Contribution to the Generic Classification of the Rhodochortaceae (Rhodophyta, Nemaliales)

Y. P. Lee and I. K. Lee

Department of Biology, Cheju National University, Cheju 590, Korea

Department of Botany, Seoul National University, Seoul 151, Korea

(Accepted 10 November 1987)

Abstract

The family names related to acrochaetioid algae are briefly surveyed and Rhodochortaceae Nasr is adopted as the correct name of the family based on the nomenclatural priority. A historical review of several generic classification schemes is presented. A new classification scheme is provided on the basis of asexual reproduction as the primary criterion and the chloroplast morphology as an additional criterion for distinguishing genera of the family. Under the new scheme, *Audouinella* Bory is restricted to taxa producing monosporangia and having parietal laminate or ribbon-shaped chloroplasts, *Acrochaetium* Naegeli to taxa producing monosporangia and having stellate chloroplasts, and *Rhodochorton* Naegeli to taxa having asexual cycles with tetraspores and not monospores.

Introduction

Acrochaetioid algae have the simplest heterotrichous organization among the Florideophyceae. The basal system is composed of a single cell or multicellular filaments. The erect system is of uniaxial, monosiphonous filaments bearing branches. There is no differentiation among any filaments of the erect system although pseudoparenchymatous structures are occasionally constructed among the basal filaments. Chloroplasts are one or several per cell, and stellate, laminate, ribbon-like or discoid in shape. The carpogonium is usually flask-shaped with a terminal or sub-terminal trichogyne. Spermatangia are born in pairs on vegetative cells or in clusters on somewhat specialized branches. The tetrasporangium is generally divided in cruciate mode or unusually in zonate mode (Lee and Kurogi 1983). The monosporangium is common on both gametangial and tetrasporangial plants with the exception of certain taxa. Bisporangia, polysporangia, or parasporangia have been reported (Børgesen 1910, 1937, Howe 1914, Jao 1936, Baardseth 1941, Klavestad 1957). Three main types of life cycles appear in acrochaetioid algae: *Polysiphonia*-type, *Liagora tetrasporifera*-type and *Audouinella rosulata*-type (Garbary *et al.* 1982).

A number of classification schemes have been proposed for the acrochaetioid algae, and there has been much discussion about generic concepts (Hamel 1925, 1927, Drew 1928, Kylin 1944, 1956, Papenfuss 1945, 1947, Woelkerling 1971, 1983, Dixon and Irvine 1977, Garbary 1979, Stegenga 1979, 1985, Lee 1980). Most classification schemes involve criteria associated with sexual reproduction and related characteristics (Rosenvinge 1909, Yamada 1944, Abbott 1962, Feldmann 1962, Woelkerling 1971, 1983, Stegenga and Vroman 1977, Stegenga 1979). Besides sexual reproduction, various characteristics such as basal system, spore germination mode, chloroplast morphology and pyrenoids have been employed in classification (Hamel 1927, Papenfuss 1945, Kylin 1956, Woelkerling 1971, Stegenga 1979). Woelkerling (1971, 1983) and Lee (1980) have discussed several characteristics associated with generic or specific criteria. Dixon and Irvine (1977) and Garbary (1979) believed that there was no logical basis for generic classification in acrochaetioid algae. Thus, there is at present no consensus among phycologists on generic concepts and classification schemes, and a great confusion of binomials for acrochaetioid algae prevails. Such confusion for taxa mentioned in this paper is presented in Table I.

Botanica Marina / Vol. 31 / 1988 / Fasc. 2

Table I. A list of the binomials of the species mentioned in the text (* basionym)

Species	name	Reference		Note
Chantransia	*alariae**	Jónsson	1901 p. 132	
Acrochaetium	*alariae*	Bornet	1904 p. 19	
Kylinia	*alariae*	Kylin	1944 p. 13	
Chromastrum	*alariae*	Papenfuss	1945 p. 320	
Audouinella	*alariae*	Woelkerling	1973 b p. 541	
Rhodochorton	*arcuatum**	Drew	1928 p. 165	
Kylinia	*arcuata*	Kylin	1944 p. 13	
Acrochaetium	*arcuatum*	Tseng	1945 p. 158	
Chromastrum	*arcuatum*	Papenfuss	1945 p. 321	
Audouinella	*arcuata*	Garbary *et al.*	1982 p. 12	
Colaconema	*bonnemaisoniae**	Batters	1896 p. 8	
Chantransia	*bonnemaisoniae*	Levring	1937 p. 94	
Acrochaetium	*bonnemaisoniae*	J. & G. Feldmann	1939 p. 458	
Audouinella	*bonnemaisoniae*	Parke & Dixon	1976 p. 590	
Callithamnion	*botryocarpum**	Harvey	1854 p. 563	
Acrochaetium	*botryocarpum*	J. Agardh	1892 p. 48	
Audouinella	*botryocarpa*	Woelkerling	1971 p. 37	
Conferva	*chalybea**	Roth	1806 p. 286	cf. Drew 1928
Colaconema	*chylocladiae**	Batters	1896 p. 8	
Acrochaetium	*chylocladiae*	Batters	1902 p. 58	
Audouinella	*chylocladiae*	Parke & Dixon	1976 p. 590	
Acrochaetium	*codicola**	Børgesen	1927 p. 33	
Rhodochorton	*codicola*	Nakamura	1944 p. 113	
Audouinella	*codicola*	Garbary	1979 p. 490	
Rhodochorton	*concrescens**	Drew	1928 p. 167	
Audouinella	*concrescens*	Parke & Dixon	1976 p. 590	
Acrochaetium	*dasyae**	Collins	1906 p. 191	
Chantransia	*dasyae*	Collins	1911 p. 185	
Audouinella	*dasyae*	Parke & Dixon	1076 p. 590	
Conferva	*daviesii**	Dillwyn	1809 p. 73	
Callithamnion	*daviesii*	Lyngbye	1819 p. 129	
Trentepohlia	*daviesii*	Areschoug	1847 p. 338	
Chantransia	*daviesii*	Le Jolis	1863 p. 106	
Acrochaetium	*daviesii*	Naegeli	1861 p. 405	
Rhodochorton	*daviesii*	Drew	1928 p. 172	
Audouinella	*daviesii*	Woelkerling	1971 p. 28	
Acrochaetium	*dictyotae**	Collins	1906 p. 193	
Chantransia	*dictyotae*	Collins	1911 p. 186	
Rhodochorton	*dictyotae*	Drew	1928 p. 190	
Audouinella	*dictyotae*	Woelkerling	1971 p. 38	
Acrochaetium	*dotyi**	Abbott	1962 p. 89	
Audouinella	*dotyi*	Garbary	1979 p. 490	
Callithamnion	*efflorescens**	J. Agardh	1851 p. 15	
Acrochaetium	*efflorescens*	Naegeli	1861 p. 405	
Chantransia	*efflorescens*	Kjellman	1875 p. 14	
Rhodochorton	*efflorescens*	Drew	1928 p. 151	
Grania	*efflorescens*	Kylin	1944 p. 26	
Audouinella	*efflorescens*	Papenfuss	1945 p. 326	
Liagorophila	*endophytica**	Yamada	1944 p. 16	
Audouinella	*yamadae*	Garbary	1980 p. 67	
Acrochaetium	*yamadae*	**comb. nov.**		
Conferva	*floridula**	Dillwyn	1809 p. 73	
Callithamnion	*floridulum*	Lyngbye	1819 p. 130	
Thamnidium	*floridulum*	Le Jolis	1863 p. 111	
Rhodochorton	*floridulum*	Naegeli	1861 p. 358	
Chromastrum	*floridulum*	Papenfuss	1945 p. 323	
Kylinia	*floridula*	Papenfuss	1947 p. 437	
Rhodothamniella	*floridula*	Feldmann	1954 p. 68	
Audouinella	*floridula*	Woelkerling	1971 p. 30	
Auduinella	*juniformis**	Bory	1823 p. 340	nonacrochaetioid
Acrochaetium	*griffithsianum**	Naegeli	1861 p. 406	cf. Papenfuss (1945)
Conferva	*hermanni**	Roth	1797 p. 164	
Chantransia	*hermanni*	Desvaux	1809 p. 310	
Audouinella	*hermanni*	Duby	1830 p. 972	
Acrochaetium	*imitator**	Abbott	1962 p. 104	
Audouinella	*imitator*	Garbary	1979 p. 490	

Table I. (continued)

