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Taxonomy of the Rhodochortaceae with Special Reference to the Plants in the Northwestern Pacific Ocean

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A normal association analysis of 10 genera hitherto referred to the Rhodochortaceae on the basis of characters of the type species results in three groups. One group is composed of two genera, *Rhodochorton* and *Rhodothamniella*, and separated by the character "absence of monosporangium". The other group, characterized by presence of monosporangium, is segregated by the characters "forming a discoid or filamentous basal system in tetrasporophyte". The group characterized by forming a discoid basal system comprises three genera, *Acrochaetium, Kylinia*, and *Chromastrum*. A cluster analysis of 36 taxa of the Rhodochortaceae in the northwestern Pacific region also results in three clusters: *Acrochaetium*-cluster, *Auduinella*-cluster, and *Rhodochorton*-cluster. The results of normal association analysis and cluster analysis correspond to the generic classification schemes suggested by Woelkerling (1983) and Lee and Lee (1988).

Key Words: taxonomy, Rhodochortaceae, *Auduinella dictyotae, Acrochaetium alariae, Rhodochorton subimmersum*

INTRODUCTION

Generic classification scheme of the Rhodochortaceae is a long standing problem (Garbary, 1979). Several generic classification schemes in order to resolve the taxonomic problem of the family have been proposed during the past 60 years and also have involved many different criteria for generic circumscription (Hamel, 1925; Kylin, 1944, 1956; Papenfuss, 1945; Feldmann, 1962; Stegenga, 1979; Lee, 1980; Woelkerling, 1983; Lee and Lee, 1988). Drew (1928) suggested the single generic concept and recognized *Rhodochorton* in the family. Nakamura (1941, 1944) and Nasr (1947) followed Drew's concept. Dixon (in Dixon and Irvine, 1977) and Garbary (1979), also following Drew's concept, recognized *Auduinella* instead of *Rhodochorton*. Woelkerling (1971) proposed a single generic concept (*Auduinella*) with a "form genus" (*Colaconema*). Lee and Lee (1988) summarized the generic classification schemes hitherto suggested in the Rhodochortaceae.

Garbary (1979) attempted to ascertain the generic circumscription in the Rhodochortaceae on the basis of numerical classification of 170 descriptions of 112 species described in the world. He concluded that there was no significant segregation of genus in the family. However, the segregation of the family into more than two genera is still received wide acceptance (Woelkerling, 1983; Stegenga, 1985; Lee, 1980; Lee and Lee, 1988). Saunders and McLachlan (1991) removed *Rhodochorton spetsbergensis* to a new genus *Meiodiscus* of the Rhodophysemataceae. Thus, it may be a more prevailing opinion that the Rhodochortaceae might be a rather heterogeneous taxon.

The intergeneric associations of the 10 genera and the interspecific relations of 36 taxa of the Rhodochortaceae from Korea and Japan are figured out with statistical methods. In this study an interpretation on the results of statistical analysis for the

Table 1. Main characteristics of the type species of the genera referred to the Rhodochortaceae

Table 1-1. Habitat

Number	Species	Habitat & Habit	References
1	*Auduinella hermanni*	freshwater saxicolous	Israelson 1942
2	*Balbiania investiens*	freshwater epiphytic	Sirodot 1876, Swale & Belcher 1963
3	*Acrochaetium secundatum*	marine epiphytic or epizoic	Dixon & Irvine 1977, Lee 1987
4	*Rhodochorton purpureum*	freshwater & marine saxicolous & epiphytic	Conway & Knaggs 1966, Jónsson 1901
5	*Colaconema bonnemaisoniae*	marine endophytic	Batters 1896, Boney 1972
6	*Kylinia rosulata*	marine epiphytic	Rosenvinge 1909
7	*Grania efflorescens*	marine epiphytic & saxicolous	Lehmann 1902, Rosenvinge 1909
8	*Liagorophila endophytica*	marine endophytic	Yamada 1944
9	*Chromastrum virgatulum*	marine epiphytic	Hooker 1833 Rosenvinge 1909
10	*Rhodothamniella floridula*	marine saxicolous & epiphytic	Dillwyn 1802, Woelkerling 1971

Table 1-2. Basal system (* under culture condition)

Species	Tetrasporophyte	Gametophyte	References
Auduinella hermanni	filamentous, interwoven	filamentous, interwoven	Israelson 1942
Balbiania investiens	filamentous, interwoven	filamentous, interwoven	Swale & Belcher 1963
Acrochaetium secundatum	filamentous, forming a disc	unknown	Lee 1987
Rhodochorton purpureum	filamentous, interwoven	*filamentous, interwoven	West 1969, Stegenga 1978
Colaconema bonnemaisoniae	no differentiation of basal and erect systems, no information on gametophytic or sporophytic phase		Batters 1896, Boney 1972
Kylinia rosulata	*filamentous, forming a disc	unicellular	Rosenvinge 1909, Boillot & Magne 1973
Grania efflorescens	filamentous	filamentous	Rosenvinge 1909
Liagorophila endophytica	unknown	filamentous	Yamada 1944, Lee *et al.* 1986
Chromastrum virgatulum	filamentous, forming a disc	unicellular	Dixon & Irvine 1977, Stegenga & Mulder 1979
Rhodothamniella floridula	filamentous, interwoven	*unicellular	Stegenga 1978

Table 1-3. Chloroplasts

Species	Chloroplast	References
Auduinella hermanni	single parietal laminate, often dissected into spirally arranged ribbons, without pyrenoids	Israelson 1942 Drew 1935
Balbiania investiens	single parietal band-shape, showing loose irregular spiral form, without pyrenoids	Swale & Belcher 1963
Acrochaetium secundatum	single, stellate with a pyrenoid	Lee 1987
Rhodochorton purpureum	several, discoid without pyrenoids	Dixon & Irvine 1977
Colaconema bonnemaisoniae	single, parietal, irregularly lobate plate with a pyrenoid	Boney 1972
Kylinia rosulata	single, parietal laminate without pyrenoids	Feldmann 1958
Grania efflorescens	1-3 band-form, often spiral form without pyrenoids	Kylin 1906, Lehmann 1902, Rosenvinge 1909
Liagorophila endophytica	single, stellate with a pyrenoid	Lee *et al.* 1986
Chromastrum virgatulum	single, stellate with a pyrenoid	Børgesen 1902
Rhodothamniella floridula	several, stellate with a pyrenoid	Kornmann & Sahling 1977, Stegenga 1978

Table 1-4. Sexuality and sexual reproductive structures (* under culture conditions)

