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A Peculiar Asplenium from the Hawaiian Islands

By OLOF H. SELLING
PALEOBOTANICAL DEPARTMENT, SWEDISH MUSEUM OF NATURAL HISTORY

INTRODUCTION

In the summer of 1852, N. J. Andersson, Swedish taxonomist and plant geographer, visited the Hawaiian Islands as a member of the Eugenie expedition. Like the bulk of his other collections from this voyage, the Hawaiian plants were not worked up but were stored in the Riksmuseum, Stockholm, and not made fully accessible until much later. Unfortunately, they share with other contemporary collections from the islands the drawback of being poorly labeled. Andersson visited the islands in time to procure plants that have now disappeared or become extremely rare. *Euphorbia Deppeana* (*E. festiva*) (Skottsberg, 23)[1] and *Tetramolopium tenerrimum* (Selling, 21), both in the Riksmuseum and determined by Skottsberg, have thus not been met with since, and *Trema amboinensis* seems to be another interesting find (Skottsberg, 23; Selling, 21). Andersson's Hawaiian ferns have hitherto yielded no notable specimens, however. Mettenius certainly left a manuscript name, *Leptolepia Anderssonii* for an Oahu fern long reported to have been collected only by Andersson (Kuhn, 14, p. 348). Christensen (9, 10), however, reduced it to synonymy with the common *Microlepia Speluncae* (Linnaeus) Moore, a view recently confirmed by me (20) on i.a. spore characters.

While examining some unidentified ferns in the Riksmuseum, I found a single specimen from the Andersson collection without definite determination (fig. 1). It had been gathered in the mountains back of Honolulu and roused my interest as I had seen no such morphological type from the islands. Attached to the sheet is a label from

[1] Numbers in parentheses refer to Literature Cited, p. 183.