Species	name	Reference		Note
Chantransia	*immersa**	Rosenvinge	1909 p. 130	
Acrochaetium	*immersum*	Hamel	1927 p. 93	
Chromastrum	*immersum*	Papenfuss	1945 p. 324	
Kylinia	*immersa*	Papenfuss	1947 p. 438	
Chantransia	*investiense**	Kuetzing	1849 p. 431	
Balbiania	*investiense*	Sirodot	1876 p. 146	
Audouinella	*investiense*	Kylin	1956 p. 87	
Rhodochorton	*investiense*	Swale & Belcher	1963 p. 281	
Audouinella	*kurogii**	Lee & Lindstrom	1979 p. 115	
Chromastrum	*kurogii*	Kuiper	1983 p. 139	
Acrochaetium	*kurogii*	**comb. nov.**		
Conferva	*lanuginosum**	Dillwyn	1809 p. 72	
Acrochaetium	*liagorae**	Børgesen	1915 p. 57	
Chromastrum	*liagorae*	Papenfuss	1945 p. 324	
Kylinia	*liagorae*	Papenfuss	1947 p. 438	
Audouinella	*liagorae*	Woelkerling	1971 p. 31	
Acrochaetium	*macropus**	Kylin & Skottsberg	1919 p. 4	
Chantransia	*macropus*	De Toni	1924 p. 47	
Kylinia	*macropus*	Kylin	1944 p. 13	
Chromastrum	*macropus*	Papenfuss	1945 p. 321	
Callithamnion	*membranaceum**	Magnus	1874 p. 67	
Rhodochorton	*membranaceum*	Hauck	1885 p. 69	
Audouinella	*membranacea*	Papenfuss	1945 p. 326	
Colaconema	*membranacea*	Woelkerling	1973 b p. 566	
Callithamnion	*microscopicum**	Kuetzing	1849 p. 640	
Acrochaetium	*microscopicum*	Naegeli & Cramer	1858 p. 532	cf. Woelkerling 1983
Chantransia	*microscopica*	Foslie	1890 p. 54	
Rhodochorton	*microscopicum*	Drew	1928 p. 163	
Audouinella	*microscopica*	Woelkerling	1971 p. 33	
Audouinella	*miniata**	Bory	1823 p. 341	see text
Chantransia	*pectinata**	Kylin	1906 p. 120	
Acrochaetium	*pectinatum*	Hamel	1927 p. 103	
rhodochorton	*pectinatum*	Rosenvinge	1935 p. 7	
Audouinella	*pectinata*	Papenfuss	1945 p. 326	
Rhodochorton	*mesocarpum*			
	f. *peniciliformis**	Kjellman	1883 p. 187	cf. Woelkerling 1973 b
Byssus	*purpurea**	Lightfoot	1777 p. 1000	
Conferva	*purpurea*	Dillwyn	1809 p. 56	
Callithamnion	*purpureum*	Harvey	1841 p. 116	
Trentepohlia	*purpurea*	C. Agardh	1824 p. 36	
Rhodochorton	*purpureum*	Rosenvinge	1900 p. 75	
Audouinella	*purpurea*	Woelkerling	1973 b p. 536	
Colaconema	*reticulatum**	Batters	1896 p. 8	
Acrochaetium	*reticulatum*	Papenfuss	1945 p. 317	
Coladodictyon	*reticulatum*	Feldmann	1955 p. 27	nonacrochaetioid
Rhodochorton	*rhizoideum**	Drew	1928 p. 182	
Acrochaetium	*rhizoideum*	Jao	1937 p. 102	
Audouinella	*rhizoidea*	Garbary	1979 p. 490	
Kylinia	*rosulata**	Rosenvinge	1909 p. 141	
Acrochaetium	*rosulatum*	Papenfuss	1945 p. 307	
Audouinella	*rosulata*	Parke & Dixon	1976 p. 590	
Conferva	*rothii**	Turton	1806 p. 1809	cf. Papenfuss 1945
Callithamnion	*daviesii*			
	β. *secundatum**	Lyngbye	1819 p. 129	
Acrochaetium	*secundatum*	Naegeli & Cramer	1858 p. 532	cf. Woelkerling 1983
Chantransia	*secundata*	Le Jolis	1863 p. 106	
Chromastrum	*secundatum*	Papenfuss	1945 p. 323	
Kylinia	*secundata*	Papenfuss	1947 p. 437	
Colaconema	*secundata*	Woelkerling	1973 a p. 94	
Audouinella	*secundata*	Woelkerling	1973 b p. 575	
Thamnidium	*spetsbergense**	Kjellman	1875 p. 31	
Rhodochorton	*spetsbergense*	Kjellman	1883 p. 187	
Audouinella	*spetsbergense*	Woelkerling	1973 b p. 585	
Rhodochorton	*subimmersum**	Setchell & Gardner	1903 p. 347	
Acrochaetium	*subimmersum*	Papenfuss	1945 p. 318	
Audouinella	*subimmersa*	Garbary & Rueness	1980 p. 22	

Table I. (continued)

Species	name	Reference			Note
Rhodochorton	*tenue**	Kylin	1925	p. 44	cf. West 1969
Audouinella	*tetraspora**	Garbary & Rueness	1980	p. 17	
Rhodochorton	*tetrasporum*	**comb. nov.**			
Chantransia	*efflorescens*				
	var. *thuretii**	Bornet	1904	p. 22	
Chantransia	*thuretii*	Kylin	1907	p. 119	
Acrochaetium	*thuretii*	Collins & Harvey	1917	p. 98	
Rhodochorton	*thuretii*	Drew	1928	p. 152	
Audouinella	*thuretii*	Woelkerling	1971	p. 36	cf. Israelson 1942
Chantransia	*violacea**	Kuetzing	1845	p. 230	
Callithamnion	*virgatulum**	Hooker	1833	p. 349	
Chantransia	*virgatula*	Le Jolis	1863	p. 106	
Trentepohlia	*virgatula*	Farlow	1881	p. 109	
Acrochaetium	*virgatulum*	Bornet	1904	p. XXII	
Rhodochorton	*virgatulum*	Drew	1928	p. 152	
Chromastrum	*virgatulum*	Papenfuss	1945	p. 323	
Kylinia	*virgatula*	Papenfuss	1947	p. 437	
Audouinella	*virgatula*	Parke & Dixon	1976	p. 532	

The primary objective of this work is to reappraise several generic classification schemes proposed by previous workers and to approach to an effective and natural classification of acrochaetioid algae.

Family Names

Acrochaetioid algae are in general considered to be a well distinguished taxonomic group separate from the other Florideophyceae. In the past, acrochaetioid algae were referred to the Ceramiaceae, the Helminthocladiaceae or the Wrangeliaceae (Naegeli 1861, Rosenvinge 1909, 1923–1924, Hauck 1885, De Toni 1924, Setchell and Gardner 1930). In recent works, acrochaetioid algae have been placed within one or two distinct families; e.g., the Chantransiaceae Rabenhorst, the Acrochaetiaceae Fritsch, the Rhodochortonaceae Nasr, the Audouinellaceae Feldmann *ex* Woelkerling (Rabenhorst 1868, Fritsch 1944, Nasr 1947, Kylin 1944, 1956, Feldmann 1962, Woelkerling 1971, 1973 b, Abbott and Hollenberg 1976, Dixon and Irvine 1977, Stegenga 1979, Lee 1980). The family concepts for acrochaetioid algae were discussed by Woelkerling (1971, 1973 b, 1983), Garbary (1978) and Garbary *et al.* (1982). Stegenga (1979) summarized the historical background on family concepts.

Feldmann (1962) proposed a classification scheme in which the Audouinellaceae was established. Woelkerling (1971) argued that the Audouinellaceae Feldmann was not validly published and had no status, and he reintroduced it with a valid description. However, following a personal communication from Papenfuss and Silva, Woelkerling (1973 b) then decided that the Audouinellaceae Woelkerling was superfluous and used the Acrochaetiaceae Fritsch as the family name of acrochaetioid algae. In recent works, the Acrochaetiaceae has been generally used for the family name (Dixon and Irvine *in* Parke and Dixon 1976, Dixon and Irvine 1977, Woelkerling 1973 b, Garbary 1979, Lee 1980, Garbary *et al.* 1982). Although the name Acrochaetiaceae was first used by Fritsch (1944), he failed to give a description of it. The first author to validate the name Acrochaetiaceae was Taylor (1957, cf. Silva 1980 a, 1980 b). Thus, the Acrochaetiaceae Fritsch *ex* Taylor (1957) is apparently predated by the Rhodochortonaceae Nasr (1947). Silva (1980 a, 1980 b) used Rhodochortaceae instead of Rhodochortonaceae under Article 18.1 of the International Code of Botanical Nomenclature (ICBN) (Voss *et al.* 1983). Therefore, the Rhodochortaceae Nasr is adopted for the family name of acrochaetioid algae in this paper under Articles 32 and 45 of ICBN.