Species	Sexuality	Reproductive structure	References
Auduinella hermanni	dioecious or monoecious	spermatangia in groups (3-4) carpogonia terminal or lateral	Israelson 1942
Balbiania investiens	monoecious	spermatangia in groups (5-6) carpogonia lateral or intercalary	Sirodot 1876, Swale & Belcher 1963
Acrochaetium secundatum	unknown	unknown	Stegenga 1985 Lee 1987
Rhodochorton purpureum	*dioecious or monoecious	*spermatangia in clusters carpogonia terminal or lateral	Knaggs 1968, West 1969, Stegenga 1978
Colaconema bonnemaisonia	unknown	unknown	
Kylinia rosulata	dioecious	spermatangia in groups carpogonia sessile on basal cells	Rosenvinge 1909, Moestrup *et al.* 1975
Grania efflorescens	monoecious	spermatangia in clusters carpogonia lateral or intercalary	Lehmann 1902, Rosenvinge 1909
Liagorophila endophytica	monoecious	spermatangia in pairs carpogonia terminal or lateral	Lee *et al.* 1986
Chromastrum virgatulum	*dioecious or monoecious	spermatangia in clusters carpogonia lateral, sessile	Rosenvinge 1909, Stegenga & Mulder 1979
Rhodothamniella floridula	*dioecious	spermatangia in clusters carpogonia terminal	Stegenga 1978

Table 1-5. Monosporangia (* under culture conditions, # on separate thallus)

Species	Tetrasporophyte	Gametophyte	References
Auduinella hermanni	present	present	Israelson 1942
Balbiania investiens	present	present	Swale & Belcher 1963
Acrochaetium secundatum	present	unknown	Stegenga 1985, Lee 1987
Rhodochorton purpureum	absent	*absent	West 1969, Stegenga 1978
Colaconema bonnemaisoniae	Monosporangia are present, but it has not been confirmed yet whether the plant represents tetrasporophyte or gametophyte.		Batters 1896
Kylinia rosulata	*present	present	Boillot & Magne 1973
Grania efflorescens	#present	unknown	Rosenvinge 1909
Liagorophila endophytica	unknown	present	Lee *et al.* 1986
Chromastrum virgatulum	present	present	Rosenvinge 1909, Stegenga & Mulder 1979
Rhodothamniella floridula	absent	*absent	Stegenga 1978

Table 1-6. Postfertilization development and carposporophyte (* under culture conditions)

Species	Postfertilization	Carposporophyte	References
Auduinella hermanni	undivided	fertilized carpogonium issuing 4-5 branches composed of a few cells bearing carposporangia	Drew 1935
Balbiania investiens	transversely divided	4-celled gonimoblast with laterals bearing carposporangia	
Acrochaetium secundatum	unknown	unknown	
Rhodochorton purpureum	*transversely divided	gonimoblast developing into tetrasporophytes which producing tetrasporangia	West 1969, Stegenga 1978
Colaconema bonnemaisoniae	unknown	unknown	
Kylinia rosulata	undivided directly	fertilized carpogonium issuing carposporangia	Feldmann 1958
Grania efflorescens	transversely divided	gonimoblast issuing several branches composed of 2-3 moniliform cells becoming carposporangia	Rosenvinge 1909
Liagorophila endophytica	longitudinally divided	4-6 celled gonimoblast developing perpendicularly to the axis of carpogonium, each cell issuing 1-3 carposporangia	Lee *et al.* 1986
Chromastrum virgatulum	transversely divided	4-5 celled gonimoblast with short branches and bearing carposporangia terminally	Rosenvinge 1909
Rhodothamniella floridula	*transversely divided	gonimoblast developing into tetrasporophytes	Stegenga 1978

Table 2. Data matrix of the characteristic units of the type species of the 10 genera T = tetrasporophyte, G = gametophyte, + = present, ? = unknown, blank = absent. See Table 1-1 for species acronyms

CHARACTERS	SPECIES		no.	Au. her. 1	Ba. inv. 2	Ac. sec. 3	Rh. pur. 4	Co. bon. 5	Ky. ros. 6	Gr. eff. 7	Li. end. 8	Ch. vir. 9	Rh. flo. 10
Habitat	epilithic		1	+			+			+			+
	epiphytic		2		+	+	+		+	+		+	+
	epizoic		3			+							
	endophytic		4					+			+		
Basal	T	filamentous	5	+	+	+	+		+	+	?	+	+
		interwoven	6	+	+		+				?		+
		forming a disc	7			+	+		+		?	+	
	G	filamentous	8	+	+	?	+	+		+	+		
		interwoven	9	+	+	?	+	+			+		
		unicellular	10			?			+			+	+
Chloroplast		single	11	+		+		+	+		+	+	
		several	12	+	+					+			+
		many	13				+						
		laminate	14	+				+	+				
		stellate	15			+					+	+	+
		ribbon-shape	16	+	+					+			
		discoid	17				+						
Pyrenoid		present	18			+		+			+	+	+
		absent	19	+			+		+	+			
Sexuality		monoecious	20	+	+	?	+	?		+	+	+	
		dioecious	21	+		?	+	?	+			+	+
Monosporangia	T	present	22	+	+	+			+	+	?	+	
		absent	23				+				?		+
	G	present	24	+	+	?		+	+	+	+	+	
		absent	25			?	+						+
Postfertilization	undivide		26	+		?		?	+			+	
	transverse div.		27		+	?	+	?		+		+	+
	longitudinal div.		28			?		?			+		
Carposporangium	present		29	+	+	?		?	+	+	+	+	
	absent		30			?	+	?					+

taxa is given to the generic classification in the Rhodochortaceae.

MATERIALS AND METHODS

All the type species of the 10 genera are examined on the basis of the characters listed in Table 1. Each characters are subdivided into several units: i.e., habitat into epilithic, epiphytic, epizoic, and endophytic; basal system of tetrasporophyte into filamentous, interwoven, and forming a disc; basal system of gametophyte into filamentous, interwo-

Table 3. List of the species examined in this study

Number	Name of species	Locality
1	*Auduinella codicola* (Børgesen) Garbary	Korea
2	*Auduinella codii* (Crouan) Garbary	Korea
3	*Auduinella daviesii* (Dillwyn) Woelkerling	Korea & Japan
4	*Auduinella dictyotae* (Collins) Woelkerling (G)	Korea
5	*Auduinella dictyotae* (Collins) Woelkerling (S)	Korea
6	*Auduinella elegans* (Drew) Lee Y-P. et Lee I.K.	Korea
7	*Auduinella infestans* (Howe et Hoyt) Dixon	Korea
8	*Auduinella phacelorhiza* (Børgesen) Garbary	Korea
9	*Auduinella thuretii* (Bornet) Woelkerling	Korea
10	*Acrochaetium canariense* Børgesen	Korea
11	*Acrochaetium catenulatum* Howe	Korea & Japan
12	*Acrochaetium densum* (Drew) Papenfuss	Korea & Japan
13	*Acrochaetium inkyuii* Lee Y-P	Korea
14	*Acrochaetium microscopicum* (Naegeli) Naegeli	Korea
15	*Acrochaetium moniliforme* (Rosenvinge) Børgesen	Korea
16	*Acrochaetium scapae* (Lyle) Papenfuss	Korea
17	*Acrochaetium secundatum* (Lyngbye) Naegeli	Korea
18	*Acrochaetium terminale* (Nakamura) Lee Y-P.	Korea
19	*Acrochaetium virgatulum* (Harvey) Bornet	Korea
20	*Rhodochorton subimmersum* Setchell et Gardner	Korea & Japan
21	*Acrochaetium alariae* (Jónsson) Bornet (G)	Japan
22	*Acrochaetium alariae* (Jónsson) Bornet (S)	Japan
23	*Acrochaetium humilis* (Rosenvinge) Børgesen	Japan
24	*Auduinella japonica* (Papenfuss) *comb. nov.*	Japan
25	*Acrochaetium kurogii* (Lee et Lindstrom) Lee Y-P.	Japan
26	*Acrochaetium sancti-thomae* Børgesen (G)	Japan
27	*Acrochaetium plumosum* (Drew) Smith	Japan
28	*Auduinella rhizoidea* (Drew) Garbary	Japan
29	*Acrochaetium sancti-thomae* Børgesen (S)	Japan & Korea
30	*Acrochaetium sessile* (Nakamura) *comb. nov.*(S)	Japan
31	*Acrochaetium sessile* (Nakamura) *comb. nov.*(G)	Japan
32	*Rhodochorton membranaceum* (Magnus) Hauck	Japan
33	*Rhodochorton purpureum* (Lightfoot) Rosenvinge (S)	Japan & Korea
34	*Rhodochorton purpureum* (Lightfoot) Rosenvinge (G)	Japan
35	*Rhodochorton spetsbergense* (Kjellman) Kjellman*	Japan
36	*Acrochaetium yamadae* (Garbary) Lee Y-P. et Lee I.K.	Japan

