

## **Towards a Better Understanding of Bird's-Nest Ferns in Hawai'i**

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## Towards a Better Understanding of Bird's-Nest Ferns in Hawai'i

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**ABSTRACT.**—For many years, the native populations of bird's-nest ferns in Hawai'i (known as 'ēkaha) have been referred to as *Asplenium nidus*. Recent morphological studies on live plants and herbarium vouchers, along with literature review, reveal that the most appropriate name is *A. musifolium*, which is primarily known from Malesia and Southeast Asia. Furthermore, *A. nidus* was a horticultural introduction and is now naturalized. This work has also elucidated the need for critical study of bird's-nest ferns in the Pacific, where several cryptic taxa may be present. Though these ferns do not possess many distinct characteristics, the shape of the midrib and the detail of the scales are diagnostic. We provide an overview of bird's-nest fern diversity in Hawai'i, a key to identify native and non-native taxa, recommendations for specimen preparation to improve visibility of diagnostic characters, and a discussion of future research directions.

**KEY WORDS.**—*Asplenium*, Hawai'i, Pacific, Morphology, Cryptic species

The name *Asplenium nidus* L., of the *Thamnopteris* group, has been broadly applied to asplenoid ferns with simple leaves forming a “nest” basket in trees, on rocks, or on the ground. These ferns collect detritus and are often microcosms for animal species in the canopy or elevated on boulders, and often the fauna in these ferns represent taxa that are typically found on the forest floor (Fayle *et al.*, 2008). *Asplenium nidus*, known colloquially as the bird's-nest fern, is often treated as a species complex (Yatabe *et al.*, 2009). The name is frequently used when referring to any fern with the bird's-nest morphology. In the context of the Hawaiian flora, this name has been applied to the native bird's-nest ferns (called 'ēkaha in Hawaiian) for roughly 200 years (Charles Gaudichaud-Beaupré collected his specimen in 1819, *Gaudichaud-Beaupré s.n* P, image seen) (Gaudichaud-Beaupré, 1826; Brackenridge, 1854; Hillebrand, 1888; Robinson, 1913; Christensen, 1925; Degener, 1946; Palmer, 2003; Vernon and Ranker, 2013; Ranker *et al.*, 2019). However, a preliminary

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morphological study of plants cultivated at Lyon Arboretum showed clear differences between cultivated *A. nidus* and 'ēkaha. This paper clarifies the morphological differences in Hawai'i between 'ēkaha and the widely cultivated and commercially available *A. nidus*. This distinction is needed with some urgency, as non-native *A. nidus* is naturalized and occasionally outplanted in restoration areas or sold as a putatively native horticultural plant due to these taxonomic misunderstandings.

*The Hawaiian islands.*—The first herbarium specimen of Hawaiian 'ēkaha was collected by Charles Gaudichaud-Beaupré while voyaging with Freycinet in the years 1817–1820 (Gaudichaud-Beaupré s.n P, image seen) and described as an endemic variety, *Asplenium nidus* var. *sandwicensis* Gaud. (Gaudichaud-Beaupré, 1826). However, photos of his specimens were sent from the Paris herbarium with a verified annotation slip by Dr. Harold St. John, and the corresponding author verified the specimen as an 'ēkaha. A few decades later, the Wilkes Expedition in 1838–1842 collected 'ēkaha and identified it as *A. nidus*. 'Ēkaha is still most commonly referred to as *A. nidus* (syn: *Neottopteris nidus* (L.) J. Sm. ex Hook.; *Thamnopteris nidus* (L.) C. Presl), including in the most recent published checklist of the Hawaiian pteridophytes (Ranker et al., 2019), Palmer's manual for the Hawaiian pteridophytes (Palmer, 2003), the U.S. Department of Agriculture (<https://plants.usda.gov/home/plantProfile?symbol=ASNI>), and The World Ferns checklist (<https://www.worldplants.de/world-ferns>), among other sources. The *Plants of the World Online* website (<https://powo.science.kew.org/>), sponsored by the Royal Botanic Gardens, Kew, ascribes the name *Asplenium australasicum* (J. Sm.) Hook. to the Hawaiian plants. One early specimen of 'ēkaha (Hillebrand s.n., BISH) was originally identified in 1867 by D.C. Eaton as *Neottopteris musifolia* J. Sm., J. Bot. (Hooker), nom. inval. The date of the collection is not known, so it could have been identified after Hillebrand's death. While *Neottopteris musifolia* was never published as a valid name (*Neottopteris nidus* var. *musifolium* (Mett.) Ridl. was published in 1926 as *A. musifolium* Mett. in 1859), we believe this specimen represents the first attempt to recognize the Hawaiian taxon as distinct from *A. nidus* and to apply a synonym of *A. musifolium*.

More recently, *Asplenium nidus* was introduced as a cultivated plant and has now naturalized across several islands (O'ahu, where it is common in exotic forests in the Ko'olau Mountain range, with scattered citizen science records on Hawai'i Island, Maui, and Kaua'i; see Citizen Science Observation section). The earliest herbarium specimen we could find is from a cultivated specimen at BISH collected on campus in 1989 (Wilson & Staples 1751 BISH). On O'ahu, a majority of the plants are found in Mānoa Valley at and around Lyon Arboretum and in various valleys in the Kāne'ohe region on the windward side of the island. According to the Arboretum staff, the earliest accession record of *Asplenium nidus* for the arboretum states "received in 1969 from a local nursery" (Katie Hatchmeister from Lyon Arboretum pers. comm.). The nursery from which these plants were purchased is unknown, indicating the species may have been in Hawai'i for some time before planting at the arboretum. A copy of The Honolulu Botanical Garden records at BISH show



that Wāhiawa Botanical Garden received their first *A. nidus* in 1963 and was sourced from Tahiti. Later records from the same garden show that plants were also imported from Australia, Samoa, Vanuatu, and the Philippines. It is also unknown where the 'Āhuimanu population came from, possibly from the same nursery stock. The forest in 'Āhuimanu where the plants are growing was clear-cut in the 1970s (Phil Kapu from Kaiāulu o Kahalu'u pers. comm.), so subsequent forest regrowth and establishment of *A. nidus* in that region likely occurred since then. The corresponding author has also seen the cultivated *A. nidus* in Hilo, Hawai'i, and Limahuli garden on Kaua'i. However, more vouchers must be collected to represent other island populations in herbaria.