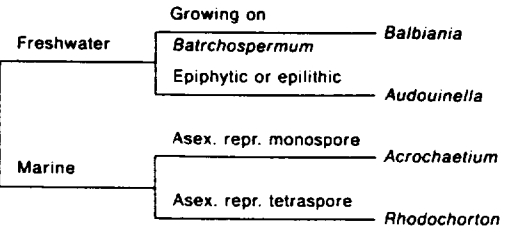
Review of Generic Concepts

More than twenty generic names have been used for acrochaetioid algae: *Byssus* Linnaeus (1753), *Conferva* Linnaeus (1753), *Ceramium* Roth (1797), *Chantransia* De Candolle (1801), *Trentepohlia* Martius (1817, cf. Lee 1980), *Callithamnion* Lyngbye (1819), *Audouinella* Bory (1823), *Acrochaetium* Naegeli (Naegeli and Cramer 1858, cf. Woelkerling 1983 and Silva *in* Farr *et al.* 1979), *Rhodochorton* Naegeli (1861), *Trentepohlia* Pringsheim (1862), *Thamnidium* Thuret (*in* Le Jolis 1863), *Balbiania* Sirodot (1876), *Colaconema* Batters (1896), *Kylinia* Rosenvinge (1909), *Pseudochantransia* Brand (1910), *Chantransiella* Brebner (cf. De Toni 1924: p. 63), *Liagorophila* Yamada (1944), *Grania* (Rosenvinge) Kylin (1944), *Chromastrum* Papenfuss (1945), *Rhodothamniella* Feldmann (1954), and *Pseu-*

rochaetium von Stosch (1965). However, most of them are not relevant to acrochaetioid algae. *Byssus* and *Trentepohlia* (*sensu* Martius) appeared to be associated with taxa of the Chlorophyta (Silva 1950, Silva *in* Farr *et al.* 1979). *Ceramium* and *Callithamnion* are genera of the Ceramiaceae, Rhodophyta. *Conferva* was suppressed as a typonym of *Hydrodictyon*, Chlorophyta (Silva 1952, Silva *in* Farr *et al.* 1979). *Chantransia* is no longer valid because none of the species originally listed by De Candolle (1801) have remained in the genus (Drew 1928, Lee 1980). *Pseudochantransia* was found to represent the prothalloid stage of *Lemanea* or *Batrachospermum* (Brand 1897, 1910). *Trentepohlia* (*sensu* Pringsheim) and *Thamnidium* were predated by *Acrochaetium* or *Rhodochorton* and should be rejected under Article 63 of the ICBN (cf. Woelkerling 1971). The remaining generic names are still used for acrochaetioid algae by phycologists.

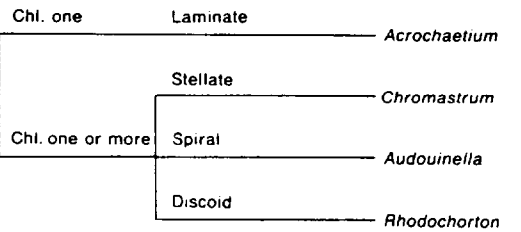
Auduinella was established by Bory (1823) for three species. Two of them, *Au. funiformis* Bory and *Au. chalybea* (Roth) Bory, are now known to be a species of *Spongomorpha*, Chlorophyta and an asexual form of *Batrachospermum*, respectively (Kuetzing 1849, Sirodot 1884, De Toni 1895, Kuckuck 1964, Cardinal 1964). The third, *Au. miniata* Bory, appeared to be conspecific with *Au. hermanni* (Roth) Duby and represented an autonomous species with isomorphic alternation of generations [Duby 1830, Desvaux 1809, Israelson 1942, Woelkerling 1971, Drew 1928; as *Rhodochorton violaceum* (Kuetz.) Drew]. Thus, *Auduinella* Bory is the oldest valid generic name in the Rhodochortaceae. The General Committee of the Botanical Congress in Berlin agreed *Audouinella* Bonnemaison (1828; p. 146) as the correct generic name instead of *Auduinella* Bory (cf. Silva 1980 b). *Acrochaetium* was established by Naegeli in 1858 (Silva *in* Farr *et al.* 1979, Woelkerling 1983). Naegeli mentioned four species of the genus viz.: *Ac. secundatum* (Lyngbye) Naegeli, *Ac. lanuginosum* (Dillwyn) Naegeli, *Ac. griffithsianum* Naegeli, and *Ac. microscopicum* (Naegeli *in* Kuetzing 1849) Naegeli (Woelkerling 1983). Later, he restricted *Acrochaetium* to taxa producing only monosporangia (= Schwärmsporen *sensu* Naegeli 1861). *Rhodochorton* was also established by Naegeli (1861) with two species viz.: *R. rothii* (Turton) Naegeli and *R. floridulum* (Dillwyn) Naegeli. Later, *R. rothii* was revealed to be conspecific with *Rhodochorton purpureum* (Lightfoot) Rosenvinge (Papenfuss 1945, Lee 1980). *Rhodochorton purpureum* has been generally cited as the type species of *Rhodochorton* (Papenfuss 1945, Stegenga 1979, Lee 1980). Naegeli (1861) circumscribed *Rhodochorton* for taxa producing only tetrasporangia. *Balbiania* was established by Sirodot (1876) on the basis of the monotypic species *B. investiens* (Lenormand) Sirodot. This genus was restricted to monoecious taxa of acrochaetioid algae. However, Swale and Belcher (1963) concluded after field and culture studies that *B. investiens* was not fundamentally different from other members of acrochaetioid algae (= *Rhodochorton* – *Acrochaetium* complex *sensu* Papenfuss 1945). Batters (1896) founded *Colaconema* on the basis of acrochaetioid algae living in the cell wall of a host and included three taxa in the genus viz.: *Co. bonnemaisoniae* Batters, *Co. chylocladiae* Batters, and *Co.? reticulatum* Batters. However, *Co. chylocladiae* was transferred to *Acrochaetium* in his later publication (Batters 1902), and *Co. reticulatum* has become the type species of *Coladodictyon* Feldmann (1955). *Kylinia* was established by Rosenvinge (1909) for the species having specialized spermatangial mother cells (= androphore cell *sensu* Rosenvinge) and longitudinal division of fertilized carpogonia. *Kylinia rosulata* Rosenbinge was the type species of *Kylinia*. However, the fertilized carpogonium of *K. rosulata* was known to cut off 2–3 carposporangia laterally or terminally without previous division (Feldmann 1958). *Grania* was established as a subgenus by Rosenvinge (1909) for taxa containing one or more band- or spiral-shaped chloroplasts. Kylin (1944) elevated *Grania* to generic status with monotypic species *G. efflorescens* (J. Agardh) Kylin. Papenfuss (1945) regarded *Grania* to be synonymous with *Audouinella* because there was no difference in generic delineation between *G. efflorescens* and the members of *Audouinella*. *Liagorophila* was established on *L. endophytica* Yamada, and restricted to taxa showing a longitudinal division of the fertilized carpogonium by Yamada (1944). Although Fan and Li (1964) and Abbott (1966) made a contribution to the knowledge of *L. endophytica*, there is some doubt about the identity of the collections examined by them. Lee *et al.* (1986) clarified the taxon, *L. endophytica*, by examination of the type and allied collections. *Chromastrum* was established for taxa containing one or more stellate chloroplasts per cell, and *Ch. virgatulum* (Harvey) Papenfuss as the type species of the genus (Papenfuss 1945). Later, Papenfuss (1947) merged *Chromastrum* into *Kylinia* on the basis of the report made by Kylin (1944), in which the type species of *Kylinia*, *K. rosulata* was said to contain stellate chloroplasts. Feldmann (1958) revealed *K. rosulata* contained a parietal laminate chloroplast without pyrenoid and not a stellate one as described by Kylin (1944). Therefore, it is likely that *Chromastrum* is distinct from *Kylinia* at least in regard to chloroplast morphology. Stegenga and Vroman (1977) and Stegenga and Mulder (1979) regarded *Chromastrum* as a distinct genus in respect to the mode of spore germination. Feldmann (1954) erected *Rhodotham-*

niella for taxa containing more than one parietal chloroplasts with one or more pyrenoids and gave *Rhodothamniella floridula* (Dillwyn) Feldmann as the type species of the genus. Christensen (1978) and Feldmann (1981) provided a generic description of *Rhodothamniella* for nomenclaturally valid publication. Lee (1980) summarized several representative characteristics of the type species of the genera mentioned above.



Asex. = asexual, repr. = reproduction.

Fig. 1. The diagramatic expression of Hamel's classification scheme (Hamel 1925).



Chl. = chloroplast.

Fig. 2. The diagramatic expression of Papenfuss' classification scheme (Papenfuss 1945).