S: sporophyte, G: gametophyte.

*This species is known as *Meiodiscus spetsbergensis* in the Rhodophysemataceae (Saunders and McLachlan, 1991).

ven, and unicellular etc. The 30 characteristic units are constructed so that every type species of the 10 genera can be scored as present (1) or absent (0) for all characteristic units (Table 2). Although it has not been known whether the plant of *Colaconema bonnemaisoniae* represents a tetrasporophyte or a gametophyte, the plant is regarded as a gametophyte in this study because the plant is supposed to be a gametophyte on the basis of *Colaconema simplex* Inagaki (as *Auduinella japonica* <Papenfuss> Lee, 1980) of which the plants produce carpogonia and spermatangia as well as monosporangia. The

Table 4. List of characters and their characteristic units employed in the statistical method

General characters	Characteristic units
1. habitat	epilithic, epiphytic, endophytic, endozoic, epizoic
2. thallus	tufted, caespitose, scattered, basal system predominating, erect system predominating
3. germinating spore	septate, aseptate
4. basal system	single cell, filamentous, discoid
5. cells of basal system	contorted, constricted, oblong, cylindrical, fusiform, ellipsoid, subglobose, globose, turbinate, various shape
6. erect system	absent, present, upright, decumbent, simple, first branch, more than second branch
7. cells of erect system	constricted, not constricted, oblong, cylindrical, clavate, barrel-shape, moniliform
8. chloroplast	single, several, stellate, laminate, discoid, ribbon-shape, patch-like
9. pyrenoid	absent, one per cell, more than one
10. hairs	present, absent
11. hair-like prolongation	present, absent
12. monosporangium	present, concatenate, solitary, in pairs, in groups, absent
13. arrangement of monosporangium	secundly serial, pinnate, spiral, fan-shape, scattered
14. spermatangium	present, absent
15. carpogonium	present, absent
16. tetrasporangium	present, absent
17. carposporangium	present, absent

characters unknown in some species, such as *Acrochaetium secundatum, Liagorophila endophytica* and *C. bonnemaisoniae* are treated as absent (0).

The material used in this examination comprises 22 taxa which are 20 species and both a gametophyte and a tetrasporophyte of one species from Korea (Lee, 1987) and 20 taxa which are 12 species and both gametophytes and tetrasporophytes of four species from Japan (Lee, 1980; Lee *et al.*, 1986). Six species are common in both localities. Either one of the species common in the both localities are employed in this study. The gametophyte and the tetrasporophyte of a species are examined as a separate entity (taxon). Following the classification scheme proposed by Lee and Lee (1988), all species referred to in the text are named (Table 3).

In this study, no assumption is made that particular characters should be emphasized for interpretation of the interspecific relation of the taxa. Seventeen morphological characters which are subdivided into several characteristic units are employed (Table 4). A total of 72 characteristic units are constructed so that every taxa can be scored as present (1) or absent (0) for all characteristic units; i.e., all characteristic units are applicable to all taxa.

The interspecific associations of the type species of the 10 genera is measured by normal association analysis (Ludwig and Reynold, 1988) which leads to the classification of species based on the presence-absence of characteristic units. The variance test is used for detecting the presence of overall associations and the index for selecting divisive characters is the sum of chi-square using Yates' correction factor. The interspecific relations of the 36 taxa of the Rhodochortaceae are figured out by cluster analysis (Ludwig and Reynold, 1988) which index is Mean Absolute Distance (MAD) and clustering is achieved by flexible strategy ($\beta = -0.25$).

RESULTS AND DISCUSSION

The plants of the Rhodochortaceae are of heterotrichose and branching filaments, and have a caespitose or a tufted habit. The basal system of the plants is one of three forms: freely entangled filaments, coherent filaments forming a monostromatic plate, and a single cell. The plants with the base composed of a single cell have been known to represent only the gametophyte of a species. However,

