

PHYTOGEOGRAPHICAL NOTES ON ACIDOPHILOUS *CLADONIA* SPECIES IN CALIFORNIA

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ABSTRACT

Several species in the lichen genus *Cladonia* (Ascomycotina: Lecanorales) and their restricted ranges in California are discussed. *Cladonia carneola*, *C. phyllophora*, *C. cervicornis* subsp. *cervicornis*, and *C. crispata* s. str. grow in small populations on azonally occurring, extremely acidic soils (pH 2.9–4.0) in Mendocino and Amador counties. The taxa at these localities are reproductively isolated from other *Cladonia* populations. Isolation is more marked at the Amador County sites, where only one subsection of the genus is represented. *Cladonia cervicornis* specimens from acidic substrata in Amador County contain the *p*-depside atranorin, an unusual and primitive chemical constituent for this species. In contrast to vascular plant species, which are represented by restricted endemic taxa at these sites, the *Cladonia* populations discussed in this paper belong to cosmopolitan taxa whose ranges are very restricted in California. These taxa are represented by relictual populations at the sites studied.

Of 32 *Cladonia* taxa in California (Hammer 1988) four taxa show distinct distributional patterns on acidic soils. Two areas in northern California are noteworthy for their azonal, conspicuously acidic soil types. Several sites in Mendocino County are characterized by shallow lateritic soils underlain by a hardpan layer that is impenetrable to plant roots. These soils and the pygmy forest that grows on them have been discussed by a number of authors (Jenny et al. 1969; Kruckeberg 1969). Unique patterns of endemism in vascular plants of the pygmy forest were noted by Mason (1946a, b) and McMillan (1956). Jenny et al. briefly mentioned the lichens of the pygmy forest and Malachowski (1975) treated the macrolichen flora of the area.

The Ione Formation, which is composed of outcroppings of a unique exhumed oxisol, lies in the foothills of the Sierra Nevada in Amador County. It shares the acidic properties and underlying hardpan of the pygmy forest. Its geological history and soil characteristics were discussed in Singer and Nkedi-Kizza (1980). Gankin and Major (1964) and Stebbins and Major (1965) discussed the flora of the Ione Formation, focusing on the endemic plant *Arctostaphylos myrtifolia* C. Parry that grows in extremely restricted populations on Ione Formation outcroppings. *Arctostaphylos myrtifolia* is taxonomically closely related to *A. nummularia* A. Gray, which is endemic to the

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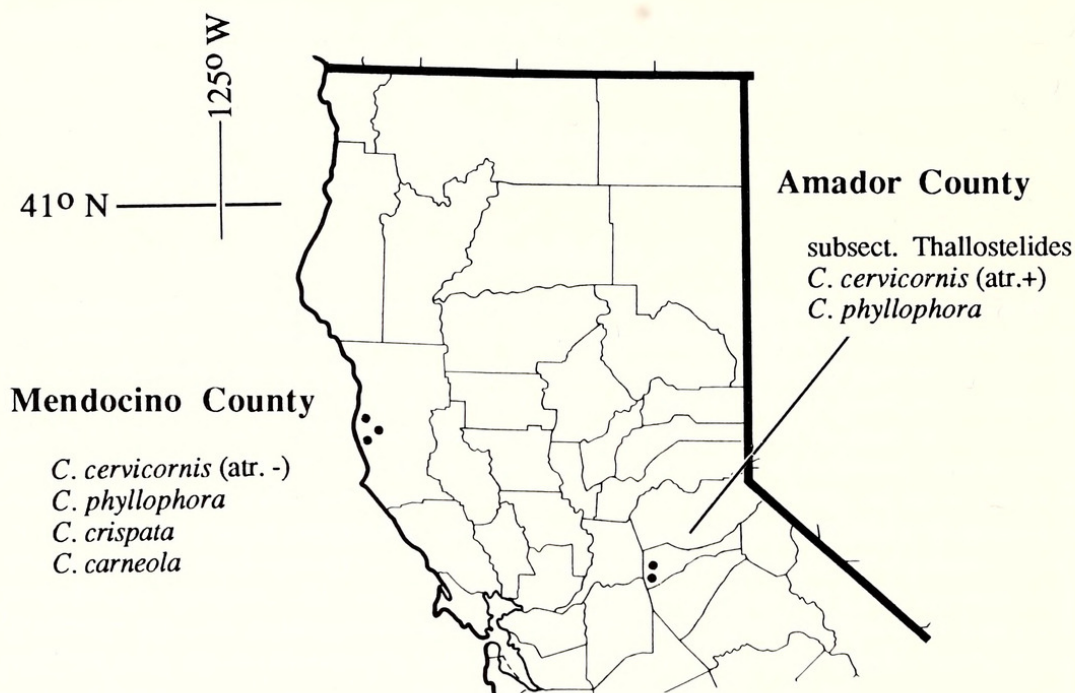


FIG. 1. Acidophilous *Cladonia* taxa found in Pygmy Forest (Mendocino County) and Ione Formation (Amador County) sites.

pygmy forest. These narrowly restricted species are both endemic to conspicuously acidic soils in California. The lichen flora of the Ione Formation was mentioned in Gankin and Major but not treated in detail.