Generic Classification Schemes

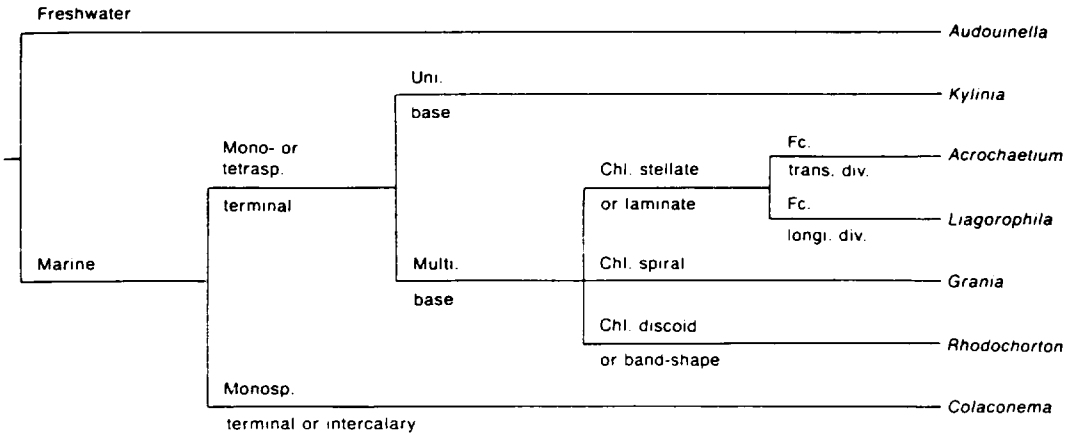
Bornet (1904) divided the acrochaetioid algae into two genera viz.: *Chantransia* for taxa having sexual reproduction, and *Acrochaetium* for taxa having no sexual reproduction. Collins (1906) followed Bornet's opinion. Woelkerling (1971) proposed an arrangement similar to Bornet's opinion and recognized a form genus, *Colaconema*, for taxa in which sexual reproduction was unknown and one natural genus, *Audouinella*, for taxa in which sexual reproduction was known. However, Woelkerling's opinion has not been generally adopted (cf. D'Lacoste and Ganesan 1972, Kumano 1978, Stegenga and van Erp 1979). The form genus concept seems not to be an effective solution to taxonomic problems of the Rhodochortaceae.

Hamel (1925) proposed a classification scheme on the basis of habitat, host specificity, and sexual reproduction (Fig. 1). He applied the chloroplast morphology as an additional criterion for circumscribing genera. However, the habitat and the host specificity are generally regarded not to be realistic as taxonomic criteria (Drew 1928, Woelkerling 1971, Lee 1980). Recently, culture studies have also indicated that acrochaetioid algae are not obligately associated with particular hosts.

Papenfuss (1945) introduced a scheme on the basis of the shape and number of chloroplast (Fig. 2). According to Papenfuss' scheme, *Rhodochorton purpureum*, *R. floridulum*, and *R. subimmersum* Setchell et Gardner should be assigned to *Rhodochorton*, *Chromastrum*, and *Acrochaetium*, respectively. In regard to sexual cycles, these three species have the same life cycle pattern (West 1969, 1970 b, Ohta and Kurogi 1979, Stegenga 1978, Lee and Kurogi 1978, Lee 1985). Therefore, the shape and number of chloroplast, if the character is applied to generic circumscription as a primary criterion, leads to a different alignment than does the pattern of life cycle.

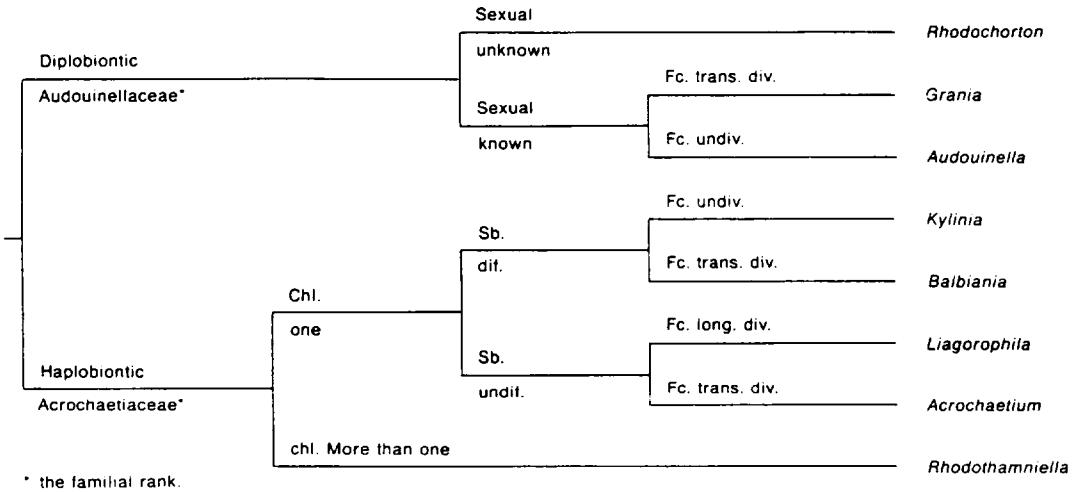
Kylin (1944, 1956) employed habitat, mode of mono- or tetrasporangium formation, basal system morphology, chloroplast morphology, and post-fertilization development for generic circumscription (Fig. 3). Drew (1928) showed that marine or freshwater habitat could not be used as a generic criterion (see also Dixon and Irvine 1977). Culture studies have shown that the life cycle of a number of species is completed with heteromorphic generations such as tretasporangial phase having a multicellular base and gametangial phase having a unicellular base: e. g., *Acrochaetium pectinatum* (Kylin) Hamel (West 1968, Abdel-Rahman and Magne 1983), *Rhodochorton floridulum* (Stegenga 1978), and *Audouinella alariae* (Jónsson) Woelkerling (Lee and Kurogi 1983). In this scheme, *Au. alariae* and *Rhodochorton floridulum* can be assigned to both genera *Kylinia* and *Acrochaetium*, and *Acrochaetium pectinatum* to both *Kylinia* and *Grania*. Therefore, this scheme is no longer effective in solving taxonomic problems of the Rhodochortaceae.

Feldmann (1962) proposed a scheme on the basis of sexual cycle, chloroplast morphology, mode of spermatangium formation, and post-fertilization development (Fig. 4). Abbott (1962) regarded the mode of spermatangium formation as an effective criterion for grouping acrochaetioid algae. *Rhodothamniella floridula*, the type species of *Rhodothamniella*, has a diphasic life cycle which is a similar pattern to that of *Rhodochorton purpureum* (West 1969, 1970 b, Stegenga 1978, Ohta and Kurogi 1979). *Kylinia rosulata* has specialized spermatangial branches (see also



Chl. = chloroplast, Fc. = fertilized carpogonium, longi. = longitudinal, trans. = transverse, div. = division, Multi. = multicellular, Uni. = unicellular, Mono- or tetrasp. = mono- or tetrasporangium, Monosp. = monosporangium.

Fig. 3. The diagramatic expression of Kylin's classification scheme (Kylin 1956).



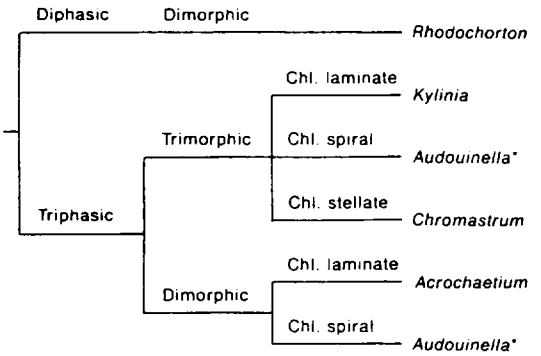
* the familial rank.
Chl. = chloroplast, dif. = differentiated, Fc. = fertilized carpogonium, long. = longitudinal, trans. = transverse, Div. = division, undiv. = undivided, Sb. = spermatangial branch, undif. = undifferentiated.

Fig. 4. The diagramatic expression of Feldmann's classification scheme (Feldmann 1962).

Moestrup *et al.* 1975). A number of species produce spermatangia in clusters on small-celled branchlets; e.g., *Acrochaetium dotyi* (Abbott 1962), *Acrochaetium botryocarpum* (Harvey) J. Agardh (Woelkerling 1970), and *Audouinella dictyotae* (Collins) Woelkerling (Lee 1987). *Audouinella kurogii* Lee et Lindstrom and *Au. alariae* usually produce spermatangia on the stalk cells of carpogonia [Lee and Linstrom 1979, Lee and Kurogi 1983, Lee 1983, Kuiper 1983; as *Chromastrum alariae* (Jónsson) Papenfuss]. Therefore, it is difficult to clearly define the differentiated spermatangial branch *sensu* Feldmann (1962).

Stegenga (1979, see also Stegenga and Vroman 1977) regarded the sexual cycle and the chloroplast morphology as the criteria to distinguish genera of the Rhodochortaceae (Fig. 5). Later, Stegenga (1895) changed some generic names in his classification scheme; *Chromastrum* to *Acrochaetium*, *Acrochaetium* to *Colaconema*, and *Kylinia* to a new name (not designated). He also regarded *Rhodothamniella* as a distinct genus on the basis of chloroplast morphology.

Woelkerling (1983) provided a scheme on the basis of sexual cycles (Fig. 6). Woelkerling (1983) emphasized



* *Audouinella* includes both dimorphic and trimorphic taxa. Chl. = chloroplast.

Fig. 5. The diagramatic expression of Stegenga's classification scheme (Stegenga 1979).

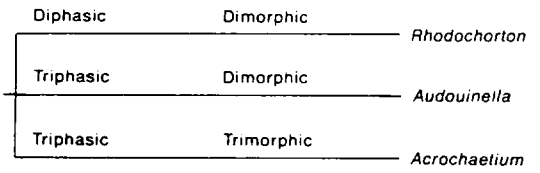
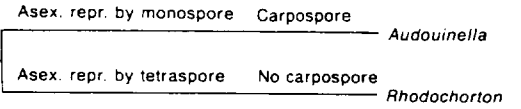


Fig. 6. The diagramatic expression of Woelkerling's classification scheme (Woelkerling 1983).

that the sexual cycle of acrochaetioid algae represented distinct lines of evolutionary development. However, both the schemes of Stegenga (1979) and Woelkerling (1983) are at present difficult to apply to taxa when the sexual cycle are unknown.

