

A Revision of the Genus *Sadleria* (Blechnaceae)¹

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ABSTRACT: The genus *Sadleria* is revised. Problems with nomenclature and species descriptions are reviewed and clarified. New keys are presented. A new species is described.

WHILE DESCRIBING A new species of *Sadleria* Kaulf., it became obvious to me that there was confusion regarding circumscription of other species of the genus, their correct names, and their descriptions, and that various published and unpublished keys for the genus did not work well. In this paper I review and define the five generally recognized species, describe a sixth, and clarify some nomenclatural problems.

Sadleria is confined to the Hawaiian Islands, but differs little from *Blechnum* (Hooker and Arnott 1832, Hillebrand 1888, Robinson 1913, Bower 1928, Copeland 1947, Joe 1960, Stone 1967, Fosberg 1976). It is usually distinguished from the latter by its pinnate-pinnatifid to bipinnate fronds and its erect to arborescent caudices (Copeland 1947, Stone 1967, Lloyd 1976). However, neither of these characteristics is completely lacking in *Blechnum*, and the arborescent caudices are absent in *S. squarrosa* and *S. unisora*. Robinson (1913) wrote that *Sadleria* conspicuously differed from *Blechnum* in its greater size, rigidity, and number of scales, but these are features also shared by some species of *Blechnum*. *Sadleria* does differ from other blechnums in that every species of *Sadleria* produces only 16 spores per sporangium. In spite of the overlapping of characters, all species in *Sadleria* are clearly related to each other and easily recognized as a group distinct from *Blechnum*.

The Hawaiian names (Pukui and Elbert 1965) for the *cyatheoides* group are 'ama'u, ma'uma'u, and pua'a 'ehu'ehu ("red pig"), or plural 'ama'uma'u. In Hawaiian theology 'ama'u is one of the forms that the pig demigod Kama-pua'a takes at will. The smaller *Sadleria squarrosa* is called 'apu'u or 'āpulu.

A red dye for *kapa* bark cloth was extracted from the trunk of larger *Sadleria* species, and occasionally the starchy pith was cooked and eaten (Degener 1930). *Palaholo*, a rolled-up frond of the 'ama'u fern or a paste made of sap from the fronds, was used to repair *kapa* or weld strips of it together (Bryan 1915, Pukui and Elbert 1965).

Sadleria plants are much photographed, frequently appearing on magazine covers and tourist advertisements, and are noted for the pink or red young leaves.

Taxonomic History

Kaulfuss (1824) described the genus *Sadleria* with the species *S. cyatheoides*, named in honor of Dr. Joseph Sadler, a physician who studied the ferns of his native Hungary. Kaulfuss based his description on material collected by Adelbert Chamisso, the naturalist aboard the Russian expedition ship *Rurick* under the command of Otto von Kotzebue (1821). Since 1824, 11 more species and three varieties of *Sadleria* have been described: *S. pallida* Hook. & Arn. (1832) [retracted by Hooker (1860), but reinstated by Hillebrand (1888)]; *Blechnum fontanesianum* Gaudich. (1827) (= *S. cyatheoides*); *S. (Blechnum) souleyetiana* (Gaudich., 1854a) Moore (1857); *S. (Blechnum) squarrosa* (Gaudich., 1854b) Moore (1857); *Blechnum kaulfussianum* Gaudich. (1854c) (= *S. cyatheoides*); *S. (Blechnum) polystichoides* (Brack., 1854) Heller (1897) (= *S. squarrosa*); *S. (Polypodium) unisora* (Baker, 1874) Robinson (1913); *Gymnogramme sadlerioides* Underw. (1897) (= *S. unisora*); *S. hillebrandii* Robinson (1913) (= *S. pallida*); *S. fauriei* Copel. (1914) (= *S. pallida*); *S. rigida* Copel. (1916) (= *S. pallida*); *S. (Blechnum) squarrosa* (Gaudich., 1854c) Moore

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(1857) β var. *tripinnatifida* Hillebr. (= *S. squarrosa*); *S. squarrosa* γ var. *intermedia* Hillebr. (= *S. squarrosa*); and *S. (Blechnum) squarrosa* (Gaudich., 1854c) Moore (1857) δ var. *depauperata* Hillebr. (= *S. unisora*).

Hillebrand (1888) was the first to publish a review of the genus, recognizing four species (*Sadleria cyatheoides*, *S. pallida*, *S. souleyetiana*, and *S. squarrosa*) with three varieties. Robinson (1913) recognized Baker's *Polypodium unisora* by adding *Sadleria unisora* as a fifth species. She also treated *S. pallida* Hook. & Arn. as a synonym for *S. cyatheoides* Kaulf. and described *S. hillebrandii* as a nomen novum for *S. pallida*, thus creating a persisting problem regarding application of these names and confusion about the correct identity of the species involved (Skottsberg 1942, Holbrook-Walker and Lloyd 1973, Degener 1974, Fosberg 1976, Lloyd 1976).

Christensen (1925) recognized seven species, including *S. fauriei* and *S. rigida*. Copeland (1947) and Stone (1967) mentioned that six or seven species existed. In recent years the five species recognized by Robinson have generally been accepted by local naturalists and are listed in unpublished fern lists by C. Lamoureux and W. H. Wagner, Jr.

MATERIALS AND METHODS

This revision is based on fieldwork on all the major Hawaiian Islands and study of herbarium specimens of MICH and BISH as well as holotypes and other important specimens from K, B, P, GL, LE, and MPPD.

Dorothy Minard-Elsaesser's thesis (1982) on the systematics of *Sadleria* was used extensively. She examined and measured 1054 herbarium specimens and photographs from B, BISH, BM, FI, GH, GL, K, MICH, NY, P, UC, and US. Her measurements were used, with permission, but with the following modifications. If my examination of plants in the field, or from more recent collections, differed from hers, I modified the measurements accordingly. She recognized *S. rigida* as a species distinct from *S. pallida*, but stated that the two might be one species. I recognize them as one species, and because *S. rigida* is generally smaller than *S. pallida*, many of the

measurements for *S. pallida* were changed when the two sets of data were combined. All measurements are given as length followed by width.

Chromosome Number

The chromosome number $n = 33$ (obtained from *Sadleria squarrosa*) (Walker 1973, F. S. Wagner 1995) falls within the aneuploid series of *Blechnum*. The precise number has been difficult to obtain because the chromosomes are quite variable in size, and although they pair nicely, some very large chromosome pairs are confusing (F. S. Wagner 1995).

Ecology and Distribution

Sadleria species are found in habitats ranging from exposed, bare, recent lava flows; to mesic and wet rain forests; and to dark, damp, steep valley walls. *Sadleria cyatheoides* is among the first invaders of exposed, new lava flows but is occasionally found in closed-canopy forests. *Sadleria pallida* is most common in wet, closed-canopy forests but is also found in exposed areas with high rainfall. *Sadleria souleyetiana* is most common in mesic to wet forests but may be found in other habitats. *Sadleria squarrosa* and *S. unisora*, as well as *S. wagneriana*, sp. nov., are limited to dark, moist environments, usually on nearly vertical walls of streams.

Origin and Relationships

Previous authors (Hooker and Arnott 1832, Hillebrand 1888, Robinson 1913, Bower 1928, Copeland 1947, Stone 1967, Fosberg 1976) accepted the probable monophyletic origin of *Sadleria* from *Blechnum* as the result of a single introduction into the Hawaiian Islands. After the original introduction the species probably arose autochthonously, with geographic isolation and genetic drift in diverse habitats on the Islands.

Sadleria can be divided into two groups based on several characters. (1) The *cyatheoides* group includes *S. cyatheoides*, *S. pallida*, *S. souleyetiana*, and *S. wagneriana*, sp. nov. These species are variable in size but with fronds usually at least 0.5 m long, often much longer, and deeply pinnate-pinnatifid to bipinnate at the bases of

larger pinnae. The bases of the sinuses have a narrow, cartilaginous, translucent bar perpendicular to the costa connecting the segments, usually making them less than completely bipinnate. All except *S. wagneriana*, sp. nov. lack glands. The spores, without perispore, are smaller than those of the next group: 42.0–70.0 (mean = 53.5) μm long, 26–45 (mean = 35.4) μm wide (Lloyd 1976); 50–64 (mean = ca. 55) μm long, 31–42 (mean = 34) μm wide (Selling 1946). (2) The *squarrosa* group includes *S. squarrosa* and *S. unisora*. Fronds are generally less than 0.5 m long, are fully bipinnate, have glandular trichomes on the pinnule margins and on the scales (most easily seen in the field, obscure on dried material), and larger spores: 58.0–81.0 (mean = 67.5) μm long, 37–45 (mean = 35.4) μm wide (Lloyd 1976); 60–75 (mean ca. 67) μm long, 37–51 (mean = ca. 44) μm wide (Selling 1946). Skottsberg's (1942) measurements of only four spores in this group showed little difference in size from his measurements of the *cyatheoides* group.

