SYSTEMATICS AND BIOGEOGRAPHY OF THE FRESHWATER RED ALGAL GENUS BATRACHOSPERMUM SECTION BATRACHOSPERMUM IN NORTH AMERICA

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BY

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Abstract

Type and historically important specimens of 46 species and infraspecific taxa from Batrachospermum sect. Batrachospermum were examined using multivariate morphometrics and image analysis. Nine species from the cluster analysis and one other species are recognised: B. anatinum, B. arcuatum, B. boryanum, B. carpocontortum, B. confusum, B. fluitans, B. gelatinosum, B. heterocorticum, B. pulchrum and B. skujae. The taxa are separated on the basis of monoecious or dioecious thalli, carpogonium size and the presence of (1) spermatangia on the involucral filaments, (2) irregular cortication, (3) monosporangia, (4) well-curled fascicles and (5) secondary fascicles.

Five new species are described from North America. Batrachospermum spermatoinvolucrum sp. nov. is distinguished by the combination of spermatangia on the involucral filaments of the carpogonial branch, relatively long carpogonia and regular cortical cells. B. trichofurcatum sp. nov. has unique forked trichogynes. The distinguishing feature of B. carpoinvolucrum sp. nov. is carpogonial branches with involucral filaments having apical carpogonia. B. involutum sp. nov. is distinct in having involute fascicle tips, spermatangia on one-celled involucral filaments and rhizoidal outgrowths from mid-fascicle cells. B. trichocontortum sp. nov. is named for the twisted appearance of the trichogyne tip and has rhizoidal outgrowths from mid-fascicle cells.

North American populations of seven previously described species were

examined and compared to appropriate type specimens. *Batrachospermum boryanum* was the most abundant and widespread species, being collected in 34 stream sites. The other six species, *B. anatinum*, *B. arcuatum*, *B. confusum*, *B. heterocorticum*, *B. pulchrum* and *B. skujae* were present in six or fewer streams. No new populations were found of *B. carpocontortum* which was first described from Washington state.

Eighty-six populations of *Batrachospermum gelatinosum* were examined from throughout its known range in North America. Pooled populations for each biome showed a north-south trend towards smaller whorl size and larger carpogonium size. *B. gelatinosum* has been collected from the north slope of Alaska and Baffin Island to Texas and Louisiana. Three populations were examined for morphological variation throughout the growing season. Carposporophyte diameter showed a spring maximum in all three populations. There were seasonal trends in whorl diameter, carposporophytes per whorl and carpogonium length in one population.

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General Introduction

The freshwater red algal genus Batrachospermum was established in 1797 by Roth and in a later paper he designated B. moniliforme as the first species to be placed in this genus (Roth, 1800). The epithet moniliforme was used until recently when Necchi (1990) and Compère (1991) concluded that Roth did not describe a new species but only made a new combination for the previously published Conferva gelatinosa L. Therefore, the type species of the genus has been designated B. gelatinosum (L.) deCandolle and B. moniliforme is an illegitimate name (Greuter et al., 1988: Art. 63.1).

Sirodot (1884) divided Batrachospermum into six sections [Setaces (= Setacea De Toni 1897), Moniliformes (= Batrachospermum), Helminthoides (= Helminthoidea Sirodot ex De Toni 1897), Turficoles (= Turfosa Sirodot 1873), Hybride (= Hybrida De Toni 1897) and Verts (= Virescentia Sirodot 1873)] on the basis of whorl size, carposporophytes pedicellate or sessile on the main axis, and trichogyne shape. Subsequently, five other sections have been proposed: Contorta (Skuja, 1931), Aristatae (Skuja, 1933), Claviformia (Reis, 1974), Carpocontorta (Sheath et al., 1986b) and Gonimopropagulum (Sheath & Whittick, 1995). These new sections are distinguished by features of the carpogonial branch, size and number of carposporophytes, carpogonium shape and the presence of typical carposporangia or gonimoblast propagules. Necchi and Entwisle (1990) revised the classification within the family Batrachospermaceae, referring the genera Sirodotia, Tuomeya and Nothocladus to sections of Batrachospermum and rejecting sections Helminthoidea, Setacea, Claviformia and Carpocontorta. However, this classification scheme has not been widely accepted (Kaczmarczyk et al., 1992; Kumano, 1993; Necchi et al., 1993; Sheath et al., 1992, 1993b, 1994a, 1994b, 1994c).