Lee (1980) proposed a classification scheme on the basis of asexual reproduction (Fig. 7). Lee (1980) postulated the corelation of production between monosporangia and carposporangia in acrochaetioid algae. The carposporangial plant can develop from a fertilized carpogonium on gametangial plants of the taxa producing monosporangia. On the other hand, the carposporophytic phase may be reduced in taxa producing no monosporangia. In this scheme, *Audouinella* includes taxa having asexual cycles with monospores and triphasic sexual cycles with gametophytic, carposporophytic, and tetrasporophytic phases. *Rhodochorton* is restricted to taxa having asexual cycles not with monospores but with tetraspores and diphasic sexual cycles with gametophytic and tetrasporophytic phases.

Drew (1928) advocated a single genus concept and employed *Rhodochorton* as the genus name for all acrochaetioid algae irrespective of habitat. Nakamura (1944), Nasr (1947) and Lee and Lee (1974) followed the contention of Drew (1928). Dixon and Irvine (1977, *in* Parke and Dixon 1976), Garbary (1979, 1980) and Garbary *et al.* (1982) concluded that there was no logical basis for the delineation of genera because of no obvious discontinuity between groups and adopted *Audouinella* as the genus name. On the contrary, Stegenga (1979; p. 23) said "... The taxonomic status of such clusters need not solely be determined by the existence of obvious discontinuities, but in addition by the magnitude of the differences between them. ... division into a number of different genera would be rather convenient in a group as large as the Acrochaetiaceae, ..." The number of genera in a family is hardly worth consideration in an effort to approach to natural classification no matter whether a group is large or small.

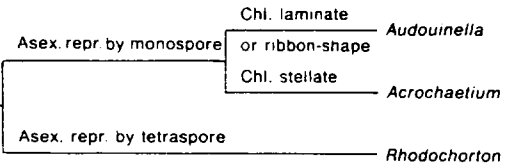


Asex. repr. = asexual reproduction.

Fig. 7. The diagramatic expression of Lee's classification scheme (Lee 1980).

Conclusion

The sexual cycle is not so satisfactory as a primary criterion for classification of acrochaetioid algae because the sexual cycles of the majority of more than 400 described taxa are still unknown (cf. Woelkerling 1983). A new classification scheme is developed from that of Lee (1980) by employing the chloroplast morphology as an additional criterion for taxa of *Audouinelle sensu* Lee (1980). Thus, three genera are adopted in the new scheme (Fig. 8): *Audouinella*, *Acrochaetium*, and *Rhodochorton*. *Audouinella* is characterized by producing monosporangia and having parietal laminate or ribbon-like chloroplasts. *Acrochaetium* is restricted to taxa producing monosporangia and containing stellate chloroplasts. *Rhodochorton* includes taxa producing no monosporangia on both gametangial and tetrasporangial plants.



Asex. repr. = asexual reproduction, Chl. = chloroplast.

Fig. 8. The diagramatic expression of the classification scheme (present study).

Woelkerling (1971) regarded the chloroplast morphology as an unreliable criterion to distinguish genera. In several taxa, the shape of chloroplast can differ depending upon the situation or position in a thallus, viz. whether a cell is in active division or not, and whether it occurs in an erect or basal system, e.g., *Chantransia immersa* Rosenvinge (Rosenvinge 1909), *Acrochaetium macropus* Kylin et Skotsberg [Lee 1980; as *Audouinella macropus* (Kylin et Skotsberg) comb. nov.], *Acrochaetium liagorae* Børgesen (Abbott 1962), *Ac. pectinatum* (West 1968, Abbott and Hollenberg 1976, Woelkerling 1971), *Acrochaetium arcuatum* (Drew) Tseng (Abbott and Hollenberg 1976), *Acrochaetium bonnemaisoniae* (Batters) J. et G. Feldmann (Boney 1972), *Audouinella codicola* (Børgesen) Garbary (Lee 1987), *Rhodochorton rhizoideum* Drew (Drew 1928), *R. floridulum* (Stegenga 1978), *Rhodochorton concrescens* Drew (1970a), *Rhodochorton membranaceum* (Magnus) Hauck (Lee 1980), *R. purpureum* (Drew 1928; as *Rhodochorton tenue* Kylin and *R. rothii*), and *Rhodochorton spetsbergense* (Kjellman) Kjellman [Drew 1928; as *Rhodochorton peniciliforme* (Kjellman) Rosenvinge], etc. However, no instance where a thallus contained both stellate and parietal laminate or ribbon-like chloroplasts was reported. Thus, chloroplast morphology is regarded as an effective criterion for classification of acrochaetioid algae which produce monosporangia.

Audouinella in this scheme may not be segregated further on the basis of the shape and number of chloroplast at present because certain taxa of the genus contain both parietal laminate and ribbon-like chloroplasts; e.g., *Au. hermanni* (Drew 1935; as *Rhodochorton violaceum*) and *Ac. pectinatum* [West 1968, Woelkerling 1971; as *Audouinella pectinata* (Kylin) Papenfuss]. Consequently, *Grania* and *Kylinia* are merged into *Audouinella* because the type species of the former two genera contain ribbon-like and parietal laminate chloroplasts, respectively.

Acrochaetium daviesii (Dillwyn) Naegeli is one of the species listed in *Acrochaetium* by Naegeli (1861). This species was cited as the type species of *Acrochaetium* (Drew 1928, Papenfuss 1945, Woelkerling 1971, Lee 1980). However, Woelkerling (1983) chose *Ac. secundatum* as the type species of *Acrochaetium* because this species was a member of the genus in the earlier publication of Naegeli (*in* Naegeli and Cramer 1858, cf. Silva *in* Farr *et al.* 1979) and *Ac. daviesii* was not. *Acrochaetium* was characterized by producing only monosporangia (Naegeli 1861). *Chromastrum* was apparently characterized by stellate chloroplasts (Papenfuss 1945). However, the type species of both *Acrochaetium* and *Chromastrum* contain stellate chloroplasts. Consequently, the two genera are congeneric, and *Acrochaetium* Naegeli should be adopted for the taxon on the basis of nomenclatural priority. *Liagorophila* is distinct in post-fertilization development and in having persistent trichogynes. However, *Liagorophila* is provisionally merged into *Acrochaetium* because the type species of the former has stellate chloroplasts, pending that more information is accumulated in acrochaetioid algae.

Rhodochorton is easily distinguished as exclusively producing tetrasporangia. It is known for some members of *Rhodochorton* that the formation of free carpospores was reduced (West 1969, Stegenga 1979, Lee and Kurogi 1978). Although *Rhodothamniella* was characterized as having stellate chloroplasts, the type species of the genus, *Rhodothamniella floridula*, had no fundamental difference from *Rhodochorton purpureum* with regard to exclusively producing tetrasporangia. Therefore, both genera, *Rhodochorton* and *Rhodothamniella*, are congeneric.

Various patterns of post-fertilization development are encountered in *Audouinella*. A carpospore is produced by transformation of a fertilized carpogonium in *Au. pectinata* (sporozygote *sensu* Abdel-Rahman and Magne 1983). Carposporangia are produced without division of a fertilized carpogonium in *Kylinia rosulata* (Feldmann 1958), or after transverse division in *Audouinella hermanni* (Drew 1935; as *Rhodochorton violaceum*) and *Au. dictyotae* (Woelkerling 1971, Lee 1987). Somewhat developed carposporophytes are encountered in *Acrochaetium dasyae* Collins (Stegenga and Borsje 1976) and *Audouinella thuretii* (Bornet) Woelkerling [Kylin 1907; as *Chantransia thuretii* (Bornet) Kylin]. Concatenate carposporangia are formed by transformation of 2–3 distal cells of branches of the carposporophyte of *Audouinella efflorescens* (J. Agardh) Papenfuss [Rosenvinge 1909; as *Chantransia efflorescens* (J. Agardh) Kjellman]. The carposporangia of *Acrochaetium imitator* Abbott are produced by repeatedly longitudinal division of the daughter cell derived from transverse division of a fertilized carpogonium (Abbott 1962).

Post-fertilization development is also varied in *Acrochaetium*. Fertilized carpogonia divided longitudinally in *Liagorophila endophytica* (Lee *et al.* 1986, Bula-Meyer 1986) and transversely in *Audouinella alariae* (Lee and Kurogi 1983, Lee 1983, Kuiper 1983; as *Chromastrum alariae*) and *Acrochaetium microscopicum* (Stegenga and Mulder 1979). Variation in spore germination mode and carposporophyte morphology has been elucidated in several members of *Acrochaetium* by Stegenga and Mulder (1979).

