stated by Hillebrand (1888 b, p. 625) to be »triquetro-globose, smooth», and in the variety *marquesense* E. Brown they are described as »22—36+ μ long with an average length of 27 ± μ, radially symmetrical, with three wings radiating from one pole, ...; the surface minutely punctate». (Brown and Brown 1931, p. 52, cf. pl. IX: g—i).

**L. repens** (Bory) Bedd. var. **macraeana** (Hook. et Arn.) C. Chr. — Pl. 5, Figs. 97, 98.

Tetrahedral, trilete, 23 (22)×28 (20—28×24—33) μ (P = 23 μ refers to measures including raised portions along the tetrad scar). Angles rounded in both polar and equatorial views. Branches of the tetrad scar reaching the equator and very prominent, followed by raised portions of the exospore all along their length. Exospore smooth, indistinctly granular-textured, about 1.5 μ thick, often somewhat dark-coloured. The spores are easily

distinguished from other Hawaiian types, by a combination of characters, chiefly the appearance of the tetrad scar and size conditions (see the key p. 7 as well as text and figures referring to the species mentioned there, under II:B:a:1). — Specimen studied: Oahu: Koolau, Pupukea-Malaekahana trail, 470 m, 15/9 1926; C. Skottsberg n. 1802 (SP).

Recent: A common species in the rain forests of all the islands.

Fossil: Occasional — rare in the analyses of all the islands, found in about 10 % of the studied samples. Not found in the series 10, 35, 71, 78, 80 and 90. Frequencies varying between traces and 1 %.

### **Diellia** Brack.

Several species, all with bilateral, monolete spores. See p. 67.

## III. Subfam. *Davallioideae.*

### **Nephrolepis** Schott.

**N. exaltata** (L.) Schott — Pl. 5, Figs. 100—102.

In the figure given by Hooker and Bauer (1838—1842, tab. XXXV, fig. 10) a sculpture is indicated on the bilateral spores of this species, but the text says nothing. Schott (1834) had earlier given some contour drawings showing bilateral type (mentioned also in the accompanying text) but no sculpture. The same statement as to type is also given by Fée (1850—1852), Mettenius (1856), Keyserling (1873), Luerssen (1879), Prantl (1892), Weaver (1896), and Diels (1902 b). Brown and Brown (1931, p. 43), in describing Marquesan material, state: »spores 34 $\pm$ $\mu$ in length, the surface conspicuously tuberculate». As Hannig has already found (1911 a, p. 342), a perispore is unlikely to occur.

Bilateral, monolete, 30×51 (28—34×47—55) $\mu$, without sculpture (immature): 26×44 (24—28×41—50) $\mu$; the spores often somewhat curved. Exospore deposit about 3 $\mu$ thick. Sculpture in the shape of very irregular warts and short, irregular ridges; contours of the spores, however, as a rule not rough as in *Polypodium atropunctatum*, but more like those in *P. pellucidum*. The spores of the present species may at first glance seem to bear a close similarity to those of the latter, but the raised portions are different. Specimen studied: Oahu: Koolau, Keeawaawa, 4/8 1922; C. Skottsberg 30 (SP).

Recent: A very common species in rain forests of all types. Heller (1897, p. 782), who kept *N. acuta* distinct from this species, emphasizes that »On Kauai, where the highest point is somewhat under 5000 feet [5170!], *N. exaltata* is plentiful at elevations of from 3000—4000 feet.»

Fossil: Not rare but as a rule only occasional. Of no particular interest.

IV. Subfam. *Pteridoideae.*

**Pteridium** Gled.

**P. aquilinum** (L.) Kuhn var. **decompositum** (Gaud.) Tryon — Pl. 5, Figs. 103, 104.

Spores described in more or less detail by a great number of authors, among which may be particularly mentioned Luerssen (1889), Lagerberg (1906; ill.), Karpowicz (1927; ill.), Waldmann (1928) and Bertsch (1942; ill.). Pictures are found also in Weaver (1896), Hegi (1906) and Erdtman (1943). In different papers their size (equatorial diameters) is given as $36.3 \times 33\ \mu$ (Weaver 1896), 29.5 (25—25.5) $\mu$ (Lagerberg 1906), 30—40 $\mu$ (Karpowicz 1927), and 28—30 $\mu$ (Waldmann 1928). As regards the endemic Hawaiian variety I know of no other description than a note in Hillebrand 1888 b, p. 631: »Spores tetraedro-globose».

Tetrahedral, trilete, $25 \times 31$ (23—$28 \times 28$—35) $\mu$. Triangular with rounded angles to subtriangular in polar view, sides straight or often slightly and evenly concave (together with adjoining parts of the proximal wall). Distal wall fairly evenly convex, only about 1 $\mu$ thick, smooth but of granular texture. The dark-coloured, finely granular sculpture generally seen in fresh material can be stripped off as a unit and thus does not appear to belong to the exospore. Branches of the tetrad scar very often not reaching the equator (cf. Luerssen, l. c., who found the same feature in the main species), bordered by ridges less distinct towards the periphery of the spore when viewed from the poles. Often the ridges $\pm$ disappear about half-way between the proximal pole and the equator. As to the features making it possible to distinguish these spores from those of *Gleichenia glauca*, *Lindsaya*, and *Microlepia setosa*, which are of the same general size (equatorial diameters), see the key p. 7 as well as text and figures referring to the said species. — Specimen studied: D. D. Baldwin: Hawaiian Ferns (SP).

Recent: Common in all the islands. In his revision Tryon (1941, p. 41) states that »it grows along field borders, in virgin land, on craters, on bare eroded slopes, on open grassy slopes and in thickets from 300 m. up to 2700 m.» This altitudinal range comes close to that given by Hillebrand (l. c. p.): »800 ft. to 8000 ft.» According to Bailey (1882, p. 27) the lower limit can be placed at about 500 ft. Hartt and Neal (1940, p. 263) also state the range to be 500—9,600 ft, and Fowler's data from Hawaii (1940, p. 15) fall within these limits. Heller noted it as »common on grassy slopes below the forest on Kauai» (1897, p. 786); Skottsberg (1926, p. 196) records it also from dry forests near Kokee.

Fossil: Not seen.

**Pteris** L.

Authors of the early days, Fée, Mettenius, and others, who had a wider genus concept, found both monolete and trilete spores in *Pteris:* so far as

hitherto known, however, all the species now recognized as belonging here have trilete spores, and this holds also for the Hawaiian. Three indigenous species are clearly valid. *P. longifolia* L., the spores of which are dealt with by for instance Mohl (1833, 1845), Presl (1836), Luerssen (1889), and Weaver (1896), was first collected by Faurie in Maui: Wailuku (Copeland 1914, p. 437), later also by Skottsberg in Kilauea, and appears to be of recent introduction (Christensen 1925, p. 17, and Skottsberg 1926, p. 197).

**P. cretica** L. — Pl. 5, Figs. 105, 106.

Mohl (1833, p. 39; 1845, p. 69) noted their type and also a sculpture, but he remarked that with the ordinary magnification used at that time they should be called smooth. Their type and smoothness is also emphasized by Bernoulli (1857) and Milde (1865); from Mettenius (1856) and Hillebrand (1888 b) information on type alone can be extracted. Luerssen (1889, p. 94) says: »Sporen rothbraun, mit groben, sehr unregelmässig warzen- und leistenförmigen Verdickungen». The illustrations published by Weaver (1896 Plate VII, fig. 13) are not particularly good, but they give an idea of the type, irregular shape, and occurrence of a sculpture. That this sculpture belongs to the exospore — a result to which also Hannig (1911 a, p. 339) later arrived as regards other species — was at the same time found by Ascherson and Graebner (1896, p. 85) and included in a description coming close to Luerssen's. About the same description is found in Warnstorf 1907 (p. 2831).

Tetrahedral, trilete, $39 \times 57$ (35—$43 \times 47$—64) $\mu$. Occasional specimens bilateral and monolete, $39 \times 60$ (33—$48 \times 47$—75) $\mu$, not to be confused with spores of *Polypodium pellucidum* (p. 60—61), to which they bear a superficial resemblance. Trilete specimens triangular in polar view, distal wall heavily arched. Tetrad scar reaching the angles. Sculpture all over the surface in the shape of irregular short ridges and wart-like projections. The equator bordered by a prominent ring, not seldom interrupted at the angles of the spore; in cross-section more or less rounded, contours somewhat undulating in polar view with an average width of about 5—6 $\mu$. Colour of the spore brown. — Specimen studied: D. D. Baldwin: Hawaiian Ferns (SP).

Recent: In somewhat varying habitats, often more or less dry, but occurs also in the rain forests. Bailey (1882, p. 25) says 3—7000 ft, Hartt and Neal (1940, p. 263): 2,700—7,000 ft; Wawra found it on Haleakala at about 2000 ft elev. (Luerssen 1875 b, p. 425).

Fossil: Not distinguished in the analyses.

**P. excelsa** Gaud. — Pl. 5, Figs. 107, 108.

Of the spores of this I know no other notes than Hillebrand's, who in his subgeneric description (1888 b, p. 627) noted their trilete type.

Tetrahedral, trilete, $29 \times 44$ (26—$31 \times 42$—45) $\mu$. Sculpture chiefly on the

distal wall: a few irregularly polygonal, low, elevated portions. Ring round the equator thick, as a rule unbroken at the angles, its contours not undulating as in the preceding. Tetrad scar as in *P. cretica*, bordering ridges very conspicuous. — Specimen studied: Oahu: Honolulu, 1852; N. J. Andersson (SP).

Recent: All the islands; woods, bottoms of gulches, etc., from 300 to over 4000 ft above sea level (Bailey 1882, p. 26, and Skottsberg 1926, p. 197, respectively).

Fossil: As the preceding.

[*P. Hillebrandii* Copel. — Of doubtful validity (cf. Copeland 1916, p. 172, and Skottsberg 1942, p. 111). The type, which came from Kauai: Kaholuamano, in semi-wet forest, has not been accessible to me].

**P. irregularis** Kaulf. — Pl. 5, Figs. 109, 110.

No description of the spores found in literature.

Tetrahedral, trilete, $30 \times 51$ ($28—33 \times 47—56$) $\mu$. Tetrad scar as in *P. cretica*, to which it bears a general resemblance also in the ring round the equator. The irregularities of this ring seem, however, generally to be somewhat different in shape, more angular and more frequent per unit length. The polygonal texture seen in Pl. 5, Fig. 109, varies in different spores. Sculpture of medium height, less raised than in *P. cretica*. — Specimen studied: Oahu: Honolulu, 1852, N. J. Andersson (SP).

Recent: In varying habitats in all the islands, particularly in the fairly dry forest types, recorded from elevations between 400 and 1200 m. Heller, who found it growing in clumps, thus collected it in »dry open places on the margin of the woods above Waimea, Kauai, at elevations of 3000 to 4000 feet» (1897, p. 787).

Fossil: As the preceding. It should be mentioned, however, that spores of what appears to be this species have been found occasionally, though in no great quantity.

## **Schizostege** Hillebr.

Besides the single Hawaiian, two Phillippine species have been referred to this genus, which was included in *Pteris* by Christ (1897, p. 167; not so in 1910) and later also by Brown and Brown (1931, p. 75 and 81).

**S. Lydgatei** Hillebr. — Pl. 5, Figs. 111—113; Pl. 6, Figs. 114—118.

Already from the notes on the spores available in literature it is fairly evident that they are entirely different from all other Hawaiian spores. Hillebrand calls them »tetraedrous, mostly angular, with 3 radiating lines» and »large and dark» (1888 b, p. 632). Brown and Brown (l. c. p. 75) have published a figure, from which may be gathered that in polar view the spores measured about $80 \times 96$ $\mu$; no sculpture is indicated, however. The tetrad scar in the drawing does not reach the angles of the spore.

Tetrahedral, trilete, 57×81 (53—60×75—87) μ, rarely bilateral, monolete, 57×84 μ (1 spore). Triangular in polar view, with fairly straight sides and as a rule well rounded angles. Occasionally the exospore thickening is thinner at the angles, which then become obtuse. Distal wall strongly arched. In optical cross section the exospore is about 6 (2.5—9) μ thick. It is sculptured, particularly on the distal wall, with irregular, fairly crowded warts of varying sizes, sometimes very coarse (see pictures). Tetrad scar distinct, bordered by less prominent ridges and occasionally not reaching the angles. — Specimen studied: Molokai: slopes of Olokui, Sept. 1912; C. N. Forbes 556-Mo (H).

Recent: A very rare terrestrial species, collected just a few times on Oahu, Molokai (see above), and at a waterfall near the head of the gulch of Waihee, W. Maui.

Fossil: Not seen.

## V. Subfam. *Gymnogrammeoideae.*

### Gymnogrammeae.

### **Coniogramme** Fée.

In his revision of this genus Hieronymus (1916, p. 280) says:

»Die Sporen sind bei allen Arten sehr ähnlich, gehören zu den triradiaten, man könnte sie als besondere Form dieser als dreilappig-tetraëdrisch bezeichnen, da sie mehr oder weniger deutlich im unteren dem dreiflächigen Scheitel gegenüberliegenden Teile Längsfalten aufweisen. Ihre Aussenmembran ist stets von hellbräunlicher Farbe, verhältnismässig dünn und zeigt winzige punktförmige, meist in Linien vereinigte, sehr feine, nur bei ganz starker Vergrösserung deutlich erkennbare chagrinartige Verzierungen, die vielleicht warzenförmige Erhöhungen des Exospors sind, bei den verschiedenen Arten von differenter Grösse zu sein scheinen, aber wegen ihrer Kleinheit als Unterscheidungsmerkmale kaum in Frage kommen können. Etwas mehr Gewicht kann man bei der Unterscheidung der Arten auf die Feststellung der Grössenunterschiede der Sporen legen.» (cf. also l. c. p. 282—283, where a note on the spores is included in the generic diagnosis).

There is one species in the islands.

**C. pilosa** (Brack.) Hieron. — Pl. 6, Figs. 119—121.

Hillebrand (1888 b, p. 551) described the spores only as »tetraedrous». Besides the general description quoted above, Hieronymus (l. c. p. 314) gives their diameter as »c. 0,3 [should be 0,03] — 0,035 mm».