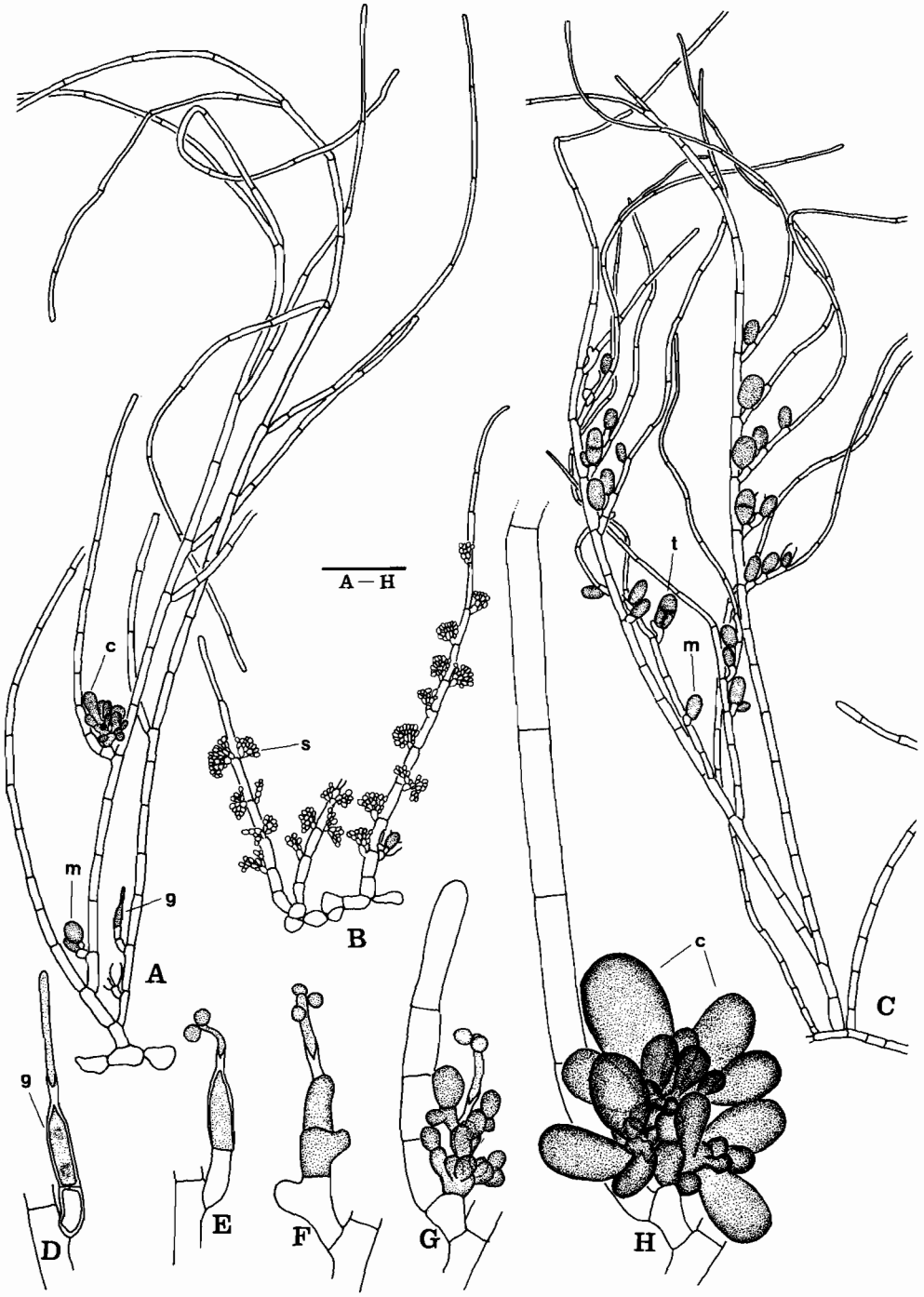

Fig. 1. *Auduinella dictyotae* (Collins) Woelkerling. A, Female gametangial plant, scale bar = 100 μm. B, Male gametangial plant, scale bar = 100 μm. C, Tetrasporangial plant, scale bar = 100 μm. D, Carpogonium, scale bar = 50 μm. E, Fertilized carpogonium, scale bar = 50 μm. F and G, Postfertilization development, scale bar = 50 μm. H, Carposporophyte, scale bar = 50 μm. Abbreviations: c = carposporangium. g = carpogonium; m = monosporangium; s = spermatangium; t = tetrasporangium.

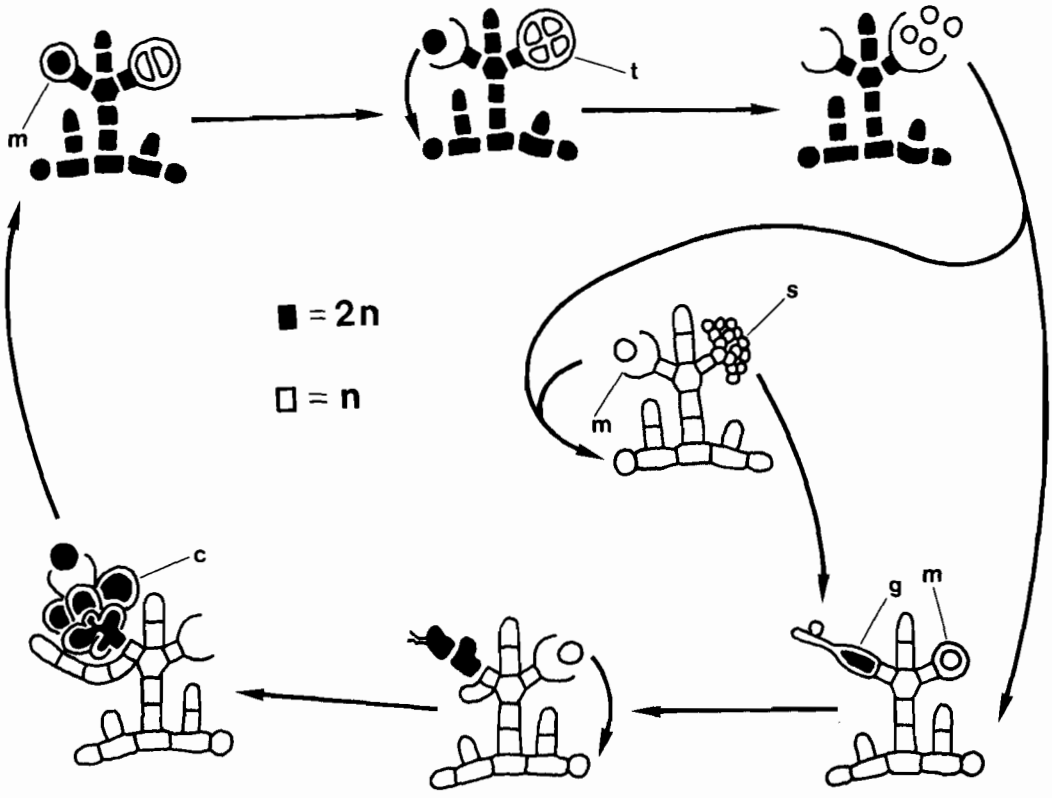

Fig. 2. Diagramatic representation of the life history of *Auduinella dictyotae* (Collins) Woelkerling. See Fig. 1. for the abbreviations.

there are many species that both gametangial and tetrasporangia plants have a multicellular filamentous base. The erect filaments are simple or branching. In some species the erect filaments are entirely reduced. The cells of erect filaments are either constricted at septum or not, and cylindrical to moniliform in shape. Hairs are occasionally formed on erect filaments. The chloroplasts are generally parietal in arrangement, single, few or several in a cell and various in shape: stellate, laminate, ribbon-shape, and discoid.

Monosporangia are born on both gametangial and tetrasporangial plants of most species for self-reproduction. In some species, tetrasporangia are known to be produced apomeiotically on both gametangial and tetrasporangial plants for self-reproduction rather than monospores. Meiotic tetrasporangia are produced on the tetrasporangial plants and divided cruciately. Carposporangia are formed on the carposporophyte which has a very simple structure.

The life history of the Rhodochortaceae has been known to be represented as three types: isomorphic trigenic alternation of generations, heteromorphic trigenic alternation of generations, and digenic dimorphic (or monomorphic) alternation of generations (Stegenga, 1979; Woelkerling, 1983). In the first type of life history, isomorphic trigenic alternation of generations, the tetrasporophyte and the gametophyte are independent, and the carposporophyte is dependent on the gametophyte (Fig. 1). Both the gametangial and the tetrasporangial plants are identical in morphology, having a multicellular filamentous base, and producing monosporangia (Fig. 2). In the second type of life history, heteromorphic trigenic alternation of generations, both the tetrasporophyte and the gametophyte are independent and the carposporophyte is dependent on

