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# Sexual Reproduction in *Audouinella alariae* (Jónsson) Woelkerling (Acrochaetiaceae, Rhodophyta) from the North Atlantic Ocean

Yong-Pil LEE*
Department of Botany, University of British Columbia
Vancouver, B.C., Canada

Carpogonia, spermatangia and carposporangia are demonstrated for North Atlantic plants of *Audouinella alariae* (Jónsson) Woelkerling for the first time. The plants are monoecious. Carpogonia are terminal on short branches and give rise to short trichogynes laterally. Spermatangia are usually borne in pairs on the supporting cells of carpogonia. Fertilized carpogonia give rise to 3—4 carposporangia. Morphology of sexual reproductive structures and postfertilization development provide characteristics for distinguishing *A. alariae* from *A. rhipidandra* (Rosenvinge) Dixon, which were previously synonymized.

## Introduction

*Audouinella alariae*, epiphytic on *Alaria esculenta* (L.) Greville, is one of the more widely distributed audouinelloid algae in the North Atlantic Ocean. Since it was described from Iceland (Jónsson, 1901), it has been reported from North Carolina (Kapraun, 1980), New England (Collins, 1906; Woelkerling, 1973), Newfoundland (South, 1976; South & Hooper, 1980), and Nova Scotia (Erskine, 1955; Edelstein *et al.*, 1969; Wilson *et al.*, 1979) in North America, and Faeroe Islands (Bφrgesen, 1902), Norway (Levring, 1937; Rueness, 1977), eastern Scotland (Wilkinson, 1979), and southwest England (Dixon & Irvine, 1977) in Europe. All of the above references mentioned plants bearing only monosporangia. From Hokkaido in the northwestern Pacific Ocean, *A. alariae* was recently found epiphytic on *Alaria crassifolia* Kjellman and bearing sexual reproductive structures and carposporangia as well as monosporangia (Lee & Kurogi, 1983).

Despite numerous collections and distribution records of *Audouinella alariae*, sexual reproduction and carposporophytes remained unknown in the North Atlantic Ocean. Woelkerling (1973) observed the type specimen and many other collections of this species from the northwestern coast of the Atlantic Ocean and described only monosporangia. South & Hooper (1980) reported *A. alariae* from Newfoundland from April through December, and observed monosporangia in May and September through December.

## Materials and methods

The material on which this study is based was collected at Cape Race, Newfoundland, Canada on August 11, 1982. Additional observations were

* Present address; Department of Biology, Cheju National University, Cheju, 590 Korea

made on the following collections: Hardhead Island, Penobscot Bay, Maine, July 1894 (*Phycotheca boreali-americana*; UBC). Ferryland, Avalon Peninsula, Newfoundland, 4 December 1968 (UBC A40352). Ketch Harbour, 7 February 1966 (NR CC 2239). Portugese Cove, Nova Scotia, 15 July 1966 (NRCC 2805). Herring Cove, Halifax County, Nova Scotia, 21 June 1966 (NRCC 7495). Peggy's Cove, Halifax County, Nova Scotia, 13 July 1981 (NRCC 8683). The abbreviations for herbaria follow Holmgren & Keuken (1974).

Permanent slides were prepared by mounting plants in 25% Karo syrup with 0.1% aniline blue. Living material, which was used in corroboration of the morphology of sexual reproductive structures, was cultured under 10°C long day (16:$\overline{8}$) conditions for two months. Part of the material from Cape Race was prepared for scanning electron microscopy as follows: thalli with a segment of the host were in 5% formalin seawater, transferred to PES medium (Provasoli 1971) for 24 hours, post fixed in 2% osmium tetroxide and PES medium (1:1) for 2 hours, dehydrated in ethyl alcohol series, dried in a critical point drying apparatus, and coated with gold.

A duplicate of the dried specimens collected by the author was deposited in the Phycological Herbarium of the University of British Columbia (UBC A67184).

