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Shorter Note

Asplenium scolopendrium* var. *americanum* (Aspleniaceae) Found in New Mexico, USA.—Asplenium scolopendrium* var. *americanum* (Fernald) Kartesz & Gandhi (the American hart's-tongue fern) is among the most distinctive and rarest members of the North American fern flora. First discovered near Syracuse, New York by Frederick Pursh in 1807, reports of new populations of this taxon have drawn considerable interest, due to its rarity, unusual distribution, and close relation to the well-known European hart's-tongue fern, *A. scolopendrium* var. *scolopendrium* L. Following Pursh's initial discovery, additional populations were found in Tennessee (Williamson, Bulletin of the Torrey Botanical Club 6:347–348. 1879), Ontario (Soper, American Fern Journal 44:129–147. 1954), Alabama (Short, American Fern Journal 69:47–48. 1979), and Michigan (Futuyma, American Fern Journal 70:81–87. 1980). Known localities in the United States, where the species is protected under the Endangered Species Act (ESA), are mostly restricted to areas with heavy lake-effect snow on limestone escarpments in the Great Lakes region, with small disjunct populations in limestone sinkholes and caves in the southeastern US. Plants from Mexico and Haiti have sometimes been treated as a distinct variety (in the segregate genus *Phyllitis* as *P. scolopendrium* var. *lindenii* (Hook.) Fernald) or even a different species (*P. lindenii* (Hook.) Maxon) but little evidence apart from geography has been presented to support their distinctiveness from *A. scolopendrium* var. *americanum*, and they have been treated as synonyms of the latter in recent treatments (e.g., Mickel and Smith, Pteridophytes of Mexico, 2004). Even under this broader taxonomic concept, the American hart's-tongue fern is restricted to a few scattered localities, and no significant range extensions have been reported since the discovery of plants in Nuevo León, Mexico, in 1983 (Arreguín-Sánchez and Aguirre-Claverán, Phytologia 60:399–403. 1986).

In February 2017, two of us (L. Baumann and E. Weaver) found a population of *A. scolopendrium* growing in a protected microsite within a small lava tube in El Malpais National Monument, near Grants, Cibola County, New Mexico. The site was discovered during regular surveys of cave features associated with the McCartys lava flow, which comprises the youngest portion of the Zuni-Bandera volcanic field (Dunbar and Phillips, New Mexico Geology 16: 80. 1994). In February 2020, the five authors coordinated a trip to survey the population and search for additional possible localities. A snowstorm delayed the start of the trip and nearly caused its cancellation, but conditions settled and we were able to get in the field by early afternoon. Even in good weather conditions, finding the *A. scolopendrium* population would be difficult; reaching it involves a 40km drive and hiking nearly 2km across a lava field of

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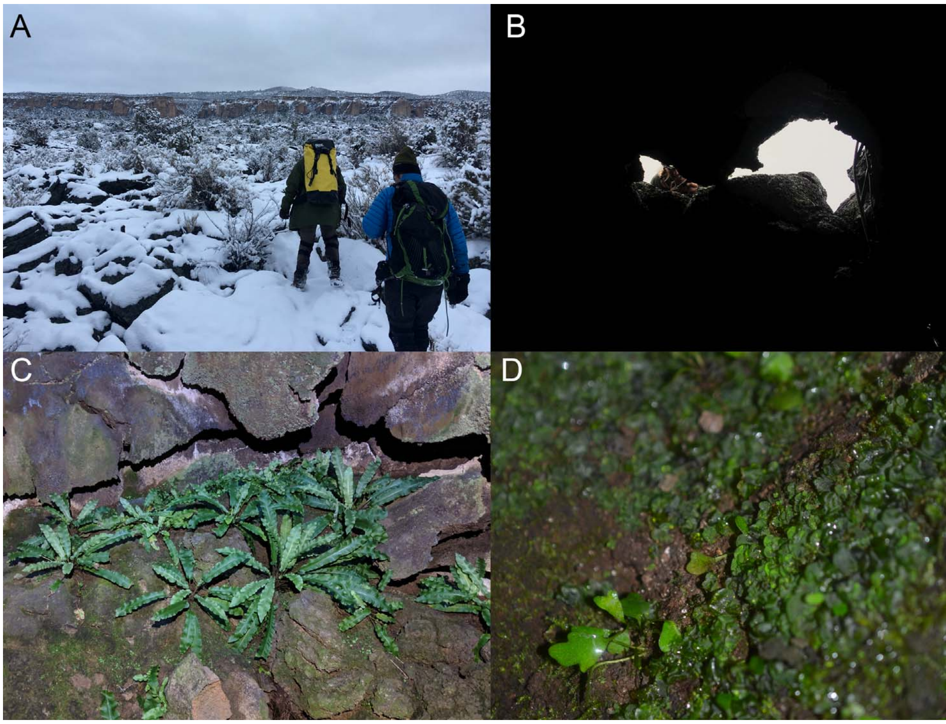