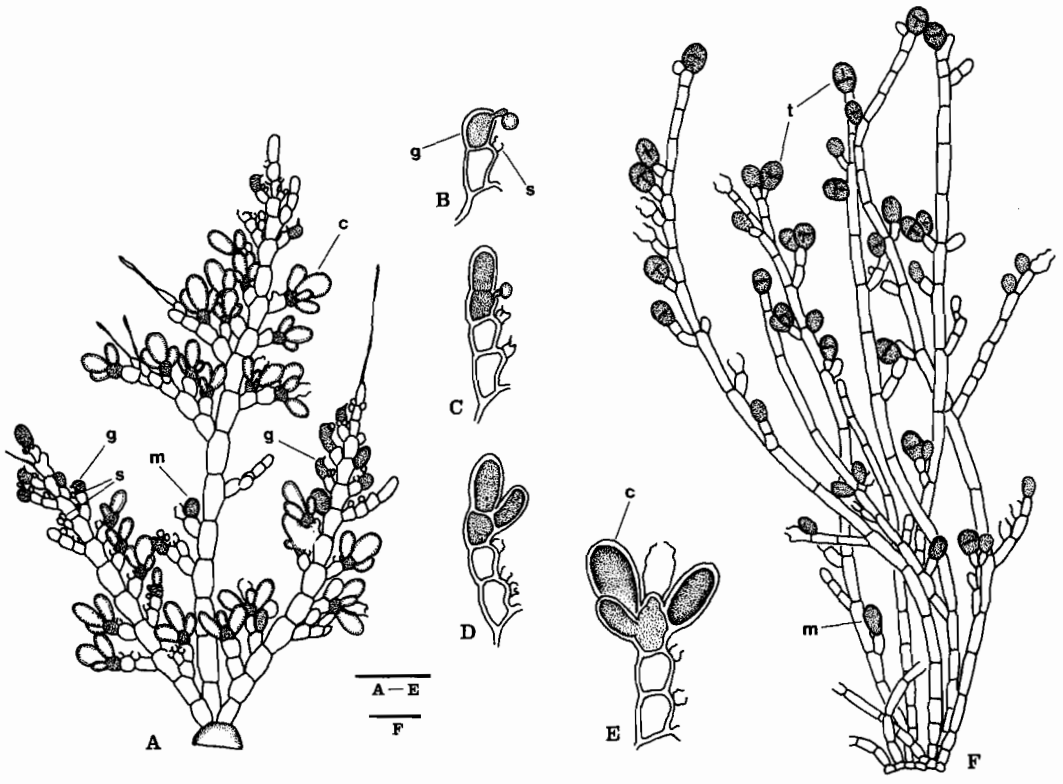

Fig. 3. *Acrochaetium alariae* (Jónsson) Bornet. A, Gametangial plant, scale bar = 50 μm. B, Carpogonium, scale bar = 20 μm. Note a spermatium attaching to a short papillate trichogyne. C and D, Postfertilization development, scale bar = 20 μm. E, Mature carposporophyte bearing three carposporangia, scale bar = 20 μm. F, Tetrasporangial plant, scale bar = 50 μm. See Fig. 1. for the abbreviations.

the gametophyte (Fig. 3). The tetrasporangial plants have a multicellular discoid base whereas the gametangial plants have a single-celled base (Fig. 4). Monosporangia are produced on both tetrasporangial and gametangial plants. In the third type of life history, digenic dimorphic (or monomorphic) alternation of generations, the carposporophyte producing carposporangia is reduced (Fig. 5). Tetrasporophyte is independent or dependent on the gametangial plants (Fig. 6). Neither tetrasporophyte nor gametophyte of this type life history produces monosporangia.

Ten genera have been referred to the Rhodochortaceae (Table 1): *Auduinella* Bory (1823, p. 340), *Acrochaetium* Naegeli (in Naegeli and Cramer, 1858, p.532), *Rhodochorton* Naegeli (1861, p. 355), *Balbiania* Sirodot (1876), *Colaconema* Batters (1896, p.8), *Kylinia* Rosenvinge (1909, p. 141), *Grania* Kylin (1944, p. 26), *Liagorophila* Yamada (1944, p. 16), *Chromastrum* Papenfuss (1945, p. 320), and *Rhodothamniella* Feldmann ex Christensen (1978, p. 67). The intergeneric relation of the genera is measured by normal association analysis on the basis of the characters of their type species. The dendrogram resulting from association analysis at p = 0.05 shows three groups of the type species of the 10 genera (Fig. 7). A group (Group 1) is separated at 9.45 level of the sum of significant chi-squares by the character "absence of monosporangium" from the other species which produce monosporangia. The rest is also divided into two groups (Group 2 and Group 3) at 4.30 level of the sum of siginificant chi-squares by the presence or absence of discoidal

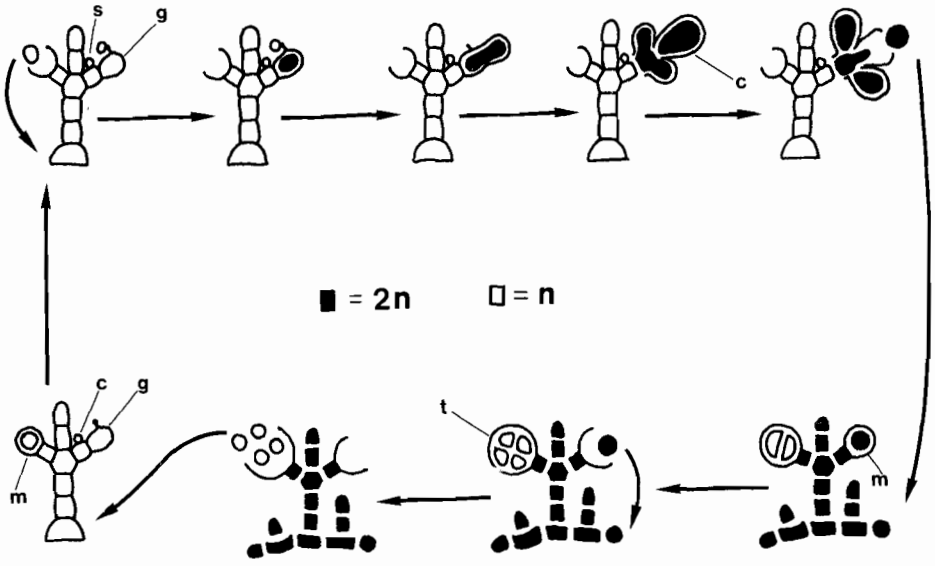

Fig. 4. Diagramatic representation of the life history of *Acrochaetium alariae* (Jónsson) Bornet. See Fig. 1. for the abbreviations.

basal system in tetrasporophyte.

Group 1 comprises the type species of two genera, *Rhodochorton* and *Rhodothamniella*. The two genera share some characters such as the absence of monosporangium, the absence of carposporophyte and carposporangium, an asexual reproduction with mitotic tetraspores. However, Group 1 is heterogeneous in terms of chloroplast morphology. The chloroplasts are many discoid without pyrenoids in *Rhodochorton* and several stellate with a pyrenoid in *Rhodothamniella*. The separation of Group 1 at 9.45 level means that the group has a more or less negative association with the other groups producing monosporangia. It may suggest a segregation of the rank of family. Saunders and McLachlan (1991) removed *R. spetsbergensis* from the Rhodochortaceae to the Rhodophysemataceae and established a new genus *Meiodiscus* with this species on the basis of the vegetative cell fusion between cells, spore germination pattern, β-phycoerythrin, presence of stalk cells subtending tetrasporangia, and asexual reproduction by mitotic tetraspores. This fact means a support of the suggestion.