## Results

Most plants of *Audouinella alariae* simultaneously bore monosporangia, sexual reproductive structures and carposporangia, however, some plants bore only monosporangia or sexual reproductive structures and carposporangia. Monosporangia are solitary and sessile in secund arrangement on the upper region of erect filaments (Fig. 9), or in pairs on a stalk cell in opposite arrangement on the middle through lower region of erect filaments. Monosporangia are obovoid to ellipsoid, 9-12$\mu m$ in diameter and 14-17 (-19)$\mu m$ long.

Male and female reproductive structures are borne on the same thallus. Spermatangia are in pairs on the adaxial side of the supporting cells of a carpogonium (Figs. 2, 3), or seldom on short branches (spermatangial branch, Fig. 1). The spermatangial branches consist of 2-3 cells which are oblong to cylindrical, 4-5$\mu m$ in diameter and 4-7$\mu m$ long. Spermatangia are globose to ellipsoid, 4-6$\mu m$ in diameter and 5-6$\mu m$ long. Spermatia attached to trichogynes are c. 4$\mu m$ in diameter (Figs. 4, 5). Carpogonia are solitary, terminal on 1- to 3-celled branches, in secund arrangement on erect filaments. Sessile carpogonia borne laterally on erect filaments were occasionally seen. The cells of the branches supporting carpogonia show no difference in appearance from the vegetative cells of erect filaments (as is the case with the stalk cells of monosporangia). Carpogonia are ellipsoid to obovoid, 5-8$\mu m$ in diameter and 9-12$\mu m$ long (Figs. 2, 3, 4). Trichogynes develop laterally on the distal portion of the carpogonium and are papillate to spatulate with a constricted base, 2-3$\mu m$ in diameter and to 9$\mu m$ long (Figs. 2, 3). Trichogynes always point to the ventral side of the carpogonium (adaxial).

Upon fertilization carpogonia elongate distally (Fig. 5) and divided by a transverse wall (Fig. 6). While the distal cell enlarges and takes the form of a carposporangium, the proximal cell gives rise to 2-3 cells subterminally or laterally (Fig. 7). Rarely the distal cell, instead of being itself a carposporangium, gives rise to terminal and lateral carposporangia. Carposporangia are obovoid to obpyriform, 12-14$\mu m$ in diameter and 18-21$\mu m$ long. Upon the release of carpospores, the old sporangial walls are retained (Fig. 8). Regeneration occurred in the old sporangial wall.

## Discussion

It seemed that *Audouinella alariae* usually tended to distributed at the ragged distal parts of the host blades. Plants from Cape Race, Newfound-

land had also 1-2 erect filaments on a single basal cell as a variety of collections and the type specimen (Woelkerling 1973). In Hokkaido, although it showed a slight seasonal variation, more than 90% of the plants consisted of 2-3 erect filaments (Lee & Kurogi, 1983). There is no consensus on the presence of unicellular hairs in *A. alariae* (Collins, 1906; Taylor, 1957; Dixon & Irvine, 1977; Woelkerling, 1973), however, some plants from Newfoundland had hairs (Fig. 9). Thus the development of hairs may show seasonal variation in this locality as Hokkaido collections (Lee & Kurogi, 1983). The cells of living material have a stellate plastid with a central pyrenoid (Fig. 10) as described by Jónsson (1901) and Levring (1937).

*Audouinella alariae* has similar morphology and development of sexual reproductive structures to *A. kurogii* Lee et Lindstrom. The latter species differs from *A. alariae* in bearing carpogonia terminally on branches and main axes, and in trichogynes with a much constricted base (Lee & Lindstrom, 1979). The carposporophyte structure of *A. alariae* is similar to *Audouinella kylinoides* (Feldmann) comb. nov.* (Stegenga & van Wissen, 1979, as *Chromastrum kylinoides*) and *A. kurogii* (Lee & Lindstrom, 1979). Woelkerling observed the type specimen of *A. rhipidandra* and synonymized it with *A. alariae*. On the other hand, Dixon & Irvine (1977) treated them as separate species. *A. alariae* is similar to *A. rhipidandra* in the size of vegetative cells and monosporangia (see Woelkerling, 1973, table 2). However, the two species are different in morphology and development of sexual reproductive structures and carposporophytes, i.e., 1) *Audouinella rhipidandra* bears spermatangia in flat, triangular clusters on 2- to 5-celled spermatangial branches; 2) *Audouinella rhipidandra* bears sessile, bottle-shaped carpogonia with a terminal trichogyne; 3) the carposporophyte structure of *A. alariae* is more simple than that of *A. rhipidandra* (cf. Rosenvinge 1909).