#### METHODS

We examined natural populations in the Ko'olau and Wai'anae Mountains, cultivated plants at Lyon Arboretum in Honolulu, dried specimens in person at the Bernice Pauahi Bishop Museum herbarium (BISH), and images at PteridoPortal (<https://www.pteridoportal.org/>). We investigated different methods to best preserve key morphological characters in pressed specimens. We dried herbarium specimens collected in the field with and without a 2 cm thick foam pad to see the effect on the midrib architecture. We compared the Hawaiian specimens to descriptions of species in the *A. nidus* complex, focusing on *A. nidus*, *A. australasicum*, and *A. musifolium*.

#### RESULTS AND DISCUSSION

The Hawaiian 'ēkaha best matches *A. musifolium* (*sensu* Holttum, 1974), as the midrib has a flattened ridge on the abaxial surface of the leaf (vs. rounded and protruding adaxially in *A. nidus*, and sharply keeled with a triangular cross-section in *A. australasicum*; Fig. 1A–E), but differs in that the leaf apex is not always broad and the leaf base is not abruptly narrowed to a narrowly winged/wingless stipe, though these features appear to vary in *A. musifolium* outside of Hawai'i (see Specimens Examined). A careful examination of the type specimen of *A. musifolium* (Cumming 89, K, image seen) clearly shows the affinities to the Hawaiian material. An alternative key (adapted from Holttum, 1974) by Dong, Wei, and Chao (2012) also leads to the Hawaiian plants matching *A. musifolium*. No other descriptions in the monograph authored by Holttum (1974) or other literature sources, match this species of bird's-nest fern midrib description.

*Morphological evidence.*—Holttum (1974) suggests that leaf arrangement (leaves ascending or not) is an important character in defining some species of the complex (a funnel-shaped nest with more upright leaves characterizes *A. australasicum*; habit of *A. nidus* and Hawaiian *A. musifolium* shown in Fig. 3), a character difficult to represent in herbaria, exacerbating the challenges of identifying preserved material. However, field observations of Hawaiian plants suggest that leaf arrangement is highly variable among individuals and/or through

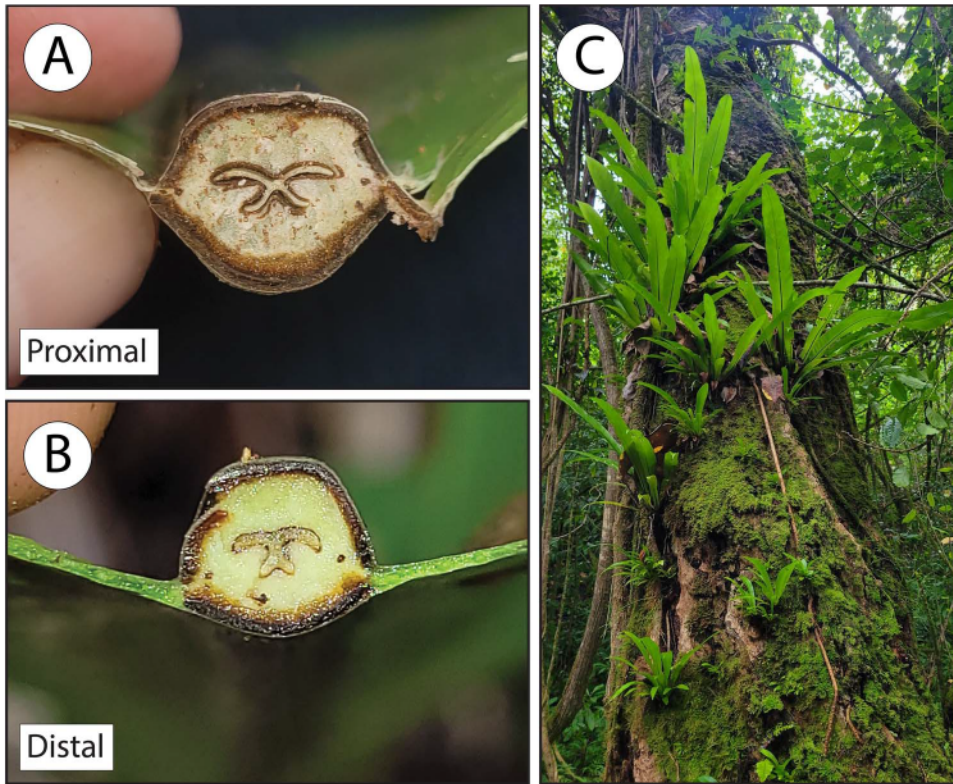


FIG. 1. Midrib detail (A-B) and habit (C) of naturalized *A. nidus* in Hawai'i. Leaves are oriented with adaxial side facing up.

time and is thus not useful for distinguishing taxa in this context. In his paper, Holttum (1974) lists Hawai'i as part of the distribution for *A. nidus*. It is highly improbable that he did not look at Hawaiian specimens, so we hypothesize that he focused on leaf shape rather than other characters. He may have disregarded the midrib characteristic, even though he highlights its importance in other parts of his key. He does, however, illustrate the need to look at living plants and that Herbarium vouchers do not accurately represent the distinctive forms associated with each species. He even cites John Smith, an employee at Kew Gardens, stating "The cultivated examples of four forms known to me, although difficult to recognize as distinct when put in the Herbarium, are however readily seen to be distinct species in the garden." (Holttum, 1974).