Group 2 comprises the type species of three genera, *Acrochaetium, Kylinia* and *Chromastrum*. These genera share some characters such as an epiphytic nature, a multicellular discoid basal disc of tetrasporophyte, and a single chloroplast in a cell. Group 2 is somewhat heterogeneous in terms of chloroplast morphology and pyrenoids. The chloroplast is single in a cell and stellate with a pyrenoid in both *Acrochaetium* and *Chromastrum*, and single in a cell and laminate without a pyrenoid in *Kylinia*. Unfortunately, no information on the gametophyte of *A. secundatum* is available. Thus, more comprehensive interpretation on Group 2 should be postpone pending the accumulation of knowledge on the life history of *A. secundatum*.

Group 3 comprises the type species of five genera, *Auduinella, Balbiania, Colaconema, Grania* and *Liagorophila*. Group 3 is characterized by a multicellular filamentous base of gametophyte. However, this group is rather heterogeneous in terms of postfertilization, chloroplast morphology and pyrenoid. A fertilized carpogonium is cut off 3-4 protuberances in *Auduinella*, divided transversely in *Balbiania* and *Grania*, and divided longitudinal-

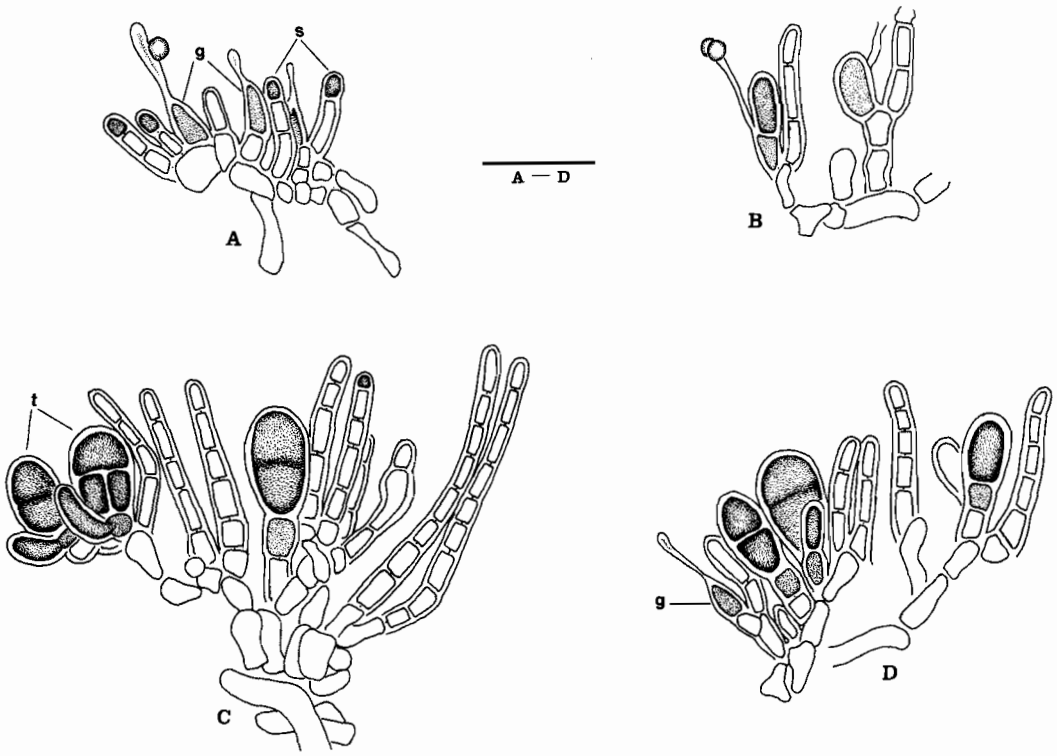

Fig. 5. *Rhodochorton subimmersum* Setchell et Gardner. A, Young plant with sessile carpogonia and short erect filaments bearing spermatangia terminally. B, Postfertilization. C, Young tetrasporangial plants derived from a fertilized carpogonium. Note the gametangial plant with more or less long erect filaments. C, Tetrasporangial plants on gametangial plant with somewhat long erect filaments. See Fig. 1. for the abbreviations.

ly in *Liagorophila*. The chloroplasts are one or several laminate or ribbon-shape without pyrenoid in both *Auduinella* and *Balbiania*, several ribbon-shape without pyrenoid in *Grania*, single laminate with a pyrenoid in *Colaconema* and single stellate with a pyrenoid in *Liagorophila*. It needs more accumulation of knowledge on the sexual reproduction of *C. bonnemaisoniae* and the tetrasporophyte of *L. endophytica* to provide a taxonomic interpretation of this group.

As a dendrogram represented by the result of cluster analysis (Fig. 8), all of 36 taxa are segregated into two clusters (Cluster I and II) at 1.14 level of Mean Absolute Distance (MAD). Cluster I comprises 19 taxa and appears in a rather defined group. Cluster II comprises 17 taxa and appears in a more or less heterogeneous group. Most of the taxa are separated at 0.06-0.2 level of MAD. It may suggest the specific circumscription in the Rhodochortaceae is drawn a line at 0.06-0.2 level of MAD. The distance of 0.06 level appears between every two taxa of *Acrochaetium catenulatum* and *A. microscopicum, A. alariae* (G) and *A. sanctithomae* (G), *A. inkyuii* and *A. terminalle*, and *A. secundatum* and *A. virgatulum*. The distance of 0. 19 level appears between *A. thuretii* and *Auduinella daviesii.* The distance between the gametophyte and the tetrasporophyte of a species in Cluster I is greater than that of a species in Cluster II.

Cluster I is characterized by a stellate chloroplast in a cell, asexual reproduction by monospore and having the second type of life history. Cluster I agrees well with Group 2 and appears to be a well defined group in the distance from the other groups. Cluster I may correspond to *Acrochaetium* sensu Hamel (1925) and *Auduinella* sensu Lee (1980) in asexual reproduction by monospore, *Chromastrum* sensu Papenfuss (1945) in a stellate chloroplast, *Chromastrum* sensu Stegenga (1979) in the second type of life history and a stellate