FIG. 1A. Snow-covered lava field near *A. scolopendrium* var. *americanum* site in Cibola County, New Mexico. FIG. 1B. Entrance to lava tube with *A. scolopendrium* var. *americanum* population, viewed from within. FIG. 1C. Mature and immature sporophytes *in situ*. FIG. 1D. Gametophytes and sporelings *in situ*.

sharp and deeply dissected basalt (Fig. 1A). Though covered with a thin layer of snow at the time of our visit, the lava field surrounding the *A. scolopendrium* site is evidently very dry for much of the year, with the local flora being comprising xerophytic species, including: *Opuntia phaeacantha* Engelm., *O. polyacantha* Haw., *Pinus edulis* Engelm., *Cylindropuntia imbricata* (Lam.) F.M. Knuth, *Fallugia paradoxa* (D. Don) Endl. ex Torr., *Atriplex canescens* (Pursh) Nutt., *Yucca baccata* Torr., and *Heterotheca villosa* (Pursh) Shinners.

Given the extreme drought sensitivity of *A. scolopendrium* (Testo and Watkins, American Journal of Botany 100:2261–2270. 2013) and its strong association with limestone elsewhere in its range, its occurrence in such a dry and exposed volcanic landscape may seem incongruous. However, the abundant fissures and lava tubes maintain microclimates with high humidity and cool temperatures year-round (Lindsey, Ecological Monographs 21:227–253. 1951). These microclimates serve as refugia for a number of mesic-adapted plants not found elsewhere in the area, including *A. trichomanes* subsp. *trichomanes* L. (Lindsey, American Fern Journal 35:109–113. 1945) and the mosses *Sanionia uncinata* (Hedw.) Loeske, *Eurhynchium pulchellum* (Hedw.) Jenn., *Paraleucobryum enerve* (Thed.) Loeske, *Platydictya jungermannioides* (Brid.) H.A. Crum, and *Tortella tortuosa* (Schrad. ex Hedw.) Limpr. (Lindsey, 1951). Ecologically, these habitats are similar to the sinkholes where *A. scolopendrium* var. *americanum* occurs in the southeastern United States and "rockhouse" habitats in the Appalachians, which also harbor unusual floristic assemblages, including members of mostly tropical fern groups, such as *Vittaria* (Farrar and Mickel, American Fern Journal 81:69–75. 1991), *Stegnogramma* (Watkins and Farrar, Brittonia 57:183–201. 2005), *Moranopteris* (Farrar, Science 155:1266–1267. 1967), and several Hymenophyllaceae genera (Pinson *et al*. International Journal of Plant Sciences 178:1–18. 2017).

The lava tube in which the *A. scolopendrium* population occurs is roughly spherical, about 4 m in diameter, with a small opening in the ceiling that is approximately 2.5 feet across (Fig. 1B). We accessed the lava tube with a cable ladder and safety line, as a vertical drop of around 3 m is required to reach the plants on the floor of the lava tube. The air inside the lava tube was very humid and warmer (~3.3°C) than the surface temperature (-4°C). The ferns were growing only on the floor of the lava tube and were most abundant on the south and west sides, presumably where adequate sunlight reaches them. A thin soil layer was present in some areas, but most plants were growing in direct contact with the underlying basalt. A whitish mineral deposit was present on some of the basalt on which the ferns were growing; we believe this to be gypsum and are conducting analyses to characterize it. The population was vigorous and large given the available habitat: we counted six fertile sporophytes and 66 immature sporophytes (longest leaf $>$ 2.5cm) and estimated there were thousands of sporelings (sensu Hunter, American Journal of Botany 9:28–36. 1922; longest leaf $<$ 2.5cm) and many thousand gametophytes (Figs 1C & 1D). No other species of fern were found in the lava tube. We found that the abundant gametophytes had capitate glandular hairs on the margins of the thalli and many possessed proliferations like those reported in lab-cultured gametophytes of *A. scolopendrium* var. *americanum* grown from spores collected from plants in New York (Testo and Watkins, Bulletin of the Torrey Botanical Society 138:400–408. 2011).

Based on our current understanding of the morphological characteristics of the gametophyte, the low probability that the population is introduced, and our current understanding of the distribution of a *A. scolopendrium*, we conclude that the population is in fact *A. scolopendrium* var. *americanum*. Mature sporophytes observed generally appear most similar (in terms of indument and leaf shape) to plants from populations from Tennessee and Alabama, USA; it is unclear at this point if these similarities reflect affinities of these populations or the fact that both occur in cave-like habitats. Interestingly, many of the mature sporophytes possessed at least some leaves with deeply hastate lamina bases, which we have observed sporadically in some specimens of *A. scolopendrium* var. *scolopendrium* but never in *A. scolopendrium* var. *americanum*. Although unusual, we do not believe this similarity reflects a close relationship with Eurasian plants, especially given the rare and sporadic appearance of this morphology in the latter.