In the Acrochaetiaceae there are monoecious and dioecious species. Dioecious ones usually have long trichogyes and abundant spermatangia (e.g., *A. microscopica* (Näg.) Woelkerling, Stegenga & Mulder, 1979; *A. rosulata* (Rosenvinge) Dixon, Stegenga & van Wissen, 1979). On the other hand, monoecious ones have rather short trichogynes and a few spermatangia. In monoecious species, male and female reproductive structures are borne close to each other, even though they may be on separate branches. Some monoecious species bear carpogonia on the lower cells of spermatangial branches (e.g., *A. halandica* (Rosenvinge) Woelkerling, Rosenvinge, 1909, figs. 21E, 22B; Stegenga & Borsje, 1977, fig. 5; *A. thuretii* (Bornet) Woelkerling, Rosenvinge, 1909, fig. 31C; *A. efflorescens* (J. Agardh) Papenfuss, Rosenvinge, 1909, fig. 62; *A. dictyotae* (Collins) Woelkerling, Woelkerling, 1971, fig. 13E). In *A. efflorescens*, Rosenvinge (1909) observed that the cells of spermatangial branches often transformed into intercalary carpogonia. In *A. halandica* grown in culture, Stegenga & Borsje (1977) observed aberrant carpogonia on which spermatangia were borne. However, none of the species known with sexual reproductive structures bear spermatangia on the supporting cells of carpogonia as in *A. alariae* and *A. kurogii*.

In the Acrochaetiaceae carpogonial morphology of *A. alariae* is also distinctive in that a papillate to spatulate trichogyne develops laterally on the distal portion of a carpogonium. Some Australian species also have similar papillate or spatulate trichogynes (Woelkerling, 1971, figs. 1, 5, 6, 7, 13), however, these trichogynes are terminal on carpogonia.

Carposporangia are only slightly larger than monosporangia in *A. alariae*, thus carposporophytes, because of their simple structure, can be mistaken for stalked monosporangia. Such characteristics as well as the distinctive morphology and development of sexual reproductive structures in *A. alariae* seem to be the reason that they

* Basionym: *Acrochaetium kylinoides* Feldmann (1958, *Bull. Soc. Bot. Fr.*, 105: 498)

have been overlooked by previous phycologists. As an example, the specimen no. 236 in *Phycotheca boreali-americana* bears abundant carposporangia and sexual reproductive structures as well as monosporangia. This suggests that the sporangia mentioned in figure 4 of Woelkerling (1973. p. 596) might be carposporangia. An elaborate figure, which may also represent carposporangia, was made from Norwegian collections by Levring (1937, fig. B).

In Hokkaido, *A. alariae* bore sexual reproductive structures and carposporangia for the period from October through February, when day length in the locality was less than 11 hours (Lee & Kurogi 1983). Culture experiments using the Hokkaido material confirmed the short day requirement for the production of sexual reproductive structures in this species. In the northwestern Atlantic, *A. alariae* bore sexual reproductive structures and carposporangia in July (New England, *Phyco. bor.-am.* no. 236; Nova Scotia, NR CC 2805 and 8683), August (Newfoundland, UBC A67184) and December (Newfoundland, UBC A 40352). In Nova Scotia, *A. alariae* bore only monosporangia in February and June (NRCC 2239 and 7495). These observations suggest that North Atlantic plants of *A. alariae* may require a different photoperiod from Hokkaido plants for the production of sexual reproductive structures and carposporangia.

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## Addendum

After this article had gone to press, an additional important paper has come to the author's attention. The paper (Kuiper, J. 1983)—The life history of *Chromastrum alariae* (Jónsson) Papenfuss (Rhodophyta, Acrochaetiaceae). *Acta Bot. Neerl.* 32(3), May 1983, 129-151.—represents detailed observations on the sexual reproductive structures and the life history of the species with the type material and some collections from the eastern coast of the North Atlantic Ocean.