Batrachospermum sect. Batrachospermum contains the largest numbers of species. This section is generally characterised by the following features: well-developed whorls, undifferentiated and straight carpogonial branches arising from both fascicle and pericentral cells, carpogonia with club- to urn-shaped trichogynes, and small, globose, pedicellate carposporophytes at various distances from the whorl axis (Mori, 1975; Starmach, 1977; Kumano, 1993). The merging of sections Batrachospermum and Helminthoidea was suggested by Sheath & Burkholder (1983). They observed the two features previously used to separate these sections, trichogyne shape and involucral filament length, to be quite variable within the same specimen and not taxonomically useful. This consolidation was adopted by Necchi & Entwisle (1990). Recently, Kumano (1993) has chosen to keep these sections separate on the basis of involucral filament length. Sect. Carpocontorta, originally distinguished on the basis of contorted carpogonia and one to two large, globose, pedicellate carposporophytes has been included in sect. Batrachospermum (Necchi & Entwisle, 1990). They proposed that these characteristics are only useful and significant at the specific level. Therefore, sect. Batrachospermum sensu lato (including sections Batrachospermum, Helminthoidea and Carpocontorta) is examined in the present study.

Sirodot (1884) first described many of the infrageneric taxa within sect.

Batrachospermum. The species and varieties have been distinguished based on the following characteristics: monoecious or dioecious thalli; whorl shape; carposporophytes contained within or protruding from the whorl; size and shape of carpogonia; and presence or absence of spermatangia on the involucral filaments of the carpogonial branch, brown cortication of the main axis or monosporangia on the gametophyte (Sirodot, 1884). However, Israelson (1942) proposed that some of these features, such as brown cortication, are due to environmental factors and many of Sirodot's taxa are simply ecotypes. Other characteristics which have been used to distinguish infrageneric taxa in sect. Batrachospermum include number of fascicles per pericentral cell, placement of carposporophytes in the whorls and shape of the carposporophyte branch cells (Mori, 1975). In addition, new species have been described with other new characteristics such as cylindrical fascicle cells, involucral filaments on one side of the carpogonial branch, heterocortication and whorl shape (Kumano, 1978; Kumano & Johnstone, 1983; Sheath & Cole, 1990; Shi et al., 1993). Therefore, an examination of all type specimens and an evaluation of characteristics for taxonomic use in this section are needed.

Batrachospermum sect. Batrachospermum infrageneric taxa have been reported from Europe, Asia, Australia, South America and North America (e.g. Sirodot, 1884; Reis, 1973; Mori, 1975; Entwisle & Kraft, 1989; Necchi, 1990; Sheath & Cole, 1990). In North America, eight species from this section have been previously reported, including B. anatinum Sirodot, B. boryanum Sirodot, B. carpocontortum Sheath, M.O.Morison, K.M.Cole et Vanalst., B. confusum (Bory) Hassall (as B. crouanianum Sirodot), B. gelatinosum (often as B. moniliforme nom. illeg.), B. heterocorticum Sheath et Cole, B. pulchrum Sirodot and B. skujae Geitler (as B. sporulans nom. illeg.) (e.g. Hylander, 1928; Vinyard, 1966; Sheath & Cole, 1992). In a survey of 1000 streams throughout North America (Sheath & Cole, 1992), populations referable to sect. Batrachospermum were collected which were unlike the species previously reported. From these populations, five new species are described on the basis of unique characteristics. In addition, there are few data on previously described species from North America. Hence, a study of the distribution and morphological variation of Batrachospermum sect. Batrachospermum species in North America would be useful.

Batrachospermum gelatinosum is one of the five most widespread macroalgae in North America occurring in all biomes except desert/chaparral and tropical rain forest (Sheath & Cole, 1992). This species has been reported from locations throughout North America ranging from Alaska and Greenland in the north to Mexico in the south (e.g. Bachmann, 1921; Sánchez-Rodríguez, 1974; Sheath & Cole, 1992). Although this species has been widely collected, there is little information on its biogeography. Additionally, there are no data on morphological variation throughout the growing season from various regions. Therefore, an examination of the distribution and spatial and temporal morphological variation in B. gelatinosum is warranted.