Tetrahedral, trilete, 38×51 (32—45×47—56) μ (average of 20 spores from two specimens of the same collection), rarely bilateral, monolete, 42× ×69 μ (1 spore). Distinctly triangular in polar view, with rounded angles; sides straight or somewhat retracted. Furrows such as spoken of by Hieronymus (see above) not present in the expanded state. Exospore of medium thickness (about 2 μ), distinctly granular-textured, generally practically smooth but occasionally minutely rough, brown-coloured. Tetrad scar reaching the angles, its contours not always sharply defined to the extreme points of the

branches. — Specimens studied: E. Maui: Haleakala, Kula; W. Hillebrand (SP): 1. 41×51 (37—45×47—55) μ. 2. 36×52 (32—39×49—56) μ.

Recent: Reported by MacCaughey (1918 a, p. 209) from all the islands, lower and middle forests, 1500—4000 ft, but I know of no positive statement as to its occurrence in Molokai. Bailey (1882, p. 55) said »in open forest at an elevation of 2—4000 feet», Hillebrand (l. c. p.) »at altitudes of 3000—5000 ft.». The stations recorded by Heller (1897, p. 781) fall within this range, which is also given by Fowler (1940, p. 13). Robinson (1912 b, p. 589), again, says »in wet woods at 900—1200 m. elevation». As a rule not common.

Fossil: No reliable record available.

Adianteae.

**Adiantum** L.

As is generally known, and was also emphasized by Hillebrand, the species of this genus are characterized by trilete spores. Occasional deviations will be noted below.

Of the two species listed here the second may not be indigenous, but the question is not yet settled (cf. below).

**A. capillus veneris** L. — Pl. 6, Figs. 122—125.

The spores of this species have been dealt with by several authors, *e. g.*, Hooker and Bauer (1838—1842), Fée (1854—1857), Bernoulli (1857), Moore (1860), Milde (1865), Luerssen (1889), Weaver (1896), Hegi (1906), Warnstorf (1907) and Beck (1918), generally rather briefly, but occasionally, as by Luerssen, Warnstorf and Beck, in some detail. They are generally called smooth, Weaver says »slightly smooth», Beck »glatt oder kaum warzig». Their size is given as 30—37 μ by Warnstorf, 48—55 μ by Beck. Weaver calls them »somewhat irregular», but eventual deviations in type do not seem to have been noted by him. I know of no description based on Hawaiian material.

Tetrahedral, trilete, triangular, with rounded angles, 39×48 (33—43×42—52) μ, or often bilateral and monolete, 36×60 (31—42×52—71) μ. All transitions between the two types were found. Distal wall heavily arched. Exospore of both types comparatively thick (about 3.5 μ), brown in colour and provided with coarse but low projections on the surface. Proximal facets less sculptured. Tetrad scar reaching the angles in the trilete spores, less extensive in the monolete. The latter are similar to those of *Psilotum*, but the sculpture is different: in *Adiantum* there is much more smooth surface between the projections, which stand out as ± independent, raised portions. — Specimen studied: E. Maui: Lower ditch trail on Haleakala, rock wall in dripping water, c. 250 m, 14/10 1922; C. Skottsberg 794 (SP).

Recent: »Moderately common at lower elevations on shaded embankments and

in wet ravines, where it sometimes may be seen covering entire walls . . . . .» (Degener, Fl. Haw., Fam. 17, 5/11/'37). Reported from all the islands.

Fossil: Not seen.

[*A. cuneatum* Langsd. et Fisch.

The spores are described by Presl (1836, p. 18; cf. also Tab. XII: III, 1—13): »In Adianto cuneato sporae sunt tetraëdricae lateribus convexis irregulariter nubeculosis», and Reinsch (1884, p. V) has given their size as »0,05 mm». The following appears to be the first description based on material from the islands.

In shape like the preceding, but only tetrahedral, trilete spores observed, 33×42 (28—38×39—47) μ. Tetrad scar and sculpture very similar, the latter possibly less thick (about 2 μ) but whether this holds also for other specimens of the species I cannot tell. Early stages of development may recall *Gleichenia*. — Specimen studied: Hawaii: Kohala, head of Waipio Valley, 7/9 1938; HBS 3119 (SP).

Recent: First recorded by Copeland (1914, p. 437) from Kauai: Kealia, later, during the HBS, also from Oahu and Hawaii (cf. Skottsberg 1942, p. 110, with a note by Christensen, who considered it introduced).

Fossil: Not seen.]

Cheilantheae.

**Pellaea** Link.

The spores of this genus are of the trilete type (see for instance Prantl 1882, p. 415). There are figures and descriptions in literature referring to several species, also to the Hawaiian: Hooker's and Greville's (1831, Tab. CXXVI, fig. 3) give little information even regarding type, while those published by Weaver (1896, Pl. VII, fig. 23) are somewhat more illustrative in this respect and also suggest a rough sculpture. Hillebrand (1888 b, p. 633) says only: »Spores tetraedro-globose».

**P. ternifolia** (Cav.) Link — Pl. 6, Figs. 126, 127.

Tetrahedral, trilete, 35×41 (32—40×35—45) μ, rounded—subtriangular in polar view, distal wall strongly arched (spore almost globular). Tetrad scar bordered by ridges and reaching the equator. According to Hannig (1911 a, p. 339) a perispore would appear most likely to be absent, as in *Pteris* and a number of other genera of the *Pteridoideae*. In the present species, however, the sculptured (irregularly tuberculate) coating does not behave as part of the exospore. Instead, it is readily found detached from it, as a unit, thus behaving like a perispore. It appears that it would — at least generally — be absent if the species is found in the fossil state. The exospore surface

thus laid bare is smooth and brown. In this state the spores appear to be indistinguishable from those of *Doryopteris* (see below). — Specimen studied: Hawaii: Mauna Loa truck road above Kilauea, 2120 m, 14/9 1938; HBS 3772 (SP).

Recent: A species of arid habitats, usually, according to Degener (Fl. Haw., Fam. 17, 6/14'33) above 4000 ft; Hartt and Neal (1940, p. 263) give the entire range as 1,950—10,400 ft, whereas Hillebrand (l. c.) says 5000—8000 ft. Fowler (1940, p. 14) reports it »from Hilina Pali [c. 2000 ft] to an elevation of about 9,500 feet» in the island of Hawaii. Recorded from all the large islands, though rare especially on Molokai and Oahu, and not approaching the humid regions.

Fossil: Not seen.

## **Doryopteris** J. Sm.

Fée (1850—1852, p. 133) described the spores of this genus as »rotundis», and Hillebrand, who dealt with it as a subgenus under *Pteris*, called them »tetraedro-globose» (1888 b, p. 629); so did Keyserling (1873, p. 1). As shown by the pictures, they do belong to the trilete type with ± rounded outline in polar view.

Two species have been found in the islands:

**D. decipiens** (Hook.) J. Sm. — Pl. 6, Figs. 128, 129.

Tetrahedral, trilete, 36×41 (30—40×36—45) μ. Distal wall heavily arched. Outline rounded to subtriangular in polar view. Tetrad scar bordered by ridges reaching the periphery. Exospore brown, smooth, and devoid of distinct texture. The sculpture seen in fresh material appears to belong to a perisporial covering. Hillebrand called the spores muricate. They appear to be indistinguishable from those of *D. decora* and of *Pellæa*. — Specimen studied: Kauai: Kokee-Milolii trail, dry country, 14/8 1938; HBS 2912 (SP).

Recent: Reported from all the islands, growing preferably at fairly low elevations, on moist, sometimes also shaded rocks, locally not uncommon. With regard to further pollen-analytical investigations in the mountains of West Maui it may be of interest to note that Bailey (1882, p. 27) found it plentifully in Wailuku valley. This author gives the altitudinal range as »300—2000 feet».

Fossil: Not seen (cf. below).

**D. decora** Brack. — Pl. 6, Figs. 130—132.

In describing this species, Brackenridge figured the spores schematically (1855, Pl. 13, fig. 1 d), but no description was published. Hillebrand (l. c. p. 630) stated them to be as in the preceding. My single slide reveals no reliable specific differences. The size values are: 35×40 (32—38×37—44) μ. — Specimen studied: Hawaii: Kau-Kona road, between Pahala and Naalehu, on a flow, 21/9 1922; C. Skottsberg 1089 (SP).

Recent: A more xerophytic species than the preceding, found in exposed situations in Kauai, Molokai, Lanai, Maui and Hawaii. Whether reported from Oahu I do not

know. The altitude figure given by Robinson (1912 b, p. 577) and MacCaughey (1918 a, p. 207), about 2000 ft, comes from Heller (1897, p. 787). Skottsberg, for instance, lists localities from 300 and 450 m elev. (1926, p. 196).

Fossil: Not seen.

VI. Subfam. *Vittarioideae.*

**Vittaria** Sm.

*V. rigida* Kaulf., with bilateral, monolete spores. See p. 72.

VII. Subfam. *Blechnoideae.*

**Sadleria** Kaulf.

Several species, all with bilateral, monolete spores. See p. 71—72.

**Doodia** R. Br.

Two species, with bilateral, monolete spores. See p. 68.

VIII. Subfam. *Asplenioideae.*

Asplenieae.

**Asplenium** L.

Numerous species, all with bilateral, monolete spores. See p. 63—66.

**Loxoscaphe** Moore.

*L. Mannii* (Eaton) Kuhn — Bilateral, monolete spores. See p. 71.

Athyrieae.

**Diplazium** Sw.

Several species, all with bilateral, monolete spores. See p. 67—68.

**Athyrium** Roth.

Four species, all with bilateral, monolete spores. See p. 66.

**Cystopteris** Bernh.

*C. Douglasii* Hook. — Bilateral, monolete spores. See p. 67. According to Hannig (1911 a, p. 340—341) and Christensen (1938, p. 542) a perispore is lacking in this genus, but as far as I can find the spiny sculpture seems to be part of a perisporial covering.

IX. Subfam. *Dryopteridoideae.*

**Dryopteris** Adans.

Most of the species have bilateral, monolete spores devoid of exospore sculpture and will be dealt with on p. 68—70. In three of them — I can speak only of those I have seen — the spores are provided with numerous short spines (up to 3 $\mu$ long) all over the surface. The origin of these spines remains to be settled. At least in certain cases the covering on which they are produced does not behave like an exospore (cf. Pl. 7, Fig. 143). The species are listed here, however. The values include the spines. The corresponding measurements, spines excluded, are found on p. 69.

**D. goggilodus** (Schk.) O. Kze emend. Fosberg — Pl. 7, Fig. 143. (Syn. *D. gongylodes*) $35 \times 54\ \mu$ (32—39 × 47—62)

Oahu: no locality, 1852; N. J. Andersson (SP)

Common in wet habitats of low elevations, in old taro patches, along streams, etc. The highest locality noted by Heller was a grassy slope at head of Pauoa in Oahu, 1000 ft elev. (1897, p. 781). Skottsberg (1926, p. 190) records it from 400 m elev. in E. Maui. According to Bailey (1882, p. 46) the altitudinal range is 2-300—1000 ft.

**D. honolulensis** (Hook.) C. Chr. — Pl. 7, Figs. 144, 145. $52 \times 66\ \mu$ (49—55 × 63—69)

Hawaiian Islands; W. Hillebrand (SP)

A common species of the wet montane regions of all the islands, reported also from the vicinity of bog areas.

**D. latifrons** (Brack.) O. Kze — Pl. 7, Figs. 146, 147. $61 \times 85\ \mu$ (54—69 × 77—96)

D. D. Baldwin: Hawaiian Ferns (SP)

Reported from all the islands, not common, at elevations of 2000—3000 ft (Hillebrand 1888 b, p. 579; cf. also Heller 1897, p. 780).

None of these species recognized in the fossil material.

**Polystichum** Roth.

*P. haleakalense* Brack. and *P. Hillebrandii* Carruth. — Bilateral, monolete spores. See p. 71.

**Cyrtomium** Presl.

*C. caryotideum* (Wall.) Presl — Bilateral, monolete spores. See p. 66.

**Tectaria** Cav.

*T. Gaudichaudii* (Mett.) Maxon — Bilateral, monolete spores. See p. 72.

X. Subfam. *Polypodioideae.*

## Polypodium L.

It has long been known that both monolete and trilete spores occur in this genus. As noted by Kaulfuss (1827, p. 107—108) and Hillebrand (1888 b, p. 552 and 558), they are also found in the Hawaiian species. I shall deal with the trilete first.

### Species with tetrahedral, trilete spores.

(*Eupolypodium*, with the exception of *P. pellucidum*)

Pl. 7, Figs. 151—157.

Spores of this group fairly uniform in shape and type of sculpture, to some extent also in size. They have been recorded as a unit in the pollen-statistical work. All of them are almost globular, and provided all over the surface with a sculpture in the form of warts, which vary in size even on the same spore. There are differences in the average coarseness of these warts, which after further study may serve to distinguish certain species or species groups. The tetrad scar, seen in polar view, reaches the periphery of the spore. After acetolysis the spores become brown to dark brown. Before entering upon the fossil occurrences, the recent species will be survyed on the principles noted below in the introduction to the list of monolete spores in the family devoid af sculpture.

**P. abietinum** D. C. Eaton — Pl. 7, Figs. 151, 152. — P × E in μ: 30 × 35 μ (28—32 × 30—38)

Kauai: Kauhao, 800 m, Febr., 1910; U. Faurie 90 (SP)

Listed by Hillebrand (1888 b, p. 557) as a variety of *P. tamariscinum*, but, as pointed out by Heller (1897, p. 784), certainly a distinct species. Whether possibly common in favorable situations — as Heller suggested — or not, I do not know. Hillebrand (l. c.) and Robinson (1913, p. 200) record it as rare on trees in Kauai, Oahu, and Hawaii.

**P. adenophorus** Hook. et Arn. — 27 × 30 μ (23—30 × 27—32)

D. D. Baldwin: Hawaiian Ferns (SP)

Less coarse warts than in the preceding.

Not uncommon in forests above 2000 ft, according to Hillebrand (l. c. p. 555). Robinson (1913, p. 198) lists it only from Kauai and Oahu: »On tree trunks in the forests above 600 m. elevation».

**P. haalilioanum** Brack. — 38 × 45 μ (32—42 × 42—49)

Oahu: Aiea, near summit, 15/3 1936; O. Degener 10508 (SP)

Hillebrand (1888 b, p. 554) who knew of this species from Oahu and Kauai, says: »On moss-covered trees, not common». Robinson (1913, p. 197) adds Hawaii and calls it rare.