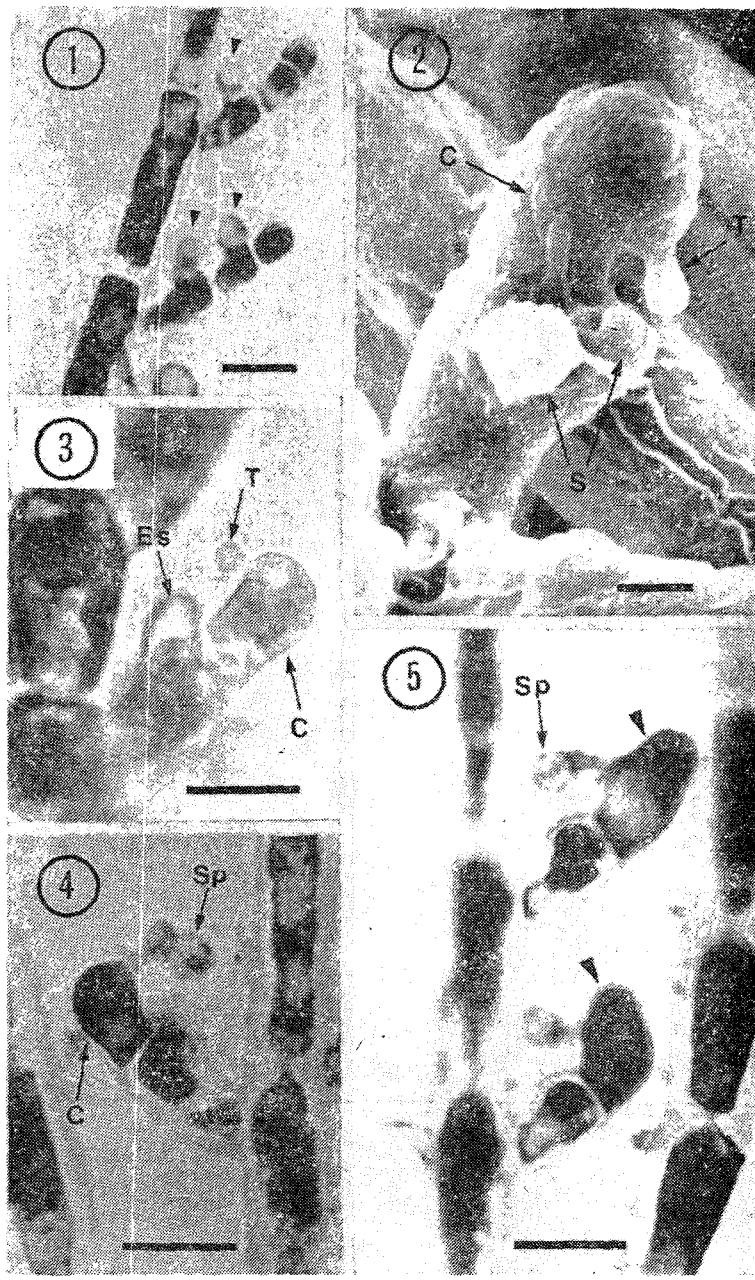


Fig. 1. Spermatangial branch bearing spermatangia (arrow heads). scale 10 $\mu m$.
Fig. 2. Carpogonium and spermatangium on the supporting cell of carpogonium (SEM). scale 2 $\mu m$.
Fig. 3. Carpogonium and empty spermatangium (in culture). scale 10 $\mu m$.
Fig. 4. Carpogonium with a spermatium attached to the trichogyne. scale 10 $\mu m$.
Fig. 5. The beginning of postfertilization development (arrow heads). scale 10 $\mu m$.
S; spermatangium, Sp; spermatium, C; carpogonium, Cg; carposporangium, Ec; emptycarposporangium, H; hairs, M; monosporangium, T; trichogyne, Es; empty spermatangium.
All the illustrations are of field collected material unless otherwise indicated.