Hybrids

Plants intermediate between any species pair of *Sadleria cyatheoides*, *S. pallida*, and *S. souleyetiana* and between *S. wagneriana*, sp. nov. and *S. souleyetiana* have been found. Intermediates between *S. squarrosa* and *S. unisora* exist. The spores of these plants usually appear normal, although they are sometimes imperfectly formed; their viability is unknown. The intermediates are recognized by the quality and distribution of their scales, by their venation (field recognition is easier, because the veins are more clearly seen on live specimens), and by the number and shape of their ultimate segments. Examination of suspected hybrids reveals that they are not entirely intermediate in character, often resembling one putative parent more than another, suggesting backcrossing and introgression.

There are no documented hybrids between the *cyatheoides* group and the *squarrosa* group, although one plant (*Palmer 1034*, BISH) has characteristics that suggest this combination.

Intermediates between the species of the *cyatheoides* group are common. They occur most frequently where two species are sympatric in

such disturbed sites as near road construction and along trailsides. In some areas intermediates are common, with or without disturbance, but in other areas they are rare.

Taxonomic Problems

The taxonomic level at which intraspecific diversity in *Sadleria* is recognized in this paper needs explanation. Hawaiian seed plant species are noted for their intraspecific variation (Carlquist 1965, 1980, Gillett 1972, W. L. Wagner et al. 1990). In Hawai'i the endemic ferns also show substantial infraspecific variability, the nonendemic indigenous species show little, and recently introduced ferns almost none. Among endemic species there may be marked variation in one or more characteristics (Hillebrand 1888, Christensen 1925), including frond size; density, distribution, size, and quality of scales and hairs; degree of blade dissection; sorus size; segment size and shape; and depth and shape of sinuses. Intraspecific variants are often connected by a cline of intermediate forms. The causes of this variation are not understood, and the variation may reflect incomplete speciation or hybridization and introgression between species.

Species are defined broadly in this paper. *Sadleria cyatheoides* is treated as a single taxonomic unit because it varies notably in only one character, its size. It is unknown whether this size variation is genetically determined or the result of environmental factors. Lloyd (1974) demonstrated that, although *S. cyatheoides* probably reproduces most frequently by intergametophytic mating, the ability for intragametophytic selfing may allow it to establish itself on new lava flows from a single spore; this may also partially explain its morphologic uniformity in characters other than size. On the other hand Ranker et al. (1996) demonstrated that even on new lava flows it is probable that most sporophytes arise from intergametophytic matings.

Sadleria pallida varies not only in size, but in length of stipe relative to rachis, the nature and distribution of scales, and the size of the proximal pinnae. These variations previously led to division of this taxon into three species (*S. pallida*, *S. hillebrandii*, and *S. rigida*). A full spectrum of intermediates between the extremes exists, and it is not even possible to recognize

varieties. In many Hawaiian vascular plants the intraspecific variation is so great that it is confusing to attempt to place a specific specimen in a particular named variety. The intraspecific variation of *S. pallida* can be partially explained by a nearly obligate intergametophytic mating system (Holbrook-Walker and Lloyd 1973) leading to continued genetic variability.

Sadleria souleyetiana varies in the presence or absence of enlarged, pinnatifid, basal pinnules overlapping the rachis, and it also varies greatly in size. The distribution and nature of the scales and the nature of the venation remain constant. This species is therefore recognized as one variable taxon.

Sadleria wagneriana, sp. nov., is recognized here as a single species because of strong characters, such as obscure veins, the nature of the scales, and the presence of glands.

Sadleria squarrosa and *S. unisora* are recognized at the specific level. Intermediates between them exist, but the polar forms vary substantially from each other, so much so that Underwood (1897) placed *S. unisora* as a species of *Gymnogramme*.

Characters Used in Classification

STIPE: The sulcate stipe of the *cyatheoides* group is usually 1/3 to 1/2 the length of the frond and is shortest when the plant grows in windy, exposed areas. Linear, light green pneumatophores are present along the entire length bilaterally, but, although obvious on living plants, they are difficult to see on dried specimens. The stipe of *S. cyatheoides* is always naked except at the very base and has a characteristic stramineous color. *Sadleria souleyetiana* and *S. wagneriana*, sp. nov., stipes vary from tan to brown, with both having a pink tinge; often the stipe of *S. wagneriana* is quite red. Both are naked except at the base. The stipe of *S. pallida* may be naked except at the base or may be covered with scales along its entire length, with many intermediates.

In the *squarrosa* group the stipes are dark brown to purple. Pneumatophores are present as a dark line. The stipe of *S. squarrosa* is thicker than that of *S. unisora* and is covered with scales, as are the rachis and costae. The stipe and rachis of *S. unisora* are only sparsely scaly.

RACHIS: The sulcate rachis of the *cyatheoides* group is naked except in very young fronds and some mature *S. pallida*, especially those *S. pallida* growing on the islands of Hawai'i, Maui, and Moloka'i.

The linear pneumatophore continues from the stipe, gradually becoming segmented on the more distal part of the rachis, and finally leaving only triangular pneumatophores on the acroscopic abaxial base of the costa.

SCALES: *Sadleria* has several kinds of scales, and each species has a characteristic type (Figure 1). The species-specific scales are most commonly found in greatest numbers in the middle of the scale-bearing portion at the base of the stipe. However, some species have a minority of their scales similar to those characteristic of other species or scales intermediate in character. Other trichomes include hairs and glands.

The trichome types and associations are as follows:

1. *Sadleria pallida* type: This scale is stiff and linear-acuminate, terminating in a straight, sharp point that may be slightly curly on specimens from the islands of Hawai'i, Maui, and Moloka'i. These scales have a dark brown medial strip and a light tan fringe that expands at the base into variable winglike auricles. This type is also seen on *S. cyatheoides*, where it is softer, has smaller auricles, and tapers to a longer curly, hairlike tip. In this species it is sometimes found in the distal portion of the scaly part of the stipe.

2. *Sadleria cyatheoides* type: This scale type is soft, linear-lanceolate to lanceolate, with a rounded or minimally expanded base, and gradually tapered distally with a long, curly, hairlike tip that is often frayed. It is tan to light brown and concolorous, although it sometimes has a dark center at its base. It is found throughout the scaly part of the stipe in *S. cyatheoides* and is the only scale at its basal end. This scale is often found at the very base of the stipe of *S. pallida*.

3. *Sadleria souleyetiana* type: This scale type is limited to this species and *S. wagneriana*, sp. nov., and is the only scale type found on these species. It is tan, thin, membranaceous, elliptic-ovate, and 1–5.6 cm long in *S. souleyetiana*, but

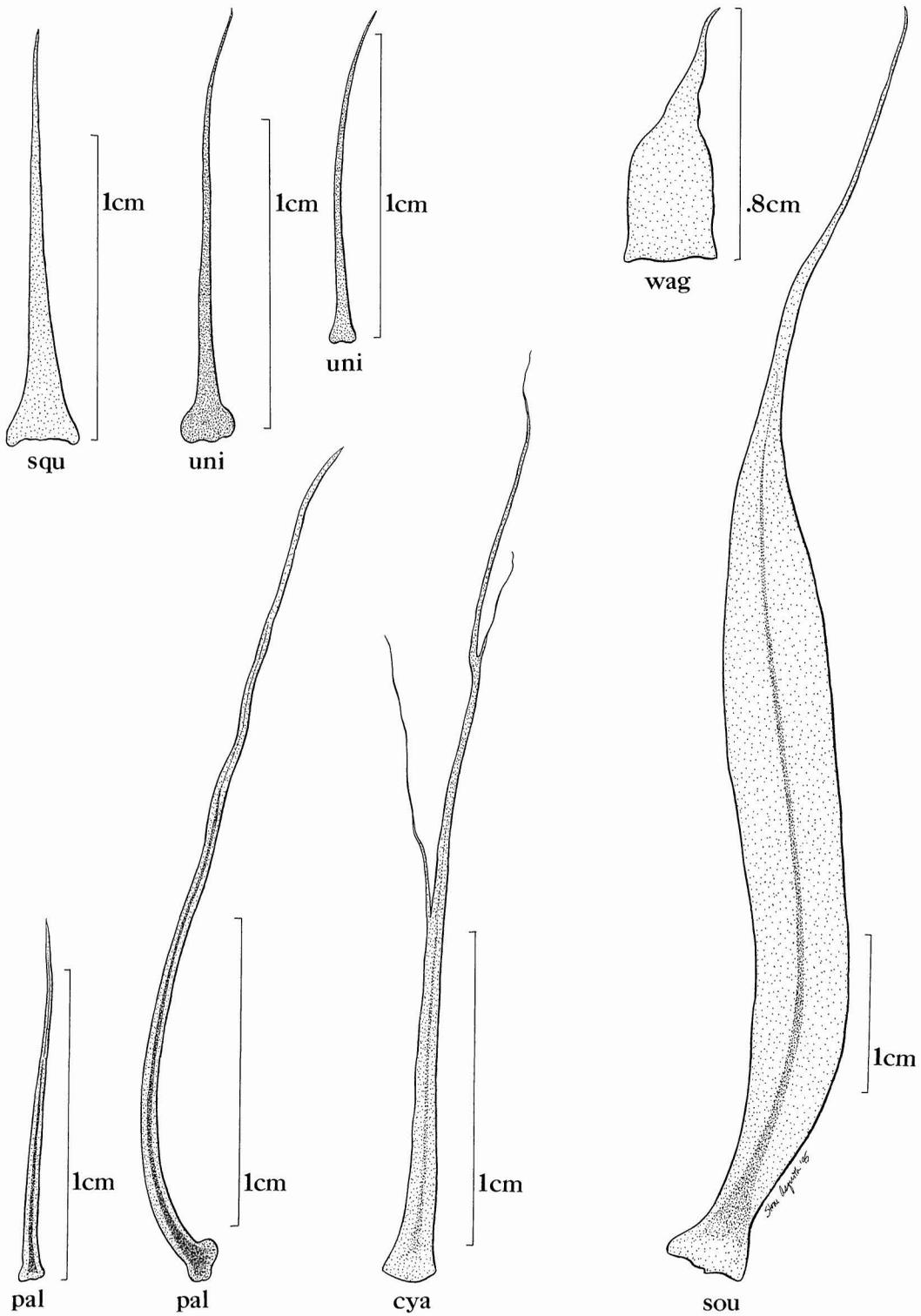


FIGURE 1. Scale morphology of *Sadleria* species. cya, *S. cyatheoides*; pal, *S. pallida*; sou, *S. souleyetiana*; sqa, *S. squarrosa*; uni, *S. unisora*; wag, *S. wagneriana*.

only 0.5–0.9 cm long in *S. wagneriana*, sp. nov. In *S. souleyetiana* it is sometimes dark at the center near its base. These scales are limited to the base of the stipe, are difficult to separate, and resemble matted wet tissue paper.