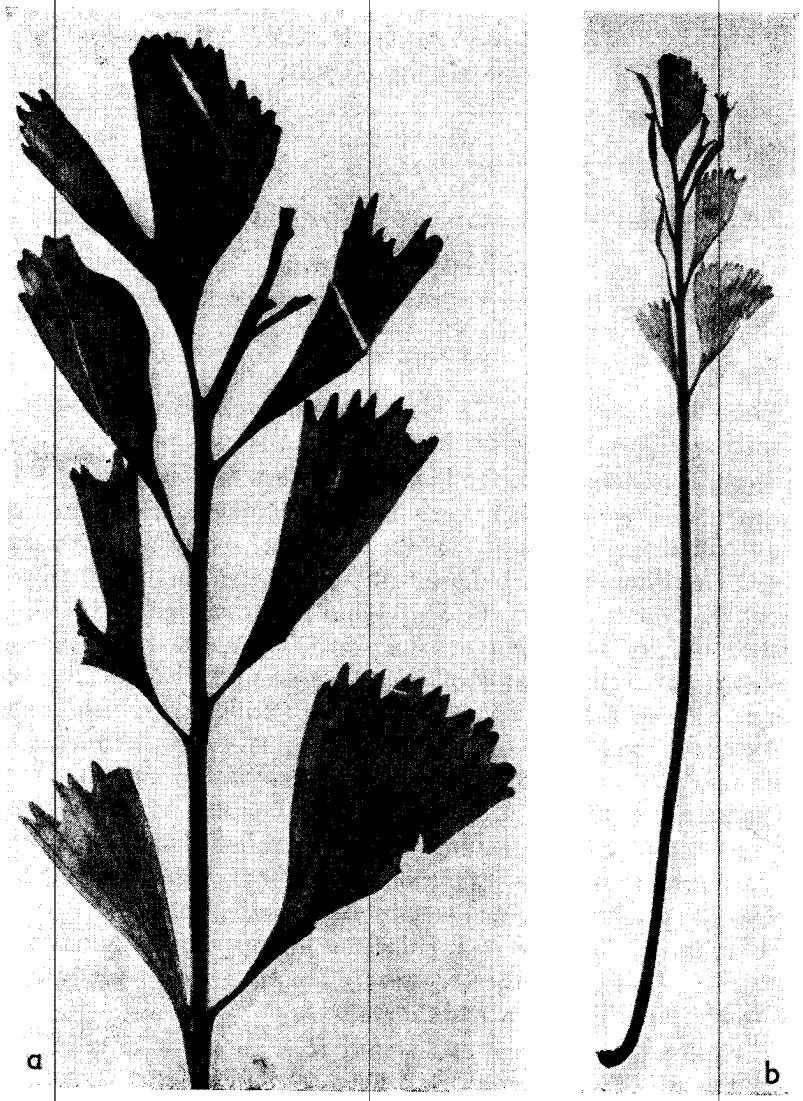

FIGURE 1.—*Asplenium Kaulfussii* f. *paradoxum:* **a**, upper part of frond × 1.4; **b**, entire frond × 0.35.

the nineteenth century with the notation "Asplenium (?) mirabile M[ihi] sp. nov."—a name not published for anything similar to this plant. The species Copeland designated thus (11) is something entirely different.

The plant looks like a living fossil. At first it could not be even properly referred to any known genus, and correspondence with leading pteridologists threw no positive light on the matter. The herbarium of Bishop Museum contained nothing like it (M. C. Neal, letter). The plant had to be made the subject of a special study, the result of which is presented below. A brief note on the specimen was included in a previous paper by me (20, p. 62). For valuable information and fruitful discussions I am particularly indebted to Dr. E. B. Copeland of Berkeley, to Dr. W. R. Maxon of Washington, D. C., and to Miss Marie C. Neal of Bishop Museum.

PREVIOUS WORK ON THE SPECIMEN

The fact that Mettenius named one of Andersson's Oahu ferns, as noted above, suggests that he had worked on other parts of the collections also, and that the unknown handwriting on the label was his. Comparison with letters from Mettenius (15) in the library of the Royal Swedish Academy of Sciences, Stockholm, proved this supposition to be correct and gave the following information.

On November 20, 1860, Mettenius received the entire collection (including extra-Hawaiian ferns) for determination. On April 12, 1861, he returned it without having concluded his study, as with the advent of the Civil War all chances of consulting Brackenridge's types (8) were indefinitely postponed. When the war was over, Mettenius was no longer alive. His study remained unpublished except for some data published by Kuhn (13, 14).

His letter of April 12, 1861 contains some passages of interest. Under *Microlepia* he mentions the *Leptolepia* referred to above, expressing doubts as to its taxonomic value:

> bei einer *Microlepia,* aus der Abtheilung *Saccoloma* [=*M. Anderssoni* Mettenius Ms. in spec. orig. (20, p. 45) =*M.* (*Saccoloma*) *Anderssonii* Mettenius in litt., 12. IV. 1861 (15) = *Leptolepia Anderssonii* Mettenius ex Kuhn (14, p. 348) = *Davallia Anders*[*!*]*onii* (Mettenius) Baker (7, p. 200; non *D. Andersonii* Mettenius in 13, p. 143; 6, p. 467, etc.) = *Microlepia Speluncae* (Linnaeus) Moore (9, 10, 20)], ist die Gewissheit, dass sie neu sei nicht so gross; Jedenfalls aber sind die Eigenthümlichkeiten dieses Farns in den Beschreibungen verwandter Arten nicht zu finden.

He also states that

Manche Arten von den Sandwich Inseln, die man mit amerikanischen oder mascarenischen Arten identifizierte, sind entschieden verschieden, so z.B. das *Acrostichum* [= *Elaphoglossum*] *micans* von *splendens* [13, p. 50; 10, p. 20], bei andern, wie z.B. *Aspidium* [= *Tectaria*] *Gaudichaudii* [13, p. 123; 10, p. 11], [*Lindsaya* (=*Lindsaea*) *Macraeana* (Hooker et Arnott) Mettenius ms. = *L. repens* (Bory) Beddome var. *Macraeana* (Hooker et Arnott) C. Christensen], *Asplenium Forsteri* musste der Name geändert werden.

