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Argyrochosma, a New Genus of Cheilanthoid Ferns

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The group of fern species related to *Notholaena nivea* (Poir.) Desv. has long been a source of taxonomic contention. In the 183 years since *N. nivea* was first described (as *Pteris nivea* Poir.), members of this alliance have been assigned to no fewer than ten genera, including *Acrostichum, Cheilanthes, Gymnogramma,* and several others no longer in use. Detailed morphological and anatomical investigations leave no doubt that these species are cheilanthoid ferns in the strict sense (Tryon & Tryon, 1982), and most recent authors place this group in either *Notholaena* or *Pellaea.* Rolla Tryon, Maxon, and others who favor placement in *Notholaena* (as typified by *N. trichomanoides*) emphasize two characters that seem to indicate an affinity to that genus: 1) the presence of a farinose indument on the abaxial leaf surface in most species and 2) the absence of a pseudoindusium formed by a modified leaf margin. Those who classify the *N. nivea* complex with *Pellaea* (i.e., Prantl, Christensen, and Morton) stress similarities in spore ornamentation, sporangial distribution and leaf architecture. Despite disagreement over the relative importance of different morphological traits, both groups of pteridologists seem to recognize the *N. nivea* complex as a natural alliance, and the sectional name *Argyrochosma* (proposed by J. Smith in 1841) has often been applied to it regardless of generic assignment.

Copeland and Weatherby recommended a different approach to the taxonomic problems raised by the *N. nivea* group. In *Genera Filicum,* Copeland (1947, p. 70) stated that "The group placed under *Pellaea* in Christensen's *Index,* p. XL, as sect. *Argyrochosma,* typified by *P. nivea* (Poir.) Prantl, has no proper place in the genus. . . . It seems to be a proper generic entity, without a name as such." In a letter to Morton dated March, 1949 (quoted in Morton, 1950, pp. 249–250), Weatherby was even more specific. He stated that "this is one of the two groups (and the better of the two) which I can see clearly as a segregate genus. If to the group of *N. nivea, N. dealbata, N. fendleri,* et cetera, you add *N. Jonesii, N. Lumholtzii, Pellaea microphylla,* and *P. formosa,* you get a coherent and, I think, natural group, which as a genus, should bear the name *Argyrochosma* (J. Smith)." Unfortunately, neither Copeland nor Weatherby lived to complete his study, and subsequent authors have not followed their recommendations.

Ongoing biosystematic investigations of *Pellaea, Notholaena,* and the *N. nivea* complex (Windham, unpubl.) serve to reinforce the idea that *Argyrochosma* is a natural (monophyletic) group worthy of generic recognition. Tryon and Tryon (1982) pointed out that sections *Argyrochosma* and *Notholaena* (the latter typified by *N. trichomanoides*) are distinct in terms of rhizome scales, leaf architecture, sporangial distribution, and spore morphology. These taxa also show consistent differences in chromosome number, gametophyte morphology, chemical composition of the farinose indument, and patterns of variability at conservative enzyme loci (Windham, 1986). Each of these characters indicates a close rela-

