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Notes on the amphipacific relations of Hawaiian Cladoniaceae

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Abstract. The total number of currently accepted species of Cladoniaceae in the Hawaiian Islands is 22. Several taxonomic problems still exist, however. The effects of isolation are clear among Cladoniaceae. Endemism is high (c. 40%); and, the number of species low. The species must have reached the archipelago via long-distance trans-oceanic dispersal, probably aided by the abundant production of lichen propagules, such as soredia and microsquamules. Although most of the species found in Hawaii are widely distributed, the Hawaiian Cladoniaceae show slight affinities to those of E and SE Asia. *Cladonia polyphylla* Mont. & v.d. Bosch is an older name for *C. fruticulosa* Krempelh., and is lectotypified from authentic material. *C. leprosula* H. Magn. is included in *C. ochrochlora* Flörke.

True oceanic islands, like the Hawaiian Islands, have never had any connection or association with continental land during geographic diversification that has been going on through geological time. These islands are volcanoes arising from the ocean floor. The Hawaiian Islands are shield volcanoes that are formed where tectonic plates move over a "hot spot" and magma wells up to the surface (e.g. Press & Siever 1982, Fosberg 1991). The estimated age of the Hawaiian archipelago is c. 50 million years. Today the nearest continent is North America (c. 3800 km to the northeast). Japan is c. 5400 km to the west, and the closest oceanic atolls are c. 800 km distant. The archipelago comprises eight major

islands (Hawaii, Kahoolawe, Maui, Lanai, Molo-kai, Oahu, Kauai, and Niihau), the largest of which - and still with volcanic activity - being Hawaii (c. 1560 sq km).

Major works on Hawaiian lichens, including Cladoniaceae, are those of des Abbayes (1947), Magnusson (1956, who summarizes exhaustively the earlier information), Klement (1966) and Smith (1981). Some ecological investigations including Cladoniaceae have also been reported (e.g. Kappen & Smith 1980).

The main purpose of the present paper is to update information on Hawaiian species of the

Cladoniaceae, including their taxonomy. In addition, we show the importance of long-distance dispersal that seems to be surprisingly effective among Cladoniaceae in many areas, especially in the Southern Hemisphere where land is scattered (see e.g. Galloway 1991, Stenroos 1993).

We emphasize that the material used for this study is not complete. Some specimens could not be determined to any known species, but on the other hand we were reluctant to describe new taxa based on sparse material. Others have not been relocated, some destroyed in World War II. The results are mainly based on specimens in H, HAW and TUR (which include the collection made by L. & Y. Mäkinen in 1966), and on field work of both authors. Several specimens were analysed by standardized thin-layer chromatographic methods (Culberson 1972, White & James 1985).

Results and discussion

Altogether 22 species of *Cladina* and *Cladonia* are recorded in this study (Table 1). The number of species reported from the area by earlier authors is almost twice as high (see Magnusson 1956, who recognized 37 species). All previously recorded species have been assigned to currently extant species in the islands; none are extinct.

The following species reported from Hawaii by earlier authors are excluded from the flora because in light of the material examined and the knowledge of the distribution of the species elsewhere they are unlikely to occur in the Hawaiian Islands, or their presence needs confirmation: *Cladia aggregata* (Sw.) Nyl., *Cladonia chlorophaea* (Flörke) Sprengel (as *C. pyxidata* var. *chlorophaea* Flörke in Magnusson 1956), *C. coniocraea* (Flörke) Sprengel, *C. corallifera* (Kunze) Nyl., *C. digitata* (L.) Hoffm., *C. erythrosperma* Vainio, *C. fimbriata* (L.) Fr., *C. furcata* (Hudson) Schrader, *C. gracilis* (L.) Willd., *C. granulosa* (Vainio) Ahti (as *C. subsquamosa* f. *granulosa* Vainio in Magnusson 1956), *C. grayi* Merr. ex Sandst., *C. macilenta* Hoffm., *C. mexicana* Vainio, *C. phyllophora* Hoffm. (as *C. degenerans* (Flörke) Sprengel in

Magnusson 1956), *C. pyxidata* (L.) Fr., *C. scabriuscula* (Delise) Nyl., *C. sphacelata* Vainio, and *C. subradiata* (Vainio) Sandst. (as *C. fimbriata* var. *balfourii* (Crombie) Vainio). Of the reindeer lichens, *Cladina rangiferina* (L.) Nyl. and *C. mitis* (Sandst.) Hustich were definitely excluded from the Hawaiian flora by Ahti (1961).