Then comes the following interesting passage:

Einen sterilen überaus merkwürdigen Farn habe ich *Asplenium mirabile* benannt, indem ich vermuthe dass dieses Blatt, ähnlich wie bei *A. dimorphum* sich zu dem fruchtragenden verhalte; doch ist dieses nur eine Vermuthung, die durch einen Durchschnitt des Blattstiels hätte geprüft werden können. Doch habe ich diese Operation unterlassen, da ich fürchtete, dass dieselbe an dem einzigen Exemplar nicht erwünscht sein werde.

A few days before this letter was discovered I had undertaken the "operation." After continued comparative studies, it gave the clue to the determination, just as Mettenius supposed.

MORPHOLOGY

Before entering on the anatomy, I give the following notes on the morphology (figs. 1-4, *a-c;* 6, *i*).

Frond sterile, 36 cm. long, carnose, brownish gray at base, otherwise grayish green (figs. 1; 2, *a*). *Petiole* 25 cm. long, about 0.5 cm. in diameter, forming a right angle just above base, slightly spiral toward right along its full length, adaxial side with a deep central furrow and a shallower furrow on each side of this (each flanking furrow with parenchymatous strands forming pneumathodes); abaxial side correspondingly bulging and with a faint median furrow, furrows vanishing toward apex (all these probably largely if not entirely absent in the living state, see below). On both sides of the petiole scattered, brown, multicellular, transparent scales, placed on very faintly elevated portions, frequent at base, and typically developed there only, unsymmetrically shieldlike, strongly pointed in upper part, ± rounded and provided with a number of projections in the lower part. These projections, or at least many of them, with an apical, dark-brown, slightly longitudinal secretion cell (figs. 2, *j;* 3, *a*). *Rachis* 11 cm. long, dichopodial (apical dichotomy only apparent), with much scattered and much reduced, ± hairlike scales (fig. 2, *i*). *Pinnae* (figs. 1; 2, *a-h;* 6, *i*) seven in number, in two rows, not strictly lateral but slightly reflexed toward adaxial side, none of them strictly opposed, uppermost pinna extending beyond apex of rachis. Each pinna 4.5 (3.9–5.0) cm. in average length, about 2.3 (1.5–3.2) cm. in average greatest width, about 0.1 cm. across at base, with a short stipe (about 0.5 cm.) evenly merging into roughly inversely-triangular lamina; two of the laminae deeply bilobate, their lobes bent toward each other and toward the rachis. Entire pinnae always unsymmetrical (see below) and slightly concave-convex, margins entire except distally; here coarsely serrate throughout and in several cases changing almost into lobes. Teeth 8–17 per pinna, of varying sizes, generally 2–3 mm. long with slightly rounded apices.