MATERIALS AND METHODS

Over 3000 collections of *Cladonia* from California were studied from fresh collections and herbarium specimens over a 2-year period. Several hundred collections of *Cladonia* were studied from five sites in the pygmy forest and the Ione Formation. The pygmy forest sites in Mendocino County lie in or adjacent to Jackson State Forest, approximately 39°15'N, within 3 km of the Pacific coast. The two collecting sites in Amador County are approximately 30 km east of Sacramento, at approximately 38°30'N, in the western foothills of the Sierra Nevada (Fig. 1). Collection citations from both sites are in Hammer (1988).

Preliminary examination of specimens was performed using a dissecting microscope and routine chemical spot tests (White and James 1985). *Cladonia phyllophora* Hoffm., *C. crispata* (Achar.) Flotow, and *C. carneola* (Fries) Fries were positively determined in this way. Several thalli of *C. cervicornis* (Achar.) Flotow subsp. *cervicornis* exhibited an equivocal reaction to the application of potassium hydroxide and were subsequently tested for chemical constit-

uents using thin layer chromatography (TLC). Specimens that performed unequivocally in the spot test (i.e., only fumarprotocetraric acid detected), were not subjected to TLC. Solvent systems "A" and "C" were used (Culberson 1974; Culberson et al. 1981; White and James 1985). Thirty-one thalli of *C. cervicornis* were tested by TLC to detect atranorin. Purified atranorin from a chemical supply company was used as a standard.

RESULTS

All four taxa discussed in this paper were collected at the pygmy forest sites. All of these taxa were rare in the pygmy forest, growing on bare soil or under *Arctostaphylos* shrubs. Only *C. cervicornis* was represented by more than 10 collections at the pygmy forest localities. The Ione Formation yielded only specimens of *C. phyllophora* and *C. cervicornis*. These species were observed as the dominant terricolous lichens at the Ione Formation sites, where they were found growing in abundance under *A. myrtifolia*.

Atranorin was detected in 16 of the 31 specimens of *C. cervicornis* subsp. *cervicornis* that were tested by TLC. This substance was found in addition to the depsidone fumarprotocetraric acid, which is typically present in *C. cervicornis*. Atranorin was detected in most (80%) of the Amador County specimens, but was rare in specimens from Mendocino County (>10%), where it was present in only trace amounts.

DISCUSSION

The four taxa of *Cladonia* examined in this paper demonstrate distinct distributional patterns in relation to their isolation on acidic substrata. *Cladonia carneola* is found at one locality outside of the pygmy forest in the Klamath Region of northwestern California. Here it comprises part of a relictual flora that is at least as old as the Pleistocene (Hammer 1989) and may be of Tertiary origins (Raven and Axelrod 1978). *Cladonia crispata* s. str. is restricted to two sites in the pygmy forest, and is not found elsewhere in the state. *Cladonia phyllophora*, rare in the pygmy forest and the Klamath Region of northwestern California, is co-dominant with *C. cervicornis* subsp. *cervicornis* at the Ione Formation sites. *Cladonia cervicornis* s. lat. is distributed widely in California, and subsp. *cervicornis*, of which a few coastal specimens contained atranorin, is present along the Pacific coast from San Diego County to Del Norte County (Fig. 1).

Analysis of the chemical data on *C. cervicornis* from the Ione Formation sites supports the hypothesis that these specimens represent an ancestral population. This population has experienced long geographical and reproductive isolation from other populations in

TABLE 1. *CLADONIA* TAXA PRESENT AT PYGMY FOREST AND IONE FORMATION SITES. Asterisks indicate acidophilous taxa discussed in this paper.