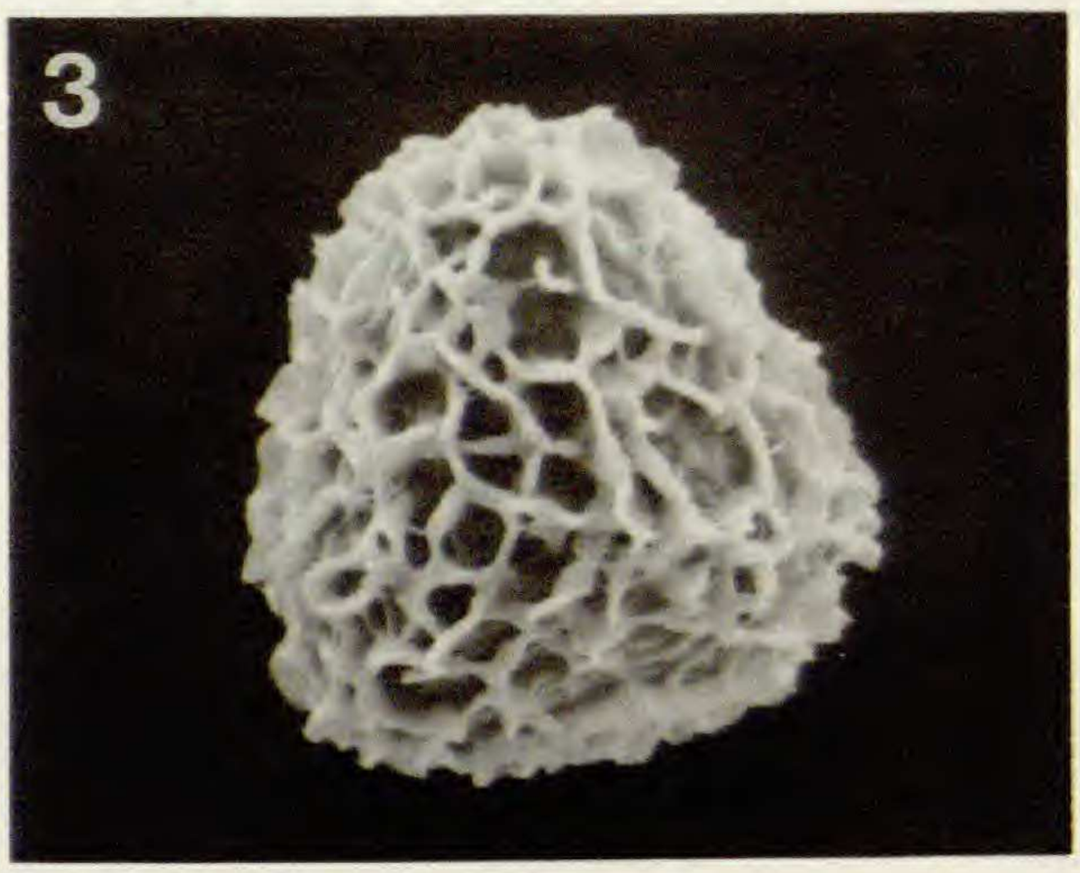
tionship between *Argyrochosma* and *Pellaea* sect. *Pellaea*, suggesting that these may be sister groups in a phylogenetic sense. However, the species of *Argyrochosma* exhibit a chromosome base number ($\bar{x} = 27$) unique among cheilanthoid ferns, and the two groups are easily distinguished using a combination of morphological features including rhizome scales, segment size and leaf dissection, nature of the leaf margin, and the occurrence of a farinose indument. The unique chromosome base number of *Argyrochosma* is here interpreted as a synapomorphy supporting the monophyletic origin of the group, and I concur with Copeland and Weatherby that *Argyrochosma* should be accorded generic rank among the cheilanthoid ferns (included in the family Adiantaceae).

My comparative study of *Pellaea*, *Notholaena*, and *Argyrochosma* is nearing completion, but this detailed work is unlikely to be published prior to deadlines established for several new floristic manuals. Therefore, to facilitate the treatment of *Argyrochosma* in the *Flora of North America*, *Flora of California*, and *The ferns and fern allies of Arizona* (Windham & Yatskievych, in prep.), I herewith describe the genus and make nomenclatural combinations for the sixteen species currently included in it.