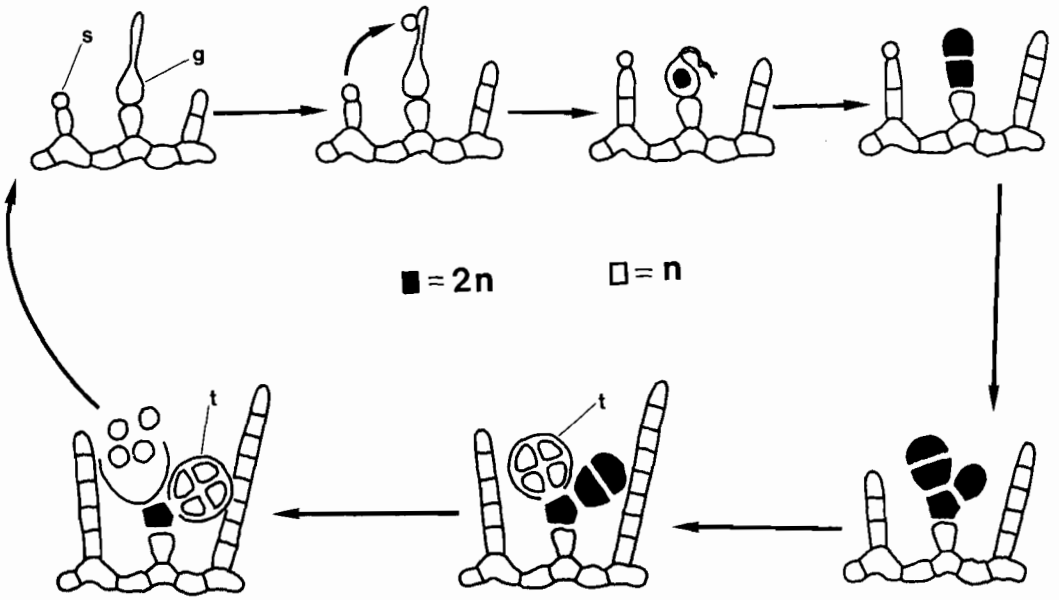

Fig. 6. Diagramatic representation of the life history of *Rhodochorton subimmersum* Setchell et Gardner. See Fig. 1. for the abbreviations.

chloroplast, *Acrochaetium* sensu Woelkerling (1983) in the second type of life history, and *Acrochaetium* sensu Lee and Lee (1988) in asexual reproduction by monospore and a stellate chloroplast.

Cluster I is segregated at 0.7 level of MAD into Group A, B. Group A comprises 8 taxa, all of which are fused together at less than 0.3 level of MAD. Group A is characterized by an unicellular base, a stellate chloroplast, production of monosporangium, and representing a gametangial phase although sexual reproductive structures are not found on the plants at hands of three taxa in this group, *Acrochaetium moniliforme, A. catenulatum* and *A. microscopicum*. Group A corresponds to *Kylinia* sensu Kylin (1944) in an unicellular base. Group B comprises 11 taxa, all of which are also fused together at less than 0.3 level of MAD. Group B is characterized by a multicellular discoid base, a stellate chloroplast, production of monosporangium and representing a tetrasporangial phase. Five taxa of the elements of Group B, *Acrochaetium alariae, A. canariense, A. virgatulum, A. sessile*, and *A. terminale*, are known to produce tetrasporangia as well as monosporangia. *A. sancti-thomae* (S) is identified as a tetrasporophyte although no tetrasporangium is found on the plants of the species at hand. Consequently, the elements of Group A may be the counterpart generation of the elements of Group B in the life history of a species, such as *A. alariae, A. sancti-thomae* and *A. sessile*.

Cluster II is also segregated into Group C and Group D at 0.7 level of MAD. Group C comprises 4 taxa, *Rhodochorton spetsbergense, R. purpureum* (S), *R. purpureum* (G), and *R. membranaceum*. Group C is rather well defined and characterized by absence of monosporangium, absence of carposporophyte, asexual reproduction by mitotic tetraspore, several or many discoid chloroplasts and having the third type of life history. Group C corresponds to *Rhodochorton* sensu Naegeli (1861), Hamel (1925), and Papenfuss (1945) in terms of several or many chloroplasts, sensu Stegenga (1979) and Woelkerl-ing (1983) in terms of the third type of life history, and sensu Lee (1980) and Lee and Lee (1988) in terms of asexual reproduction by tetraspore. Group C also corresponds to *Rhodothamniella* sensu Feldmann (1962) in terms of several or many chloroplasts. Group C agrees quite well with Group 1.

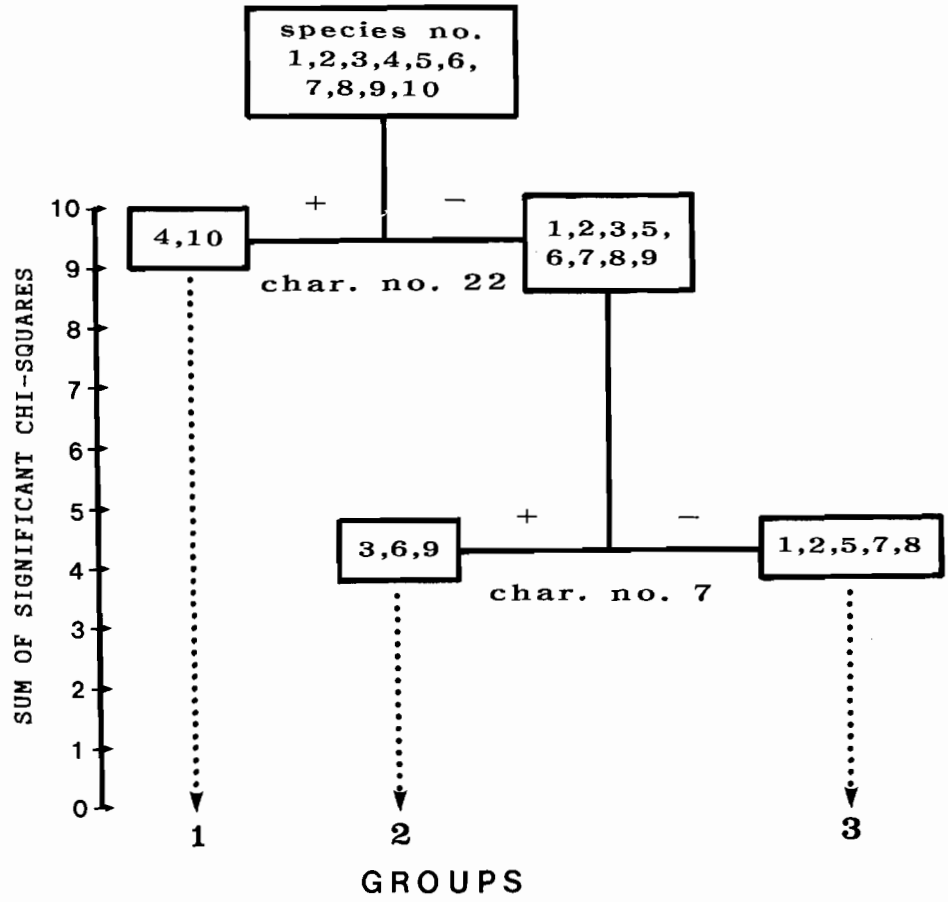

Fig. 7. Division of the type species of 10 genera in the Rhodochortaceae, using a normal association analysis based on the presence-absence of 30 characteristic units. Each box includes the number of type species either positive (+) or negative (-) for that character. See Table 2 for explanation.

Group D, comprising 13 taxa, is rather heterogeneous because of some elements: *Acrochaetium yamadae, Auduinella japonica, Auduinella dictyotae* (G) and *Rhodochorton subimmersum*. Group D, except these taxa, is well defined and agrees well with Group 3. Group D is characterized by a multicellular filamentous base, a laminate chloroplast and having the first type of life history, and corresponds to *Acrochaetium* sensu Papenfuss (1945) in terms of a laminate chloroplast, *Acrochaetium* sensu Stegenga (1979) in terms of the first type of life history and a laminate chloroplast, *Auduinella* sensu Woelkerling (1983) in terms of the first type of life history, and *Auduinella* sensu Lee and Lee (1988) in terms of asexual reproduction by monospore and laminate or ribbon-shape chloroplasts.