In addition, the following taxa reported from the Islands are reduced to synonymy, further reducing the total number of accepted species present: *Cladonia congregata* H. Magn. (= *C. didyma* (Fée) Vainio, see des Abbayes 1966, Stenroos 1986a), *C. fauriei* des Abb. (= *C. kauaiensis* Merrill, see Stenroos 1986a), *C. leprosula* H. Magn. (= *C. ochrochlora* Flörke, T. Ahti pers. comm.), *C. subsquamosa* (Nyl.) Crombie (= *C. squamosa* Hoffm., see Huovinen & Ahti 1988), and *C. vulcanica* Zoll. & Moritzi (= *C. didyma* (Fée) Vainio, see Huovinen et al. 1989). *C. polyphylla* Mont. & v.d. Bosch (as *C. pityrea* **polyphylla* (Mont. & V.D. Bosch) des Abb. in Magnusson 1956) was found here to be conspecific with *C. fruticulosa* Krempelh. However, although *C. polyphylla* (lectotype, here selected: Java, Junghuhn, PC-Hue; syntypes, L, PC-Hue) is an older name for this taxon, it is not accepted here because *C. fruticulosa* shall be proposed for conservation according to the new Art. 14.1 in the Botanical Code as approved in the XV International Botanical Congress in Yokohama in 1993.

Finally, in addition to *Cladina magnussonii* (Ahti) Ahti, which was reported by Ahti (1961), the following taxa are recorded here as additions to Magnusson's (1956) list of Cladoniaceae of the Hawaiian Islands: *Cladonia* cf. *corniculata* Ahti & Kashiw., *C. merochlorophaea* Asah. var. *merochlorophaea*, *C. pleurota* (Flörke) Schaeffer s.lat., and *C. poeciloclada* des Abb. One specimen (Kauai, Hanalei, Bowler 1517, H), with farinose soredia, imperfectly scyphose podetia, and fumarprotocetraric acid, probably belongs to an undescribed species ("sp. 1" in Table 1). Specimens (Kauai, Kokee, L. & Y. Mäkinen 66-2031, TUR; Oahu, Waianae Range, L. & Y. Mäkinen 66-1627, TUR; Hawaii, Volcanoes Nat. Park, Stenroos 3918, H) determined here as "sp. 2" are related to *C.*

Table 1. List of Hawaiian Cladoniaceae and their major secondary substances. BAR=barbatic acid (incl. 4-O-demethylbarbatic acid), DID=didymic acid, FUM-complex=fumarprotocetraric and protocetraric acids and Cph-2 (Cph-1 present or absent), HSEK=homosekikaic acid, IUSN=isousnic acid, MCRY=4'-O-methylcryptochlorophaeic acid, MER=merochlorophaeic acid, PER=perlatolic acid, PSO=psoromic acid, SQU=squamatic acid, THA=thamnolic acid, USN=usnic acid.

Species	Major secondary substances
<i>Cladina</i>	
<i>leiodea</i> (H. Magn.) Ahti	USN, FUM-complex
<i>magnussonii</i> (Ahti) Ahti	ATR, FUM-complex
<i>skottsbergii</i> (H. Magn.) Follm.	USN, PER
f. <i>fuscescens</i> (Ahti) Ahti	PER
<i>Cladonia</i>	
<i>angustata</i> Nyl.	USN, BAR
cf. <i>cenotea</i> (Ach.) Schaerer	SQU
cf. <i>corniculata</i> Ahti & Kashiw.	FUM-complex
<i>didyma</i> (Fée) Vainio	THA, DID or BAR
<i>farinacea</i> (Vainio) A. Evans	FUM-complex
<i>fruticulosa</i> Krempelh.	PSO or FUM-complex
<i>kauaiensis</i> G.K. Merrill ex H. Magn. & Zahlbr.	USN, THA
<i>mauiensis</i> H. Magn.	BAR, DID
<i>merochlorophaea</i> Asah. var. <i>merochlorophaea</i>	MCRY, MER, FUM-complex
<i>oceanica</i> (Vainio) Zahlbr.	USN, BAR, DID
<i>ochrochlora</i> Flörke	FUM-complex
<i>pleurota</i> (Flörke) Schaerer	USN, IUSN, ZEO
<i>poeciloclada</i> des Abb.	FUM-complex
<i>ramulosa</i> (With.) Laundon (incl. <i>C. adspersa</i> Mont. & Bosch)	FUM-complex, HSEK, ATR
<i>solitaria</i> H. Magn.	USN
<i>squamosa</i> Hoffm.	SQU
<i>subsquamosa</i> Krempelh.	FUM-complex