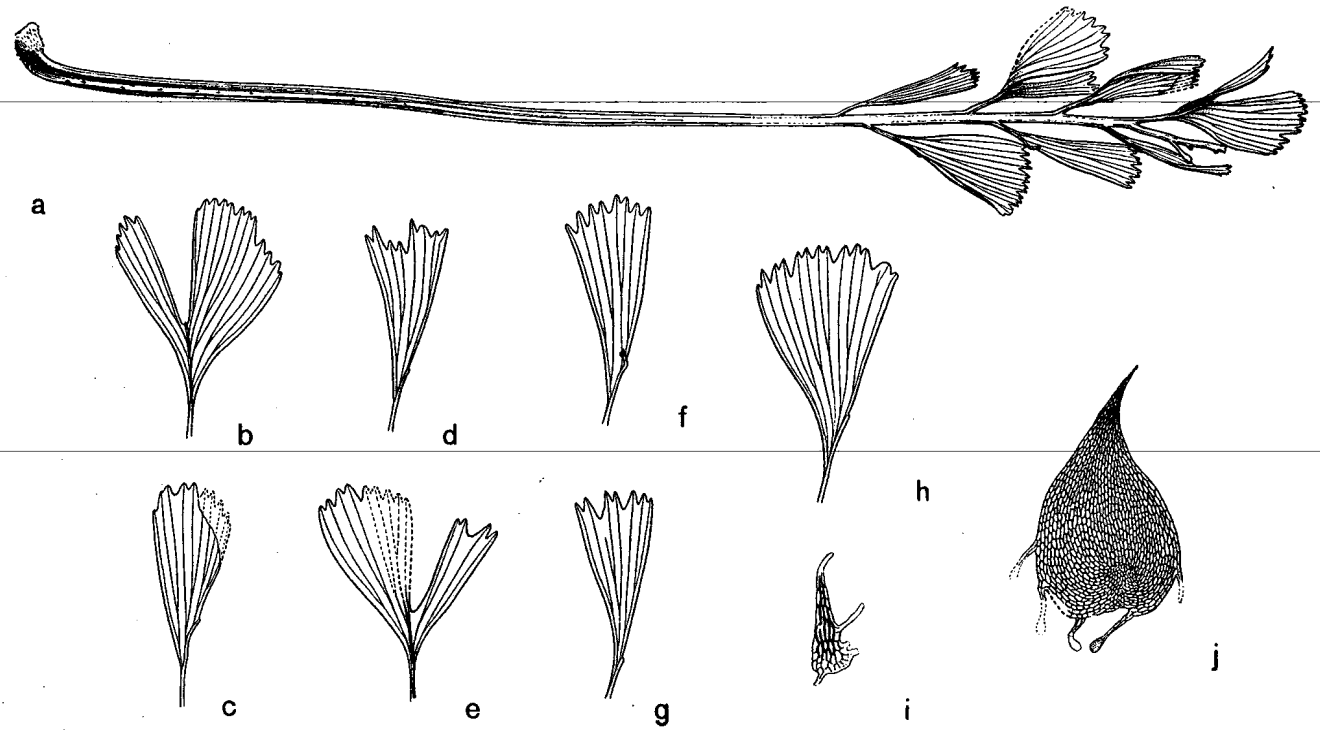

FIGURE 2.—*Asplenium Kaulfussii* f. *paradoxum:* **a,** restoration of living plant, × 0.45; **b-h,** pinnae (missing parts known from impressions on other pinnae; impressions lost in boiling specimen for examination), all × 0.9; **i,** scale from upper part of petiole, about × 9; **j,** scale from basal part of petiole, about × 18.

Main nerve generally only 0.25 to 0.50 as long as corresponding pinna [in one case continuing into a rather short (3 mm. long), not flattened branch, strongly bent toward the rachis and distinctly forked, that is, acting like a whole pinna], its branching dichopodial-helicoid, or in two cases (with early arrested attempts at) scorpioid (pinnae entire or bilobate, respectively), the branches dividing once dichotomously, each end almost invariably extending to the apex of one tooth (no fully developed tooth without nerve). *Epidermis* with vestiges of scales even on the laminae, not particularly strongly cutinized, not glossy, surface minutely rough when dry (fig. 3, *b*), its cells only slightly longitudinal or isodiametrical in surface view, though often angular, especially on adaxial side (fig. 4, *a*). On abaxial side of the frond cells with more undulating lateral walls and numerous, ± evenly dispersed and little characteristic longitudinal stomata (fig. 4, *b*, on the rachis following pneumathodes; see below), averaging about 54 × 30 μ (fig. 4, *c*).