**P. Hillebrandii** Hook. — 24×30 μ (19—27×26—35)

Oahu: Koolau, Pupukea-Malaekahana trail, 470 m, 15/9 1926; C. Skottsberg n. 1797 (SP)

A rare species in forests of relatively low altitudes (Hillebrand l. c. p. 557; Robinson 1913, p. 200). The latter author records localities from Oahu and Hawaii, and gives the altitudinal range »400—700 m.»

**P. Hookeri** Brack. — Pl. 7, Fig. 153. — 28×31 μ (25—31×28—36)

W. Maui: N slope of Puu Kukui at Nakalalua, 28/7 1938; O. Selling (spore sample only) — 1 specimen: 20×24 μ

An epiphytic species, known from all the islands, though as a rule not common. Locally it may be fairly abundant. Occurs in all types of rain forest, acc. to Hartt and Neal (1940, p. 263) from 2,000 to 7,000 ft elev. Fowler (1940, p. 15), dealing with the Kilauea-Mauna Loa Section of Hawaii National Park calls it »common epiphyte throughout rain forest.»

**P. hymenophylloides** Kaulf. — 27×31 μ (22—32×27—36)

Molokai: above Waikolu valley, near Pepeopae bog, 12/7 1938; HBS 2543 (SP)

A rain forest species recorded from all the islands. It is not always rare, as Hillebrand (1888 b, p. 556) thought, but may be common, as in the forest between Kokee and Kilohana in Kauai (Skottsberg 1926, p. 198). Fowler (1940, p. 15) found it in »rain forest at elevations of 3,000 to 4,000 feet» in Hawaii.

**P. Knudsenii** Hieron.

A rare relative of *P. Hookeri*, known from a few localities in Kauai, about 2000—5000 ft elev. (Hillebrand 1888 b, p. 554; Heller 1897, p. 786); not seen. Hillebrand says: »Spores as in *P. Hookeri*», Hieronymus (1905, p. 80): »Sporis subglobosis, usque ad 0,05 mm crassis, ubique minute granuloso-tuberculatis, fuscescentibus.»

**P. pseudogrammitis** Gaud. — 34×41 μ (30—37×39—45)

Oahu: Poamoho, 18/8 1935; O. Degener 10166 (SP)

A very common epiphytic species known from the rain forests of all the islands, rarely terrestrial. This species (and *P. tamariscinum*) probably furnished a good deal of the spore contents of the slides.

**P. pumilum** Rob. — (—×40 μ)

Not seen; known only from the type locality in Oahu (Robinson 1913, p. 195—196). Its specific status remains to be settled, at any rate the name is invalid (cf. Christensen 1925, p. 18). Comes close to *P. Knudsenii*. Robinson calls the spores »yellow, tetrahedral, 0,040 mm. in diameter, very minutely tuberculate».

**P. Saffordii** Maxon — 29×32 μ (26—31×30—34)

W. Maui: N slope of Puu Kukui, wet forest at Nakalalua, 28/7 1938: O. H. Selling (spore sample only)

A generally scarce epiphytic rain forest species known from all the islands. Guppy (1906, p. 593) records it as *P. serru-*

*latum* from 3,000—6,000 ft elev. Hillebrand (1888 b, p. 553) called it rare, Robinson (1913, p. 197) common. Fowler (1940, p. 15) found it to be occasional in the region studied by him.

**P. sarmentosum** Brack. — Pl. 7, Fig. 154. $37 \times 42\ \mu$ ($32—40 \times 38—45$)

D. D. Baldwin: Hawaiian Ferns (SP)

A common species in all the islands, epiphytic as well as terrestrial in the rain forests.

**P. tamariscinum** Kaulf. — Pl. 7, Fig. 155. $34 \times 39\ \mu$ ($29—41 \times 34—47$)

Total of the following (30 spores)

1) Oahu: Koolau, back of Tantalus, c. 600 m, 7/8 1922; C. Skottsberg 58 (= the main species) (SP) $33 \times 39\ \mu$ ($31—36 \times 34—43$)
2) W. Maui: summit of Puu Kukui, 25/7 1938; HBS 2705 (= var. *montanum* Hillebr.) (SP) $36 \times 43\ \mu$ ($29—41 \times 38—47$)
3) Kauai: vicinity of Kokee, 13/8 1938; E. Plews (HBS distrib. nr) 2858 (= var. *tripinnatifidum* (Gaud.) Hillebr.) (SP) $32 \times 36\ \mu$ ($21—33 \times 35—38$)

A common species recorded from all the islands. Both epiphytic and terrestrial in the rain forest. Heller (1897, p. 786) considered it best developed in the wetter parts. Cf. also *P. pseudogrammitis*.

Fossil occurrences (the above group of species): Found in 98 % of all samples. On Kauai they are not absent anywhere, and in the few samples from the other two islands, in which they were not recorded, they would no doubt be found if the analyses were extended. They occur in every series, in almost all (1, 34, 57, 71, 80) or all samples (remaining series).

The values vary between traces and 341 %, generally between 1 and 9 % (7/10 of all occurrences), 3 % is the commonest value (13 % of d:o), followed next by 2 % and 4 % (almost 12 % of d:o). The average, all occurrences taken together, is 13.7 %. In the samples with the commonest values (1—9 %) the average is 4 %. The highest values, apparently caused by local conditions are: 341 % in 410 (84), 143 % in 205 (35), 127 % in 356 (81), 95 % in 206 (35) and 90 % in 413 (84).

### Species with bilateral, monolete spores.

Very few Hawaiian species belong to this type. Besides those listed below, Hillebrand recorded *P. lanceolatum* L., which was stated to have been collected by Nuttall in Kauai (1888 b, p. 555). Christensen (1925, p. 19) seems right in excluding it from the list of Hawaiian ferns. A fifth species, *P. scolopendria* Burm. f., listed with a query by Christensen, is most probably of recent introduction. Its history in the islands is dealt with by Degener (Fl. Haw., Fam. 17, May 20, 1940). Its spores have a thick exospore, with dense, very minute projections, and measure $41 \times 67$ ($36—47 \times 62—72$) $\mu$

(HBS 3291). That *P. aureum* L. is a recent escape is generally agreed. Its spores are dealt with by for instance Mohl (1833, p. 39, Tab. I, fig. 13, 14; 1845, p. 69 and 81, Tab. II, fig. 13, 14).

**P. atropunctatum** Gaud. — Pl. 7, Figs. 156, 157.

Bilateral, monolete, 56×89 (49—64×80—95) μ, covered all over the surface with dark brown, coarse and angular projections, unique in appearance among the Hawaiian spores. Tetrad scar bordered by ridges and measuring 1/2—3/4 of the length of the spore. Hillebrand (1888 b, p. 552) has given a short description: »Spores ovoid-reniform, laterally compressed, verruculose». Early stages of this sculpture recall the pitted sculpture in *Psilotum*, especially *P. complanatum*, to the spores of which those of the present species may occasionally bear a close resemblance. As a rule they are of larger size, however, and have other proportions of polar to equatorial diameters. The exospores of immature spores of this species are also thinner than those of mature spores of *Psilotum*. — Specimens studied: W. Maui: N slope of Puu Kukui at Nakalalua, 28/7 1938; O. H. Selling (spore sample only): 58×90 (52—64×80—95) μ; W. Maui: forest patch on summit of Puu Kukui, 24—25/7 1938; HBS 2638 (SP): 55×88 (49—59×82—93) μ.

Recent: A common fern, recorded from all the islands, on both rocks and trees, from elevations varying from 700 to 6,800 ft (Hartt and Neal 1940, p. 263 as *P. lineare;* cf. also Fowler 1940, p. 15). It occurs on the summit of Puu Kukui, W. Maui, where it was collected during the HBS 1938. Heller (1897, p. 785) says that in Kauai it ranges »from the lower forests to 3500 feet», but it goes higher there too.

Fossil: Spores of this species were found in 13 % of all samples: in about 1/5 of those from Maui, but only about half as common in those from Molokai and Kauai. Not recorded in the series 84, only rarely in 10, 35, 37, and 78, and by no means common in any of the other series. The values are always low, generally traces (2/3 of the occurrences) or 1 %. Only in 4 (1) the frequency reached 2 %.

**P. pellucidum** Kaulf. — Pl. 7, Figs. 158, 159.

The spores are very similar to those of *P. vulgare* L., which seem to be the first fern spores ever reported to have been examined microscopically (W. Cole in 1669, according to Kaulfuss 1827) and of which there are numerous pictures and descriptions. The similarity makes it hard to fix the taxonomic position of a number of Tertiary spores now suggested to represent *P. vulgare* (Rudolph 1935, Thiergart 1937, 1940). The spores of the Hawaiian species do not seem to have been figured before. They are briefly described by Hillebrand (1888 b, p. 558): »Spores verrucose or reticulate».

Bilateral, monolete, 34×57 (32—37×53—62) μ. Tetrad scar and surrounding ridges as in the preceding. Exospore covered by numerous, fairly large

and irregular warts, rounded when seen from aside, and separated by narrow furrows. The colour is brown. Easily distinguished from aberrant, monolete spores of *Pteris cretica* (p. 49), to which they bear but a superficial resemblance. — Specimen studied: Hawaii: Kohala pipe line above Kamuela c. 1100 m, 29/9 1922; C. Skottsberg 732 (SP).

Recent: A common species, terrestrial and epiphytic, on all the islands. Reported by Robinson (1913, p. 198) in altitudes from 300 to 2000 m above the sea, by MacCaughey (1918 a, p. 211) from 1800 to 6000 ft, by Hartt and Neal (1940, p. 263) from 750 to 9,500 ft. The lowest limit was placed at 1 foot elev. by Bailey (1882, p. 52). In the crater of Haleakala it grows to at least 2600 m, though represented by a form given varietal rank by Skottsberg (1941, p. 25), var. *vulcanicum*. This is common also in Hawaii. The main species is found in the mountain bogs, too.

Fossil: Recorded in 75 % of the analysed samples and from all three islands (Kauai: 55 %, Molokai: 88 %, Maui: 77 %). The spores are rather regularly distributed, being found in most of the samples of all series except no. 90, where they occurred in only 8 of 26 analyses. The values vary from traces to 37 %, generally between traces and 3 %, 1 % being the commonest (half of the occurrences) and followed by traces (1/4 of d:o) and 2 % (1/8 of d:o). The average is 1 %. The highest frequencies are: 37 % in 406 (84), 13 % in 407 (84), 7 % in 6 (1) and 46 (1), 6 % in 405 (84). In Maui the highest value is 4 %, recorded in 239 (57).

No reaction to climate could be detected.

**P. spectrum** Kaulf. — Pl. 7, Fig. 160.

The spores of this species, which have a smooth exospore, are dealt with on p. 71. They differ from the bulk of the polypodiaceous spores devoid of sculpture in their thick exospore, which makes them easy to distinguish from other Hawaiian types. They are mentioned by Hillebrand (1888 b, p. 559): »Spores ovoid-reniform, with one dorsal line, which bifurcates at one or both ends». Bifurcations generally absent. Exospore about 3 $\mu$ thick.

Recent: A terrestrial and epiphytic species recorded from all the islands. Hillebrand (l. c. p. 560) says »not uncommon», but this may refer only to Oahu, where it seems to be of more common occurrence than elsewhere (cf. also Degener, Fl. Haw., Fam. 17, May 20, 1940). Heller (1897, p. 786), who made excursions in Kauai and Oahu, calls it »common in the lower woods», which agrees fairly well with Bailey's data: »in damp forest at 500—3000 feet elevation» (1882, p. 55). Robinson (1913, p. 202) says only »in dense shade of woods», Degener, »dense woods at medium elevations» (l. c.).

Fossil: Not seen.

## XI. Subfam. *Elaphoglossoideae.*

### **Elaphoglossum** Schott.

Several species, with bilateral, monolete spores. See p. 70.

Genus inc. sed.

In the collections of the Riksmuseum, Stockholm, is a very peculiar fern collected on Oahu in 1852 by N. J. Andersson. I have not been able to refer it to any living or fossil genus, not even as a highly isolated (or monstrous) type. It will be described in a paper under preparation (Selling mscr.). Unfortunately the single frond is sterile. The plant does not appear to have been collected by anybody else, and, if not extinct, it must be extremely rare.

## APPENDIX TO THE POLYPODIACEAE.

*Bilateral, monolete polypodiaceous spores without sculpture in a fossil state.*

The bulk of the polypodiaceous species — several of them very common — belong to this type. In recent material the spores are provided with a ± delicate perispore; these coverings often contribute diagnostic characters. In the fossil state the perispore is absent, and all the species belonging here must therefore be recorded as a unit. Such spores occur in all samples, and in widely varying frequencies; from traces to 3800 %, generally about 25 %. It is true that the spores of certain recent species differ greatly in size, but in fossil material none can be exactly determined on the basis of single spore-size values. It may on the other hand be possible to trace with some probability the affinities of spores of a certain size, especially if the fossil material is large and indicates a common origin, permitting a tentative comparison of averages.

In the analyses I put on record three conventional groups of spores: about 30 $\mu$, 45 $\mu$ and 60 $\mu$ in largest equatorial diameter. I did this in order to determine whether there had been any notable changes in the relative number of spores of different size during different periods of time, but found none. For that reason it did not seem worth while to determine the spore sizes of each living species. In the series 57 (W. Maui: summit of Puu Kukui), however, a vast number of spores were found to have been deposited a short period at the beginning of period III. The question arose whether these spores originated from plants covering the tremendous precipice below the bog, a couple of thousand feet high, down into the Iao valley (apparently chiefly species of *Sadleria*), or whether they had come from plants growing in the bog itself. If the former was the case, this fact might be of essential importance to the interpretation of wind conditions during the Late Quaternary,

and accordingly to an understanding of the history of the vegetation. For that reason I resolved to look through the entire group as completely as possible in order to find out whether the average size of the fossil spores might point to any given recent species or species group. Although the result, which will be discussed in the paper containing the general results of the pollen analyses, did not give any clue to the interpretation of the wind conditions, they seem worth publishing. The survey might be of some value to future investigations.