The midrib of the leaf is useful for identifying species of bird's-nest ferns. The abaxial midribs of most Hawaiian collections of *A. musifolium* are trapezoidal in cross-section, but some seem to have a more rounded (vs. a more angular) ridge, suggesting either intraspecific variability or the presence of multiple native bird's-nest taxa in Hawai'i. In Indonesia, Yatabe *et al.* (2001) showed that a number of cryptic species may co-occur in a single area. The



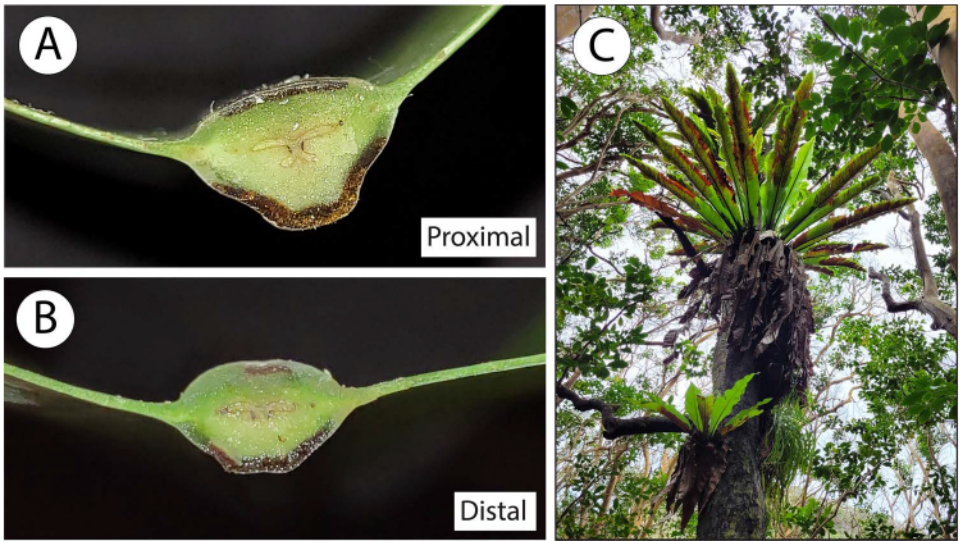


FIG. 2. Midrib detail (A-B) and habit (C) of native *A. musifolium* in Hawai'i. Leaves are oriented with adaxial side facing up.

adaxial portion of the midrib is pronounced but not as much as in *A. nidus* (See Table 1 for measurements). Palmer (2003) mentions variation in leaf mid-ribs, but he later states that he was possibly looking at a mix of individuals of introduced (*A. nidus*) and native (*A. musifolium*) plants, and that some of that variation was likely from naturalizing populations of *A. nidus* (D. Palmer, pers. comm.). The observed differences in midrib architecture of *A. musifolium* and

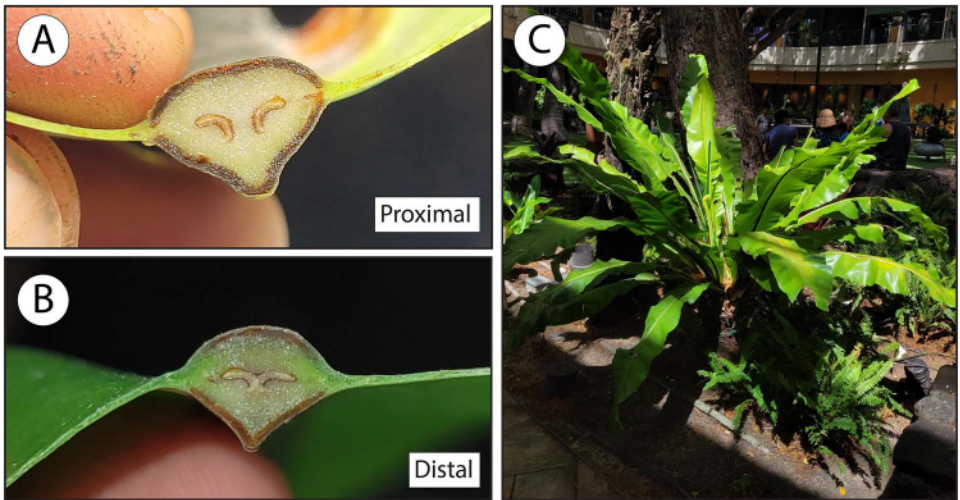


FIG. 3. Midrib detail (A-B) and habit (C) of cultivated *A. australasicum* in Hawai'i. Leaves are oriented with adaxial side facing up.

TABLE 1. Comparison of the 3 bird's-nest ferns found in the Hawaiian islands. The leaf character descriptions for *A. australasicum* are based on a cultivated plant in the Hawaiian islands, the scale dimensions are based on a specimen from Rapa (Fosberg 11493, BISH). The scale dimensions for *A. musifolium* were taken from a Hawai'i specimen that is typical of the local populations.

Characters	<i>Asplenium nidus</i>	<i>Asplenium musifolium</i>	<i>Asplenium australasicum</i>
Distribution	SE Asia, Indo-Pacific, Pacific islands, Madagascar, East Africa.	Indonesia, Malaysia, Philippines, New Guinea, Solomon Islands, Hawai'i.	Australia, New Caledonia, Norfolk island, Southwest Polynesia through French Polynesia.
Upper surface of midrib	Well pronounced, rising ~ 3–5 mm.	Minutely pronounced, rising ~ 0–2 mm.	Minutely pronounced to somewhat pronounced, rising ~ 0–3 mm.
Lower surface of midrib	Up to 4 mm at the base of the leaf, 0–1 mm in the upper 2/3rds, rounded in cross section.	Well pronounced, ~1 cm, upper 2/3rds 3–5 mm with a blunt ridge trapezoidal in cross section.	Well pronounced, ~1 cm, with a sharp ridge triangular in cross section.
Scale color	Amber, concolorous.	Irregularly colored with large portions hyaline with cells partially pigmented.	Amber, concolorous.
Scale cell length in micrometers	Min: 56.02 Mean: 198.67 Max: 412.27	Min: 155.22 Mean: 317.69 Max: 458.61	Min: 81.30 Mean: 196.1 Max: 418.62
Scale cell width in micrometers	Min: 36.20 Mean: 52.22 Max: 68.01	Min: 59.11 Mean: 91.34 Max: 161.57	Min: 31.48 Mean: 44.36 Max: 57.83