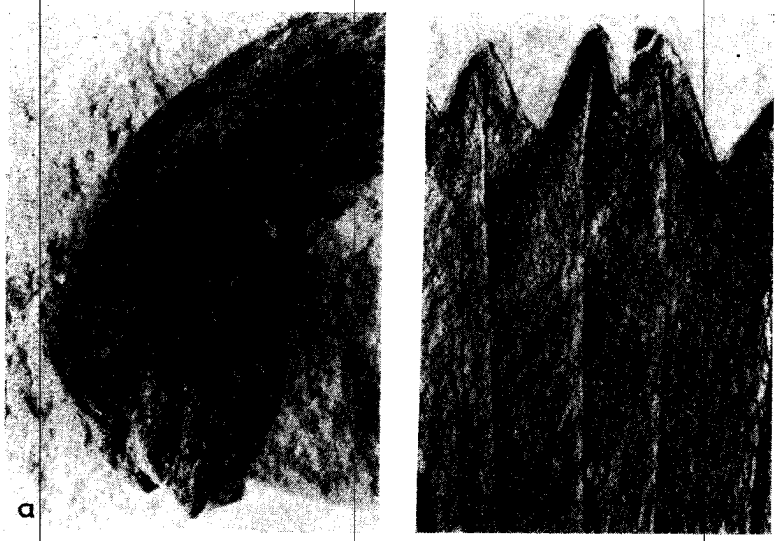

FIGURE 3.—*Asplenium Kaulfussii* f. *paradoxum:* **a,** basal part of petiole with scales, one fairly well-preserved, numerous fragments; **b,** detail of upper part of pinna shown in figure 2, *h,* showing appearance of surface before boiling and presence of several much reduced scales (both × 6.5).

ANATOMY

A cross section of the petiole 9 cm. from the base was examined (fig. 4, *d-e*). It remained much compressed even after boiling. The furrows mentioned above are no doubt largely, if not entirely, absent in the natural state, and the meristeles less strongly bent. The picture shows distelic organization, the convex sides of the bow-shaped meristeles facing each other. Probably the two branches unite higher up

in the rachis; this is indicated by the abaxial hooks on each and by the presence of an isolated xylem strand close to one of these hooks. The protoxylem occurs at both ends of each bow. Surrounding parenchyma with scattered fibers close to the meristeles and enclosed by a sclerenchymatous sheath only broken by two—originally probably lateral—strands of parenchyma (pneumathodes) (see further Potonié, 18) now sunk into the above-mentioned furrows. These strands are continuous with a hypodermal parenchymatous sheath about five cells thick.

DISCUSSION

The gross morphology is strange. Had this fern been found in the fossil state, represented merely by an impression, the establishment of a new peculiar genus would have been far from remarkable. At first glance, the large, triangular, coarsely dentate pinnae of mainly dichotomous venation suggest schizaeaceous affinities. That supposition is refuted, however, by the anatomy of the petiole, which is clearly aspleniaceous. The stele is of Ogura's *Asplenium* type (17, pp. 114-115, 382-384), which is found in most species of *Asplenium, Phyllitis, Camptosorus,* and *Ceterach.* Considering all characters cumulatively, *Asplenium* is the only choice here. There is complete agreement with this genus in the other anatomical features, in the epidermis and scales (appearance as well as distribution), and in all parts of the gross morphology except the laminae of the pinnae. No such agreement is found outside the genus. The idea of a monstrosity of unexpected appearance then comes into the foreground. The question is whether any species in the islands could have produced this pseudoarchaic type. If so, the peculiar behavior of the main nerve of the pinna would be satisfactorily explained, as well as the retarded apical growth of the frond in spite of its being evidently comparatively young.

I have examined every Hawaiian *Asplenium,* and originally every Hawaiian fern, in the Riksmuseum herbarium, supplementing these studies with data in literature. Judging by this survey, there is one species that might have produced the frond—the polymorphous *A. Kaulfussii* Schlechtendahl (s. lat.)—unless there was a closely related species which is now extinct. *A. enatum* Brackenridge is somewhat different (Skottsberg, 22, p. 68 ff.). A typical frond of *A. Kaulfussii* is shown in figure 5, *a.* In others, the shapes of the pinnae, especially