ramulosa and *C. phyllopoda* (Vainio) Stenroos (Stenroos 1988) but differ from them by their very slender, more branched, granulose, and partly escyphose podetia. Specimens generally referred to as *C. scabriuscula* or *C. farinacea* are here included in *C. farinacea* s.lat. The present material is often richly squamulose (in contrast to *C. farinacea* s.str. in South America) and the podetial squamules and parts of podetial surface are farinose-soresiate (contrary to *C. scabriuscula* s.str.). Similar material is found in Eastern Asia

as well. However, this complex still needs a thorough revision. For some of the more poorly known taxa of those accepted here, the reader is referred to some previous papers: *Cladonia angustata* Nyl. (Stenroos 1986a), *C. fruticulosa* Krempelh. (as *C. decipiens* des Abb. in Magnusson 1956, see Stenroos 1988), *C. mauiensis* H. Magn. (Stenroos 1986a), *C. oceanica* (Vainio) Zahlbr. (Stenroos 1986a), and *C. solitaria* H. Magn. (Stenroos 1986b).

The effects of prolonged isolation of the Hawaiian Islands are clear in taxa of the Cladoniaceae. The degree of endemism in lichens is high, viz. c. 40% (parmelioid lichens 8%, alectorioid lichens 0%, umbilicarioid lichens 0%, lichens total 38% (see Magnusson 1956), mosses 46% (see Hoe 1979), ferns & fern allies 70% (C. H. Lamoureux, pers. comm.), and angiosperms 95%), and the number of species is relatively low. Because of the isolation of the archipelago, taxa in the Cladoniaceae must have reached the area via long-distance trans-oceanic dispersal or, in the case of endemics, evolved on the islands.

Long-distance dispersal is apparently aided by the abundant production of lichen propagules such as soredia and microsquamules which are very common in the Cladoniaceae. The priority of vegetative dispersal is supported by the fact that spore-production seems to be poor, at least in many present-day Cladoniaceae, even if the species is frequently fertile.

Ancestors of the esorediate and esquamulose endemics of genus *Cladina* as well as of *Cladonia* sect. *Unciales* (viz. *C. solitaria*) may have reached the islands by means of easily disintegrating thallus fragments. Most of the other species possess either farinose or granulose soredia (*C. angustata*, *C. cf. cenotea*, *C. cf. corniculata*, *C. fruticulosa*, *C. merochlorophaea*, *C. ochrochlora*, *C. pleurota* s.lat., *C. poeciloclada*, *C. farinacea* s.lat., and the endemics *C. mauiensis*, *C. oceanica*, and *C. sp. 1*) or microsquamules or granules (*C. didyma*, *C. ramulosa*, *C. squamosa*, and *C. sp. 2*). The endemic *C. kauaiensis* produces relatively large, attached granules but those of its ancestors may have been more suitable for long-distance dispersal.

Most of the species which also occur outside Hawaii, have a relatively wide total range (*C. didyma*, *C. merochlorophaea*, *C. ochrochlora*, *C. pleurota*, *C. ramulosa*, *C. farinacea* s. lat., and *C. squamosa*). However, as with the phanerogams (Carlquist 1970) the Hawaiian Cladoniaceae flora seems to show some affinities with that of E and SE Asia (Fig. 1). On the other hand, the alectorioid and parmelioid lichens of Hawaii

have weak affinities with Central and South America (Smith 1993, 1994).

Successful dispersal is not only a problem of how to reach an area but also of establishment once there. Asexual propagules, produced abundantly in most Cladoniaceae, have both biotypes present. Yet most species are slow in their development and need stable conditions without much competition or disturbance. Both competition and disturbance are encountered on Hawaii, where luxurious vascular vegetation with many aggressive alien plants has taken over many areas. Cladoniaceae are also absent from large arable and cultivated areas and areas under grazing (mainly cattle). Feral pig activity in natural forests results in a dramatic decrease in cladonioid species except on rotting logs which are rarely disturbed. Volcanic activity is extremely destructive: lava flows may bury large areas, and bare volcanic rock and heat certainly set limits to the growth of many Cladoniaceae. On the other hand, ash fields and lava flows in wet areas provide excellent habitats for some species. The invasion of alien bunchgrasses this century has not only crowded out cladonioid lichens from the many areas of exposed lava, but also dramatically increased the incidence and severity of wildfires (Smith and Tunison 1992). The immediately adjacent regions of thermal areas also provide habitats e.g. for the endemic *C. oceanica* (Kapen & Smith 1980, Smith 1981). The Islands, therefore, provide a wide array of habitats though many of them are now inimical to lichens.