With but few exceptions I have not quoted the occasional measurements presented earlier or to be extracted from figures in literature, not because I consider mine sufficient or necessarily superior to others, but for the chief reason that no Hawaiian material has yet been examined after acetolysis, the method employed by me all through the work (see p. 10), and a uniform preparation method is of fundamental importance to a comparison of this kind. Besides, it is of course of little use to cite measurements without any data of preparation, and most of those hitherto published do not give any. A comparison of fossil spores with values which may or may not comprise the perispore is moreover of no value at all. In the following measurements the perispore is excluded. The methods, number of measurements, etc., are the same as those generally used for this paper.

Indications of the known distribution of each species would have been useful, but the attempt was not made because too many of the literary references are unsatisfactory in some respect or other, and would require a consultation of herbarium material not available on account of the war.

Synonyms are as a rule not quoted, nor doubtful or introduced species. Since a couple of groups are critical, the recognition of certain species is only tentative.

## **Asplenium** L.

Measures in $\mu$ (P × E)

**A. acuminatum** Hook. et Arn. — 28 × 43 (26—29 × 40—48)

W. Maui: N slope of Puu Kukui, between Haelaau and Nakalalua, 1/8 1938; HBS 2742 (SP)

[10 spores, a specimen from New Caledonia, Noumea; Franc (SP): 28 × 41 (25—31 × 38—48) $\mu$]

**A. adiantum nigrum** L. — 28 × 42 (25—31 × 36—46)

Hawaii: E slope of Mauna Loa, at end of truck road, 2120 m, 14/9 1938; HBS 3276 (SP)

**A. contiguum** Kaulf. — 20 × 34 (17—22 × 32—36)

Hawaii: Kilauea, Fern Jungle; 17/9 1938; HBS 3322 (SP)

Skottsberg 1942, p. 80: 24—39 $\mu$ (cf. p. 86).

**A. enatum** Brack. — 35×55 (31—38×51—59)

Kauai: Alakai, between Lehua maka noe and Kawaikoi, 25/8 1938; HBS 2963 (SP)

**A. falcatum** Lam. subsp. **subcaudatum** Skottsb.

Total of the following, including varieties (40 spores) — 29×49 (24—34×41—58)

1) D. D. Baldwin: Hawaiian Ferns (called *A. caudatum*) (SP) — 29×46 (24—32×42—49)
2) W. Maui: N slope of Puu Kukui, above Nakalalua in swampy forest, 28/7 1938; HBS 2731 (SP) — 28×53 (25—32×50—58)
3) var. *nitidulum* (Hillebr.) Skottsb. — Hawaii: Kilauea, Fern jungle, 1200 m, 17/9 1922; C. Skottsberg 569 (SP) — 31×53 (29—34×51—56)
4) var. *sectum* Hillebr. emend. Skottsb. — Hawaii: Kilauea iki, 1200 m, 21/9 1926; C. Skottsberg n. 1904 (SP) — 27×43 (25—29×41—45)

**A. Hillebrandii** C. Chr.

Not seen. — Found only on Oahu.

**A. horridum** Kaulf. — 22×41 (20—25×39—44)

Oahu: Waianae Mts, Kaala, 25/9 1938; HBS 3569 (SP)

Sometimes slightly curved. Skottsberg 1942, p. 81: »36—39 μ». Cf. Brown and Brown 1931, pl. XIII, A and D.

**A. insiticium** Brack. — 37×64 (32—42×54—70)

Molokai: forest above Waikolu Valley, 6/7 1938; HBS 2509 (SP)

Sometimes slightly curved. Skottsberg 1942, p. 76: »51—57 μ (perispore wing not included)».

**A. kauaiense** (Hillebr.) Rob.

Not seen. — Found only on Kauai.

**A. Kaulfussii** Schlecht. — 32×51 (29—37×48—54)

Oahu: Palolo, Kaau crater, 480 m, 23/10 1922; C. Skottsberg 906 (SP)

Skottsberg 1942, p. 71: »Their size is subject to little variation: (45—) 48—51 (—54) μ in all» (perispore excluded, acc. to personal communication).

**A. Knudsenii** Hillebr. — 20×30 (18—22×28—32)

Oahu: Kalihi, 1909; U. Faurie 305 (SP)

**A. lobulatum** Mett. — 25×44 (22—26×41—47)

Hawaii: Kohala, Upper Hamakua ditch trail between Koiawe and Alakahi valleys, 8/9 1938; HBS 3151 (SP)

Skottsberg 1942, p. 73: »The spores are 42—48 μ long» (excluding perispore; personal comm.)

**A. Macraei** Hook. et Grev. — Pl. 7, Fig. 136.

Total of the following (20 spores) — 19×28 (16—22×24—32)

Kauai: Kohua ridge, Kawaia trail, 19/8 1938; HBS 2994 (SP) — 20×28 (17—22×24—32)

Oahu: Waianae, Palehua iki, 23/8 1922; C. Skottsberg 285 [f. *sphenolobium* (Kze) Skottsb.] (SP) 18×28 (16—20×25—30)
Skottsberg 1942, p. 65: »The size is about the same in all (*A. erectum*, *Macraei* and *lunulatum*), 24—30 μ». Besides, the same is true of *A. Macraei* var. *rapense* E. Brown: »27 ± μ (Brown and Brown 1931, p. 65)

**A. monanthes** L. 26×39 (22—30×35—43)

D. D. Baldwin: Hawaiian Ferns (SP)

**A. mirabile** Copel.

Not seen; described by Copeland (1914, p. 440) from Kauai: Keihia, alt. 300 m. — Close to *A. horridum?*

**A. nephelephyllum** Copel. 24×42 (22—26×38—46)

Kauai: Alakai, forest at Kawaikoi stream, 16/8 1938; HBS 2968 (SP)
Skottsberg 1942, p. 106: »39—45 μ long» (excluding perispore; personal comm.).

**A. nidus** L. — Pl. 7, Fig. 137. 35×51 (32—40×46—58)

Oahu: Koolau, Kawaiiki ditch trail, on trees, c. 300 m, 15/9 1922; C. Skottsberg 221 (SP)

**A. normale** Don. 34×46 (29—36×42—48)

W. Maui: N slope of Puu Kukui, rain forest above Nakalalua, 28/7 1938; O. H. Selling (spore sample only)

**A. patens** Kaulf. 30×47 (28—32×42—50)

Oahu: Waianae, near Green Peak, c. 800 m, 23/8 1922; C. Skottsberg 290 (SP)
Occasionally somewhat curved. Possibly only a large state of *A. rhipidoneuron;* cf Skottsberg 1942, p. 78.
Skottsberg l. c. p.: »39—45 μ» in n. 998; n. 290 (in G) offered no good spores.

**A. rhipidoneuron** Rob. 30×48 (26—32×42—52)

W. Maui: Wailuku Valley; H. Beraz (SP; det. C. Skbg)
Skottsberg 1942, p. 76: »42—51 μ (perispore wing not included) varying in different specimens between 42—45 and 48—51 μ.»

**A. rhomboideum** Brack.

Not seen.

**A. schizophyllum** C. Chr. 24×42 (21—27×40—44)

Kauai: Kohua ridge, Kawaia trail, in very wet rain forest; 19/8 1938; HBS 3021 (SP)

**A. sphenotomum** Hillebr.

Not seen.
Christensen (1925, p. 14) considers the species may be only a form of *insiticium*, and according to Skottsberg (1942, p. 74) he may be right in this.
Skottsberg 1942, p. 74: »The spores measure 45—48 μ in n. 1942 and 48—57 μ or occasionally 60 μ in n. 2928; in n. 2929 they are not ripe».

**A. trichomanes** L. 24×35 (19—30×29—42)

Hawaii: Mauna Loa, E slope near end of truck road, 2120 m, 14/9 1938; HBS 3271 (SP)

**A. unilaterale** Lam. 19×28 (17—21×25—30)

E. Maui: Olinda, 16/6 1927; O. Degener and H. Wiebke 3999 (SP)

**A. varians** Hook. et Grev. 25×37 (22—27×34—40)

D. D. Baldwin: Hawaiian Ferns (SP)

**A. vexans** Heller

Not seen; reported only from Oahu. Acc. to Alston (1933, p. 178) it seems to be identical with *Athyrium microphyllum*, »which might be referred to *Asplenium* with equal reason».

## Athyrium Roth.

**A. esculentum** (Retz.) Copel.

Recorded by Copeland (1914, p. 437) from Kauai as new to Hawaii. Not seen.

**A. microphyllum** (Sm.) Alston — Pl. 7, Fig. 140. 25×43 (22—28×40—46)

Synonyms (acc. to Alston 1933, p. 178); *A. Baldwinii* (Hillebr.) C. Chr. and *A. Poiretianum* (Gaud.) Presl. — Cf. above under *Asplenium vexans*.

Hawaii: head of Waipio Valley, 7/9 1938; HBS 3145 (SP)

Slightly curved. Exospore finely punctulated.

**A. proliferum** (Kaulf.) C. Chr. 29×43 (26—33×39—46)

Oahu: Koolau, Kawaiiki ditch trail, c. 300 m, 15/8 1922; C. Skottsberg 235 (SP)

**A. pseudoarboreum** Copel.

Copeland 1916, p. 171: Lanai. Not seen.

## Cyrtomium Presl.

**C.** (?) **Boydiae** (Eaton) Rob.

Excluded from the genus by Christensen (1930, p. 43), who remarks that its whole habit is different from all species of this genus. He felt, however, uncertain about its taxonomic position. Earlier he considered Hillebrand (1888 b, p. 572) was probably right in listing it but as a variety of *Dryopteris cyatheoides* (Kaulf.) O. K. (1925, p. 25). — Found, according to Robinson (1913, p. 204) in Hawaii, Maui, and Oahu. Not seen.

**C. caryotideum** (Wall.) Presl — Pl. 7, Fig. 149. 32.5×50 (29—36×45—56)

Oahu: Ekahanui, rocky, grassy woods, 1500 ft, 19/4 1936; O. Degener, Martinez, Topping and Bush 11967 (SP)

### **Cystopteris** Bernh.

**C. Douglasii** Hook. — Pl. 7, Fig. 141. $\frac{28 \times 42}{(24—32 \times 39—44)}$

D. D. Baldwin: Hawaiian Ferns. Cf. also p. 46. (SP)

### **Diellia** Brack.

As to the species of this genus, see Smith 1934.

**D. Alexandri** (Hillebr.) Diels $\frac{23 \times 36}{(22—26 \times 34—38)}$

D. D. Baldwin: Hawaiian Ferns (SP)

**D. centifolia** (Hillebr.) Diels

Found only on Kauai; cf. Smith 1934, p. 5; not seen.

**D. erecta** Brack. — Pl. 5, Fig. 99. $\frac{25 \times 37}{(23—27 \times 33—40)}$

E. Maui; H. Beraz (SP)

**D. falcata** Brack. $\frac{22 \times 40}{(21—23 \times 35—45)}$

Oahu: Makaleha valley, west central branch, in rocky, damp Kukui (*Aleurites moluccana*) forest, 23/10 1936; O. Degener, N. Krauss, and M. Martinez 11031 (SP)

**D. Knudsenii** (Hillebr.) Diels

A very rare species, found only on Kauai (cf. Smith 1934, p. 5); not seen.

**D. laciniata** (Hillebr.) Diels

As the preceding.

**D. pumila** Brack. $\frac{22 \times 35}{(20—24 \times 30—38)}$

W. Maui: Iao valley, Aug. 1909; U. Faurie (SP)

### **Diplazium** Sw.

**D. fenzlianum** (Luerss.) C. Chr. $\frac{31 \times 45}{(28—34 \times 43—52)}$

Oahu: Waianae, S part of Puu Hapapa, 3/9 1938; HBS 3357 (SP)

Skottsberg 1942 p. 109: spores in 3357 37 $\mu$ long.

**D. japonicum** (Thunb.) Bedd. $\frac{29 \times 39}{(25—31 \times 36—42)}$

Hawaii: Kohala, Upper Hamakua ditch trail, between Koiawe and Alakahi valleys, 8/9 1938; HBS 3179 (SP)

Skottsberg 1942, p. 109, says about this number: »39 $\mu$ (average of 10)» (perispore excluded, acc. to personal comm.).

**D. kaalanum** (Copel.) C. Chr.

Close to *D. japonicum;* described from Kauai: Kaala (Copeland 1914, p. 438). Not seen.

**D. marginale** (Hillebr.) C. Chr.

Not seen.

**D. mauianum** (Copel.) C. Chr.

Close to *D. japonicum;* described from E. Maui: Makawao, 800 m (Copeland 1914, p. 437). Not seen.

**D. meyenianum** Presl — 33×49 (29—35×44—54)

Molokai: head of Waikolu valley along pipe line trail, 13/7 1938; HBS 2631 (SP)

**D. molokaiense** Rob. — 27×36 (25—31×32—40)

Oahu: Waianae, Makaleha gorge, c. 450 m, 30/8 1922; C. Skottsberg 396 (SP)

**D. sandwichianum** (Presl) Diels — Pl. 7, Fig. 139. — 29×49 (26—31×45—52)

Molokai: Pukoo, 600 m, 1910; U. Faurie 297 (SP)

## Doodia R. Br.

**D. kunthiana** Gaud. — Pl. 6, Fig. 135. — 31×44 (28—34×42—48)

Kauai: Waimea, [Kaholuamanu, in *Metrosideros* forest], 1300 m, 29/4 1905; B. P. G. Hochreutiner 3601 (SP)

**D. Lyonii** Degener — 31×44 (29—36×40—46)

W. Maui: N side of Honokowai-Amalu valley, in a small ravine below Haelaau, 2/8 1938; HBS 2784 (SP)

## Dryopteris Adans.

**D. acutidens** C. Chr.

Not seen.

**D. carvifolia** (Kze) C. Chr.

A rare species; not seen.

**D. crinalis** (Hook. et Arn.) C. Chr. — 27×42 (26—30×38—46)

Hawaii: Kohala range; W. Hillebrand (SP)

**D. cyatheoides** (Kaulf.) O. K. — Pl. 7, Fig. 142. — 26×39 (25—28×34—44)

Oahu: Manoa valley, 11/5 1926; O. Degener 9231 (SP)

**D. dentata** (Forsk.) C. Chr. — 26×39 (22—28×34—42)

Hawaii: Hilo, 1910; U. Faurie 338 (SP)

**D. glabra** (Hook. et Arn.) C. Chr. — 24×38 (22—26×34—41)

Oahu: Waianae, Palehua iki, 700 m, in forest, 23/8 1922; C. Skottsberg 282 (SP)
Somewhat curved.