In Group D four taxa, *A. yamadae, A. japonica, A. dictyotae* (G) and *R. subimmersum*, are fused together in a small bunch at 0.33 level of MAD. *A. yamadae* and *A. japonica* are fused at 0.24 level of MAD. *A. dictyotae* (G) and *R. subimmersum* are fused at 0.29 level of MAD. This bunch is characterized by an endophytic nature and the presence of carpogonium and spermatangium. However, this bunch is rather heterogeneous in some characters: *A. yamadae* having a stellate chloroplast and producing monosporangium; *A. japonica* and *A. dictyotae* (G) having a laminate chloroplast, producing monosporangium and producing spermatangium and carpogonium; *R. subimmersum* having several chloroplasts and producing neither monosporangium nor carposporangium. *A. dictyotae* (G) has the first type life history whereas *R. subimmersum*

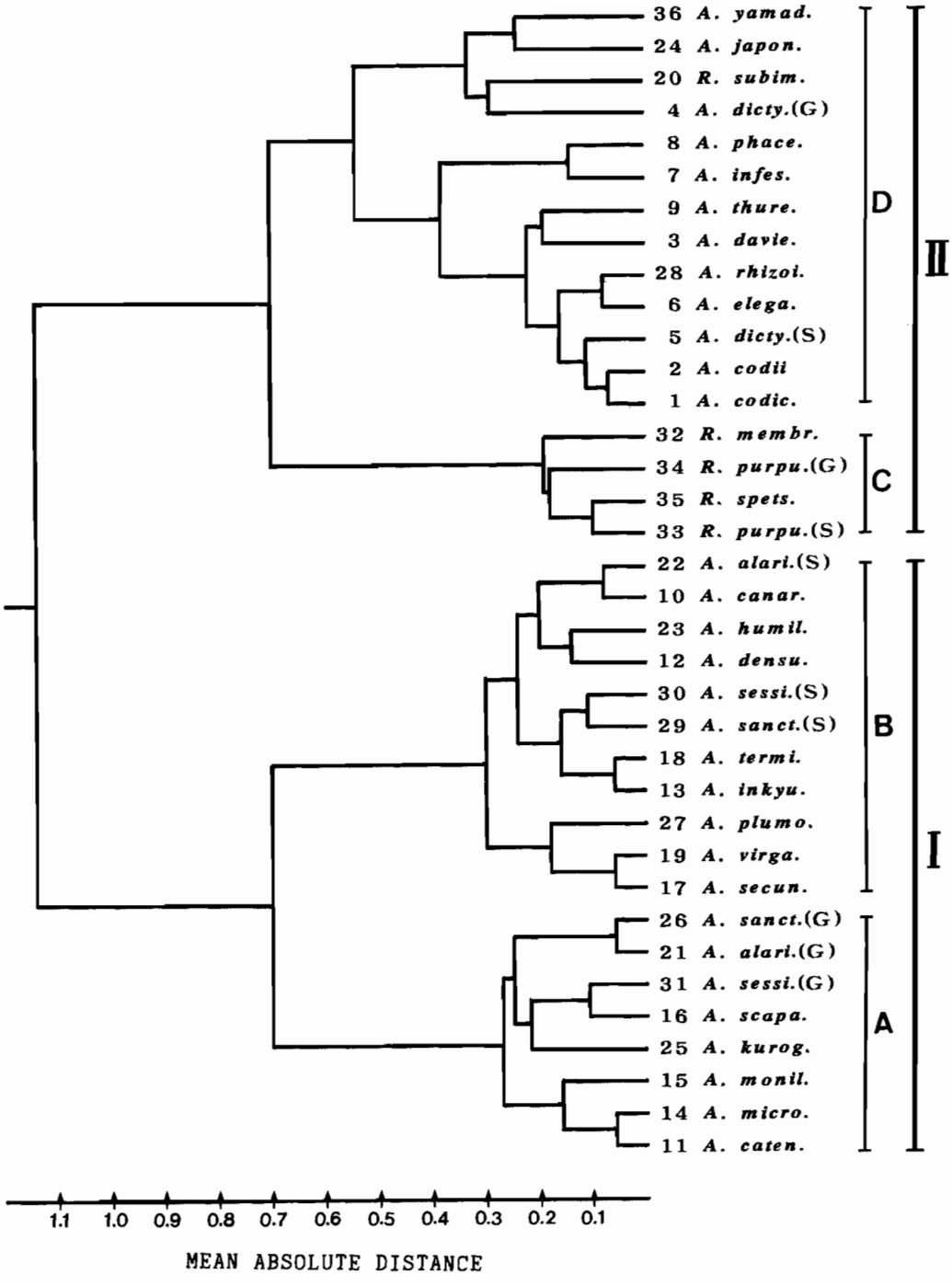

Fig. 8. Dendrogram for cluster analysis of 36 taxa of the Rhodochortaceae, using mean absolute distance and the flexible strategy; $\beta = -0.25$. See Table 3 for explanation of species acronyms.

has the third type of life history. The appearance of this bunch in Group D may be said to be a limitation in the taxonomic interpretation of the result of cluster analysis. However, the limitation may be expected to be removed when the life history of most taxa of the Rhodochortaceae are known.

The result of normal association analysis on the type species of the 10 genera suggests that *Rhodochorton* and *Rhodothamniella* comprised in Group 1 may be a well defined taxon as a separate genus or a family. The result of the cluster analysis on 36 taxa showes Cluster I being a well defined taxon. The segregation of Cluster I into Group A and B suggests that Cluster I has a heteromorphic nature in the life history. Both the results of normal association analysis on the type species of the 10 genera and cluster analysis on the 36 taxa from the northwestern Pacific Ocean strongly suggest the segregation of the Rhodochortaceae into 3 genera. These results support the classification schemes suggested by Woelkerling (1983) and Lee and Lee (1988). Garbary (1979) demonstrated that the result of numerical taxonomy with 170 OTUs (operational taxonomic units) of 112 species in the Rhodochortaceae in the world supported the single genus concept suggested by Drew (1928). Consequently, it needs an attention that the result may differ entirely according to establishment of characteristic units for statistical analysis.

APPENDIX

List of proposed new combinations:

1) *Auduinella japonica* (Papenfuss) Lee comb. nov. Basionym: *Colaconema simplex* Inagaki (1935, p. 44). Papenfuss (1945, p. 315) proposed a new name, *Acrochaetium japonicum* Papenfuss, for this taxon.

2) *Acrochaetium sessile* (Nakamura) Lee comb. nov. Basionym: *Rhodochorton sessile* Nakamura (1941, p. 278). *Acrochaetium sessile* (Nakamura) Aziz (1965, p. 156) is an illegitimate name in Articles 29 and 32 of International Code of Botanical Nomenclature (Sydny Code, 1981).

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