4. *Sadleria squarrosa-unisora* type: This scale is concolorous, brown to dark brown, small (1.8–9.5 mm long, 0.1–1.5 mm wide at the base), linear-triangular, with hastate basal lobes and glandular marginal trichomes. The scale of *S. squarrosa* is tan to brown and triangular, whereas that of *S. unisora* is dark brown and linear-triangular tapering to an acuminate, hair-like tip.

5. Evanescent scale type: This scale type occurs on the distal parts of the larger species and is present on young croziers. It is evanescent except on some specimens of *S. pallida*, where it is found on the more distal portions of the stipe and on the rachis. It is ovate-lanceolate with an acuminate tip, thin, light tan, occasionally with a dark center at the rounded base.

6. Fibrils: These are uniseriate hairs, sometimes with two cells at the base. On most species they are common on the abaxial surfaces of the segments and less common on the adaxial surfaces, costae, and distal parts of the stipe.

7. Glands and glandular hairs: Glandular hairs are present on the margins of the segments and scales of *S. squarrosa* and *S. unisora*. The abaxial surfaces of the segments of *S. wagneriana*, sp. nov., bear many small, translucent, lemon-colored, globular glands. It is the only member of the *cyatheoides* group with glands.

FRONDS: The fronds of the *cyatheoides* group are pinnate-pinnatifid to bipinnate at the base of larger pinnae, whereas the *squarrosa* group fronds are fully bipinnate.

PINNAE: The pinnae are linear, long and acuminate to short and obtuse (Figure 2). The presence of a cartilaginous bar perpendicular to the costa (1–3 mm long) separating the segments at the base of the sinuses of the *cyatheoides* group makes it difficult to determine if a particular pinna is deeply pinnatisect or fully bipinnate. Most pinnae have this bar between the segments, but at the base of larger pinnae, especially in *S.*

souleyetiana, the bar is absent and the plant is fully bipinnate.

The distance between the pinnae is variable between species, some with close to overlapping pinnae and some with widely separated pinnae.

SEGMENTS: There is much overlap in the appearance of the segments depending on the maturity and size of the frond and the amount of wind and sun exposure. *Sadleria cyatheoides* usually has obtuse to acute, slightly falcate segments with a dark and somewhat glossy adaxial surface. *Sadleria pallida* tends to have wider segments that are more rectangular and obtuse, and the adaxial surface tends to be a lighter, duller green. The segments of *S. souleyetiana* are falcate and much longer and narrower, with a dull, shallowly rugose adaxial surface. *Sadleria wagneriana*, sp. nov., has obtuse segments with sinuses cut only 2/3 to the costa and adaxial surfaces resembling those of *S. cyatheoides*.

The basal segments of the pinnae of the *cyatheoides* group are often enlarged, crenulate to pinnatifid, and overlapping the rachis. *Sadleria souleyetiana* often has a very large, deeply pinnatifid basal segment overlapping the rachis, but occasionally this enlarged segment is minimally developed or is lacking altogether. *Sadleria cyatheoides* frequently has enlarged basal segments, sometimes slightly pinnatifid, but never as large as those seen in *S. souleyetiana*. *Sadleria pallida* also exhibits this character, but less often and less marked than in the other taxa. Extensive examination of herbarium specimens and living material in the field has shown that the enlarged pinnatifid basal segments, when present and well developed, are diagnostically valuable, but their absence does not help with identification.

VENATION: The veins branch close to their bases, one branch arching and uniting into a continuous series of arches near the costa. Sori are borne on these arching veins. Beyond the arches the veins may or may not fork again.

Venation of the segments of the larger species is easily observed in the field. When fresh, the veins of both *S. pallida* and *S. souleyetiana* are evident and pellucid. Veins of *S. pallida* all extend to and touch a translucent, cartilaginous margin with a terminal raised, waxy hydathode

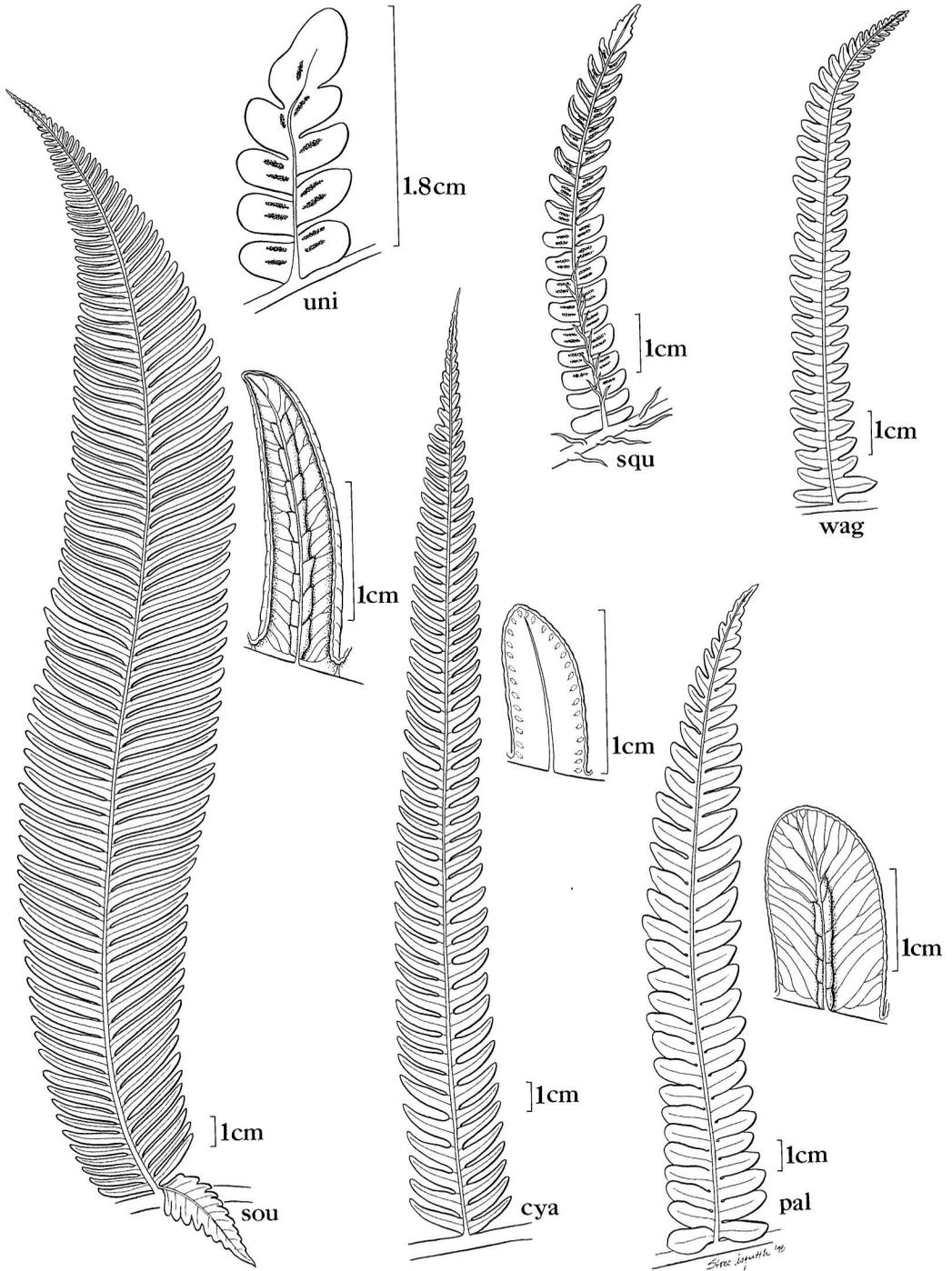


FIGURE 2. Pinna shape of all *Sadleria* species and venation pattern of some. The venation patterns of *S. wagneriana*, *S. unisora*, and *S. squarrosa* are similar to that of *S. cyatheoides* (obscure except at distal 1/8 where a hydathode is found). cya, *S. cyatheoides*; pal, *S. pallida*; sou, *S. souleyetiana*; sqa, *S. squarrosa*; uni, *S. unisora*; wag, *S. wagneriana*.

on the dorsal surface in contact with this margin; veins of *S. souleyetiana* all terminate in a hydathode, and none touch the margin. The proximal 7/8 of the veins of *S. cyatheoides* is obscured, but the distal 1/8 is pellucid, terminating in hydathodes, with none touching the margin. These three species may be distinguished in the field, with the aid of a hand lens and transmitted light, by examining the veins of a single mature segment from any part of the frond. On dried specimens examination of the margins of the revolute segments shows that the hydathodes of *S. cyatheoides* and *S. souleyetiana* are clearly separated from this margin, whereas the hydathodes of *S. pallida* overlap with it.