**D. globulifera** (Brack.) O. Kze — 30×51 (28—34×48—55)

Hawaii: Mauna Kea, 2000 m, 1909; U. Faurie 334 (SP)
Exospore ± thick.

[**D. goggilodus** (Schk.) O. Kze emend. Fosberg — Pl. 7, Fig. 143. [31×49 (26—37×43—57)]

Cf. p. 56. Values with spines excluded.]

**D. hawaiiensis** (Hillebr.) Rob. 23×37 (20—26×33—40)

Oahu: Waianae, Mt Kaala, 25/9 1938; HBS 3748 (SP)
Skottsberg 1942, p. 45: »The spores are .... only 42 μ».

[**D. honolulensis** (Hook.) C. Chr. — Pl. 7, Figs. 144, 145. [48×61 (45—51×57—64)]

Cf. p. 56. Values with spines excluded.]

**D. hudsoniana** (Brack.) C. Chr.

Not seen.

**D. keraudreniana** (Gaud.) C. Chr. 25×41 (22—27×37—45)

Oahu: Koolau, Keeawaawa, c. 500 m, 1922; C. Skottsberg 41 (SP)
± thick-walled

[**D. latifrons** (Brack.) O. Kze — Pl. 7, Figs. 146, 147. [58×81 (52—66×72—93)]

Cf. p. 56. Values with spines excluded.]

**D. paleacea** (Sw.) C. Chr.

Total of the following (20 spores) 32×50 (26—37×42—56)
Kauai: Alakai, along trail between Kokee-Mohihi road and Lehua maka noe, 16/8 1938; HBS 2964 (= var. *fuscoatra* (Hillebr.) C. Chr.) (SP) 33×50 (26—37×44—56)
Hawaii: Kohala, Upper Hamakua ditch trail at head of Koiawe valley, 7/9 1938; HBS 3142 (= var. *truncata* (Brack.) C. Chr.) (SP) 32×50 (28—34×42—56)

Skottsberg 1942, p. 43: »Spore size (largest diam., average of 10) 56 μ (n. 3142), 60 μ (2964), and 62 μ (n. 3579 [= var. *fuscoatra*]).»

**D. parvula** Rob. 22×35 (21—24×32—38)

Kauai: Kohua ridge, Kawaia trail, in wet forest, 19/8 1938; HBS 2991 (= f. *minuta*) (SP)
Skottsberg (1942, p. 46) gives a longest diameter of 12 μ for this number, and 12,5 and 13 μ for other numbers; these are the figures as read on the micrometer scale which by oversight were not multiplied by 3 before inserted in the MS; read 36, 37,5 and 39 μ (personal communication).

**D. rubiformis** Rob.

Considered by Christensen (1925, p. 8) to be a variety of *D. keraudreniana* (Gaud.) C. Chr. Not seen.

**D. rubiginosa** (Brack.) O. K. 23×37 (18—25×32—43)

Kauai: Waimea, 1910; U. Faurie (SP)
Sometimes slightly curved.

**D. sandwicensis** (Hook. et Arn.) C. Chr. 29×44 (26—31×40—48)

Lanai; W. Hillebrand (SP)

**D. squamigera** (Hook. et Arn.) Hook. 35×52 (31—42×48—56)

Oahu: Waianae, 1910; U. Faurie 331 (SP)

**D. stegnogrammoides** (Bak.) C. Chr. 31×48 (28—34×42—55)

Hawaii: Kilauea, Fern forest, c. 1200 m, 17/9 1922; C. Skottsberg 566 (SP)

**D. unidentata** (Hook. et Arn.) C. Chr. 25×45 (20—29×41—52)

D. D. Baldwin: Hawaiian Ferns (SP)

## **Elaphoglossum** Schott.

**E. aemulum** (Kaulf.) Brack. 29×45 (27—32×40—48)

Oahu: Waianae, Palehua iki in forest, c. 800 m, 23/8 1922; C. Skottsberg 283 (SP)

**E. crassicaule** Copel. (cfr.) 34×48 (32—38×44—51)

Kauai: Alakai, near Kilohana, 16/8 1938; HBS 2986 (SP)
Skottsberg 1942, p. 124; »spores 36—48 μ, average 42 μ».

**E. Fauriei** Copel. 31×49 (29—34×48—51)

Molokai: in the wet forest above Waikolu valley between Upper Maunahui camp and Pepeopae, 12/7 1938; HBS 2567 (SP)
Skottsberg 1942, p. 121: »Spores (average of averages) 39 μ. The table gives detailed values: aver.: 33—43 μ, extr.: 30—48 μ».

**E. gorgoneum** (Kaulf.) Brack. s. str. — Pl. 7, Fig. 161. 36×50 (33—41×41—57)

W. Maui: rain forest at Nakalalua, 28/7 1938; O. H. Selling (spore sample only)
Skottsberg 1942, p. 118: »longest diameter (39—) 42—48 (—51) μ, average 45 μ, perisporial crests not included».

**E. hirtum** (Sw.) C. Chr. 33×48 (30—36×44—52)

Oahu: Honolulu, 1852; N. J. Andersson (SP)

**E. micradenium** (Fée) Moore 26×40 (24—29×36—44)

Oahu: Honolulu, 1852; N. J. Andersson (SP)

**E. parvisquameum** Skottsb. 33×48 (29—36×43—52)

W. Maui: between Haelaau and Nakalalua, c. 1200 m, 28/7 1938; HBS 3741 (SP)
Skottsberg 1942, p. 124: »spore circ. 44—45 μ large; p. 126 (table): aver. 43—46 μ extr. 36—51 μ.

**E. reticulatum** (Kaulf.) Gaud. 33×48 (32—35×44—51)

W. Maui: N slope of Puu Kukui, between Haelaau and Nakalalua, 1/8 1938; HBS 2718 (SP)

**E. Wawrae** (Luerss.) C. Chr. 25×39 (22—29×35—42)

Kauai: Kohua ridge, Kawaia trail, c. 1100 m, 19/8 1938; HBS 3014 (SP)

### **Hypolepis** Bernh.

**H. punctata** (Thunb.) Mett. — Pl. 5, Figs. 94, 95. $\frac{30 \times 43}{(27—32 \times 41—46)}$

Cf. p. 46. Values with spines excluded.

### **Loxoscaphe** Moore.

**L. Mannii** (Eaton) Kuhn — Pl. 7, Fig. 138. $\frac{22 \times 33}{(20—24 \times 29—36)}$

D. D. Baldwin: Hawaiian Ferns (cf. also p. 46). (SP)

### **Nephrolepis** Schott.

[**N. exaltata** (L.) Schott — Pl. 5, Figs. 100—102. $\frac{26 \times 44}{(24—28 \times 41—50)}$

Cf. p. 47. Values with sculpture excluded.]

### **Polypodium** L.

(See further p. 57—61.)

**P. spectrum** Kaulf. — Pl. 7, Fig. 160.

Total of the following (20 spores) $\frac{44 \times 69}{(35—50 \times 64—77)}$

Oahu: Koolau, Kaluanui trail, near Punaluu boundary, c. 600 m, 27/9 1938; O. H. Selling (cf. also p. 61) (spore sample only) $\frac{46 \times 69}{(40—50 \times 62—76)}$
Hawaiian Islands; D. D. Baldwin: Hawaiian Ferns (SP) $\frac{43 \times 69}{(35—50 \times 64—77)}$

### **Polystichum** Roth.

**P. halaekalense** Brack.

Not seen.

**P. Hillebrandii** Carruth. — Pl. 7, Fig. 148. $\frac{27 \times 36}{(23—31 \times 32—39)}$

E. Maui: Haleakala, 1500 m, Aug. 1909; U. Faurie 361 (SP)

### **Sadleria** Kaulf.

**S. cyatheoides** Kaulf. $\frac{34 \times 54}{(31—37 \times 50—56)}$

Oahu: Koolau, Keeawaawa, lower ridges, 4/8 1922; C. Skottsberg 38 (SP)
Skottsberg's spore data (1942, p. 51) include the perispore.

**S. Fauriei** Copel.

Close to *S. cyatheoides*; first recorded from Oahu: Kalihi, 600 m, in Copeland 1914, p. 438—439. Not seen.

**S. pallida** Hook. et Arn. — Pl. 6, Fig. 134. $\frac{39 \times 57}{(36—43 \times 52—64)}$

W. Maui: summit of Puu Kukui, 24—25/7 1938; HBS 2639 (SP)
Skottsberg (1942, p. 51) found the spores mostly slightly smaller than in *S. cyatheoides*.

**S. rigida** Copel.

Copeland 1916, p. 172: Kauai: near summit swamp of Waialeale, alt. 1500 m, leg. Rock, Sept. 1909. Also recorded from Lanai. — Belongs to *S. pallida*? Not seen.

**S. souleyetiana** (Gaud.) Moore — 38×56 (34—42×49—59)

W. Maui, N slope of Puu Kukui, between Nakalalua and the summit, 26/7 1938; HBS 2702 (SP)
Skottsberg 1942, p. 52: »Size, without perispore 45—54×33—39 μ».

**S. squarrosa** (Gaud.) Mann — 46×70 (41—51×65—75)

Hawaii: Kohala, Upper Hamakua ditch trail, in a cave at the road-side near Koiawe valley, 10/9 1938; HBS 3196 (SP)
Skottsberg 1942, p. 53: Spore size (without perispore, cf. p. 54): 66—75×45—48 μ in n. 2591, 63—70×39—48 μ in n. 3196».

**S. unisora** (Bak.) Rob. — 42×65 (37—47×60—68)

Kauai: Kohua ridge, Kawaia trail, very wet forest, 19/8 1938; HBS 3003 (SP)
Skottsberg 1942, p. 54: »The spores . . . . are of the same general shape and size as in *squarrosa*, 66—72×40—51 μ in n. 3003, 57—72×36—48 μ in 3078, perispore not included».

## Stenoloma Fée.

**S. chusanum** (L.) Ching — Pl. 5, Fig. 96. — 30×49 (24—34×42—52)

Hawaii: Kohala, Kehena trail, 17/6 1938; HBS 3455 (SP)
Perispore (not included in the measurements) with irregular warts, about 3—8 μ wide. Brown and Brown (1931, p. 51) also measured spores of Forbes 422 (fr. Molokai): 52 ± μ with perispore.

## Tectaria Cav.

**T. Gaudichaudii** (Mett.) Maxon — Pl. 7, Fig. 150. — 23×35 (20—25×29—38)

Oahu: Koolau, in the inner parts of Manoa valley, 300—400 m, 27/8 1922; C. Skottsberg 357 (SP)

## Vittaria Sm.

**V. rigida** Kaulf. — Pl. 6, Fig. 133. — 29×62 (26—32×56—67)

Hawaii: Hiulani forest, SW of Olaa, c. 500 m, 8/9 1922; C. Skottsberg 445 (SP)
Sometimes slightly curved. Note the relation P: E.

Fam. MARSILIACEAE.

**Marsilia** L.

Hillebrand (1888 b, p. 651) listed two species from the islands, *M. villosa* Kaulf. and *M. crenulata* Desv., the latter brought to the *species inquirendae* by Robinson (1912 a, p. 233) and provisionally excluded by Christensen (1925, p. 20).

*M. villosa* is a rare plant in old taro patches at low elevations in Oahu (Forbes 1920). Owing to the mode of dissemination of its spores the probability that they would be met with in pollen-statistical studies is very small. At any rate, no material of the species has been available for study. Cf. further Hanstein 1865—66 and Russow 1871.

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A couple of additions to the surveys of recent distribution are available in CH. PICKERING, The Geographical Distribution of Animals and Plants, Pt II, Plants in their wild state, Salem, Mass., 1876, a work long neglected. It contains extensive lists of plants of the most peculiar designations, which entirely disregard the official reports on the same collection published by BRACKENRIDGE (1854; see above) and GRAY (1854). Still, it often gives more detailed information on localities than is found in the other works. Deviating statements also occur (see, *e. g.*, *Lycopodium*). It should be noted, however, that the data were partly taken direct from »memorandum books and original rough notes» without revision (l. c. p. 489).

## INDEX TO LATIN PLANT NAMES.

Invalid species names in ordinary type. Names not referring to indigenous ferns bracketed.

## EXPLANATION OF PLATES.

(Since the variation in each species is not shown, the plates should not be used in identification without consulting the text)

In all figures the magnification is × 400. The negatives, taken by Mr. K. E. Samuelsson, are kept in the Palaeobotanical Department, Swedish Museum of Natural History, Stockholm.

Particulars of the collections are found under each species in the preceding text.

All spores were prepared by the acetolysis method except those shown in Figs. 7—9 (this material, too scanty to allow preparation by the said method, was boiled in KOH). For data relating to preparation, see p. 10.

*d* = distal view; *l* = lateral view; *p* = proximal view (referring to the original position of the spores in the tetrads).

**Plate 1.** Lycopodiaceae and Selaginellaceae.

Lycopodiaceae

**Fig. 1.** *Lycopodium erubescens* Brack. — Kauai; Selling s. n. (*d*).

**Figs. 2—3.** *L. Haleakalae* Brack. — W. Maui; Skottsberg 1094. Fig. 2: normal spore (*d*), Fig. 3: aberrant d:o.

**Fig. 4.** *L. serratum* Thunb. — W. Maui; Selling s. n. (*d*).

**Figs. 5—7.** *L. polytrichoides* Kaulf. — W. Maui; HBS 2715. Figs. 5, 6: *d;* 6: photographed at a lower level than 5. Fig. 7: *l.*

**Figs. 8—9.** *L. phyllanthum* Hook. et Arn. — Oahu; Andersson s. n. Fig. 8: *d*, Fig. 9: *p* (surface views).

**Figs. 10—12.** *L. nutans* Brack. — Oahu; Skottsberg n. 1865. Fig. 10: *l.* Figs. 11, 12: *d;* 11 surface view, 12 photographed at a lower level.

**Figs. 13—15.** *L. Mannii* (Hillebr.) Skottsb. — W. Maui; Ewart and Swezey 136. Same spore photographed at successively lower levels (*d*).

**Fig. 16.** *L. cernuum* L. — Oahu; Andersson s. n. (*d*).

**Figs. 17—19.** *L. volubile* Forst. — New Zealand: North Isl. (specimen credited to Hawaii not available); G. E. and G. Du Rietz 2769. Fig. 17: *d*, Figs. 18, 19: *p;* 19 photographed at a lower level than 18.