Of the endemics, *Cladina leiodea*, *C. skottsbergii*, *Cladonia oceanica*, and *C. sp. 2* are distributed on most islands, whereas the others seem to be confined to a smaller area: *Cladina magnussonii* (Maui), *Cladonia kauaiensis* (Kauai), *C. mauiensis* (Maui), *C. solitaria* (Maui), *C. sp. 1* (Kauai); *Cladina magnussonii* and *Cladonia solitaria* are actually confined to a very small area at the summit of W. Maui.

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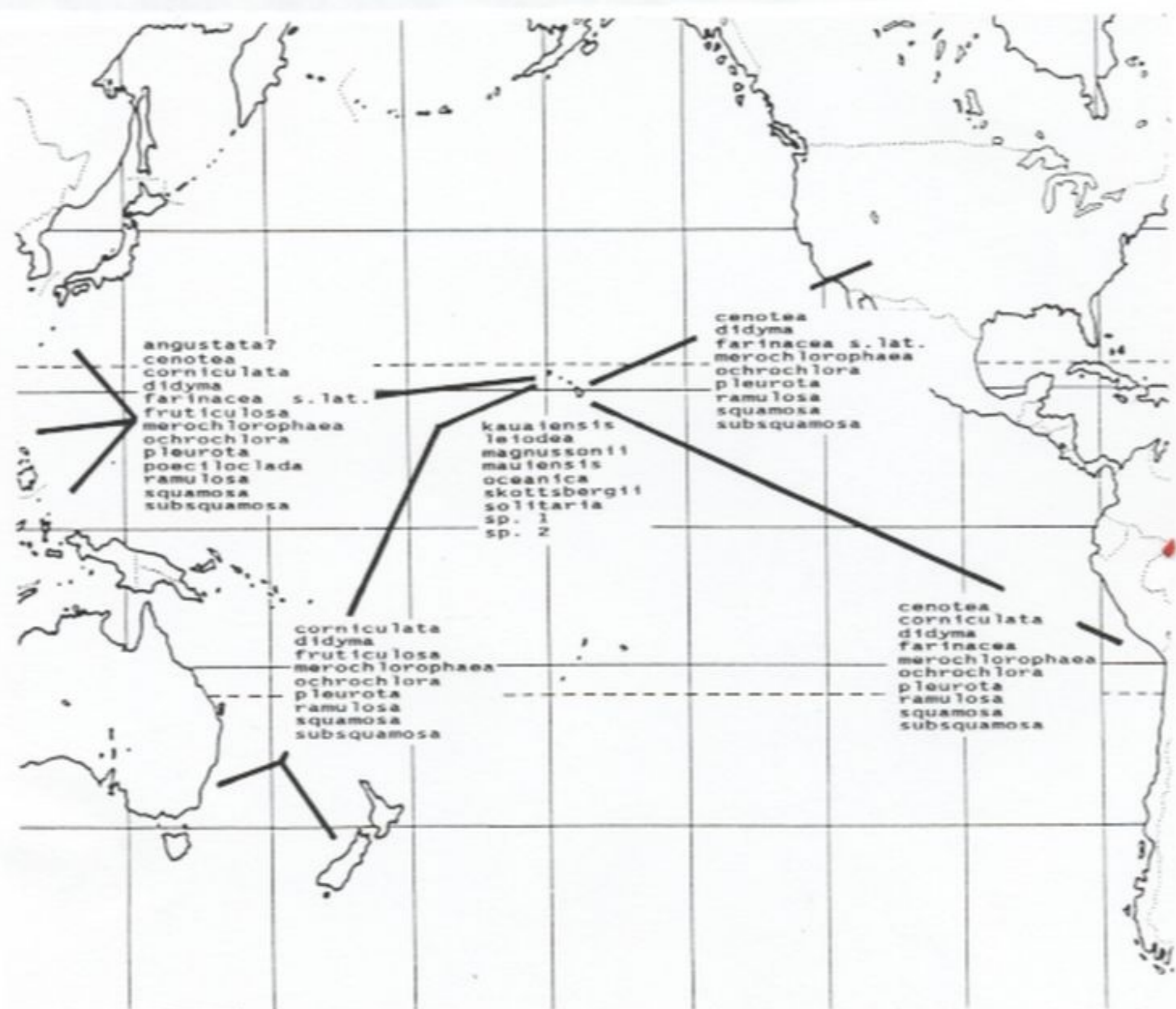


Fig. 1: The amphipacific relations of Hawaiian Cladoniaceae.

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