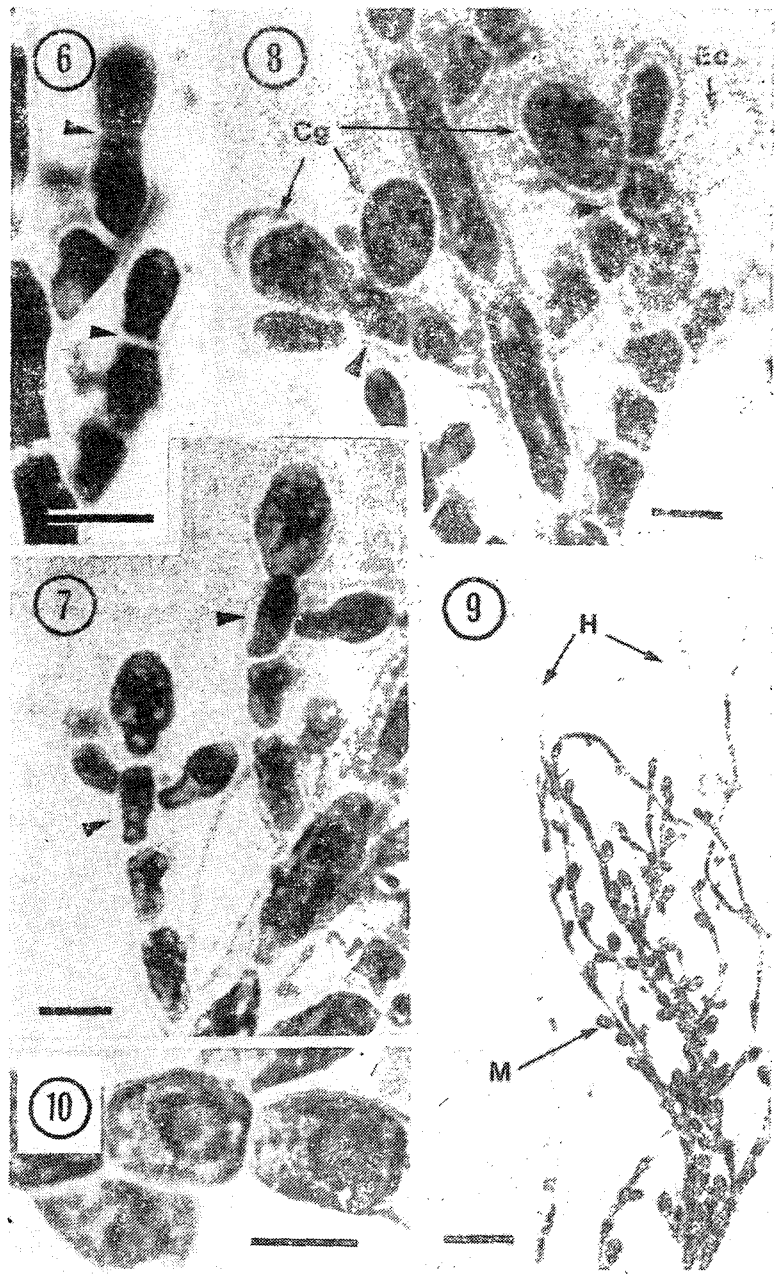


Fig. 6. Postfertilization development. Note the first division of the fertilized carpogonium by a transverse wall (arrow heads). scale 10 $\mu m$.
Fig. 7. Immature carposporophytes (arrow heads). scale 10 $\mu m$.
Fig. 8. Mature carposporophytes (arrow heads). scale 10 $\mu m$.
Fig. 9. Thallus bearing hairs. Note monosporangia. scale 50 $\mu m$.
Fig. 10. Stellate plastids (in culture). scale 10 $\mu m$.

# 北大西洋産 *Aubouinella alariae* (Jónsson) Woelkerling의 有性生殖

이 용 필
Canada British Columbia大學 植物學科

北大西洋産 *A. alariae*의 造果器는 가지의 끝에 發生하며 側生하는 짧은 受精毛를 갖는다. 造精器는 造果器의 支持細胞上에 發生한다. 果胞子體는 3~4個의 果胞子囊을 形成한다.