Pygmy forest (Mendocino County)	Ione formation (Amador County)
Sect. <i>Cladonia</i>	
Subsect. <i>Cocciferae</i> (Del. in Duby) Mattick	
<i>C. polydactyla</i> (Flörke) Sprengel s. lat.	
<i>C. transcendens</i> (Vainio) Vainio	
<i>C. macilenta</i> Hoffm.	
<i>C. bellidiiflora</i> (Achar.) Schaer.	
Subsect. <i>Ochroleucae</i> (Fries) Mattick	
* <i>C. carneola</i> (Fries) Fries	
Subsect. <i>Thallostelides</i> (Vainio) Mattick	
* <i>C. phyllophora</i> Hoffm.	
* <i>C. cervicornis</i> (Achar.) Flotow subsp. <i>cervicornis</i>	
<i>C. cervicornis</i> subsp. <i>verticillata</i> (Hoffm.) Ahti	
<i>C. pyxidata</i> (L.) Hoffm.	
<i>C. chlorophaea</i> (Flörke) Sprengel	
<i>C. fimbriata</i> (L.) Fries	
<i>C. subulata</i> (L.) Wigg.	
Sect. <i>Perviae</i> (Fries) Mattick	
Subsect. <i>Chasmariae</i> (Achar.) Mattick	
Series <i>Furcatae</i> E. Dahl	
<i>C. furcata</i> (Hudson) Schrader	
Series <i>Squamosae</i> E. Dahl	
<i>C. carassensis</i> Vainio s. lat.	
<i>C. squamosa</i> (Scop.) Hoffm.	
var. <i>squamosa</i>	
<i>C. squamosa</i> (Scop.) Hoffm. var. <i>sub-squamosa</i> (Nyl. ex Leighton) Vainio	
* <i>C. crispata</i> (Achar.) Flotow s. str.	
	Subsect. <i>Thallostelides</i>
	* <i>C. phyllophora</i>
	* <i>C. cervicornis</i> subsp. <i>cervicornis</i>
	* <i>C. chlorophaea</i>

western North America. Atranorin was present in most specimens of *C. cervicornis* subsp. *cervicornis* from the Ione Formation sites. It was rare in over 100 specimens of *C. cervicornis* from outside of Amador County. Culberson (1986) discussed the loss of atranorin as a derived trait in the *C. chlorophaea* group, which is closely related to *C. cervicornis* (subsect. *Thallostelides*). The influence of gene flow in populations of lichens on their chemical constituents was demonstrated by Culberson et al. (1988). *Cladonia cervicornis* in the pygmy forest has remained in contact with contiguous populations that range along the Pacific coast of California from the Mexican border to Oregon. Gene flow and the subsequent evolution of derived chemotypes (presence of fumarprotocetraric acid only and loss of atranorin in most individuals), may be inferred for these populations. The Amador County population of *C. cervicornis* has been geographically isolated from coastal populations. Its concomitant

reproductive and genetic isolation may be inferred from its retained primitive chemical characteristics.

Geographic isolation at the Ione Formation sites has influenced the diversity of *Cladonia* species as well as their chemical characteristics. In contrast to the pygmy forest, where 17 species and four subsections are represented, only one subsection and three species are represented at the Amador County sites (Table 1).

The pygmy forest of Mendocino County and the Ione Formation of Amador County are areas where low soil pH is correlated with unique distributions of phanerogams. Cryptogams such as the lichen genus *Cladonia* demonstrate unique patterns of distribution in these areas as well. Vicariance and subsequent isolation on specialized soils has led to speciation and endemism in many vascular plants such as *Arctostaphylos nummularia* and *A. myrtifolia*. Many widely distributed taxa of the genus *Cladonia* are relictual at these localities, and possess primitive characters. Where contact with widespread populations has been maintained, as in coastal populations, derived characters may be observed.

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NOTEWORTHY COLLECTIONS

MONTANA

GOODYERA REPENS (L.) R. Br. (ORCHIDACEAE).—Judith Basin Co., Little Belt Mts., Sandpoint Cr. of Lost Fork of Judith R., 42 km SW of Stanford, T12N R10E SE¼ sect. 10, 1860 m, 3 Aug 1987, *Phillips 870803-34* (MRC) (verified: J. S. Shelly, P. F. Stickney, MRC). Approximately 200 plants were found in a 400-square-meter area on a north-facing slope in dense shade of an old-growth Douglas-fir/lodgepole pine forest. The site is an *Abies lasiocarpa/Linnaea borealis* habitat type on limestone substrate. The orchids were found in an unburned island in the center of a large 1985 burn, growing in thick mats of the mosses *Drepanocladus uncinatus*, *Hylocomnium splendens*, and *Pleurozium schreberi* (det: J. C. Elliott). Other associated species include *Linnaea borealis*, *Pyrola secunda*, *Galium boreale*, *Clematis columbiana*, *Thalictrum occidentale*, *Smilacina stellata*, *Juniperus communis*, *Pseudotsuga menziesii*, *Abies lasiocarpa*, and *Picea engelmannii*.

Significance. Second record for MT. Previously known from a single collection (6 Aug 1980, *J. DeSanto*, GNP) from Glacier National Park near Upper Kintla Lake 370 km northwest of the location reported here. This site is also disjunct by 600 km from next closest known U.S. station in the Black Hills, SD. In addition to MT, western U.S. distribution includes CO, NM, and AZ, but the species is not known from the adjacent states of WY and ID.—H. WAYNE PHILLIPS, Lewis and Clark National Forest, P.O. Box 871, Great Falls, MT 59403.



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