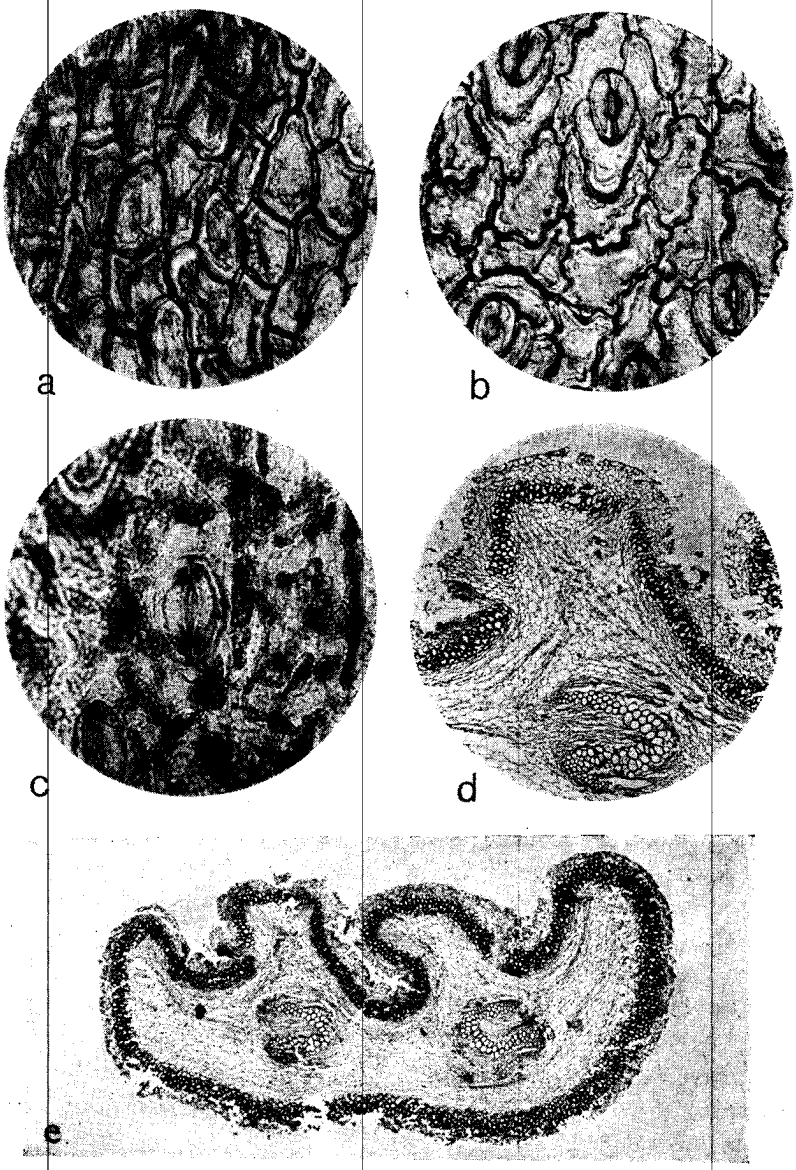

FIGURE 4.—*Asplenium Kaulfussii* f. *paradoxum:* **a,** epidermis from upper part of pinna, × 195; **b,** epidermis with stomata from lower part of pinna, × 195; **c,** guard cells, × 240; **d,** detail of cross section of petiole, showing one of the meristeles and one of the parenchymatous strands penetrating sclerenchymatous sheath, × 35; **e,** cross section of petiole; much less compressed in the living state, × 21.