Patterns of venation become obscured on dried specimens, and the distal parts of the veins are difficult to see because of curling of the margins; however, the raised waxy hydathodes on the dorsal margins of the revolute segments clearly show the termination of the veins. Veins of *S. pallida* and *S. souleyetiana* are usually observed as dark or raised lines on the abaxial surface. Strong back-lighting will sometimes show the veins, and the application of 90% ethanol before examination makes the veins more visible.

The abaxial surface of the segments is covered by a thickened, light-colored epidermis bearing many stomata. This layer entirely covers the proximal 7/8 of the veins of *S. cyatheoides* and *S. wagneriana*, sp. nov., but is thin or absent over the veins of *S. souleyetiana* and *S. pallida*. This explains the translucence of the veins on living specimens and the visibility of the veins on dried specimens.

Veins of *S. squarrosa* and *S. unisora* are obscured in the same manner as in *S. cyatheoides*, and they terminate in slightly bulbous expansions short of the margins.

Veins of the hybrids are intermediate between those of the parents and are clearly seen in the field, but are difficult to examine on dried specimens.

SORI: Sori are continuous, linear, and parallel to and near the costa. The introrse indusia are usually firm. The length of the sori and the distance they cover to the tip of the segments have been considered helpful diagnostic characters (Hillebrand 1888, Robinson 1913), but extensive

field and herbarium observation has shown this character to be of little diagnostic value.

Sadleria unisora often has a single sorus parallel to the costa, or there may be two sori parallel to the midvein of the segment. Indusia of this species are thin, narrow, chartaceous, and often interrupted.

SPORES: Spores of *Sadleria* are bilateral, monolete, somewhat concave in lateral view and ovate in polar view, with the external spore wall composed of several distinct layers that vary from species to species. Studies dealing with spore size and shape were done by Skottsberg (1942), Selling (1946), Carlquist (1966), and Holbrook-Walker and Lloyd (1973) and are discussed under each species. Lloyd (1976) observed spore morphology under the scanning electron microscope and showed that the external spore wall consists of several layers. The innermost layer in all species is smooth and without ornamentation; it probably represents the exospore. One to three additional loosely attached layers represent a perispore. The outer perispore of *S. cyatheoides* is smooth. Spores of *S. pallida* were found to be composed of thin, irregular plates of various sizes and shapes. The perispore of *S. souleyetiana* is highly irregular and tuberculate, whereas the perispores of *S. squarrosa* and *S. unisora* are composed of a reticulum of anastomosing rods of various sizes and shapes. The finding of Tryon and Lugardon (1991) that the spores of *S. souleyetiana* [sic] have a foliaceous exospore needs further examination.

The spores of the *squarrosa* group are larger and exhibit the large size associated with precinctiveness, as discussed by Carlquist (1965, 1966, 1980).

TAXONOMIC TREATMENT

Sadleria Kaulfuss, Enum. Fil., 161, 1824.

Type species: *Sadleria cyatheoides* Kaulfuss.

Terrestrial, small, medium-sized, or large ferns, small forms without a caudex, large forms decumbent with terminal upright caudices, bearing brown, nonclathrate scales. Fronds borne in rosette, pinnate-pinnatifid to bipinnate, coria-

ceous, sterile fronds like the fertile ones but usually without a pericostal vein arch, the younger fronds often quite red. Stipes stramineous or dark, adaxially sulcate, scales borne at base of stipe to over entire stipe and rachis, pneumatophores linear, tan to dark, bilateral on entire length of stipe, several vascular bundles forming an arch following the abaxial surface of the stipe in large species, fewer bundles in smaller species. Pinnae alternate, sessile or short-stipitate, basal segments sometimes arising

from rachis. Segments falcate to obtuse, numerous, adnate. Veins forked near costa, uniting to form a pericostal arch from which free veins arise. Coenosori continuous over pericostal vein arches, as in *Blechnum*; indusia opening toward costa, coriaceous or chartaceous. Sporangia large, globose, annulus with 13–30 indurated cells. Spores 16 per sporangium, large, monolete, with perispore.

DISTRIBUTION: Hawaiian Islands.

KEY TO THE SPECIES OF *Sadleria* (DRIED SPECIMENS)

- 1. Fronds >0.3 or more long, deeply pinnate-pinnatifid, or bipinnate at base of larger pinnae; ultimate segments >0.8 cm long; scales without glandular trichomes 2
- 1. Fronds usually <0.3 m long, bipinnate; ultimate segments <5 mm long; scales with glandular trichomes 5
- 2(1). Scales at base of stipe thin, >3 mm wide, tan, lanceolate, resembling matted tissue paper 3
- 2. Scales at base of stipe thick, <2.5 mm wide, light brown concolorous or with dark midrib and tan margin, linear-elongate, not resembling matted tissue paper 4
- 3(2). Deeply pinnate-pinnatifid to bipinnate; ultimate segments elongate-falcate; basal segments of pinna often pinnatifid and overlapping rachis or not; veins visible, usually as dark line; stipe diameter 0.8–3.0 cm; all major Islands 3. *S. souleyetiana*
- 3. Pinnatifid, ultimate segments oblong, obtuse; basal segments of pinna not pinnatifid and not overlapping rachis; veins obscure or partially evident; stipe diameter 0.25–0.7 cm; Kaua'i only 6. *S. wagneriana*, sp. nov.
- 4(2). Veins on abaxial surface of segments prominent as dark or raised lines; scales extending partially or completely up petiole, predominantly stiff, linear-elongate, acuminate, bicolorous with dark center and light brown margin 2. *S. pallida*
- 4. Veins on abaxial surface of segments obscure; scales limited to base of petiole, soft, linear-lanceolate, with torn margins and long, curly, hairlike tip, predominantly concolorous, tan to brown 1. *S. cyatheoides*
- 5(1). Petiole diameter 1.2–2.5+ mm; pinnae linear to linear-lanceolate, 1.8–11 cm long, acute-tipped; ultimate segments 4–13+ pairs per pinna, ovate to ovate-lanceolate, scales linear-triangular, light brown to dark brown to red-brown, abundant on entire petiole and rachis; all major Islands 4. *S. squarrosa*
- 5. Petiole diameter 0.7–1.0 mm; pinnae 1.9–3.5 cm long, obtuse; ultimate segments 4–8+ pairs per pinna, ovate to round; scales linear-triangular with thin tapering tip, dark red-brown, sparse on petiole and rachis; Kaua'i only 5. *S. unisora*

FIELD KEY FOR THE *cyatheoides* GROUP

(The group with fronds >0.3 m long, ultimate segments >8 mm long, pinnatifid or bipinnate only at base of larger pinnae and not limited to steep, wet, dark valley walls. Venation of mature fronds viewed from the abaxial surface, by transillumination.)

- 1. Veins evident; acroscopic basal pinna segment enlarged, pinnatifid, and overlying rachis or not; scales thin, tan, wide, and resembling matted tissue paper, or linear-triangular with hastate base, dark midrib, and tan margins 2

1. Veins obscure except at distal 1/8 where they end in hydathodes; acroscopic basal pinna segment seldom enlarged and overlying rachis; scales limited to base of stipe, linear-ovate, tan, and concolorous or thin, broad, tan, resembling matted tissue paper 3
- 2(1). Basal pinna segments enlarged, pinnatifid or not; veins evident, ending in hydathode, not touching margin of segments; scales thin, broad, tan, resembling matted tissue paper; all major Islands 3. *S. souleyetiana*
2. Basal pinna segments usually not enlarged and pinnatifid; veins evident, extending to cartilaginous margins of segments; scales at base of stipe predominantly dark, bicolorous with dark center and light brown margins, and basal hastate wings, linear-triangular, stiff, acuminate-tipped; all major Islands 2. *S. pallida*
- 3(1). Segments elongate, obtuse to falcate; glands absent on abaxial surface of ultimate segments; scales soft linear-triangular, tan to brown, predominantly concolorous, margins torn, with long, curly, hairlike tip; usually in open sunny mesic areas; all major Islands 1. *S. cyatheoides*
3. Segments obtuse; glands translucent, tan, plentiful on abaxial surface of ultimate segments; scales thin, broad, tan, resembling matted tissue paper; on damp, steep, dark walls of streams. Kaua'i only 6. *S. wagneriana*, sp. nov.

1. *Sadleria cyatheoides* Kaulf., Enum. Fil., 162, 1824.—Type: Hawaiian Islands: Oahu, *Chamisso s.n.* (LE, photo BISH!).