*A. nidus* in Hawai'i closely match those observed elsewhere in the Pacific (e.g., Singapore; Fig. 5). There are two O'ahu specimens that were collected within the past 4 years (by Phil Kapu in Maunawili and by Kevin Faccenda in Waimano) that have the upper surface of the midrib slightly more pronounced than specimens collected from other areas (including Niu, Wailupe, Palikea, Mākaha, and Pāhole), but that fall within the range of variation for the Hawaiian populations of *A. musifolium*. Though Yatabe *et al.*, 2001 state that hybridization was rare in their studies, genetic studies on the Hawaiian taxa could confirm if introgression between native and non-native populations has led to morphological variability.

There are also scales attached to the base of the leaves, which can be useful in species identification (see the key presented in Dong, Wei, and Chao, 2012) but are often missing from herbarium specimens. Scales are easily harvested among the young unfurling leaves in the center of the "nest". The length-to-width ratio of the scales themselves has been highlighted as an important diagnostic feature, but more studies on the scale size and color appear useful in differentiating some taxa (especially 'ēkaha vs. *A. nidus*; see Fig. 4 and Table 1). Thus, we also recommend that collectors ensure scales are present on any vouchers, and

ideally some scales should be stored in fragment packets to ensure they are available for observation.

Several characteristics of the scales (taken from the unfurling leaves in the center of the “nest”) separate the Hawaiian plants from the cultivated *A. nidus* found in the Hawaiian islands: the color, margin, and general size of the cells (Fig. 4, Table 1). Cultivated *A. nidus* has brown scales, comparatively smaller cells than ‘*ēkaha*, and margins with recurved hooked-appendages (See Fig. 4 for detail of *A. nidus* scales). The Hawaiian plants have scales that lack recurved hooked-appendages, are more pale, and the cells are often twice the size of those in *A. nidus* (Fig. 4, Table 1). The color of the cell walls is often dark red to black, while *A. nidus* are typically only dark red. This color difference can be misleading because often the young scales of ‘*ēkaha* are uniformly dark red and appear to become black with age. Some scales on the Hawaiian plants seem to lack color completely when viewed under a microscope. When color does appear, the cells are irregularly pigmented (Fig. 4). Sometimes, a film of debris develops on the scales and will obscure the true color, so some cleaning may be necessary. The scales from the O‘ahu plants have consistent morphology with specimens from Maui (*H.L. Lyon s.n.*) and Hawai‘i Island (*B.C. Stone 3012 BISH*), so scales are thus likely consistent throughout the Hawaiian Islands.

We collected material from a cultivated specimen of bird’s-nest fern at Ho‘omaluhia Botanical Garden in Kāne‘ohe, O‘ahu. The leaves of the plant are typical of *A. musifolium* from the Philippines in the petiolate leaf base and the flattened ridge on the underside of the midrib. The scales, however, are very different from the Hawaiian plants and more closely resemble *A. nidus* and *A. australasicum*: they are brown and have smaller cells (Fig. 4). The cell walls on this specimen are also noticeably thin (roughly half the thickness of the Hawaiian material). Comparison to a specimen labeled *A. musifolium* from Latangai, Papua New Guinea (*Croft & Lelean LAE65465*, BISH) shows that the scales are indistinguishable to the Ho‘omaluhia specimen. This Latangai specimen is typical of the species throughout Malaysia/Malesia. Further research on scale morphology is needed to further assess the relationships between the Hawaiian plants and the extra Hawaiian plants of *A. musifolium*.

*Molecular evidence.*—Previous studies that used molecular data to infer relationships within the *A. nidus* complex suggest that the name *A. nidus* has been widely and broadly applied to many cryptic lineages within the complex, but that *A. musifolium* is a well supported, monophyletic species based on DNA from Malaysia (Dong *et al.*, 2012; Xu *et al.*, 2020). A recent phylogenetic analysis of *Asplenium* L. included relatively dense sampling of the *A. nidus* complex (Xu *et al.*, 2020), but did not include any Hawaiian individuals. The analysis included three specimens of *A. musifolium* from Sabah (Malaysia) and Indonesia, which form a well-supported clade (posterior probability = 100%, bootstrap support = 96%), nested within other members of *A. nidus sensu lato*. Dong, Wei, and Chao (2012) similarly recovered a well-supported (bootstrap support = 97%) clade of *A. musifolium*, sister to a monophyletic *A. australasicum*.