Argyrochosma (J. Smith) Windham, stat. nov.—*Notholaena* sect. *Argyrochosma* J. Smith, J. Bot. (Hooker) 4:50. 1841.—Lectotype (chosen by Christensen, 1906, Ind. Fil., p. XL): *Pteris nivea* Poir. [*Argyrochosma nivea* (Poir.) Windham]. – 6939

Rhizome compact, short-creeping, erect to more or less decumbent, bearing scales and many fibrous roots. Rhizome scales thin, light brown to reddish brown, concolorous, up to 1 cm long, linear to lanceolate with an acuminate tip, entire to minutely denticulate. Leaves monomorphic, clustered, up to 40 cm long. Petiole terete to very shallowly sulcate, shorter than to slightly longer than the lamina, with a single vascular bundle; castaneous, atropurpureous, or blackish in color; glabrous, glaucous, sparsely ceraceous, or bearing small widely scattered scales or trichomes. Lamina imparipinnate (Fig. 1), linear-lanceolate, ovate or deltate; bipinnate to pentapinnate at the base, with up to 15 pairs of subopposite or alternate pinnae; coriaceous or (rarely) herbaceous, the upper surface glabrous or sparsely ceraceous, the lower glabrous or usually densely white (rarely yellow) ceraceous. Rachis similar to the petiole but occasionally flexuous. Pinnae lanceolate to deltate, generally remote, divided into numerous ultimate segments. Segments small, oblong to roundish or cordate, entire to shallowly lobed, petiolulate or (rarely) sessile; segment margins unmodified, rarely reflexed to protect sporangia. Veins free, 1- or 2-forked, the unmodified ultimate branches bearing sporangia for much of their length (Fig. 2). Sporangia with 64 or 32 spores. Spores trilete, light to dark brown, with cristate (Fig. 3) or rugose surfaces. Gametophytes usually cordate with wide notches, symmetrical and glabrous (lacking farina-producing trichomes). Chromosome number: $x = 27$ (Fig. 4).

Distribution.—A strictly American genus of approximately 20 species occupying rupestral or (rarely) terrestrial habitats from near sea level to an elevation of 4200 m in the Andes. Ranging from Missouri, Wyoming, and California to Chile (including the Juan Fernandez Islands), Argentina, and the highlands of southeastern Brazil. There is a large geographic gap between the North and South



FIGS. 1–4. Characteristics of the genus *Argyrochosma*. 1. Whole plant of *Argyrochosma nivea* (*Correll & Smith P743*, GH) showing habit and imparipinnate leaf architecture, × ⅓. 2. Leaf from the same individual showing sporangia distributed along the veins for much of their length, × 2. 3. Typical cristate spore of *A. formosa* (*Windham et al. 551*, *KANU*), × 750. 4. Meiotic chromosome squash of *A. delicatula* (*Windham et al. 482*, *KANU*) showing 27II, × 1000.

American elements of the genus (only *A. incana* is found in Central America and the West Indies), with the greatest diversity of species occurring in the highlands of central and northern Mexico.

ENUMERATION OF SPECIES (AND MAJOR SYNONYMS)

1) **Argyrochosma chilensis** (Fée & Remy) Windham, comb. nov.—*Cincinalis chilensis* Fée & Remy in Gay, Hist. Chile (Bot.) 6:497. 1853.—*Notholaena chilensis* (Fée & Remy) Sturm—*Pellaea chilensis* (Fée & Remy) C. Chr.

2) **Argyrochosma dealbata** (Pursh) Windham, comb. nov.—*Cheilanthes dealbata* Pursh, Fl. Amer. Sept. 2:671. 1814.—*Notholaena dealbata* (Pursh) Kunze—*Pellaea dealbata* (Pursh) Prantl.

Although this diploid taxon shows a strong morphological resemblance to the agamosporous triploid *A. limitanea* (Tryon, 1956), isozyme analyses indicate that the species, in its present form, was not involved in the origin(s) of that polyploid.

3) **Argyrochosma delicatula** (Maxon & Weath.) Windham, comb. nov.—*Notholaena delicatula* Maxon & Weath., Contr. Gray Herb. 127:7. 1939.

Preliminary isozyme data indicate that this is quite distinct from *A. incana* and should be maintained as a separate species despite the existence of a few intermediate individuals discussed by Maxon and Weatherby (1939) and Wollenweber (1984).