Blechnum fontanesianum Gaudich., Voy. Freyc. Bot., 397, pl. 15, 1826.—Type: (P, photo BISH!).

Blechnum kaulfussianum Gaudich., Voy. Bonite Bot., 43, pl. 78, 1854. Illustration without description.

Woodwardia cyatheoides (Kaulf.) Mett., Fil. Hort. Lips., 25, 1856.

HAWAIIAN NAME: 'ama'u, pua'a 'ehu'ehu; plural: 'ama'uma'u.

Stems 30–400+ × 6–20 cm, erect to decumbent then erect at terminal portion, where they are 20–300 cm tall, erect part of stem clothed in skirt of retained fronds, scales retained throughout stem; *fronds* pinnate-pinnatifid to bipinnate at base of larger pinnae, lance-elliptic, 55–293 × 27–72 cm; *stipes* 24–192 × 0.4–2.8 cm, stramineous, sulcate, naked except at base; *scales* limited to base of stipes, except on very young fronds, predominantly soft, brown, concolorous, linear-lanceolate with torn margins, tapering to a long, curly, often torn, hairlike tip, scales on distal part of scaly stipe occasionally stiffer with dark center, lighter margins, and shorter, sharper tip; *rachises* glabrous, sulcate with central groove surrounded by rounded, elevated margins, this groove not continuous with groove of costa; *blades* 31–153

× 27–72 cm, upright with tip recurved and pointing down, often in a shuttlecock arrangement on stem; *pinnae* 13.5–36 × 1.6–2.9 cm, often 19–62 pairs per frond linear-lanceolate, cut 7/8 to costa to fully pinnate at base of larger pinnae, segments separated by a narrow cartilaginous bar; *ultimate segments* linear-oblong or falcate, tips often acute, 0.5–1.7 × 1.5–4.0 mm, 29–63 pairs per pinna with segments sometimes larger, slightly pinnatifid, and deflected over the rachis; *veins* obscured by thick abaxial epidermal layer, except in distal 1/8 where they terminate in a bulbous expansion short of the margin (easily seen only on trans-illuminated living material); *coenosori* 2 per segment, often extending to segment apex; *indusia* firm, opening toward costa; *sporangia* with 13–21 indurated annulus cells; *spores* 38.0–58.0 × 26–27 μm, perispore smooth.

REPRESENTATIVE SPECIMENS: Kaua'i: Koloa District, Wahiawa Mts. ESE of Puukolo, *Flynn 1990.315* (BISH); O'ahu: Honouliuli Forest Reserve, Palehua-Palikea trail, summit of Pali Kea, *Sohmer 6148* (BISH); Punaluu, Castle Trail, *Ozaki 1576* (BISH); Lāna'i: Puu Alii, Kealia Aupuni, Kaunolu divide, *Eames 18709* (BISH); Moloka'i: west ridge of Honomuni, *St. John 25,206* (BISH); Maui: Haleakala, Paliku, *Olson 106* (BISH); Hawai'i: Hawai'i Volcanoes National Park, Chain of Craters Road, Oceanside, *Newell 90* (BISH).

The holotype is a very small, fertile plant.

Sadleria cyatheoides is most common in open, drier forests at elevations of 75–2200 m and is often a primary invader of newer lava flows. It is less common in mesic forests and dark, moist, closed-canopy forests.

Sadleria cyatheoides has been incorrectly reported to occur in Sumatra (Christensen 1906, Robinson 1913).

Mature fronds, which are lance-elliptic, appear ovate-lanceolate on live plants because the basal pinnae curve forward. Living fronds often arch with the tip pointing down. Stems retain a skirt of dead fronds, a feature particularly apparent on recent lava flows.

The rhizome, when seen exposed, may be more than 4 m long, creeping on the ground with the terminal portion erect, and what appears to be a group of plants may prove to be a clone resulting from repeated branching of the rhizome. The base of the creeping rhizome eventually decays, leaving a shredded tangle. In the Maka'ala Natural Area Reserve on the island of Hawai'i it develops an erect caudex, 3 or more meters tall, with a base expanding to 30 cm; sometimes, when tilted, the buttressed base assumes a triangular cross section, the longest dimension being up to 45 cm. There is no information regarding the age of these plants.

Sadleria cyatheoides is recognized in its habitat by the caudex retaining dead fronds; by pale tan stipes naked except at the base; characteristic scales; a dark green, glossy adaxial blade surface; and obscure veins when viewed abaxially.

2. *Sadleria pallida* Hook. & Arn., Bot. Beech. Voy., 75, 171, 1832.—Type: Hawaiian Islands: "Tahiti" [but actually O'ahu], lectotype, here designated: *Beechey s.n. s.d.* (GL!). *Blechnum pallidum* Brack., Fil. U.S. Expl. Expd., 133, 1854.
- Sadleria fauriei* Copel., Philipp. J. Sci. Bot. 9:436–439, 1914.—Type: Hawaiian Islands: Oahu, Kalihi, Oct. 1909, *Faurie 95* (MICH!).
- Sadleria hillebrandii* Robinson, Bull. Torrey Bot. Club 40:226, 1913.—Type: Hawaiian Islands: Kauai, *Hillebrand 80* (B!).
- Sadleria rigida* Copel., Philipp. J. Sci. Bot. 11:171–172, 1916.—Type: Hawaiian Islands: Kauai, near swamp on summit of Waialeale, Sept. 1909, *Rock s.n.* (MICH, 2 sheets!).

HAWAIIAN NAMES: 'ama'u 'i'i, 'i'i, 'i'i'i.

Stems 0.4–4 m × 4–10 cm, decumbent to erect at terminal portion, 0.4–2.1 m tall, bare of old fronds; *fronds* elliptic to ovate-lanceolate, 29–105(–187) × 17–37 cm; *stipes* 11–77 × 0.3–0.8 cm wide, sulcate, scaly entire length or only at base; *scales* linear-triangular, stiff, light brown margins and dark central rib with sharp acuminate tip, base broad with thin, light brown hastate wings, some scales concolorous, thinner and tapering to a threadlike tip, scales limited to base of stipe or variously distributed, sometimes covering entire stipe; *rachises* and *costae* glabrous to very scaly; *blades* 18–58 × 17–37 cm, deeply pinnate-pinnatifid to bipinnate at base of larger pinnae, linear-lanceolate to lance-elliptic, often with rapidly diminishing apex; *pinnae* 6.5–26 × 1–2.5 cm, linear-lanceolate to lance-elliptic, usually cut 7/8 to the costa, pinnate on larger fronds, basal pinnae not reduced or reduced to 1/5 size of middle pinnae, 7–37 pairs per frond; *ultimate segments* 6–19 × 2.5–7 mm, 14–36 pairs per pinna, separated by a hyaline bar, tips obtuse; *veins* evident, usually as dark or elevated lines on abaxial surface (translucent in living material, hydathodes terminating the veins visible on the revolute margins of the dorsal surface on dried specimens), all reaching hyaline segment margin; *coenosori* 2 per segment, parallel to midvein, often short of apex; *indusia* firm, opening toward costa; *sporangia* with 15–23 annulus cells; *spores* 36–61 × 20–44 μm, perispore surface rough.

REPRESENTATIVE SPECIMENS: Kaua'i: headwaters of N fork of Wailua River, "The Blue Hole" E. of Mts. Waialeale & Kawaikini, *Lorence et al. 23.VII.1987* (BISH); Lāna'i: Lanaihale, Palawai, *Hosaka 18855* (BISH); Moloka'i: Manuahi Ridge (W side of Pelekunu Valley), *Lorence et al. 2.VIII.1987* (BISH); Maui: Olinda Flume Trail, *Hendrickson 3791* (BISH); Kipahulu Forest Reserve, Nuanualoa Stream, *Higashino & Mizuno 3115* (BISH); Hawai'i: Kulani Trail, O'laa Forest Res., O'laa, Puna Dist., *St. John 24,989* (BISH).

Sadleria pallida is most frequently found in closed-canopy mesic to wet forests or on open,

rainy, cloudy, windswept ridges at elevations from 25 to 2150 m and is uncommon in drier, exposed areas.

On O'ahu and Kaua'i *S. pallida* usually has stipes naked except at the base, with occasional patches of scales on the stipes and rachises of some plants; at higher elevations and on the more southeasterly islands, the stipe, rachis, and costae tend to be scaly, often losing much of the scaliness on older fronds. Plants of both extremes may be found on all the major Islands, and a cline in this single character can be found in plants that are otherwise identical.

In sheltered areas *S. pallida* develops a decumbent, branching caudex up to 4 m long that is terminally erect, occasionally rising to over 1.5 m. The oldest portion of the caudex decays and leaves a shredded end. What at first appears to be a group of plants may, on closer examination, prove to be a clone arising from a branching caudex. The fronds are arranged in a shuttlecock pattern and, except in sheltered areas, are deciduous, leaving the stem clean.

This species is rare in the swamp at the summit of Mt. Ka'ala on O'ahu, where *Cibotium* species grow abundantly, but is abundant at the margins and slopes draining the bog.