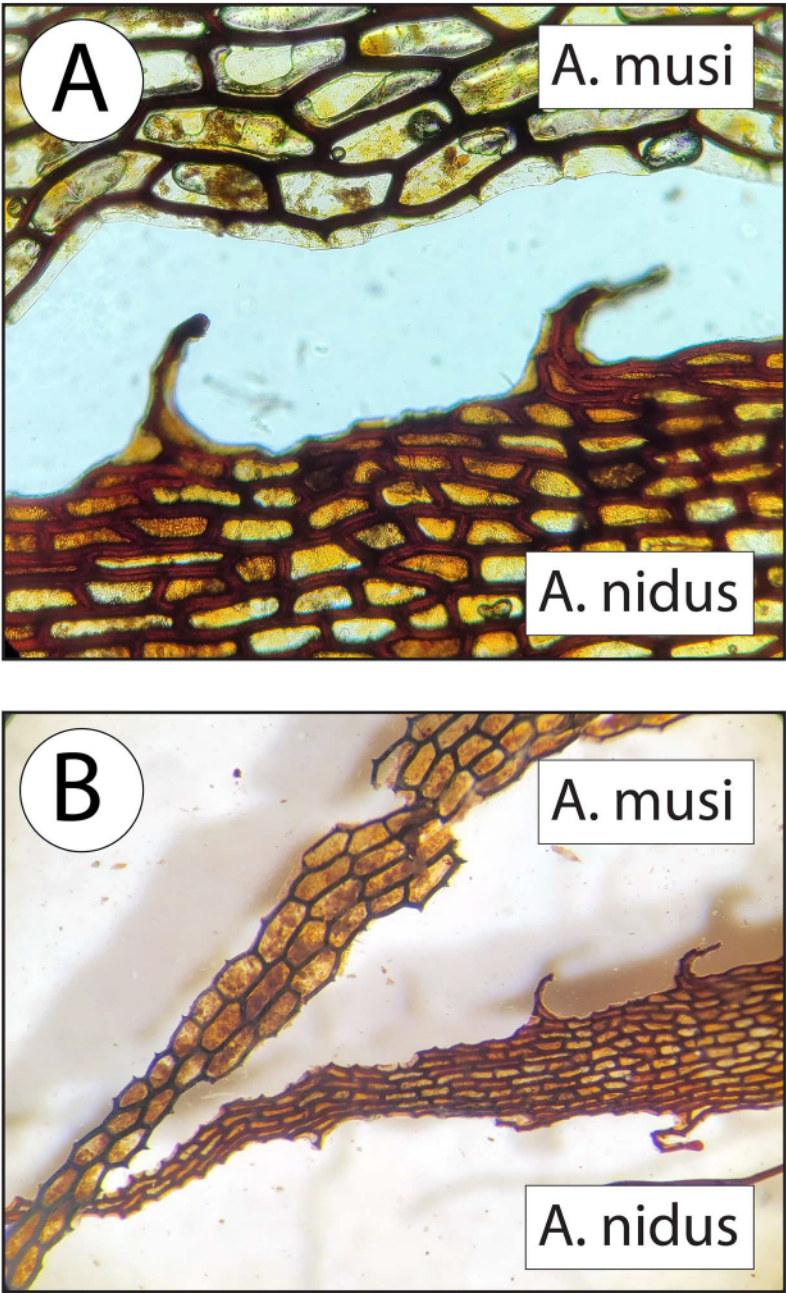


FIG. 4. Scales from Hawaiian *A. musifolium* (top of A and B) and *A. nidus* (bottom of A and B) showing differences in coloration, cell wall thickness, and cell size.



FIG. 5. Comparison of *A. musifolium* (left) and *A. nidus* (right) in Singapore. Photograph by Cerlin Ng. Leaves are oriented with adaxial side facing up.

In Xu *et al.* (2020), most specimens identified as *A. australasicum* or *A. cf. australasicum* fail to form a clade, unlike in the earlier Dong, Wei, and Chao (2012) study. We suspect that taxonomy was applied inconsistently to specimens in this large, global analysis and that the lack of consistent and coherent specimen identification has led, at least in part, to this apparent lack of monophyly. For example, a specimen from Huahine (Society Islands) labeled *A. nidus* (K. R. Wood 10991, PTBG image seen) was found to be sister to a specimen identified as *A. cf. australasicum*. Upon inspection of the Wood 10991 specimen, we believe that this plant presents a typical *A. australasicum* morphology, including the presence of a sharply keeled midrib (*e.g.*, Fig. 1D). This suggests that thorough examinations of the specimens included in Xu *et al.* (2020) is warranted (though outside the scope of the present study), and that Xu *et al.* (2020) did not use a consistent morphological concept of *A. nidus* or *A. australasicum*.

Additional genetic studies of the *A. nidus* complex have demonstrated that clear reproductive barriers do exist between some lineages (Yatabe *et al.*, 2009), suggesting that the complex represents multiple species whose boundaries we are still discerning. Cytological data suggest that the bird's-nest ferns complex includes many polyploids and multiple ploidy levels (Dong, 2011). It is thus possible that ploidy contributes to patterns of reproductive isolation and may also obscure evolutionary histories in previous molecular work that did not use polyploid-aware phylogenetic methods (see discussion in Rothfels, 2021). Yatabe *et al.* (2001, 2002) uncovered multiple cryptic lineages among co-occurring tetraploids in West Java, suggesting that ploidy is unlikely to be the sole cause of cryptic diversity in the bird's-nest fern complex. Yatabe *et al.* (2003) also document extensive cryptic diversity among taxa identified as *A. nidus* and lack of monophyly with respect to other named taxa in the complex, including *A. australasicum* (*sensu* Holttum, 1974). No *A. musifolium* or Hawaiian material was included in these studies, so it is difficult to extrapolate from these results in the context of this study.

Genetic sampling of the Hawaiian members of the complex could lend additional support to the results presented in this manuscript. In the meantime, however, morphology is sufficient to distinguish the native Hawaiian *‘ēkaha*

from the traditional definition of *A. nidus*, and closely allies the Hawaiian taxon with *A. musifolium* in a broad sense, but future studies may reveal the Hawaiian plant as a distinct variety based on the differences in scale morphology.