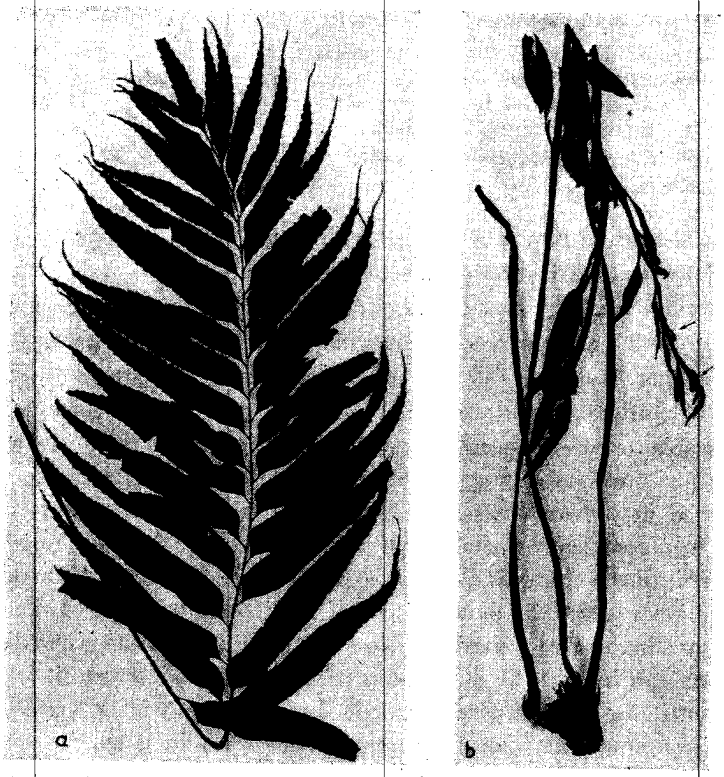

FIGURE 5.—*Asplenium Kaulfussii:* **a,** pinnae typical (Oahu, in mountains, 1852, *Andersson,* without number); **b,** fairly young specimen showing part of short rhizome with scales, long petiole with torsions, and some aberrant, obtuse pinnae (Kauai, Kauhao, 800 m., 1910, *Faurie 210*). Specimens in Riksmuseum, Stockholm; both × 0.33.

the basal ones, are somewhat modified, and there are slight indications that growth is suppressed apically as well as on the basipetal side of the pinnae and concentrated on the basal part of the acropetal side. These features are by no means confined to *A. Kaulfussii* (figs. 5, *b;* 6, *a-h;* see also plates in Mettenius, 16), but their combination with excellent agreement in the texture and color of the frond, in the anatomy, scales (see Skottsberg, 22, p. 69, as to differences between *A. Kaulfussii* and *A. enatum* in the scales), and in other characters warrants the tentative reference of the frond to *Asplenium Kaulfussii* as a new form:

Asplenium Kaulfussii Schlechtendahl forma **paradoxum,** new form.

Ab A. Kaulfussii differt pinnis sat paucis, c. 4.5 × 2.3 cm., laminis pinnarum obtriangularibus, interdum dichotome incisis, apice dentibus 8–17, c. 2–3 mm. longis dentatis, nervatura basi dochopodialibus, helicoidaliter vel leviter scorpiodialiter ramosis, ceterum dichotomis.

Hab. in insulis Hawaiiensibus, insula Oahu, Koolau, 1852; N. J. Andersson (Museum Holmiense).

It should be remembered that Hillebrand (12; Skottsberg, 22, p. 68 ff.) recognized several varieties of *A. Kaulfussii,* and described three closely related species later rejected by Christensen (10, p. 26), who considered them merely abnormally cut forms. It is also worth noting that Robinson (19, p. 207) designates the pinnae of *A. Kaulfussii* "obtuse at apex; broadly ovate," a description which is not applicable to typical specimens; possibly, the passage refers to slightly abnormal forms showing indications of the tendency that is so pronounced in f. *paradoxum. A. Kaulfussii,* taken in its widest sense, may be a genetically unstable species. The form *paradoxum* might be an occasional mutant that never became fertile, in which the arrested apical growth and the development of the remaining parts of the pinnae have become very marked. No external causes of its unique development can be traced. The type is of considerable interest, as it supplements our picture of the morphological range of the genus and indicates numerous morphogenetic potentialities in a species of the *Kaulfussii* type. *A. Kaulfussii* might be a suitable object for genetic and physiological experiments with a view to interpreting the underlying causes.