Plants from the Beechey voyage were kept in Arnott's herbarium, now at GL; a few specimens were kept in Hooker's herbarium, now at K (Staffleu and Cowan 1967). The lectotype here designated is on a GL sheet containing two specimens, both consisting only of pinnae; the upper left specimen is *S. cyatheoides*, and the lower right specimen (the lectotype) is *S. pallida*. It is labeled *S. pallida* in Hooker's handwriting, and it had been collected on O'ahu (Degener 1974), although that location had been crossed out and relabeled "Tahiti," where *Sadleria* does not grow. The presence of two species on this sheet may, in part, explain Hooker's ambiguous acceptance of this species.

Hooker and Arnott (1832) described *S. pallida* based on specimens almost certainly collected on O'ahu during Capt. Beechey's voyage (Degener 1974). They indicated that the species differed from *S. cyatheoides* in having a paleaceous rachis, shorter pinnae, broader pinnules with visible veins, and a pale color to the whole frond. This description clearly separates *S. pallida* from all other *Sadleria* species. Hooker

(1860) and Hooker and Baker (1874) revised this opinion and stated that *S. pallida* was merely a variety of *S. cyatheoides*. Their confusion regarding the existence of *S. pallida* is understood when the two specimens collected on the Beechey Expedition (now at Kew) are examined. Both are *S. cyatheoides* but one is much paler than the other and is labeled *S. pallida*. The sheet at GL with a pinna from each species further explains this confusion.

Smith (1875) considered *S. pallida* and *S. souleyetiana* to be only different states of *S. cyatheoides*. Hooker and Baker (1874) related *S. pallida* Hook. & Arn. to *Blechnum pallidum*, described by Brackenridge (1854). (Brackenridge described the form of *S. pallida* with a scaly stipe and rachis.)

Hillebrand (1888) reinstated *S. pallida* Hook. & Arn. as a species. However, he did not refer to an original type specimen but applied the name to specimens from "Hawaii! Kilauea; Maui! Specimens with naked frond and rhachis from Oahu and Kauai!" His description of *S. pallida* coincides with the scaly form seen commonly on the island of Hawai'i, although, as seen above, he mentioned the naked form on O'ahu and Kaua'i in his discussion of the taxon.

The Sadleria pallida, S. hillebrandii Problem

In 1913 Robinson described a new species, *Sadleria hillebrandii*, as a substitute for *S. pallida* Hook. & Arn., which she believed had been identified incorrectly, and as a result caused a continuing problem with the proper disposition of these taxa (Skottsberg 1942, Degener 1974, Fosberg 1976). The names *S. pallida* and *Sadleria hillebrandii* have both been used (Christensen 1925, Fosberg 1942, Degener 1930, 1974, Stone 1967, Lloyd 1976) for what was believed to be two closely related species separated only by the degree of scaliness of the stipe and rachis.

Fosberg (1976) reviewed this taxonomic problem and showed that Robinson had published a new species that was based on the type specimen (*Hillebrand 80, B*); he gave no opinion regarding its validity or its relationship to *S. pallida* and stated that Hillebrand's Kaua'i specimen must be accepted as the type (neither he nor, apparently, any of the other above authors had seen this specimen).

Robinson picked as the holotype for *Sadleria hillebrandii* a collection from Kaua'i (*Hillebrand 80, B*). This inadequate specimen is a single sheet containing only the distal 1/3 of the blade. Its veins are obscured by an opaque abaxial epidermal layer, there is no stipe, and the rachis and costae are naked except for scattered fine scales on the abaxial surface of the segments. This holotype is very different from the written description of *S. hillebrandii*. The lack of a stipe, scales, and much of the rachis makes this a difficult specimen to diagnose with certainty with current knowledge of the genus. The segments have an abaxial surface typical of *S. cyatheoides*, but they are more obtuse and wider than usually seen in that taxon. It may be an atypical *S. pallida* or a hybrid between *S. cyatheoides* and *S. pallida*. The specimen cited as the holotype for *S. hillebrandii* does not correspond with the published description of the specimen. This makes it impossible to determine what Robinson's concept of *S. hillebrandii* really was.

Robinson was incorrect on two points in her discussion of the *Sadleria* species. Fosberg (1976) showed that she was incorrect in considering *S. pallida* Hook. & Arn. as synonymous with *S. cyatheoides*. She was also incorrect in stating that *S. pallida*, a shade- and moisture-loving plant, was the first to grow on open lava flows, that being the habit of *S. cyatheoides*.

Sadleria pallida Hook. & Arn. is the correct name for this species. A full spectrum of plants intermediate in the single character of scaliness rules against the recognition of two taxa.

The holotype of *S. fauriei*, with its stiff, bicolored stipe base scales with attenuate tips and prominent dark veins that extend to the margins of obtuse segments is typical of *S. pallida*.

In the field *S. pallida* is recognized by its characteristic scales, often scaly stipes, translucent veins that touch the margins of the segment, and the shorter, light-colored pinnae with usually less than 30 pairs of segments.

3. *Sadleria souleyetiana* (Gaudich.) T. Moore, Ind. fil., xxvi, 1857 (as "souleytiana"); *Blechnum souleyetianum* Gaudich., Voy. Bonite Bot. pl. 2, fig. 7 & 8, pl. 134, 1846-1849. Without description.—Type: Hawaiian

Islands: Sandwich Islands, *Gaudichaud, s.n.* (holotype: P!, photo BISH!).

Sadleria souleyetiana (Gaudich.) T. Moore forma *brevisora* H. Christ, Hochreutiner, Ann. Conserv. Jard. Bot. Geneve, 1911-1912: 204.—Type: Hawaiian Islands: (Sandwich Islands): Ile de Kauai, Weimea (= Waimea), Kalalu (= Kalalau), 19 avril 1905, *Hochreutiner 3552* (holotype: G: clastotype! and photo BISH!).

Sadleria souleyetiana is the spelling used by Gaudichaud in his original description. Hillebrand (1888), Christensen (1906), Robinson (1913), and others have since misspelled it as *souleytiana*.

Stems erect or decumbent 0.4-3.0(-7.0) m × 3-10 cm; *fronds* lance-ovate, 50-345 × 71-104 cm; *stipes* tan, sulcate, 53-189 × 0.8-3.0 cm, naked except near base, where it is thickly covered with a mat of scales; *scales* thin, paperlike, tan, 10-60 × 1-8 mm, often stalked, with a dark linear central portion near base, matted and tangled appearance suggesting wet tissue paper; *rachises* glabrous; *blades* ovate-lanceolate, deeply pinnate-pinnatifid to bipinnate, 85-156 × 71-104 cm; *pinnae* lance-elliptic, closely set, 35-52 × 3.2-6.6 cm, widest in the middle, falcate with attenuate apices, cut 7/8 or completely to costa, 36-63 pairs per frond; *ultimate segments* elongate-falcate, 18-33 × 4-6 mm, (40-) 62-89 pairs per pinna, adaxial surface light green, slightly rugose, separated by a hyaline bar, falcate with acute to rounded apices, basal segments often overlapping rachis, frequently much larger (sometimes not enlarged), the larger pinnatifid to pectinate; *veins* visible, usually as a dark line, free beyond costal arch, not reaching the margin (translucent in living material); *coenosori* 2 per segment, long, extending nearly to tip of segment; *indusia* firm, opening toward costa; *sporangia* with 13-22 indurated annulus cells; *spores* without perispore, 38-72 μm long, 24-43 μm wide, perispore tuberculate, 16 spores per sporangium.

REPRESENTATIVE SPECIMENS: Kaua'i: Kalalau Lookout, *Degener & Hatheway 20,425* (BISH); O'ahu: North Halawa, Heeia Divide, Haiku Valley, Koolau Range, *St. John 20,422* (BISH); Moloka'i: top of cliff at head of Wailau

Valley, *Fosberg 1337* (BISH); Maui: Olinda Pipeline, *St. John 24,725* (BISH); Hawai'i, 22 Mile Road, 2 1/2 miles N.E. of Glenwood, Oloo, Puna Dist., *St. John et al. 18,480* (BISH).

Sadleria souleyetiana is scattered in mesic to wet forests, where it may grow in full sun or in heavy shade. It is common in its habitat at 400–1550 m, and its reputation for being uncommon probably results from lack of recognition. In the Waikamoi area of Haleakalā on Maui it is very common.

Degener (1974) called this taxon a confusing aggregate of ferns. It is quite variable in size and its larger representatives, usually seen on the steep sides of valleys in wet forests, are the largest of all *Sadlerias*. In most situations the frond is of intermediate size, and in some places, including the summit of Mt. Ka'ala on O'ahu, mature fronds may be only 0.5 m long.

In the field *S. souleyetiana* is recognized by the distinctive mat of scales at the base of the stipe; the large, falcate pinnae with a dull, shallowly rugose, adaxial surface; and translucent veins that do not reach the margins of the long, falcate segments. When present, the often-enlarged, pinnatifid basal segments are a valuable diagnostic character; however, this feature may be absent. The illustration in the original description of this species shows no enlargement of this segment.

4. *Sadleria squarrosa* (Gaudich.) T. Moore, Ind. fil., xxvi, 1857; *Blechnum squarrosus* Gaudich., Voy. Bonite Bot. 42, pl. 2, fig. 1–6, 1854. Illustration without description.

Blechnum polystichoides Brack., Fil. U.S. Expl. Exp., 134, 1854.—Type: Hawaiian Islands, Hawaii, Saw Mill, Wilkes Exp. (holotype: 59499 US).