*A pressing matter.*—Relying on herbarium material alone can be challenging when identifying members of the *A. nidus* complex because the drying process and how the plants are pressed affect the architecture of the midrib, especially when dried slowly vs. quickly and with vs. without foam pads between the cardboard pieces in plant presses. Study of fresh material is ideal, but based on our experience with the drying process, we determined that one can position the midrib to see the shape of the ridge and on which side the ridge is most prominent. Using no foam pads resulted in flat specimens with a hard to discern midrib in the upper half of the leaf. However, the basal portion of the leaves had a mostly discernable midrib architecture despite being compressed. When prepping for mounting, we recommend that specimens be mounted with the lower midrib positioned with the abaxial surface visible, which facilitates using the midrib for identification. Removing the mounting tape to closely examine the midrib for specimens mounted with the leaf folded may be necessary. Instead of folding, we recommend cutting the leaves and positioning the cut exposure at the edge of the sheet, as it is then possible to see the shape of the midrib when viewing the sheet at eye level. For the drying process, we recommend using one to two 2+ cm thick foam pads to preserve the midrib architecture. The collector can also make a cross section of the midrib and mount it on the herbarium sheet or mention the shape of it on the specimen label.

The base of the leaf, if intact, can be useful for identifying various bird's-nest ferns. For instance, *A. musifolium* and *A. australasicum* will have a prominent ridge on the abaxial surface that is well developed at the base of the leaves and is less pronounced in the distal third when the leaves are dried.

The scales attached to the base of the leaves can be useful in species identification (see the key presented in Dong, Wei, and Chao, 2012), but are often missing from herbarium specimens. Scales are easily harvested among the young unfurling leaves in the center of the “nest”. The length-to-width ratio of the scales themselves has been highlighted as an important diagnostic feature, but more studies on the scale size and color appear useful in differentiating some taxa (especially ‘*ēkaha* vs. *A. nidus*; see Fig. 4 and Table 1).

*Future work.*—It should also be noted that plants in Tahiti warrant closer attention. Upon inspection of herbarium material at BISH and NY (Fa'a'a, Huahine, and Taha'a), some specimens labeled as *A. nidus* have what appear to be very stiff leaves, sori that are more widely spaced than typical *A. nidus*, and the midrib very prominent on the upper surface while also strongly ridged on the bottom. The leaves also appear to be consistently lanceolate. These have been annotated by J. Flume as “*Asplenium societatis* Flume nom ined.”, but this is not yet published. Other populations of *A. australasicum* from Polynesia and Australia have the upper portion of the midrib much less prominent and sori closer together.

Though studies have been done on various taxa of bird's-nest fern (Dong, Wei, and Chao, 2012; Kim and Tae, 2002; Murakami *et al.*, 1999; Xu *et al.*, 2020), a



thorough investigation of morphological traits paired with genetic analysis is greatly needed, especially of those in Southeast Asia and the Pacific. Morphology of the midrib and leaf scales appear to be useful in delineating species boundaries; however, the midrib morphology is not always discernible in herbarium vouchers and scales may be neglected when collecting and pressing specimens. Further collection and study of these ferns needs to be standardized to make the herbarium vouchers easily discernible. Tahiti and Hawai'i are not the only regions that need attention—remote primary forests and hard-to-access landscapes of Papua New Guinea and the Indo-Pacific region should be carefully considered, since these areas have not been thoroughly studied. Much is yet to be learned about the *Thamnopteris* group of asplenoid ferns.

### CONCLUSIONS

Our study clarifies key morphological features, the midrib architecture in particular, that may be used within Hawai'i to distinguish between native and introduced taxa in the bird's-nest fern complex, as well as outlining the reasons why the name *A. musifolium* should be used for the Hawaiian 'ēkaha fern. This clarification will assist botanists and conservation practitioners seeking clarity on the identity of the native 'ēkaha compared to naturalized or cultivated *A. nidus*. Below is a key to summarize the morphological differences between the known bird's-nest ferns in Hawai'i:

#### KEY TO THE NATIVE AND NON-NATIVE SPECIES OF BIRD'S-NEST FERNS IN HAWAII

- 1 Midrib at the midpoint of the leaf prominent at least ( $\frac{3}{4}$  of it or more) on adaxial surface (+/- two angled) and nearly flat to slightly rounded on abaxial surface ..... *Asplenium nidus*
- 1 Midrib of leaf at the midpoint prominent on the adaxial surface (at least  $\frac{3}{4}$  or more) and slightly rounded/bulging on the abaxial surface (2).
- 2(1) Midrib of leaf with a sharp keel on abaxial surface; cross section of midrib triangular ..... *A. australasicum*
- 2 Midrib of leaf with a flattened ridge on abaxial surface; cross section of midrib trapezoidal ..... *A. musifolium*

CITIZEN SCIENCE OBSERVATIONS.—

#### *Asplenium nidus*:

**KAUA'I.** <https://www.inaturalist.org/observations/150463998>

**MAUI.** <https://www.inaturalist.org/observations/208316442>

**HAWAII ISLAND.** <https://www.inaturalist.org/observations/150463712>

#### *Asplenium musifolium*:

**MOLOKA'I.** <https://www.inaturalist.org/observations/189222897>

**MAUI.** <https://www.inaturalist.org/observations/205166624>

**HAWAII ISLAND.** <https://www.inaturalist.org/observations/171287263>

**SINGAPORE.** <https://www.inaturalist.org/observations/99635666>

SPECIMENS EXAMINED.—

All specimens and images examined for this project have been studied by the corresponding author, Miles K. Thomas

***Asplenium australasicum* (J. Sm.) Hook.:**

Type specimen: AUSTRALIA, cultivated plant at Kew Gardens, 1863, *Anonymous collector s.n.* (BM, image seen)

**AUSTRALIA:** Vicinity of Mossman, Mossman Gorge, 60 km north of Cairns, 100 m, 31 Aug 1981, *D.C. Wasshausen 1164* (US); Kiama, New South Wales, Sep–Oct 1912, *J.E. Tilden 594* (BISH); Norfolk Island, New South Wales, Jul 1899, *I. Robinson s.n.* (BISH); New South Wales, Newell Falls Creek, 6 miles east of Dorrigo, 3000 ft, 7 Feb 1954, *D. Werner 18* (UC); New South Wales, Orara East State Forest, Coffs Harbour, 150 m, 2 May 1956, *E.F. Constable P7404* (UC).