**Figs. 20—21.** *L. venustulum* Gaud. — W. Maui; Skottsberg 775 (*d*). Fig. 20: surface view, Fig. 21: optical cross section.

Selaginellaceae

**Figs. 22—23.** *Selaginella arbuscula* Kaulf. — Oahu; Degener 5663. Fig. 22: *l*, Fig. 23: *p.*

**Figs. 24—25.** *S. deflexa* Brack. — W. Maui; Selling s. n. Tetrahedral tetrads in different positions. The spores also occur singly.

**Plate 2.** Psilotaceae, Ophioglossaceae, Marattiaceae, Schizaeaceae.

Psilotaceae

**Figs. 26—27.** *Psilotum complanatum* Sw. — Hawaii; HBS 3446 (*l*). Fig. 26: surface view, Fig. 27: optical cross section.

**Fig. 28.** *P. nudum* (L.) Griseb. — Oahu; Skottsberg 134 (*l*).

Ophioglossaceae

**Figs. 29—30.** *Botrychium subbifoliatum* Brack. — Baldwin: Haw. Ferns s. n. Fig. 29: *d*, Fig. 30: *l.*

**Figs. 31—32.** *Ophioglossum falcatum* (Presl) Fowler — Hawaii; Faurie 182. Fig. 31: *p*, Fig. 32: *d.*

**Figs. 33—35.** *O. concinnum* Brack. — Baldwin: Haw. Ferns. s. n. Fig. 33: *p*, Fig. 34: *d* (surface views), Fig. 35: detail of spore with abnormal local thickenings of the sculpture.

Marattiaceae

**Figs. 36—37.** *Marattia Douglasii* (Presl) Bak. — W. Maui; Selling s. n. Fig. 36: mature spore (*l*), Fig. 37: immature spore (*p*) with supposed perisporie (later disappearing).

Schizaeaceae

**Figs. 38—39.** *Schizaea robusta* Bak. — W. Maui; Selling s. n. (*l*). Fig. 38: optical cross section; Fig. 39: surface view, showing minute projections of the exospore.

**Figs. 40—44.** *Schizaea Skottsbergii* Selling (known only in the fossil state).

Figs. 40—41. The main species (*l*). — Molokai: Pepeopae bog; Selling, peat sample 158 (type specimen). Fig. 40: surface view (= Selling 1944, Pl. V, Fig. 48), Fig. 41: optical cross section (= l. c., Pl. V, Fig. 51).

Figs. 42—44. Var. *mauiensis* Selling (*l*). — W. Maui: Puu Kukui; Selling, peat sample 191 (type of the variety). Fig. 42: surface view (= l. c., Pl. V, Fig. 52), Fig. 43: optical cross section (= l. c., Pl. V, Fig. 55), Fig. 44: Immature spore, optical cross section, showing the thickness of the primary exospore membrane, on which a first thin layer of the secondary thickening has just been deposited. The texture of the latter is indicated in the lower part and along the margins.

**Plate 3.** Gleicheniaceae and Hymenophyllaceae.

Gleicheniaceae

**Figs. 45—46.** *Gleichenia emarginata* (Brack.) Moore — Hawaii; Skottsberg 418. Fig. 45: *p*, Fig. 46: *l*.

**Figs. 47—49.** *G. glauca* (Thunb.) Hook. — W. Maui; HBS 2740. Fig. 47: *p*, Figs. 48, 49: *l*.

**Figs. 50—51.** *G. linearis* (Burm.) Cl. — Oahu; Skottsberg 154. Fig. 50: *p*, Fig. 51: *l*.

**Figs. 52—53.** *G. owhyhensis* Hook. — Kauai; HBS 2939. Fig. 52: *p*, Fig. 53: *l*.

Hymenophyllaceae

**Figs. 54—55.** *Hymenophyllum lanceolatum* Hook. et Arn. — Kauai; HBS 3001. Fig. 54: *p*, Fig. 55: *d*, surface view.

**Fig. 56.** *H. obtusum* Hook. et Arn. — Oahu; Skottsberg 921 (*p*).

**Fig. 57.** *H. recurvum* Hook. et Arn. — W. Maui; Selling s. n. (*p*).

**Fig. 58.** *Trichomanes Baldwinii* (Eaton) Copel. — W. Maui; HBS 2676 (*p*).

**Figs. 59—61.** *T. cyrtotheca* Hillebr. — Oahu; Hillebrand s. n. Fig. 59: *p*, surface view, Fig. 60: *p*, almost optical cross section, Fig. 61: *l*, surface view.

**Figs. 62—64.** *T. davallioides* Gaud. — Haw. Islds (s. l.); Hillebrand. Fig. 62: *p*, surface view, Fig. 63: *p*, optical cross section, Fig. 64: *l*, surface view.

**Fig. 65.** *T. draytonianum* Brack. — Hawaii; Faurie 109 (*p*).

**Figs. 66—67.** *T. saxifragoides* Presl — Oahu; Yuncker 3026. Fig. 66: surface view, intermediate between *p* and *l*, Fig. 67: d:o, *l*.

**Plate 4.** Dicksoniaceae.

**Figs. 68—72.** *Cibotium Chamissoi* Kaulf. s. str., different collections. — Figs. 68, 69; E. Maui; Beraz s. n. Fig. 68: *d*, surface view, Fig. 69: *l*. — Figs. 70, 71: Oahu; HBS 3583. Fig. 70: *p* of abnormal specimen with structures recalling conditions in *Hemitelia*, Fig. 71: *p* of normal specimen showing perforations along the lists bordering the tetrad scar (faintly visible in the basal part). — Fig. 72: Kauai; HBS 2958, alete spore from otherwise normal collection.

**Figs. 73—76.** *C. glaucum* (J. E. Sm.) Hook. et Arn., different collections. — Fig. 73: E. Maui; Beraz (*d*, surface view). — Fig. 74: Hawaii; HBS 3141 (*d*. almost optical cross section). — Fig. 75: Same coll. as in 73 (*l*, optical cross section). — Fig. 76: Same coll. as in 74, (*p*, surface view).

**Figs. 77—79.** *C. hawaiiense* Nakai et Ogura — Hawaii; Skottsberg 428. Fig. 77: *d*, surface view. Fig. 78: *p*, optical cross section. Fig. 79: *l*, optical cross section. — Cf. *C. splendens*.

**Figs. 80—87.** *C. splendens* (Gaud.) Kraj. — Oahu; Skottsberg 70. — Figs. 80—82: Normal, mature spores. Fig. 80: *d*, surface view, Fig. 81: *p*, optical cross section, Fig. 82: *l*, optical cross section. — Fig. 83: Abnormal spore (mature) with two branches of the tetrad scar very much reduced; view intermediate between *p* and *l*. — Figs. 84—87: Immature spores.

**Fig. 88.** *C. St. Johnii* Kraj. — Kauai; Hochreutiner 3547 (= number referred by Krajina 1938 to var. *fallax* Kraj. subvar. *integrilobatum* Kraj.). (*p*, almost optical cross section). Spore apparently immature, no additional material available.

**Plate 5.** Polypodiaceae (I).

(As a rule the spores are shown such as they occur (or can be expected to occur) in the fossil state — without perispores, if such be present in the corresponding species. In genera showing little variation in exospore morphology only certain species are illustrated; these examples are marked by an asterisk.)

Dennstaedtioideae: Dennstaedtieae

**Figs. 89—91.** *Microlepia setosa* (Sm.) Alston — Oahu; Skottsberg 200. Fig. 89: *p*, surface view, Fig. 90: *p* of well expanded spore, almost optical cross section, Fig. 91: *l*, optical cross section (distal wall often more rounded).

**Figs. 92—93.** *M. speluncae* (L.) Moore — Kauai; Heller 2650. Fig. 92: *p*, optical cross section, Fig. 93: *l*, surface view.

Dennstaedtioideae: Hypolepideae

**Figs. 94—95.** *Hypolepis punctata* (Thunb.) Mett. — W. Maui; Selling s. n. (*l*). Fig. 94: almost optical cross section of spore with non-corroded spines of the perispore, Fig. 95: optical cross section (perispore absent).

Lindsayoideae

**Fig. 96.** *Stenoloma chusanum* (L.) Ching — Hawaii; HBS 3455 (*l*, almost optical cross section of spore with adherent fragments of characteristically coarsely warty perispore and showing the smooth surface of the exospore as well).

**Figs. 97—98.** *Lindsaya repens* (Bory) Bedd. var. *macraeana* (Hook. et Arn.) C. Chr. — Oahu; Skottsberg n. 1802. Fig. 97: *p*, surface view, Fig. 98: *l*, optical cross section.

**Fig. 99.** **Diellia erecta* Brack. — E. Maui; Beraz (*l*).

Davallioideae

**Figs. 100—102.** *Nephrolepis exaltata* (L.) Schott — Oahu; Skottsberg 30 (*l*). Fig. 100: immature spore, optical cross section, Fig. 101: mature d:o, surface view, Fig. 102: d:o, optical cross section.

Pteridoideae: Chaetopterides

**Figs. 103—104.** *Pteridium aquilinum* (L.) Kuhn — Baldwin: Haw. Ferns s. n. Fig. 103: *p*, almost surface view, Fig. 104: *l*, optical cross section.

Pteridoideae: Lepidopterides

**Figs. 105—106.** *Pteris cretica* L. — Baldwin: Haw. Ferns s. n. Fig. 105: *d*, almost optical cross section, Fig. 105: *l*, d:o.

**Figs. 107—108.** *P. excelsa* Gaud. — Oahu; Andersson. Fig. 107: *d*, optical cross section, Fig. 108: *l*, d:o.

**Figs. 109—110.** *P. irregularis* Kaulf. — Oahu; Andersson. Fig. 109: *d*, almost optical cross section, Fig. 110: *l*, optical cross section.

**Figs. 111—113.** *Schizostege Lydgatei* Hillebr. — Molokai; Forbes 556-Mo. Fig. 111: *p*, surface view, Fig. 112, *p*, optical cross section of coarsely warty spore, Fig. 113: d:o of almost smooth spore. — See also Figs. 114—118.

**Plate 6.** Polypodiaceae (II).
(Cf. text under Pl. 5)

Pteridoideae: Lepidopterides (continued).

**Figs. 114—118.** *Schizostege Lydgatei* Hillebr. — Molokai; Forbes. Fig. 114: *p* (somewhat oblique), Fig. 115: *d* of minutely granular spore, Fig. 116: *d* of coarsely warty spore (both 115 and 116 = surface view), Fig. 117: *l* of normal (trilete) spore with minutely granular sculpture, Fig. 118: *l* of aberrant (monolete) spore. — See also Figs. 111—113.

**Figs. 119—121.** *Coniogramme pilosa* (Brack.) Hieron. — E. Maui; Hillebrand s. n. Fig. 119: *l* of aberrant (monolete) spore with an additional, ± straight scar close to the main one, Fig. 120: *p*, surface view of normal (trilete) spore, Fig. 121: *l* of d:o, optical cross section.

Gymnogrammeoideae: Adianteae

**Figs. 122—125.** *Adiantum capillus veneris* L. — E. Maui; Skottsberg 794. Fig. 122: *p*, surface view of normal (trilete) spore, Fig. 123: *l*, almost optical cross section of d:o,

Fig. 124: *l*, surface view of aberrant (monolete) spore, Fig. 125: *l*, optical cross section of d:o.

Gymnogrammeoideae: Cheilantheae

**Figs. 126—127.** *Pellaea ternifolia* (Cav.) Link — Hawaii; HBS 3272. Fig. 126: *p*, surface view, Fig. 127: *l*, optical cross section.
**Figs. 128—129.** *Doryopteris decipiens* (Hook.) J. Sm. — Kauai; HBS 2912. Fig. 128: *p* (somewhat oblique), surface view, Fig. 129: *l*, optical cross section.
**Figs. 130—132.** *Doryopteris decora* Brack. — Hawaii; Skottsberg 1089. Fig. 130: *p*, surface view, Fig. 131: *d*, optical cross section, Fig. 132: *l*, optical cross section.

Vittarioideae

**Fig. 133.** *Vittaria rigida* Kaulf. — Hawaii; Skottsberg 445 (*l*). In the plate the colour has become too light as compared with spores of other species.

Blechnoideae

**Fig. 134.** **Sadleria pallida* Hook. et Arn. — W. Maui; HBS 2639 (*l*).
**Fig. 135.** **Doodia kunthiana* Gaud. — Kauai; Hochreutiner 3601 (*l*). Remark: same as made for Fig. 133.

**Plate 7.** Polypodiaceae (III).
(Cf. text under Pl. 5)

Asplenioideae: Asplenieae

**Fig. 136.** **Asplenium Macraei* Hook. et Grev. — Kauai: HBS 2994 (*l*).
**Fig. 137.** **A. nidus* L. — Oahu; Skottsberg 221 (*l*).
**Fig. 138.** *Loxoscaphe Mannii* (Eaton) Kuhn — Baldwin: Haw. Ferns s. n. (*l*).

Asplenioideae: Athyrieae

**Fig. 139.** **Diplazium sandwichianum* (Presl) Diels — Molokai; Faurie 297 (*l*).
**Fig. 140.** **Athyrium microphyllum* (Sm.) Alston — Hawaii; HBS 3145 (*l*).
**Fig. 141.** *Cystopteris Douglasii* Hook. — Baldwin: Haw. Ferns s. n. (*l*).