Rhodochorton is an assemblage of taxa containing variously shaped chloroplasts, viz. stellate in *Rhodochorton floridulum* (Kornmann and Sahling 1977, Kuckuck 1897), discoid in *R. purpureum* (Kuckuck 1897, Lee 1980) and *R. spetsbergense* [Woelkerling 1973 b; as *Audouinella spetsbergense* (Kjellman) Woelkerling], an irregularly partite form in *R. membranaceum* (Kuckuck 1897, Lee 1980), and parietal laminate in *R. subimmersum* (Drew 1928, Nakamura 1941, Lee and Kurogi 1978) and *Audouinella tetraspora* Garbary et Rueness (Garbary and Rueness 1980).

Appendix

List of proposed new combinations

1) *Acrochaetium kurogii* (Lee *et* Lindstrom) Lee *et* Lee *comb. nov.* Basionym: *Audouinella kurogii* Lee *et* Lindstrom (1979), p. 115.
2) *Acrochaetium yamadae* (Garbary) Lee *et* Lee *comb. nov.* Basionym: *Liagorophila endophytica* Yamada (1944), p. 16. Garbary (1980; p. 67) proposed a new name, *Audouinella yamadae* Garbary, for this taxon.
3) *Rhodochorton tetrasporum* (Garbary *et* Rueness) Lee *et* Lee *comb. nov.* Basionym: *Audouinella tetraspora* Garbary *et* Rueness (1980), p. 17.

Acknowledgements

We are grateful to Prof. Dr Y. H. Chung, Department of Botany, Seoul National University, Korea, and Prof. Dr J. W. Kang, Department of Marine Biology, National Fisheries University of Pusan, Korea, for their continuous guidance and advice during the course of this study. We wish to express our sincere gratitude to Dr S. C. Lindstrom, Nori Aquafood Systems Inc., British Columbia, Canada, for her favor of reading this manuscript and giving valuable comments. Thanks are due to Dr D. Garbary, Department of Biology, St. Francis Xavier University, Nova Scotia, Canada, and Dr G. T. Boalch, The Laboratory, Citadel Hill, Plymouth, Great Britain, for their critical reading and revision of this paper. This paper represents a part of the work supported by the Korea Science and Engineering Foundation (KOSEF) to the first author for the years 1984–1986.

References

Abbott, I. A. 1962. Some *Liagora*-inhabiting species of *Acrochaetium*. *Occa. Pap. Bernice P. Bishop Mus. 23*: 77–120.

Abbott, I. A. 1966. Observations on *Liagorophila endophytica*, a rare species in the Acrochaetiaceae (Rhodophyta). *J. Phycol. 2*: 145–150.

Abbott, I. A. and G. J. Hollenberg. 1976. *Marine Algae of California*. Stanford University Press, California, pp. 827.

Abdel-Rahman, M. H. and F. Magne. 1983. Existence d'un nouveau type de cycle de développement chez les Rhodophycées. *C. R. Acad. Sc., Paris 269*: 641–644.

Agardh, C. A. 1824. *Systema Algarum*. Lund, Literis Berlingianis, pp. 312.

Agardh, J. G. 1851. *Species, Genera et Ordines Algarum*. Vol. 2, Part 2: 1. Part 1. Lund, pp. 336.

Agardh, J. G. 1892. Analecta algologica. Observations de speciebus algarum minus cognitis earumque dispositione. *Lunds Univ. Arrskr. 28*: 1–182.

Areschoug, J. E. 1847. Phycearum, quae in maribus Scandinaviae crescunt, enumeratio. *Nova Acta Regiae Soc. Sci. Ups. 13*: 223–382.

Baardseth, E. 1941. The marine algae of Tristan da Cunha. *In*: *Results of Norwegian Scientific Expedition to Tristan da Cunha*. Vol. 9. Det. Norske Videnskaps-Akademii, Oslo, pp. 173.

Batters, E. A. 1896. Some new British marine algae. *J. Bot., Lond. 34*: 6–11.

Batters, E. A. 1902. A catalogue of the British marine algae. *J. Bot. Lond. 40 (Suppl.)*, pp. 107.

Børgesen, F. 1910. Some new or little-known West Indian Florideae. II. *Bot. Tidsskr. 30*: 177–207.

Børgesen, F. 1915. The marine algae of the Danish West Indies. Vol. II. Rhodophyceae. *Dansk. Bot. Ark. 3*: 1–80.

Børgesen, F. 1927. Marine algae from the Canary Islands. III. Rhodophyceae. *Det. Kgl. Dansk. Vid. Selsk. Biol. Medd. 6*: 1–97.

Børgesen, F. 1937. Contributions to a south Indian marine algal flora. *J. Indian Bot. Soc. 16*: 1–56.

Boney, A. D. 1972. *In vitro* growth of the endophyte *Acrochaetium bonnemaisoniae* (Batt.) J. *et* G. Feldmann. *Nova Hedwigia 23*: 173–186.

Bonnemaison, T. 1828. Essai sur les Hydrophytes loculées ou articulées de la famille des Epidermées et des Ceramiées. *Mem. Mus. His. nat. Paris 16*: 49–148.

Bornet, E. 1904. Deux *Chantransia corymbifera* Thuret. *Acrochaetium* et *Chantransia*. *Bull. Soc. Bot. Fr. 51 (Suppl.)*: XIV–XXIII.

Bory de Saint Vincent, J. B. M. 1823. *Auduinella*. *In*: *Dictionnaire Classique d'Historie Naturelle*, Vol. 3 Rey et Gravier, Paris, pp. 349–341.

Brand, F. 1897. Über "*Chantransia*" und die einschlägigen Formen der Bayrischen Hochebene. *Hedwigia 36*: 300–319.

Brand, F. 1910. Über die Süßwasserformen von *Chantransia* (D. C.) Schmitz. *Hedwigia 49*: 107–118.

Bula-Meyer, G. 1986. *Liagorophila endophytica* (Acrochaetiaceae, Rhodophyta) in the Caribbean Sea: a new record for the Atlantic Ocean. *Br. phycol. J. 21*: 263–268.

Cardinal, A. 1964. Etude sur les Ectocarpacées la Manche. *Nova Hedwigia 15*: 1–86, Figs 1–41.

Christensen, T. 1978. Annotations to a textbook of phycology. *Bot. Tidsskr. 73*: 65–70.

Collins, F. S. 1906. *Acrochaetium* and *Chantransia* in North America. *Rhodora 8*: 189–196.

Collins, F. S. 1911. Notes on algae. X. *Rhodora 13*: 184–187.

Collins, F. S. and A. B. Harvey. 1917. The algae of Bermuda. *Proc. Am. Acad. Arts Sci. 53*: 1–95.

De Candolle, A. P. 1801. Extrait d'un raport sur les Conferves. *Bull. Soc. Philomath. Paris 3*: 17–21.

Desvaux, N. A. 1809. Plantes trouvés dans le Haut-poitou, les unes nouvelles, les autres point indiquées dans la Flore de France. *J. Bot. Soc., Paris 2*: 307–318.

De Toni, G. B. 1895. *Sylloge algarum omnium hucusque cognitarum Vol. 3. Sylloge Fucoidearum*. Padua pp. 638.

De Toni, G. B. 1924. *Sylloge algarum omnium hucusque cognitarum Vol. 6. Sylloge Floridearum (5)*. Padua pp. 767.

Dillwyn, L. W. 1802–1809. *British Confervae*. London. pp. 87, pls 318.

Dixon, P. S. and L. M. Irvine. 1977. *Seaweeds of British Isles Vol. 1. Rhodophyta, Part 1. Introduction, Nemaliales, Gigartinales*. London. pp. 252.

D'Lacoste, L. E. and E. K. Ganesan. 1972. A new freshwater species of *Rhodochorton* (Rhodophyta, Nemaliales) from Venezuela. *Phycologia 11*: 233–238.

Drew, K. M. 1928. A revision of the genera *Chantransia*, *Rhodochorton*, and *Acrochaetium* etc. *Univ. Calif. Publs Bot. 14*: 139–224.

Drew, K. M. 1935. The life-history of *Rhodochorton violaceum* (Kuetz.) comb. nov. (*Chantransia violacea* Kuetz.) *Ann. Bot. 59*: 439–450.

Duby, J. E. 1830. *Bontnicon Galicum*. Paris. pp. 968–977.

Fan, K. C. and W. S. Li. 1964. Studies on the reproductive organs of red algae V. *Liagorophila*. *Acta Bot. Sinica 12*: 376–383.

Farlow, W. G. 1881. The marine algae of New England. *Rep. of Commissioner of Fish and Fisheries* Appendix A–I: 105–201.

Farr, E. R., J. A. Leussink and F. A. Stafleu, eds. 1979. *Index Nominum Genericorum (Plantarum) Vols 1–3*. Bohn, Scheltema and Holkema, Utrecht, Netherlands. pp. 1869.

Feldmann, J. 1954. Inventaire de la flore marine de Roscoff. Algues, Champignons, Lichens et Spermatophytes. *Trav. Stn. Biol. Roscoff Suppl. 6*: 1–151.