Sadleria polystichoides (Brack.) Heller, Minn. Bot. Stud. 1:788, 1897.

5. *squarrosa* (Gaudich.) T. Moore β var. *tripinnatifida* Hillebrand, Fl. Haw. Is., 583, 1888.—Type: Hawaiian Islands: *Hillebr. s.n., s.d.* (holotype B!).

5. *squarrosa* (Gaudich.) T. Moore γ var. *intermedia* Hillebrand, Fl. Haw. Is., 583, 1888.—Type: Hawaiian Islands: Oahu, Konahuanui, *Lydgate s.n., s.d.* (holotype B!).

HAWAIIAN NAMES: 'apu'u, 'āpulu.

Stems decumbent to erect, 2.0–10 \times 1–3 cm; *fronds* lance-ovate to elliptic, 16–61 \times 3.5–22 cm; *stipes* dark, 3–12 cm \times 1.2–2.5 mm, densely covered with scales; *scales* dark brown to red-brown, 1.8–8.1 \times 0.1–0.6 mm, 0.4–1.5 mm wide at hastate base, linear-triangular, elongate with marginal glandular trichomes; *rachises* and *costae* covered with scales; *blades* bipinnate, coriaceous, 15–31 \times 3.5–22 cm; *pinnae* 1.8–11 \times 0.5–1.5 cm, linear to linear-lanceolate with acute tip, 8–36 pairs per frond, usually reduced in length basally; *ultimate segments* ovate to ovate-lanceolate, adnate, concave abaxially, slightly contracted at base, 3–6 \times 2–4 mm, 4–13 pairs per pinna, tips obtuse to acute, glandular trichomes present on margins; *veins* obscure except in distal 1/8 where they terminate in a bulbous expansion short of the margin; *indusia* thick, continuous, and overlapping sorus; *coenosorus* 1–3 mm long; *sporangia* with 16–30 annulus cells; *spores* without perispore, 50–67 μ m long, 31–47 μ m wide, perispore rough and reticulate.

REPRESENTATIVE SPECIMENS: O'ahu: Koolauloa Mts. between Punaluu & Kaipapau, *Nov./14–21/08 Forbes s. n.* (BISH); Moloka'i: head of Waikolu Valley, *July 13, 1938, Cranwell, Skottsberg s. n.* (BISH); Lāna'i: Lanaihale, *Munro 940* (BISH); Maui: Olinda Flume Trail, *Hendrickson 3781* (BISH); Hawai'i: Kohala Mts., Kehena Ditch Trail, *Carlquist 1858* (BISH).

Sadleria squarrosa is thought to be rare, but it is often very common in its preferred habitat at elevations of 400 to 2050 m. It grows best in partially to very shaded, steep, damp walls of loose cinder, often near streambeds; it tolerates very little sun exposure. A solid wall of plants whose visible fronds, sometimes covering 15 m², may be found, but single plants grow in appropriate microhabitats.

5. *Sadleria unisora* (Baker) Robinson, Bull. Torrey Bot. Club 40:227, 1913; *Polypodium unisorum* Baker, in Hook. & Baker, Synops. Fil., 307, 1868.—Type: Hawaiian Islands: Hawaii,

Mount Rauai, Sandwich Isles, *Hillebrand s.n.* (holotype B!).

Sadleria squarrosa (Gaudich.) T. Moore δ var. *depauperata* Hillebrand, Fl. Haw. Is., 583, 1888 (holotype B!).

Gymnogramme sadlerioides Underw., Minn. Bot. Stud. 1:781, 1897 (holotype: MPPD!).

Stems decumbent, 1.0–8.5 \times 0.8–2.5 cm; *fronds* 17–43 \times 3.8–6.4 cm, lance-elliptic to lanceolate; *stipes* dark brown to purplish black, 2.6–14 cm \times 0.7–1.0 mm, sparsely covered with scales, abundant glandular hairs present; *scales* brown to dark red-brown, 2.1–9.5 \times 0.1–1.1 mm, 0.3–3.1 mm wide at hastate base, linear-triangular with thin, tapering tip, marginal glandular trichomes; *rachises* and costae with sparse scales, many glandular hairs; *blades* bipinnate, subcoriaceous, 13.9–28.3 \times 3.8–6.4 cm, with obtuse tip; *pinnae* 1.9–3.5 \times 0.8–1.3 cm with obtuse tip, 14–16 pairs per frond; *ultimate segments* adnate, ovate, concave abaxially, somewhat contracted at base, 4–7 \times 3–5 mm, 4–8 pairs per pinna, with rounded tips and glandular trichomes on the margins; *veins* obscure except distal 1/8, ending in a bulbous expansion: *coenosori* short, 1–2 mm long, parallel to midvein or parallel to pinna rachis; *indusia* thin, sparse, and interrupted; *sporangia* with 15–24 annulus cells; *spores* without perispore, 53–75 \times 33–45 μ m, perispore surface rough and reticulate.

REPRESENTATIVE SPECIMENS: Kaua'i: Kokee, [Kaua'ikinana] Stream tributary below Mohihi Road, *Flynn et al.* 2263 (BISH); Kaholuamanu, *Rock 1412* (BISH); Waimea District, Waimea, Alakai Swamp, Kawaikoi stream just upstream from the Alakai Trail, *Herbst 2901* (BISH); Kokee, [Kaua'ikinana] Stream bank, *Palmer 1196* (BISH); side of Stream on the Alakai Swamp trail on the way to the Kilohana Overlook, *Palmer 900* (BISH).

Sadleria unisora occupies the same habitat as *S. squarrosa* and is closely allied with it; yet it is distinct enough that Underwood (1897) placed it in the genus *Gymnogramme*. It differs from *S. squarrosa* in having narrower stipes and rachises that are sparsely covered with dark, nar-

row scales tapering to a hairlike tip, pinnae that are more obtuse, closer to each other, and fewer pinnules per pinna. In addition, it has vestigial indusia, short or interrupted sori parallel with the costae or costules, and commonly free venation, without pericostal areoles. Stipes and rachises are more heavily clothed with glandular hairs.

Sadleria unisora is limited to Kaua'i, where it is found in narrow, dark defiles with damp walls composed of cinder. In its typical form it is clearly distinct from *S. squarrosa*. There are plants on the north coast of Moloka'i and in the Olinda area on Maui that are intermediate between the two species. In its native habitat on Kaua'i it is often sympatric with *S. squarrosa* and yet maintains its separate character.

6. *Sadleria wagneriana* D. Palmer & T. Flynn, sp. nov. Holotype: Hawaiian Islands: Kaua'i, Kokee, [Kaua'ikinana] Gulch, on steep damp walls 60 m beyond the Alakai Swamp Trail, from Mohihi Road to Pihea, 16 Nov. 1992, *Palmer 1028* (BISH!).

Sadleria souleyetianae similis sed squamis minoribus, stipite tenuiore, venis obscuris, et segmentis glanduliferis forma segmentorum *S. cyatheoidis* similis.

Similar to *Sadleria souleyetiana*, but with smaller scales, thinner stipe, veins obscure except in distal part, pinnae pinnate not pinnatisect, segments obtuse and glandular, and lamina deltate.

Stems decumbent to erect, protruding from vertical walls, up to 25 \times 2–7 cm; *fronds* deltate, 54–95 cm long; *stipes* pink to red, 28–56 \times 0.25–0.7 cm, naked except at very base where they are lightly covered with a mat of scales resembling wet tissue paper, scales often caducous; *scales* thin, tan, concolorous, lanceolate, 10–20 \times 1–4 mm; *rachises* glabrous; *blades* pinnate-pinnatifid, never bipinnate, 26–39 \times 23–33 cm, deltoid, dark green on adaxial surface, pale green on abaxial surface; *pinnae* 8–16 pairs per frond, 14–17 \times 1.0–1.7 cm, cut only 3/4–7/8 to costa, many uniseriate hairs and globular, translucent, tan, stalked, glands on abaxial surface, especially overlying the veins and cos-

tae, fewer on adaxial surface; *ultimate segments* 27–35 per largest pinna, oblong, obtuse with rounded tip, 6–9 × 3–4 mm, separated by a cartilaginous bar at base of sinus; *veins* obscured by epidermal layer except distal 1/8, or minimally translucent, terminating in hydathode short of margin; *coenosori* 3–7 mm long, extending 1/2–2/3 the length of the segments; *indusia* firm, covering the entire sorus, margins and surface with many glands; *sporangia* with 20–21 cells; *spores* 42–65 × 30–37 μm without perispore, tuberculate.

PARATYPES: Hawaiian Islands: Kaua'i, Kokee, Kauai Kinana [Kauai Kinana] Valley, on steep moist stream bank, *Palmer et al. 2197* (BISH); Kokee, Kauai Kinana [Kauai Kinana] Gulch, 60 m beyond the Alakai Swamp trail from Mohihi Road to Pihea, *Palmer 1028* (BISH, 3 sheets).