Dryopteridoideae

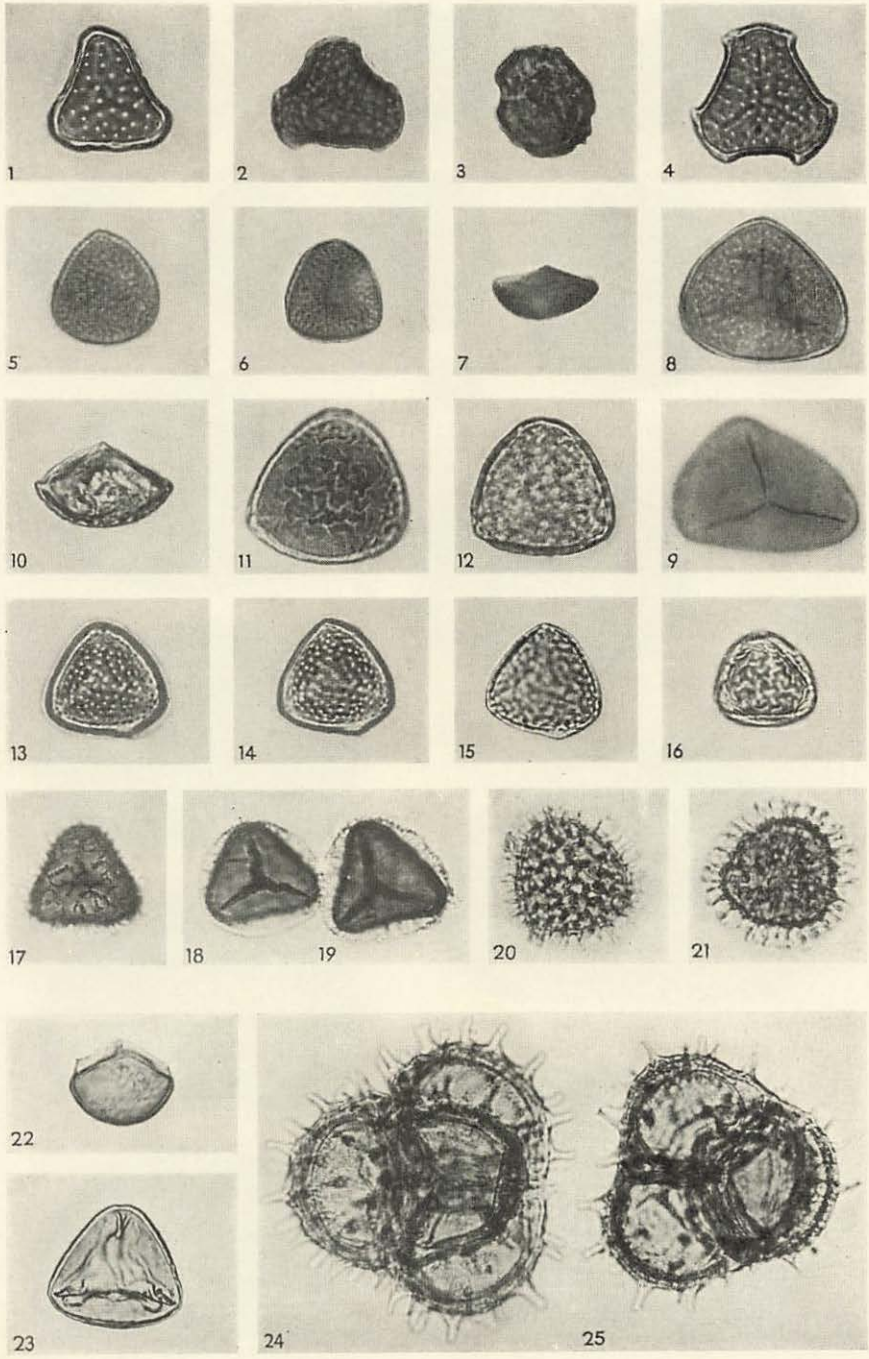
**Fig. 142.** **Dryopteris cyatheoides* (Kaulf.) O. Kze — Oahu; Degener 9231 (*l*).
**Fig. 143.** *D. goggilodus* (Schk.) O. Kze emend. Fosberg — Oahu; Andersson s. n. (*l* of spore with but fragments of spiny coating left).
**Figs. 144—145.** *D. honolulensis* (Hook.) C. Chr. — Haw. Islds: s. l.; Hillebrand (*l*). Fig. 144: surface view, Fig. 145: optical cross section. (Spores with spiny coating present).
**Figs. 146—147.** *D. latifrons* (Brack.) O. Kze — Baldwin: Haw. Ferns s. n. Fig. 146: *l*, optical cross section, Fig. 147: *p*, d:o. (Spores with spiny coating present).
**Fig. 148.** **Polystichum Hillebrandii* Carruth. — E. Maui; Faurie 361 (*l*).
**Fig. 149.** *Cyrtomium caryotideum* (Wall.) Presl — Oahu; Degener, Martinez, Topping and Bush 11967 (*l*).
**Fig. 150.** *Tectaria Gaudichaudii* (Mett.) Maxon — Oahu; Skottsberg 357 (*l*).

Polypodioideae

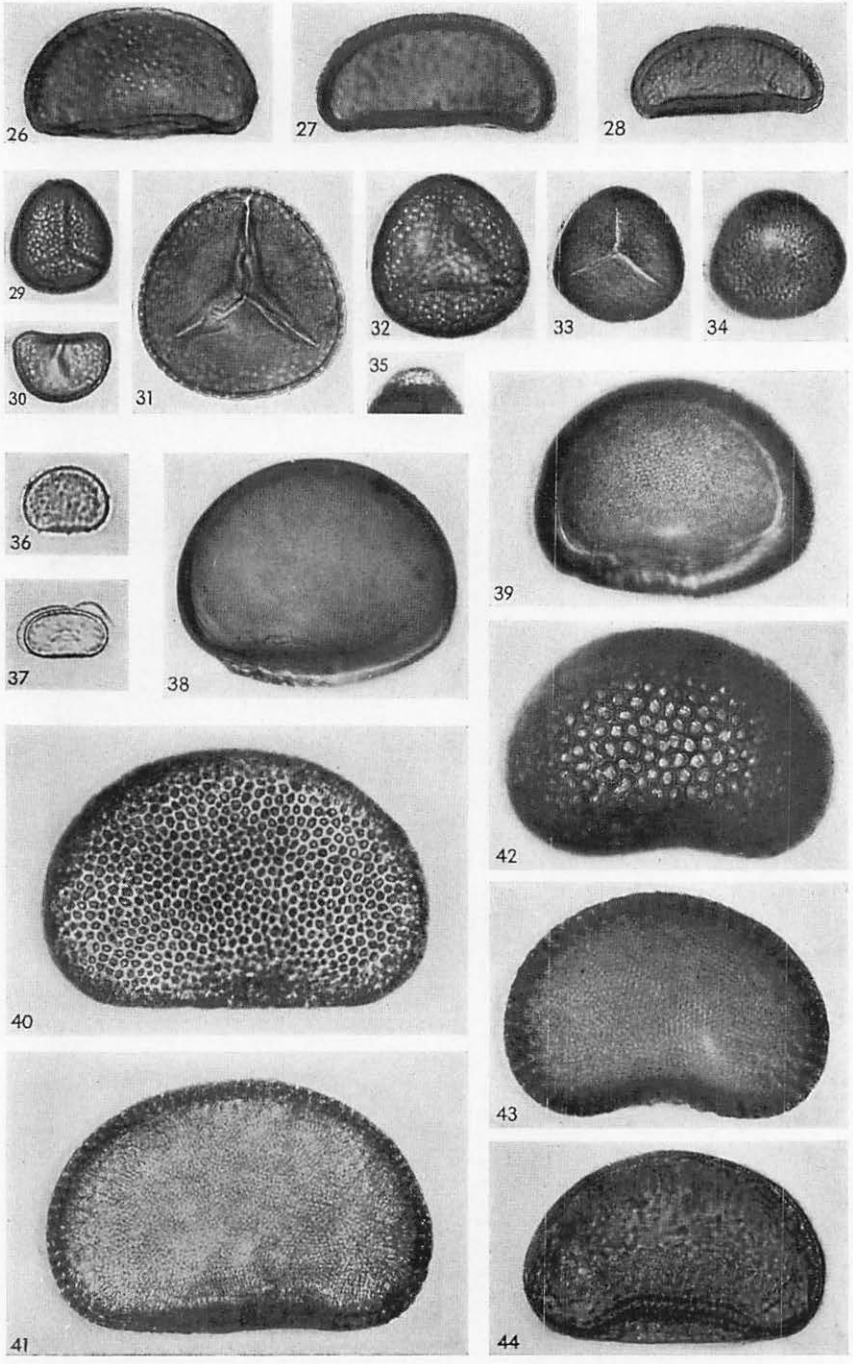
**Figs. 151—152.** **Polypodium abietinum* D. C. Eaton — Kauai; Faurie 90. Fig. 151: *l*, Fig. 152: *p* (both = surface view).
**Fig. 153.** **P. Hookeri* Brack. — W. Maui; Selling s. n. (intermediate between *p* and *l*, surface view).
**Fig. 154.** **P. sarmentosum* Brack. — Baldwin: Haw. Ferns s. n. (*p*).
**Fig. 155.** **P. tamariscinum* Kaulf. — Oahu; Skottsberg 58 (*l*, surface view).
**Figs. 156—157.** *P. atropunctatum* Gaud. — W. Maui; HBS 2638 (*l*). Fig. 156: surface view of immature spore, Fig. 157: d:o of mature spore.
**Figs. 158—159.** *P. pellucidum* Kaulf. — Hawaii; Skottsberg 732. Fig. 158: *l*, surface view, Fig. 159: *p*, optical cross section.
**Fig. 160.** *P. spectrum* Kaulf. — Baldwin: Haw. Ferns s. n. (*l*, optical cross section).

Elaphoglossoideae

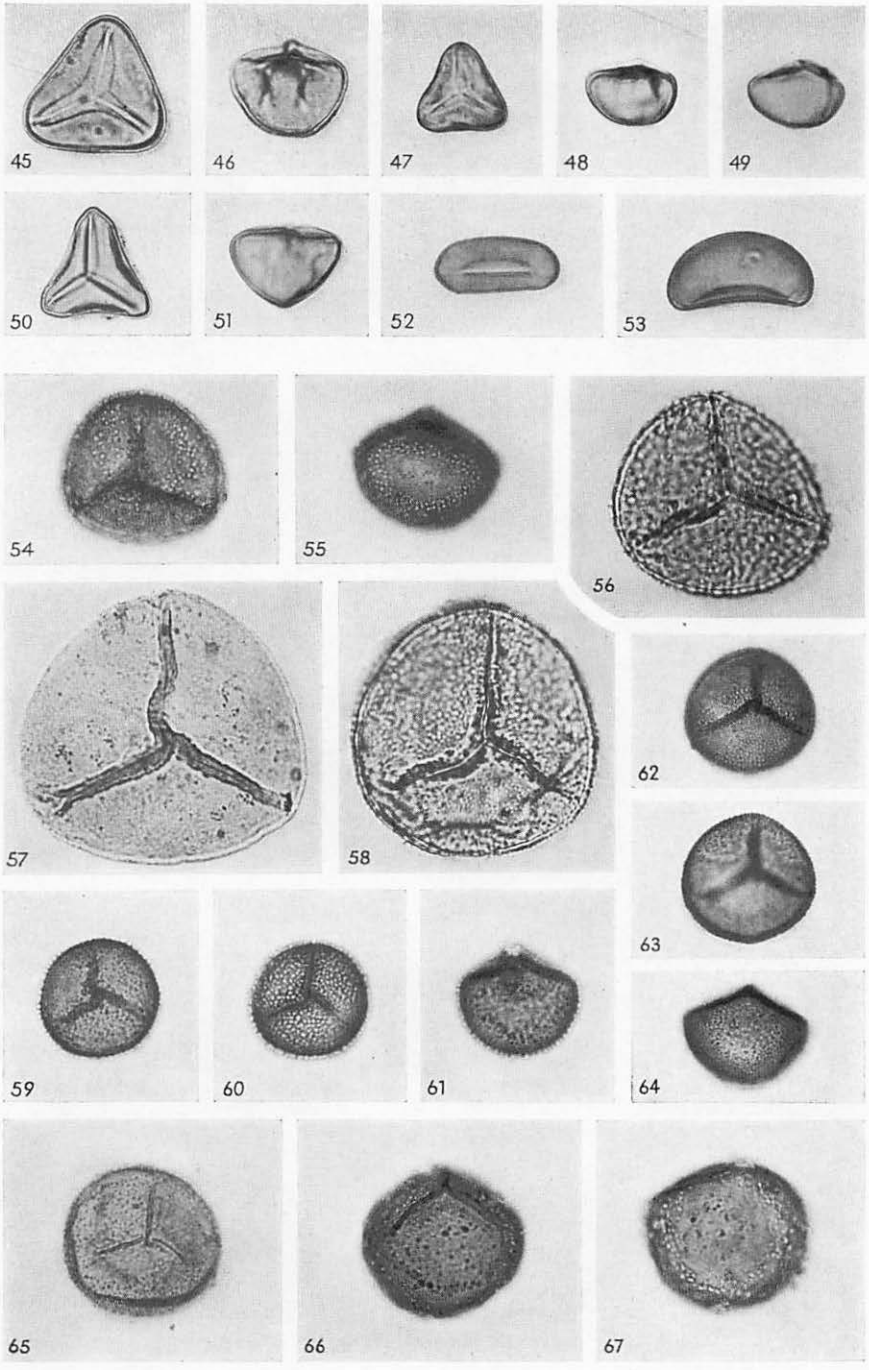
**Fig. 161.** **Elaphoglossum gorgoneum* (Kaulf.) Brack. s. str. — W. Maui; Selling s. n. (*l*).