**FIJI:** Vanua Levu, Thakaundrove, southern slope of Valanga Range, 200–400 m, 11 Nov 1933, *A.C. Smith 382* (BISH); Viti Levu, Namosi Province, in trees along the Waidina, 400 m, 5 Sep 1927, *J.W. Gillespie 2656* (BISH); Kandavu, Namalata isthmus region, 30 m, 11–18 Oct 1933, *A.C. Smith 34* (BISH).

**HAWAII:** O'ahu, Kalihi, cultivated plant purchased from Home Depot garden shop as *Asplenium nidus*, 30 Dec 2023, *M.K. Thomas 615* (BISH).

**MARQUESAS:** Hiva Oa, above Atuona, 700 m, 6 Oct 1930, *Pacific Ent. Survey Ex 46* (BISH); Uahuka, 700 m, 10 Nov 1922, *W.B. Jones 1690* (BISH); Uapou, high ridge, 700 m, 13 Sep 1922, *W.B. Jones 1193* (BISH); Nukuhiva, 1922, *E.H. Quayle 1227* (BISH).

**NIUE:** Eas of Alofi, in deep forest on rocks, 65 m, 6 Feb 1940, *T.G. Yuncker 10066* (BISH).

**RAPA:** Maitua, cliffs at the foot of Mt. Tautautu, talus at foot of cliff among other ferns, 210 m, 11 Jul 1934, *F. R. Fosberg 11493* (BISH)

**TONGA:** Vava'u, on humus in forest shade near top of seaward side of cliffs of northwestern side of island, 150 m, 25 May 1953, *T.G. Yuncker 16171* (BISH); Kao, on dead tree on steep slopes in forest, 270 m, 6 May 1953, *T.G. Yuncker 15885* (BISH); Eua, Liku cliffs and plateau, 200–300 m, Jun & Jul 1926, *H.E. Parks et al. 16258* (BISH); Tongatapu, in forests near the coast back of Fatai village, 10 Mar 1953, *T.G. Yuncker 15266* (BISH).

***Asplenium musifolium* Mett.:**

Isotype: PHILIPPINES. Luzon, *H. Cumming 89*, Herbarium Hookerianum 1867 (K, image seen).

**HAWAII:** Sandwich islands, 1819 *C. Gaudichaud-Beaupré* (P); Sandwich islands, O'ahu, 1838–1842, *Wilkes s.n.* (BISH); Kaua'i, along Hanapēpē River near the falls, 24 Jul 1895, *A. A. Heller 2056* (BISH); Kaua'i, Hā'upu, moist forest, 650

ft, 25 Dec 1933, *H. St. John & F. R. Fosberg 13678* (BISH); Kaua'i, Southwest of Hā'ena 4 miles along the Nā Pali Coast Trail, 500 ft, 30 Jul 1969, *J. Hendrickson 3980* (BISH); Kaua'i, Hanakāpī'ai, 600 ft, 1 Jan 1948, *H. St. John et al. 23178* (BISH); O'ahu, half way up Pu'u Hāpapa, Wai'anae Mts, Hono'uli'uli, 20 Oct 1930, *Nakagawa s.n.* (BISH); O'ahu, without specific locality, *H. Mann & W. Brigham 137* (BISH); O'ahu, Kīpapa Trail, O'ahu Forest National Wildlife Refuge, 481 m, 15 Jun 2006, *L. S. Reynolds & R. Walker 146* (BISH); O'ahu, 'Aiea, epiphytic, 300–680 m, 29 Aug 1998, *M. Kato H-1045* (BISH); O'ahu, Hawai'i Loa, southeastern Ko'olau Mountains, on wooded slope facing Niu, 441 m, 9 Apr 2022, *M.K. Thomas 333* (BISH); O'ahu, Palawai Gulch, southern Wai'anae Mountains, 680 m, 6 Apr 2022, *M.K. Thomas et al. 331* (BISH); O'ahu, Hau'ula, Ko'olau Range, near head of Papali Gulch, 1,900 ft, 26 Oct 1952, *K.A. Wilson & E. Ozaki 159* (BISH); O'ahu, Kaliuwa'a Valley, Aug 1908, *Rock 5* (BISH); O'ahu, Waikāne, Waikāne-Waiāhole divide, 1,200 ft, 13 Mar 1932, *E.P. Hume 507* (BISH); Moloka'i, Ka'uhako Crater, 7 Dec 2004, *M. Wysong 508* (BISH); Moloka'i, Hālawā Stream, 200 ft, 27 Dec 1932, *H. St. John et al. 12656* (BISH); Moloka'i, Mapulehu Valley in gulch, 1,200 ft, 28 Dec 1932, *H. St. John et al. 12777* (BISH); Moloka'i, Wailau, 500 ft, 3 Jul 1933, *H. St. John et al. 13220* (BISH); Moloka'i, Waikolu Valley, steep valley wall below Pu'u Ka'eo, 2,500 ft, 22 Dec 1948, *H. St. John et al. 23460* (BISH); Moloka'i, west ridge of Honomuni, 1,500 ft, 23 Dec 1953, *H. St. John 25209* (BISH); Lāna'i, mountains east end, Jun 1913, *C.N. Forbes 97 L* (BISH); Maui, West Maui, Wailena Gulch, 850–950 ft, 15 Jul 1964, *M.R. Crosby & W.R. Anderson 1833* (BISH); Maui, on the way to Kīpahulu, 8 Dec 1919, *C.N. Forbes 1769 M* (BISH); Maui, East Maui, Upper trail, 18 Dec 1908, *H.L. Lyon s.n.* (BISH); Hawai'i, Honomālini, South Kona District, 1,700 ft, 31 Dec 1946, *H. St. John et al. 22501* (BISH); Hawai'i, Kona, Manukā, Government Road, 1,600 ft, Jun 1927, *G.W. Russ 42* (BISH); Hawai'i, forest near Hilo, 1910, *B.M. Newell s.n.* (BISH); Hawai'i, near Maku'u, Puna, 20 May 1966, *O. Degener & I. Degener 30689* (BISH); Hawai'i, between Kalapana and Kapoho by road, 4 Aug 1929, *M.C. Neal s.n.* (BISH); Hawai'i, Puna, Kupa'ahu & N.W. area, 4 Jul 1959, *B.C. Stone 3012* (BISH).