Feldmann, J. 1955. Un nouveau genre de Protofloridée: *Coladodictyon*, nov. gen. *Bull. Soc. Bot. Fr. 102*: 23–28.

Feldmann, J. 1958. Le genre *Kylinia* Rosenvinge (Acrochaetiales) et sa reproduction. *Bull. Soc. Bot. Fr. 105*: 493–500.

Feldmann, J. 1962. The Rhodophyta order Acrochaetiales and its classification. *Proc. 9th Pacific Sci. Congr., 1957. 4*: 219–221.

Feldmann, J. 1981. Sur une nouvelle espèce de *Porphyra* (*P. drachii* J. Feldm.) et remarques sur l'évolution des plates chez les Rhodophycées (Bangiophycées et Acrochaetiales). *Vie Milieu 28–29*: 425–435.

Feldmann, J. and G. Feldmann. 1939. Additions à la flore des algues marines de l'Algérie. *Bull. Soc. Nat. Bot., Ser. 11. 3*: 75–175.

Foslie, M. 1890. Contribution to knowledge of the marine algae of Norway. 1. East-Finmaiken. *Tromsoe Mus. Arsh. 13*: 48–54.

Fritsch, F. E. 1944. Present-day classification of algae. *Bot. Rev. 10*: 233–277.

Garbary, D. J. 1978. On the phylogentic relationships of the Acrochaetiaceae (Rhodophyta). *Br. phycol. J. 13*: 247–254.

Garbary, D. J. 1979. Numerical taxonomy and generic circumscription in the Acrochaetiaceae (Rhodophyta). *Bot. Mar. 22*: 477–492.

Garbary, D. J. 1980. On the systematic position of *Liagorophila* (Acrochaetiaceae, Rhodophyta). *Taxon 29*: 67–69.

Garbary, D. J., G. I. Hansen and R. F. Scagel. 1982. The marine algae of British Columbia and Northern Washington: Division Rhodophyta (red algae), Class Florideophyceae, Orders Acrochaetiales and Nemaliales. *Syesis 15 (Suppl. 1)*: 1–102.

Garbary, D. J. and J. Rueness. 1980. *Audouinella tetraspora*, a new member of the Acrochaetiaceae (Rhodophyta) from Norway. *Norw. J. Bot. 27*: 17–22.

Hamel, G. 1925. Floridees de France. III. *Rev. Alg. 2*: 39–67.

Hamel, G. 1927. *Recherches sur les genres* Acrochaetium *Naeg. et* Rhodochorton *Naeg.* Imprimerie R. Jacqueline, Paris, France. pp. 117.

Harvey, W. H. 1841. *A Manual of the British Algae*. London. pp. 103–118.

Harvey, W. H. 1854. Some account of the marine botany of the colony of Western Australia. *Trans. R. Ir. Acad. 22*: 525–566.

Hauck, F. 1885. Die Meeresalgen, Deutschlands und Oesterreichs. *In*: (L. Rabenhorst ed.) *Kryptogamenflora von Deutschland, Oesterreich und der Schweitz. Zweite Aufl. Zweiter Band*. Leipzig. pp. 575.

Hooker, W. J. 1883. *The English Flora of Sir James Edward Smith. Class XXIV Cryptogamia Vol. V*. London. pp. 248–432.

Howe, M. A. 1914. The marine algae of Peru. *Mem. Torry Bot. Club 15*: 1–85, pl. 66.

Israelson, G. 1942. The freshwater Florideae of Sweden. *Symb. Bot. Upsal. 6*: 1–134, pls 1–3.

Jao, C. C. 1936. New Rhodophyceae from Woods Hole. *Bull. Torrey Bot. Club 63*: 237–257.

Jao, C. C. 1937. New marine algae from Washington. *Pap. Michigan Acad. Sci. Arts and Letters 22*: 99–116, pls 12–14.

Jónsson, H. 1901. The marine algae of Iceland. 1. Rhodophyceae. *Bot. Tidsskr. 24*: 127–155.

Kjellman, F. R. 1875. Om Spetsbergens marina, Klorofyllförande Thallophyter. 1. *Bihang K. Sven. Vet. Akad. Handl. 3*: 1–34.

Kjellman, F. R. 1883. The algae of the Artic Sea. *K. Sven. Vet. Akad. Handl. 20*: 1–350.

Klavestad, N. 1957. Paraspores in *Rhodochorton rothii* Naeg. *Nytt. Mag. Bot. 5*: 61–62.

Kornmann, P. and P. H. Sahling. 1977. Meereslagen von Helgoland. *Helgol. Wiss. Meeresunt. 29*: 1–289.

Kuckuck, P. 1897. Beiträge zur Kenntnis der Meeresalgen. 2. Über *Rhodochorton membranaceum* Magnus, eine chitinbewohnende Alga. *Wiss. Meeresunt. Abt. Helgoland, N. F. 2*: 337–348.

Kuckuck, P. 1964. *Ectocarpaceen – Studien IV*. Hamburg. p. 139.

Kuetzing, F. T. 1845. *Phycologia Germanica, d. i. Deutschlands Algen*. Nordhausen. pp. 340.

Kuetzing, F. T. 1849. *Species Algarum*. Leipzig. pp. 922.

Kuiper, J. 1983. The life history of *Chromastrum alariae* (Jónsson) Papenfuss (Rhodophyta, Acrochaetiaceae). *Acta Bot. Neerl. 32*: 129–151.

Kumano, S. 1978. Occurrence of a new freshwater species of the genus *Acrochaetium*. *Jap. J. Phycol. 26*: 105–108.

Kylin, H. 1906. Zur Kenntnis einiger schwedischer *Chantransia*-Arten. *In*: (F. R. Kjellman ed.) *Botaniska Studier till*. Uppsala. pp. 113–126.

Kylin, H. 1907. *Studien über die Algenflora der schwedischen Westküste*. Akad. Abhand. Uppsala. pp. 114–190.

Kylin, H. 1925. The marine red algae in the vicinity of the Biological Station at Friday Harbor, Wash. *Lunds Univ. Arsskr. Avd. 2. 21*: 1–87.

Kylin, H. 1944. Die Rhodophyceen der schwedischen Westküste. *Lunds Univ. Arsskr. N. F. Avd. 2. 40*: 1–140. Tafs 32.

Kylin, H. 1956. *Die Gattungen der Rhodophyceen*. Lund. pp. 669.

Kylin, H. and C. Skottsberg. 1919. Zur Kenntnis der subantarktischen und antarktischen Meeresalgen. II. Rhodophyceen. *Wiss. Ergebn. Schwed., Südpolar-Exped. 1901–1903. Vol. 4*. pp. 88.

Lee, I. K. and Y. P. Lee. 1974. Some members of *Rhodochorton* (Rhodophyta) in Korea. *Korean J. Bot. 17*: 36–52.

Lee, Y. P. 1980. Taxonomic Study on the Acrochaetiaceae (Rhodophyta). Dr. Sci. thesis, Hokkaido Univ., Sapporo. pp. 302.

Lee, Y. P. 1983. Sexual reproduction in *Audouinella aluriae* (Jónsson) Woelkerling (Acrochaetiaceae, Rhodophyta) from the North Atlantic Ocean. *Bull. Korean Fish. Soc. 16*: 265–272.

Lee, Y. P. 1985. Notes on reproduction in *Rhodochorton purpureum* (Lightfoot) Rosenvinge (Rhodophyta) with special reference to Hokkaido plants. *Korean J. Bot. 28*: 45–55.

Lee, Y. P. 1987. Taxonomy of the Rhodochortonaceae (Rhodophyta) in Korea. *Korean J. Phycol. 2*: 1–50.

Lee, Y. P. and M. Kurogi. 1978. Sexual reproductive structures and postfertilization in *Rhodochorton subimmersum* Setchell et Gardner. *Jap. J. Phycol. 26*: 115–119.

Lee, Y. P. and M. Kurogi. 1983. The life history of *Audouinella alariae* (Jónsson) Woelkerling (Rhodophyta, Acrochaetiaceae) in nature and culture. *J. Fac. Sci., Hokkaido Univ., Ser. V (Bot.) 13*: 57–76.

Lee, Y. P. and S. C. Linstrom. 1979. *Audouinella kurogii*, a new marine red alga (Acrochaetiaceae) from northern Japan. *Jap. J. Phycol. 27*: 115–122.

Lee, Y. P., T. Yoshida and M. Kurogi. 1986. Observations on the type of *Liagorophila endophytica* Yamada (Acrochaetiaceae, Rhodophyta). *Jap. J. Phycol. 34*: 171–176.

Le Jolis, A. 1863. Liste des algues marines de Cherbourg. *Mem. Soc. Sci. Nat. de Cherbourg 10*: 1–168, pls 6.

Levring, T. 1937. Zur Kenntnis der Algenflora der norwegischen Westküste. *Lunds Univ. Arsskr., Avd. 2. 33*: 1–147.

Lightfoot, J. 1777. *Flora Scotica. Vol. 2*. London. pp. 902–1007.

Linnaeus, C. 1753. *Species Plantarum II*. Stockholm. pp. 1131–1171.