Given the difficulty in separating infraspecific taxa of *Asplenium scolopendrium* and the uncertainty surrounding the evolutionary history of the group, additional study of the New Mexican populations in a broader context is badly needed. The discovery of this population, which is over 1200 km away from the nearest known locality in Nuevo León, Mexico, and 2500 km away from the core populations of *A. scolopendrium* var. *americanum* in the Great Lakes region of the United States and Canada, adds an additional layer of complexity to our understanding of this species. In addition, though weather conditions during our expedition prevented the exploration of other sites, earlier surveys suggest that at least one additional population occurs in the area. Establishing the taxonomic affinities of these newfound populations is a priority for future research, and we collected several leaves as vouchers (*W. L. Testo 2431*, NY, UNM, US) and additional leaf fragments for future genomic analyses, under permit ELMA-2020-SCI-0003.

Given the occurrence of this population in an isolated area with minimal human traffic, it is unlikely to be disturbed by human activity. The population is demographically balanced and the plants we observed were healthy, with the only damage observed being several leaves scattered on the floor of the lava tube, presumably as a result of herbivory, perhaps by packrats (*Neotoma* spp.). Finally, the population's occurrence within a national monument provides it additional protection and monitoring by the National Park Service. The U.S. Fish and Wildlife Service has initiated a 5-Year Review (89 FR 39113) of the federal listing status of *A. scolopendrium* var. *americanum* in accordance with Section 4(c)(2) of the ESA, and this new population and range extension will be included in this review.

This discovery of *Asplenium scolopendrium* in a xeric lava field in New Mexico also adds to the list of fern species with disjunct populations in the southwestern United States and adjacent Mexico. Rock-dwelling species of *Asplenium* are prominent on this list; along with *A. scolopendrium*, *A. adiantum-nigrum* L., *A. dalhousiae* Hook., *A. exiguum* Bedd., *A. monanthes* L., *A. platyneuron* (L.) Britton, Sterns, & Poggenb., and *A. trichomanes* all are represented in this region by populations well outside of their core ranges (Wagner et al., Aspleniaceae, in: Flora of North America Editorial Committee (eds.), The Flora of North America, Vol. 2. Oxford University Press, New York, NY, pp. 228–245. 1993). Some of these disjunctions are truly remarkable: apart from occurrences in the southwestern United States and northern Mexico, *A. dalhousiae* and *A. exiguum* are restricted to eastern Asia, and *A. adiantum-nigrum* is otherwise almost entirely a Eurasian species.The occurrence of these taxa thousands of kilometers outside of their contiguous ranges attest both to the capacity of fern spores for long-distance dispersal and to the potential of climatically buffered microsites—particularly those associated with rock formations—to harbor unusual biota (Smith, MacNeill, and Richard, Madroño 40:174–176. 1993; Farrar, Journal of the Torrey Botanical Society 125:91–108. 1998).

The existence of such isolated populations of *A. scolopendrium* and other mesophytic fern taxa in xeric regions of western North America also raises questions about how they successfully established. Given the long distances involved in any dispersal scenario, it is most probable that these populations arose following colonization events involving a single spore. Of the *Asplenium* species discussed above, only *A. monanthes* is known to be apomictic (Smith and Mickel, Brittonia 29:391–398. 1977), suggesting that initial establishment of populations of the remaining species involved intragametophytic selfing (gametophyte selfing). Although frequently invoked in discussions of fern biogeography (Barrington, Journal of Biogeography 20:275–279. 1993), this reproductive strategy appears to be uncommon in most fern lineages (Soltis and Soltis, American Fern Journal 80:161–172. 1990; Haufler *et al.*, BioScience 66:928–937. 2016) and lab experiments suggest that *A. scolopendrium* var. *americanum* is an obligate outcrosser (Testo and Watkins, 2011). Although this observation on the taxon's reproductive biology is seemingly incongruous with the existence of disjunct populations like the one reported here, there are several possible explanations. First, it is possible, if unlikely, that the population's founder event involved multiple spores that dispersed as a unit (Kramer, Gardeners' Bulletin, Singapore 30:79–83. 1977), or even a whole sporangium (Gastony, American Journal of Botany 61: 672–680. 1974). Alternatively, the proliferations observed on gametophytes in the newly discovered population may have allowed for the establishment of a multi-gametophyte colony via vegetative reproduction, with subsequent intergametophytic mating. Similar scenarios have been posited to explain patterns of long-distance dispersal in tropical epiphytic ferns (Dassler and Farrar, Brittonia 53:352–369. 2001). A third possibility is simply that there is population-level variation in selfing capacity in *A. scolopendrium* var. *americanum*, and the New Mexico population did in fact establish through intragametophytic selfing. Intraspecific variation in mating systems is known to occur in ferns (Sessa, Testo, and Watkins, New Phytologist 211:1108–1119. 2016), including marked differences between American and Eurasian varieties of *A. scolopendrium*. More detailed study of the reproductive biology of this taxon with a focus on the recently discovered New Mexican population should help address these questions.

Acknowledgments

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