**INDONESIA:** Riouw Archipelago, 29 May 1919, *HAB Bunnemeijer 6011* (L); Sumatra, Jambi, 19 September 1925, *O. Posthumus 1084* (L).

**MALAYSIA:** Borneo, East Kalimantan: Sebulu lowland rain forest, 2 Dec 1980, *Kato & Wiradinata 6962* (L); Sabah, Ranau District, Mesilau River between Mt. Kinabalu golf course site Mesilau Cave, *J.H. Beaman et al. 9105* (MICH); PNG, slopes of Mt. Rossel, Rossel Island, Milne Bay Province, 19 Mar 1979, *J.R. Croft LAE 71358* (L); Tawao, Elphinstone Province, British North Borneo, Oct 1922–March 1923, *A.D.E. Elmer 21406* (BISH).

**NEW GUINEA:** New Ireland, N.W. Lavongai (New Hanover) 5 km south of Lai Bay, Subdistrict Lamet, New Ireland, 100 m, 10 May 1974, *Croft & Lelean LAE 65465* (BISH).

**PHILIPPINES:** Quezon, Tayabas, Brgy. Lalo approach, Mt. Banahaw de Tayabas Abang towards Kawa (loco dicto), 19 Oct 2002, *J.F. Barcelona 1429* (MU); Panay, Antique Province, Culasi Mun. Barangay Alojipan, Hanggud-tubig (W. face of Mt. Madia-as), 1100–1200 m, 9 Apr 1992, *J.F. Barcelona et al. 586* (US).



***Asplenium nidus* L.:**

Lectotype: INDONESIA. Java. *Osbeck s.n.* (LINN, image seen)

**CAROLINE ISLANDS:** Kusiae Island, on decomposed trees, 26 Jan 1936, *M. Takamatsu 437* (BISH); Sholiap Islet, Woleai Atoll, terrestrial in dense forest between taro pit and outer beach ridge, 1 m, 8 Aug 1965, *F.R. Fosberg 47042* (BISH); Namonuito Atoll, Magur Islet, epiphyte in forest, 22 Jun–5 Jul 1957, *B.C. Stone 2121* (BISH); Truk, on rocks, 10 ft, leaves to 3 ft long, 24 Sep 1947, *C.C.Y. Wong 121* (BISH); Palau, Paulo Anna Island, epiphytic on *Cocos* and on ground, 13 Jul 1992, *A.K. Kepler 92-249* (BISH); Anguar Island, ridge on northwest corner of island, dense wet forest on ridge of rough dissected limestone, 40 m, 26 Jul 1946, *F.R. Fosberg 25941* (BISH).

**CHAGOS ARCHIPELAGO:** Diego Garcia, in swampy area, 15 Jun 1967, *C. Rhyne 430* (BISH).

**FIJI:** Rotuma, Haua Meamea Island, 30 ft, 1 Aug 1938, *H. St. John 19367* (BISH); Rotuma, Kilinga, Itutiu District, 15 ft, 8 Jul 1938, *H. St. John 19097* (BISH); Rotuma, “Solnaku Island”, 150 ft, 18 Aug 1938, *H. St. John 19605* (BISH).

**HAWAII:** O‘ahu, Mānoa Valley, Lyon Arboretum, epiphytic on *Albizia* tree, escaping cultivation and naturalizing throughout the garden, 28 Mar 2022, *M.K. Thomas 301* (BISH); O‘ahu, Pauoa, growing in cinnamon tree on side of Pauoa Flats trail, 487 m, 25 Dec 2022, *M.K. Thomas 568* (BISH); O‘ahu, Mānoa, Mānoa Falls trail, southeastern Ko‘olau Mountains, ahupua‘a of Waikīkī, secondary lowland wet forest with *Falcataria moluccana* and other exotic species, 122m, 17 Oct 2022, *M.K. Thomas 460* (BISH); O‘ahu, Hawai‘i Loa Ridge, southeastern Ko‘olau Mountains, wooded slope facing Niu, disturbed mesic forest dominated by guava, only one plant seen, 440 m, 9 Apr 2022, *M.K. Thomas 332* (BISH). O‘ahu, Bishop Museum courtyard, 19 Jul 1989, *Wilson & Staples 1751* (BISH).

**INDONESIA:** Java, near Nongkodjajar, Mar 1909, *M. Mousset 114* (BISH); Java, Tengger Mountains, 1320 m, Apr 1906, *E. Rosenstock 19* (BISH); Java, Bogor, epiphyte in garden, 8 Jan 1899, *H. Dihm 31* (BISH); Indonesia, Feb 1877, *H. Poli s.n.* (F); Maluku Islands, Ambon, 3 m, 28 July 1913–30, Nov 1913, *C. Robinson 448* (US).

**KAPINGAMARANGI:** Werua Islet, occurring on bases of coconut, old stumps, and coconut husks in plantations, 20 Jul 1954, *W.A. Niering 622* (BISH).

**POHNPEI:** Madoenihmw Municipality. Tipwen, Enipoas, in agroforest, fern 1 m tall, 24 Oct 2001, *E. Albert 12* (BISH); Nett Municipality, Eirke, agroforest near house and road, 20 Feb 2006, *R. Lengsi et al. 9* (BISH).

**SOCIETY ISLANDS:** Without specific locality, *Whitney Expedition 2215* (BISH); without specific locality, *Whitney Expedition 2217* (BISH).

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