The label of form *paradoxum* says "Honolulu: på bergen [in the mountains]. 1852." Andersson's Hawaiian labels are occasionally attached to specimens which were certainly collected elsewhere. In this case the label is most likely correct. I have gone through Andersson's Hawaiian ferns, and found no instance of confusion. The exact locality in the mountains cannot be determined, however. Andersson, who visited Oahu from June 22 to July 3 and from August 25 to 26, 1852, made several excursions to the Koolau Range back of Honolulu, two of which he described, but only in general terms, as far as botany is concerned (4, pp. 44-48, 53-61; 5). These refer to Nuuanu Valley, the adjoining mountain crests, and the lowlands below Nuuanu Pali. During his August excursion he visited only "a luxuriant valley [possibly Pauoa Valley] adjoining the aforementioned Nuuanu Valley"

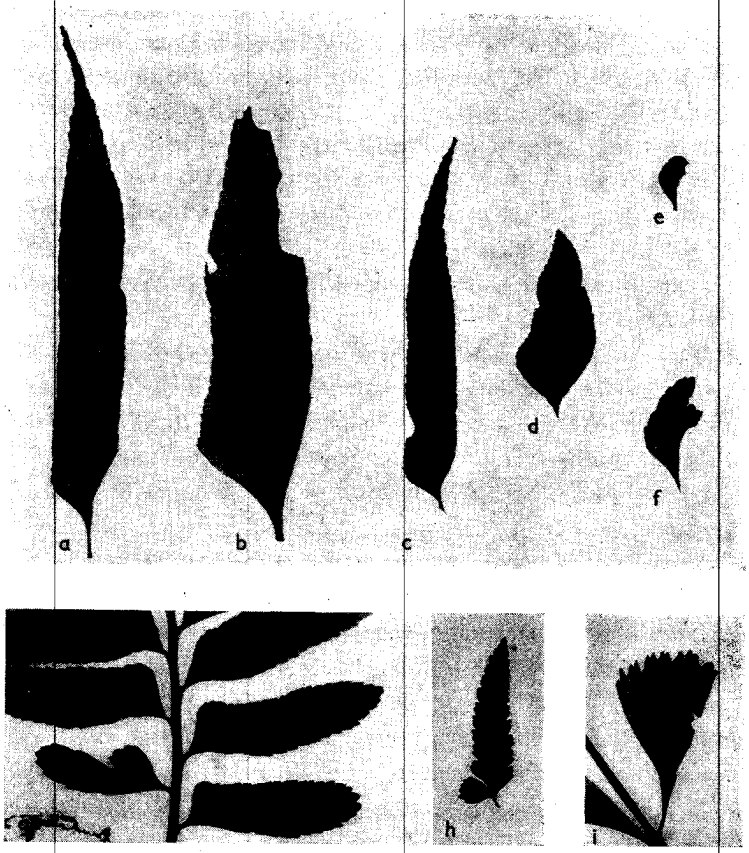

FIGURE 6.—Pinnae of *Asplenium Kaulfussii* and some related species, showing transitions toward the pinna type in *A. Kaulfussii* form *paradoxum:* **a,** *A. Kaulfussii,* typical pinna (Oahu, 1852, *Andersson,* without number); **b,** *A. Kaulfussii* variety *membranaceum* Hillebrand, broad pinna with stronger development of acropetal basal part (Hawaii, *Faurie 211*); **c,** *A. enatum* Brackenridge, pinna fairly typical in general outline, with lobation in acropetal basal part (Kauai, *Faurie 210*); **d,** same species, atypical (basal) pinna with stronger development of acropetal basal part (Baldwin: Hawaiian Ferns); **e, f,** same species, atypical (basal) pinnae with growth restricted to the acropetal basal part (West Maui, *Faurie 214*); **g,** *A. compressum* Swartz, various transitions (St. Helena, cultivated in Hort. Berol.; *Urban,* without number); **h,** *A. anomodon* Colenso, basal lobe developed, though without suppression of apical growth of pinna (New Zealand, *Du Rietz 1641:1*); **i,** *A. Kaulfussii* form *paradoxum,* entire pinna, supposed to correspond to acropetal basal part of a typical pinna (Oahu, *Andersson,* without number). All specimens in Riksmuseum, Stockholm; best transitional types available. All × 0.5.

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