This species' known range is limited to Kaua'i at around 1100 m in Kauai Kinana and Mōhihi Valleys, and on the north face of Pihea Peak in upper Hanakoa Valley. Fronds are sparse on the caudex with red to pink, thin stipes growing horizontally from steep, shaded, moist walls of defiles. It is easily identified by segments that resemble *S. cyatheoides*, having veins obscured except in the distal 1/8 or only faintly visible, and light tan scales limited to the frond base resembling those of *S. souleyetiana* in color, texture, and matted appearance. However, the scales are smaller than in *S. souleyetiana*, cover only the extreme base of the stipe, and are caducous. The ultimate segments are obtuse and glandular, as contrasted with the narrow, falcate segments of *S. cyatheoides* and the narrow, long, falcate, nonglandular segments of *S. souleyetiana*. This is the only taxon in the *cyatheoides* group with glands. It is not a hybrid between *S. cyatheoides* and *S. souleyetiana* because the scales, the venation, and the segments are not intermediate.

The polar form of this taxon is very distinct from *S. souleyetiana*; however, a cline of intermediates between the two is present in the type locality. These show qualities intermediate in the translucence of the veins; the size, shape, and color of the segments; the degree of glandu-

larity; the size and color of the stipe; the size and distribution of the scales; and the shape of the blade (Table 1). The reason for this cline of intermediacy is not known. Full speciation with introgression or incomplete speciation are both possibilities.

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TABLE 1
COMPARISON OF *Sadleria wagneriana* WITH *S. souleyetiana*

CHARACTER	<i>Sadleria wagneriana</i>	<i>S. souleyetiana</i>
Stipe color	Pink to red	Tan
Stipe diameter	0.25–0.7 cm	0.8–3.0 cm
Stipe scales	10–20 × 1–4 mm	10–60 × 1–8 mm
Blade	Deltate	Ovate-lanceolate
Adaxial surface	Dark green, relatively smooth	Light green, slightly rugose
Glands	Many translucent, globular, stalked, on abaxial and adaxial surfaces, over the veins, on the rachis, costae, and indusia, fewer on adaxial surface	Glands absent
Pinnae	Cut 2/3–7/8 to costa, usually not bipinnate	Cut 7/8 to costa or bipinnate
Pinna pairs	8–16	36–63
Ultimate segments	6–9 × 3–4 mm, obtuse to falcate, 27–35 pairs per pinna	18–33 × 4–6 mm, falcate, 40–89 pairs per pinna
Veins	Obscure except for distal 1/8	Translucent throughout

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LITERATURE CITED

- BAKER, J. G. 1874. Page 307 in Hooker and Baker, Synops. Fil. 2nd ed. Robert Hardwicke, London.
- BOWER, F. O. 1928. The ferns, vol. III. Cambridge Press, England.
- BRACKENRIDGE, W. D. 1854. Fil. U.S. Explor. Exped. Bot. Vol. Bot. 2.
- BRYAN, W. A. 1915. Natural history of Hawaii, p. 574. The Hawaiian Gazette Co., Ltd., Honolulu.
- CARLQUIST, S. 1965. Island life: A natural history of islands of the world. The Natural History Press, Garden City, New York.
- . 1966. The biota of long-distance dispersal. III. Loss of dispersibility in the Hawaiian flora. *Brittonia* 18:310–335.
- . 1980. Hawaii, a natural history, 2nd ed. Pacific Tropical Botanical Garden, Lāwa‘i, Hawai‘i.
- CHRISTENSEN, C. 1905–1906. Index Filicum. Reprinted by Otto Koeltz Antiquariat Koenigstein-Ts./B.R.D., Western Germany, 1973.
- . 1925. Revised list of Hawaiian Pteridophyta. *Bernice P. Bishop Mus. Bull.* 25:1–30.
- COPELAND, E. B. 1914. *Philipp. J. Sci. Bot.* 9:435–441.
- . 1916. Hawaiian ferns collected by J. F. Rock. *Philipp. J. Sci. C. Bot.* 11:171–173.
- . 1947. *Genera filicum*. *Chronica Botanica*, Waltham, Massachusetts.
- DEGENER, O. 1930. Ferns and flowering plants of Hawaii National Park, p. 40. Honolulu Star-Bulletin, Honolulu.
- . 1974. *Sadleria* about Kilauea, Hawaii. *Hawaii. Bot. Soc. Newsl.* 13(5): 21–23.
- FOSBERG, F. R. 1942. Uses of Hawaiian ferns. *Am. Fern J.* 32:15–23.
- . 1976. Typification of *Sadleria hillebrandii* Robinson. *Taxon* 25:187–188.
- GAUDICHAUD, C. 1826. Voyage autour du monde . . . S. M. l’*Uranie* et la *Physicienne* . . . M. Louis de Freycinet, *Botanique*, p. 397, pl. 15.
- . 1854a. Voyage autour du monde . . . la *Bonite*. *Botanique*, p. 43, pl. 2, figs. 7,8, pl. 134, figs. 1–6.
- . 1854b. Voyage autour du monde . . . la *Bonite*. *Botanique*, p. 43, pl. 78.
- . 1854c. Voyage autour du monde . . . la *Bonite*. *Botanique*, p. 42, pl. 2, figs. 1–6.
- GILLETT, G. W. 1972. The role of hybridization in the evolution of the Hawaiian flora. Pages 205–219 in D. H. Valentine, ed. *Taxonomy, phytogeography and evolution*. Academic Press, London.
- HELLER, A. A. 1897. Observations on the ferns and flowering plants of the Hawaiian Islands. *Minn. Bot. Stud.* 1:788.
- HILLEBRAND, W. 1888. *Flora of the Hawaiian Islands*, facsimile ed. Hafner, New York.
- HOLBROOK-WALKER, S., and R. M. LLOYD. 1973. Reproductive biology and gametophyte morphology of the Hawaiian fern genus *Sadleria* (Blechnaceae) relative to habitat diversity and propensity for colonization. *Bot. J. Linn. Soc.* 67:157–174.
- HOOKE, W. J. 1860. *Species filicum*, vol. II. William Pamplin, London.
- HOOKE, W. J., and G. A. W. ARNOTT. 1832. *The botany of Captain Beechey’s voyages*, Part III. Henry G. Bohn, London.
- HOOKE, W. J., and J. G. BAKER. 1874. *Synopsis filicum*, 2nd ed. Robert Hardwicke, London.
- JOE, B. 1960. Ferns cultivated in California: *Sadleria*. *Am. Fern J.* 60:232–235.
- KAULFUSS, G. F. 1824. *Enumeratio Filicum*. Sumptibus C. Cnobloch, Lipsiae.
- KOTZEBUE, O. 1821. Voyage of discovery in the south sea and to Behring’s Straits in search of a north-east passage. Sir Richard Phillips and Co., London.
- LLOYD, R. M. 1974. Reproductive biology and evolution in the Pteridophyta. *Ann. Mo. Bot. Gard.* 61:318–331.
- . 1976. Spore morphology of the Hawaiian genus *Sadleria* (Blechnaceae). *Am. Fern J.* 66:1–7.
- MINARD-ELSAESSER, D. 1982. Systematics of *Sadleria* (Blechnaceae), an endemic genus of Hawaiian ferns. M.S. thesis, Ohio University, Athens.

- MOORE, T. 1857. Index filicum, Part 1. xxv–xxvi, Williams and Norgate, London.
- PUKUI, M. K., and S. H. ELBERT. 1965. Hawaiian-English dictionary. University of Hawai'i Press, Honolulu.
- RANKER, T. A., C. E. C. GEMMILL, P. G. TRAPP, A. HAMBLETON, and K. HA. 1996. Population genetics and reproductive biology of lava-flow colonising species of Hawaiian *Sadleria* (Blechnaceae) *In*: J. M. Camus, M. Gibby, and R. J. Johns, eds. Pteridology in perspective. Royal Botanic Gardens, Kew.
- ROBINSON, W. J. 1913. A taxonomic study of the Pteridophyta of the Hawaiian Islands—II. Bull. Torrey Bot. Club 40:193–228.
- SELLING, O. H. 1946. Studies in Hawaiian pollen statistics, I. The spores of the Hawaiian pteridophytes. Bernice P. Bishop Mus. Spec. Publ. 37:71–72.
- SKOTTSBERG, C. 1942. Vascular plants from the Hawaiian Islands, III. Pteridophytes collected during the Hawaiian Bog Survey, 1938. Acta Horti Gothob. 15:35–148.
- SMITH, J. 1875. Historia Filicum. Pages 306–307. MacMillan & Co., London.
- STAFLEU, F. A., and R. S. COWAN. 1967. Taxonomic literature. Utrecht.
- STONE, B. C. 1967. A review of the endemic genera of Hawaiian plants. Bot. Rev. 33:216–251.
- TRYON, A. F., and B. LUGARDON. 1991. Spores of the Pteridophyta. Springer-Verlag, New York.
- UNDERWOOD, L. M. 1897. *Gymnogramme sadleroides*. Minn. Bot. Stud. 1:781–784, pl. 43.
- WAGNER, F. S. 1995. The chromosomes of *Sadleria* (Blechnaceae). Contrib. Univ. Mich. Herb. 20:239–240.
- WAGNER, W. L., D. R. HERBST, and S. H. SOHMER. 1990. Manual of the flowering plants of Hawai'i. University of Hawai'i Press, Bishop Museum Press, Honolulu.
- WALKER, T. G. 1973. Cytology in fern classification. Page 99 *in* A. C. Jermy and J. A. Crabbe, eds. Phylogeny and classification of the ferns. Academic Press, London.