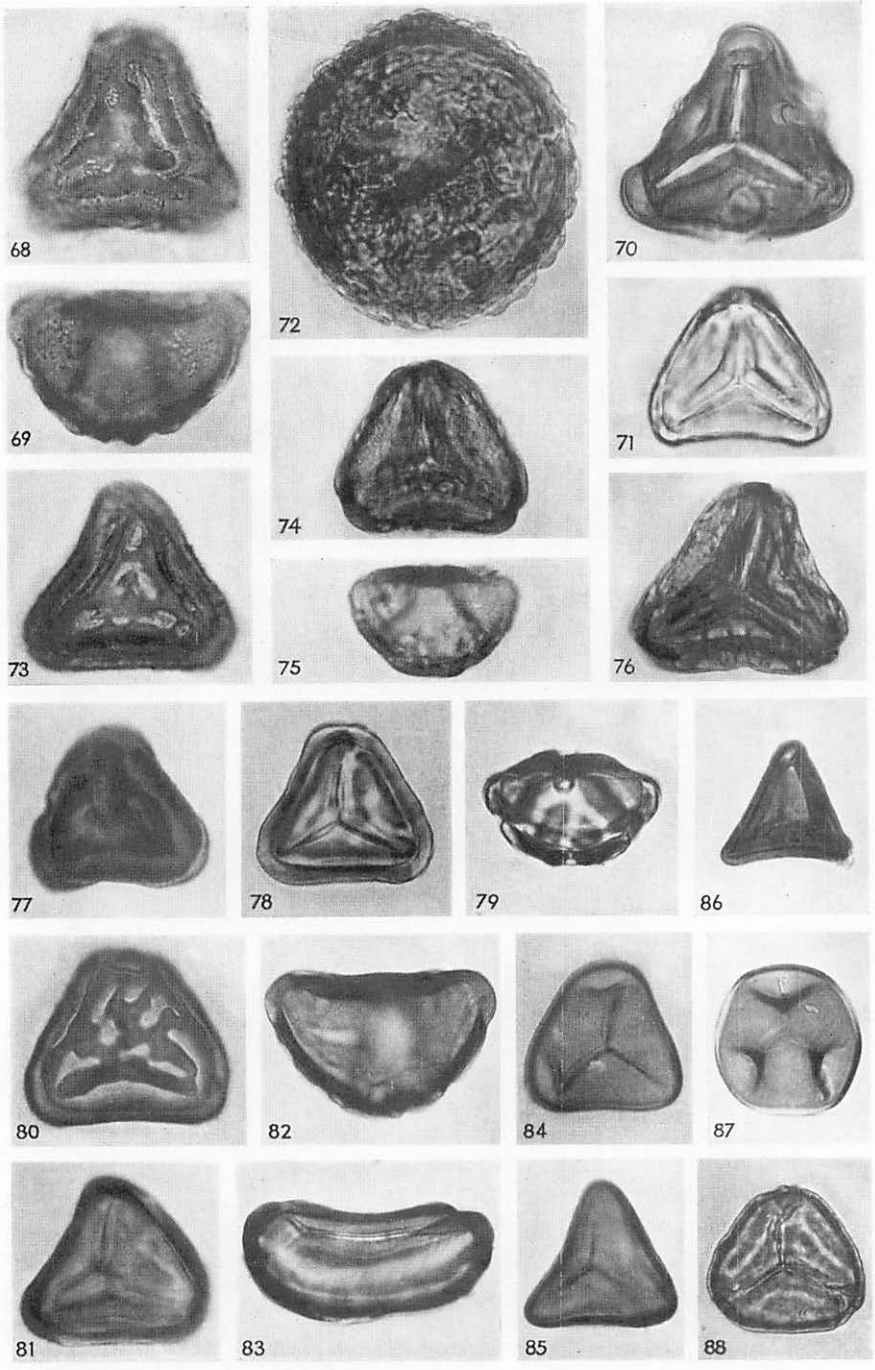

*Lycopodiaceae* (1—21) and *Selaginellaceae* (22—25).



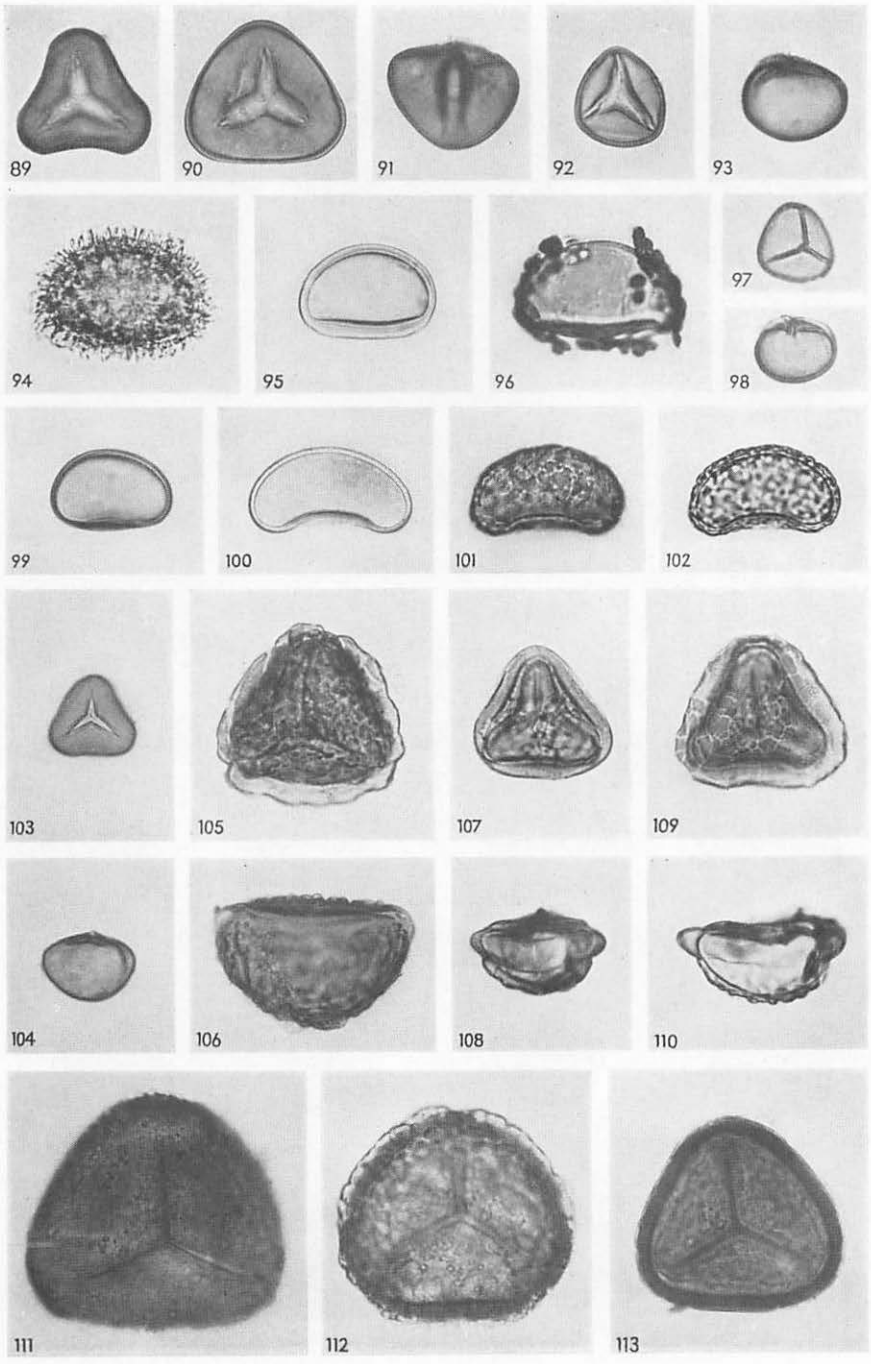

*Psilotaceae* (26—28), *Ophioglossaceae* (29—35), *Marattiaceae* (36—37), and *Schizaeaceae* (38—44).



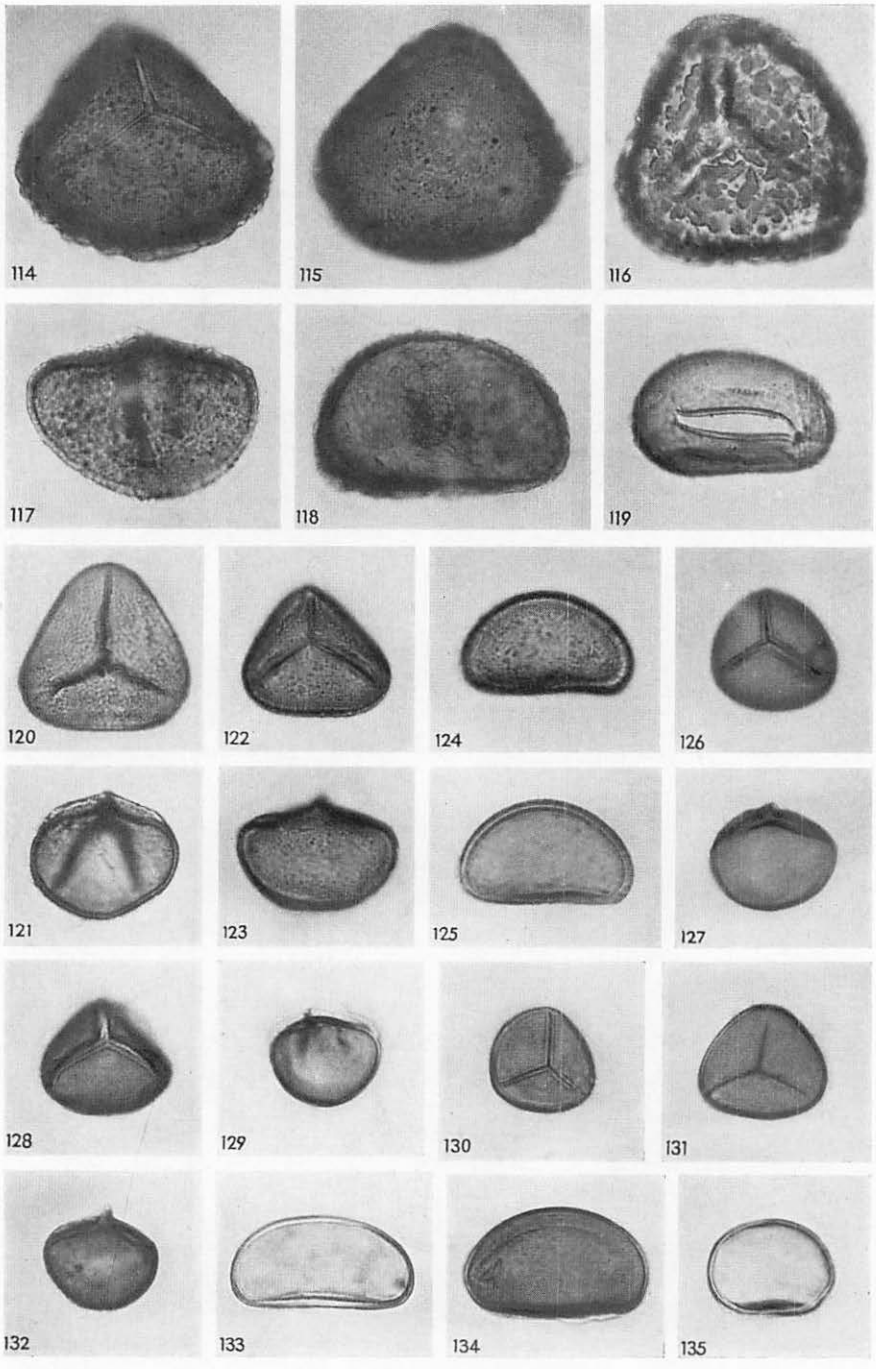

*Gleicheniaceae* (45—53) and *Hymenophyllaceae* (54—67).



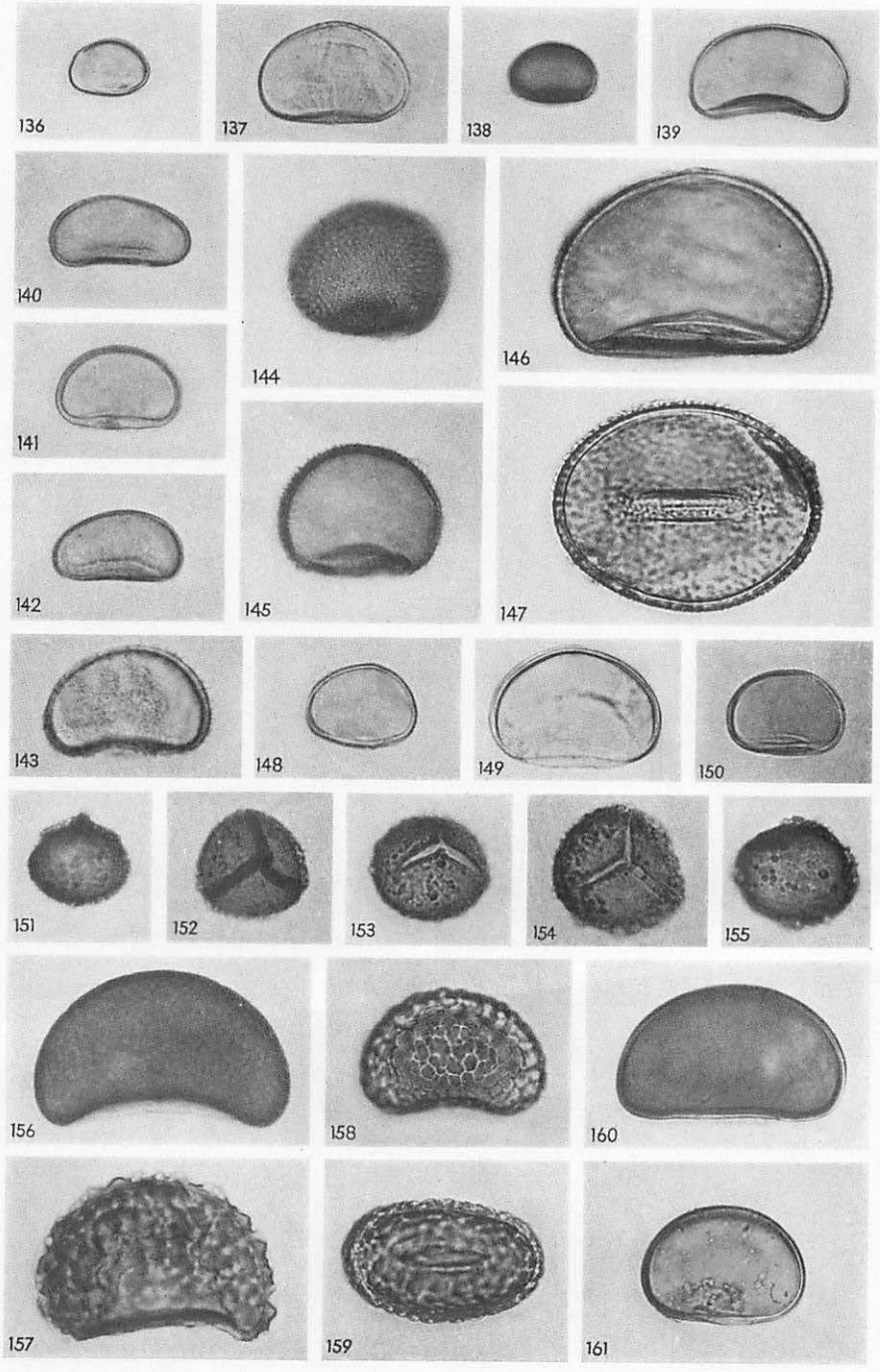

*Dicksoniaceae.*




*Polypodiaceae* (I).




*Polypodiaceae* (II).




*Polypodiaceae* (III).