Lyngbye, H. 1819. *Tentamen Hydrophytologiae Danicae*. Copenhagen. pp. 248.

Magnus, P. 1874. Die botanischen Ergebnisse der Nordseefahrt vom 21. Juli bis 9. September 1872. *Jahresb. Komm. Unters. deutschen Meere, Kiel 2*: 61–79.

Martius, C. F. P. 1817. *Flora Cryptogamia Erlangensis*. Nuremberg. pp. 508.

Moestrup, Ø., I. Nicolaisen, H. Nielsen and P. M. Pedersen. 1975. Some new or noteworthy marine benthic algae from Denmark. *Bot. Tidsskr. 69*: 257–261.

Naegeli, C. 1861. Beiträge zur Morphologie und Systematik der Ceramiaceae. *Sber. bayer. Akad. Wiss. 2*: 297–415.

Naegeli, C. and C. Cramer. 1858. *Pflanzenphysiologische Untersuchungen. Vol. 2. Die Stärkekörner*. Zurich, Switzerland.

Nakamura, Y. 1941. The species of *Rhodochorton* from Japan I. *Sci. Pap. Inst. Algol. Res., Hokkaido Univ. 2*: 273–291.

Nakamura, Y. 1944. The species of *Rhodochorton* from Japan II. *Sci. Pap. Inst. Algol. Res., Hokkaido Univ. 3*: 99–119.

Nasr, A. H. 1947. Synopsis of the marine algae of the Egyptian Red Sea coast. *Bull. Fac. Sci. Egypt. Univ. 26*: 1–55.

Ohta, M. and M. Kurogi. 1979. On the life history of *Rhodochorton purpureum* (Lightf.) Rosenvinge. *Jap. J. Phycol. 27*: 161–167.

Papenfuss, G. F. 1945. Review of the *Acrochaetium-Rhodochorton* complex of the red algae. *Univ. Calif. Publs Bot. 18*: 229–334.

Papenfuss, G. F. 1947. Further contributions toward an understanding of the *Acrochaetium-Rhodochorton* complex of the red algae. *Univ. Calif. Publs Bot. 18*: 433–447.

Parke, M. and P. S. Dixon. 1976. Check-list of British marine algae. 3rd revision. *J. Mar. Biol. Ass. U. K. 56*: 527–594.

Pringsheim, N. 1862. *Beiträge zur Morphologie der Meeresalgen*. Abh. Preuss. Akad. Wiss. pp. 37, pls 8.

Rabenhorst, L. 1868. *Flora europaea algarum aquae dulcis et submarinae. Sect. 3*. Leipzig. pp. 461.

Rosenvinge, L. K. 1900. Note sur une Floridée aériene (*Rhodochorton islandicum* nov. sp.). *Bot. Tidsskr. 23*: 61–81.

Rosenvinge, L. K. 1909. The marine algae of Denmark I. Rhodophyceae 1. *K. Dan. Vid. Selsk. Biol. Skr. 7*: 1–151.

Rosenvinge, L. K. 1923–1924. The marine algae of Denmark. I Rhodophyceae 3. *K. Dan. Vid. Selsk. Biol. Skr. 7*: 285–487.

Rosenvinge, L. K. 1935. Distribution of the Rhodophyceae in the Danish waters. *K. Dan. Vid. Selsk. Biol. Skr. 6*: 1–44.

Roth, A. G. 1797. *Catalecta botanica quibus plantae novae et minus cognitae describuntur atque illustratur. Fasc. 1*. Lipsiae. pp. 145–218.

Roth, A. G. 1806. *Catalecta botanica quibus plantae novae et minus cognitae describuntur atque illustratur. Fasc. 3*. Lipsiae. pp. 350, 12 pls.

Setchell, W. A. and N. L. Gardner. 1903. Algae of northwestern America. *Univ. Calif. Publs Bot. 1*: 165–419.

Setchell, W. A. and N. L. Gardner. 1930. Marine algae of the Revillagigedo Islands Expedition in 1925. Proc. *Calif. Acad. Sci., Ser. 4. 19*: 109–125.

Silva, P. C. 1950. Generic names of algae proposed for conservation. *Hydrobiologia 2*: 252–280.

Silva, P. C. 1952. A review of nomenclatural conservation in the algae from the point of view of the type method. *Univ. Calif. Publs Bot. 25*: 241–323.

Silva, P. C. 1980 a. Remarks on algal nomenclature VI. *Taxon 29*: 121–145.

Silva, P. C. 1980 b. *Names of Classes and Families of Living Algae*. Netherlands. pp. 156.

Sirodot, S. 1876. Le *Balbiania investiens* étude organogénique et physiologique. *Ann. Sci. Nat. (Bot.) 3*: 146–174.

Sirodot, S. 1884. Les *Batrachospermes*. Libraire de l'academie de Medicine. Paris. pp. 210–283.

Stegenga, H. 1978. The life histories of *Rhodochorton purpureum* and *Rhodochorton floridulum* (Rhodophyta, Nemaliales) in culture. *Br. phycol. J. 13*: 279–289.

Stegenga, H. 1979. *Life Histories and Systematics of the Acrochaetiaceae*. Total Photo/Total Print. Amsterdam, Holland. pp. 34.

Stegenga, H. 1985. The marine Acrochaetiaceae (Rhodophyta) of southern Africa. *S. Afr. J. Bot. 51*: 291–330.

Stegenga, H. and W. J. Borsje. 1976. The morphology and life history of *Acrochaetium dasyae* Collins (Rhodophyta, Nemaliales). *Acta Bot. Neerl. 2*: 15–29.

Stegenga, H. and A. S. Mulder. 1979. Remarks on the *Audouinella microscopica* (Naeg.) Woelkerling complex, with a brief survey of the genus *Chromastrum* Papenfuss (Rhodophyta, Nemaliales). *Acta Bot. Neerl. 28*: 289–311.

Stegenga, H. and N. D. van Erp. 1979. Morphological variation in the genus *Acrochaetium* (Rhodophyta, Nemaliales). *Acta Bot. Neerl. 28*: 425–448.

Stegenga, H. and M. Vroman. 1977. The significance of life history characters for the systematics of the Acrochaetiaceae. *J. Phycol. 13 (Suppl.)*: 64.

Swale, E. M. F. and J. H. Belcher. 1963. Morphological observations on wild and cultured material of *Rhodochorton investiens* (Lenormand) nov. comb. [*Balbiania investiens* (Lenorm.) Sirodot]. *Ann. Bot. N. S. 27*: 281–290.

Taylor, W. R. 1957. *Marine algae of the Northeastern Coast of North America*. Univ. Michigan Press, Ann Arbor. pp. 507.

Tseng, C. K. 1945. New and unrecorded marine algae of Hong Kong. *Pap. Mich. Acad. Sci. Arts and Lett. 30*: 157–172.

Turton, W. 1806. *A General System of Nature. 3*. London.

von Stosch, H. A. 1965. The sporophyte of *Liagora farinosa* Lamour. *Br. phycol. Bull. 2*: 468–496.

Voss, E. G., H. M. Burdet, W. G. Chaloner, V. Demoulin, P. Hiepko, J. McNeill, R. D. Meikle, D. H. Nicolson, R. C. Rollins, P. C. Silva and W. Greuter, eds. 1983. *International Code of Botanical Nomenclature. Adopted by the Thirteenth International Congress, Sydney, August 1981*. Bohn, Scheltema & Holkema. The Hague/Boston. pp. 1–75.

West, J. A. 1968. Morphology and reproduction of the red alga *Acrochaetium pectinatum* in culture. *J. Phycol. 4*: 89–99.

West, J. A. 1969. The life histories of *Rhodochorton purpureum* and *R. tenue* in culture. *J. Phycol. 5*: 12–21.

West, J. A. 1970 a. The life history of *Rhodochorton concrescens* in culture. *Br. phycol. J. 5*: 179–186.

West, J. A. 1970 b. A monoecious isolate of *Rhodochorton purpureum*. *J. Phycol. 6*: 368–370.

Woelkerling, W. J. 1970. *Acrochaetium botryocarpum* (Harv.) J. Ag. in southern Australia. *Br. phycol. J. 5*: 159–171.

Woelkerling, W. J. 1971. Morphology and taxonomy of the *Audouinella* complex (Rhodophyta) in southern Australia. *Aust. J. Bot., Suppl. 1*: 1–91.

Woelkerling, W. J. 1973 a. The *Audouinella* complex (Rhodophyta) in the western Sargasso Sea. *Rhodora 75*: 78–101.

Woelkerling, W. J. 1973 b. The morphology and systematics of the *Audouinella* complex (Acrochaetiaceae, Rhodophyta) in northeastern United States. *Rhodora 75*: 529–621.

Woelkerling, W. J. 1983. The *Audouinella* (*Acrochaetium* – *Rhodochorton*) complex (Rhodophyta): present perspectives. *Phycologia 22*: 59–92.

Yamada, Y. 1944. Notes on some Japanese algae X. *Sci. Pap. Inst. Algol. Res., Hokkaido Univ. 3*: 11–25.