4) **Argyrochosma fendleri** (Kunze) Windham, comb. nov.—*Notholaena fendleri* Kunze, Farnkr. 2:87, t. 136. 1851.—*Pellaea fendleri* (Kunze) Prantl

5) **Argyrochosma formosa** (Liebm.) Windham, comb. nov.—*Allosorus formosus* Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., V. 1:220 (Mex. Bregn. 68). 1849.—*Notholaena formosa* (Liebm.) R. Tryon—*Pellaea formosa* (Liebm.) Maxon.

6) **Argyrochosma incana** (Presl) Windham, comb. nov.—*Notholaena incana* Presl, Rel. Haenk. 1:19, t. 1, fig. 2. 1825.

Variations in flavonoid chemistry (Wollenweber, 1984) and spore size (Windham, unpubl.) within this widespread taxon suggest that it may include at least two distinct species.

7) **Argyrochosma jonesii** (Maxon) Windham, comb. nov.—*Notholaena jonesii* Maxon, Amer. Fern J. 7:108. 1917.—*Pellaea jonesii* (Maxon) Morton.

As currently defined, this species includes diploid and tetraploid cytotypes which tend to occupy different portions of the range. The type specimen, collected in Inyo County, California, probably represents the tetraploid.

8) **Argyrochosma limitanea** (Maxon) Windham, comb. nov.—*Notholaena limitanea* Maxon, Amer. Fern J. 9:70. 1919.—*Pellaea limitanea* (Maxon) Morton.

Both the typical form and var. *mexicana* (Maxon) Broun are agamosporous triploids which probably arose through different polyploidization events (Windham, unpubl.). If and when the diploid progenitors are identified, it may be necessary to recognize these varieties as distinct species.

9) **Argyrochosma lumholtzii** (Maxon & Weath.) Windham, comb. nov.—*Notholaena lumholtzii* Maxon & Weath., Contr. Gray Herb. 127:16. 1939.

10) **Argyrochosma microphylla** (Mett. ex Kuhn) Windham, comb. nov.—*Pellaea microphylla* Mett. ex Kuhn, Linnaea 36:86. 1869.—*Notholaena parvifolia* R. Tryon.

11) **Argyrochosma nivea** (Poir.) Windham, comb. nov.—*Pteris nivea* Poir., Encycl. 5:718. 1804.—*Notholaena nivea* (Poir.) Desv.—*Pellaea nivea* (Poir.) Prantl.

Although the typical form and var. *tenera* (Hook.) Griseb. both reproduce by means of agamospory, recent chromosome counts indicate that var. *nivea* is triploid while at least some individuals of var. *tenera* are diploid (Windham, unpubl.). The status of all four infraspecific taxa comprising *A. nivea* will need to be reassessed when additional genetic data become available.

12) **Argyrochosma pallens** (Weath. in R. Tryon) Windham, comb. nov.—*Notholaena pallens* Weath. in R. Tryon, Contr. Gray Herb. 179:78. 1956.

13) **Argyrochosma palmeri** (Baker) Windham, comb. nov.—*Notholaena palmeri* Baker, Hook. Icon. Pl. 17: t. 1678 & text. 1887.

14) **Argyrochosma peninsularis** (Maxon & Weath.) Windham, comb. nov.—*Notholaena peninsularis* Maxon & Weath., Contr. Gray Herb. 127:15. 1939.

15) **Argyrochosma pilifera** (R. Tryon) Windham, comb. nov.—*Notholaena pilifera* R. Tryon, Contr. Gray Herb. 179:79. 1956.

16) **Argyrochosma stuebeliana** (Hieron.) Windham, comb. nov.—*Pellaea dealbata* var. *stuebeliana* Hieron., Hedwigia 48:225, t. 12, fig. 15. 1909.—*Notholaena stuebeliana* (Hieron.) R. Tryon.

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