The objectives of this research are as follows: (1) to determine the number of well-distinguished species worldwide in Batrachospermum sect. Batrachospermum based on type specimens; (2) to describe five new species which have unique morphological characteristics from North America; (3) to summarize the known distribution of species within this section in North America and to characterize morphological variation within each species throughout its entire geographic range; (4) to study the biogeography and morphological variation, spatial and temporal, in B. gelatinosum.

Morphometric analysis of Batrachospermum section Batrachospermum (Batrachospermales, Rhodophyta) type specimens

2.1 Introduction

Sect. Batrachospermum of the freshwater red algal genus Batrachospermum is generally characterised by the following features: undifferentiated carpogonial branches arising from both fascicle and pericentral cells, carpogonia with club- to urn-shaped trichogynes, and small, globose, pedicellate carposporophytes at various distances from the whorl axis (Mori, 1975; Starmach, 1977; Kumano, 1993). Sheath & Burkholder (1983) suggested merging sections Batrachospermum and Helminthoidea since they found the two features previously used to separate these sections, trichogyne shape and involucral filament length, to be quite variable. Necchi & Entwisle (1990) agreed with this conclusion, but recently Kumano (1993) chose to keep the two sections separate based on length of involucral filaments. Sect. Carpocontortum has been included in sect. Batrachospermum because the distinguishing features of contorted carpogonia and one to two large, globose, pedicellate carposporophytes are thought to be of significance only at the specific level (Necchi & Entwisle, 1990). In the present study sect. Batrachospermum sensu lato is considered to include species formerly classified in sections Batrachospermum, Helminthoidea and Carpocontortum.

Within sect. Batrachospermum, infrageneric taxa were first distinguished by Sirodot (1884) based on the following features: monoecious or dioecious thalli; whorl shape; carposporophytes contained within or protruding from the whorl; size and shape of carpogonia; and presence or absence of spermatangia on the involucral filaments of the carpogonial branch, brown cortication or monosporangia. However, some of these features, such as the degree of protusion of carposporophytes from the whorl and the presence or absence of brown cortication are likely to be influenced by environmental conditions (Israelson, 1942). Subsequently, Mori (1975) proposed use of the number of fascicles per pericentral cell, the placement of carposporophytes in the whorls and shape of the carposporophyte branch cells as characters to separate species from Japan. More recently, numerous species have been described on the basis of the presence or absence of new criteria, such as cylindrical fascicle cells, involucral fascicle development on one side of the carpogonial branch, and inflated, irregular cortication (Kumano, 1978; Kumano & Johnstone, 1983; Sheath & Cole, 1990). There has been no major comparison of type specimens to determine the general utility of these characters and few morphometric data are available on most species belonging to Batrachospermum sect. Batrachospermum. Thus, this study was undertaken to examine all available type specimens.

Nomenclature within Batrachospermum sect. Batrachospermum is problematical. In his monograph of the genus, Sirodot (1884) frequently renamed validly published taxa, thereby making some of his species names illegitimate and superfluous (Greuter et al., 1988: Art. 63.1). However, these names have persisted in the literature and some have been used to make new combinations at both the specific and varietal levels (Israelson, 1942; Starmach, 1977). The nomenclature of a few species has been clarified (Necchi, 1990; Compère, 1991), but no attempt has been made to date to study the section as a whole. Therefore, a re-examination of the taxa in Batrachospermum sect. Batrachospermum is warranted.

2.2 Materials and methods

2.2.1 Materials

Type and historically important specimens (HIS) of taxa referable to Batrachospermum sect. Batrachospermum [herbarium abbreviations according to Holmgren et al. (1990)] were analysed and where possible, multiple specimens were measured in order to account for morphological variability within taxa as follows.

1. B. alpestre Shuttlew. ex Hassall (1845: 111). In rivulo prope Reichenbach, 25 iii 1838, R. J. Shuttleworth & Dr. J. K. Schmidt, lectotype here designated, **BM**.
2. B. anatinum Sirodot (1884: 249).
   a. Ruisseau sortant de l'etang du moulin de la Chèvre, près Plelan, Forêt de Paimpont, France, 12 v 1878, historically important specimen (HIS), **PC** (This refers to the general collection).
   b. Ruisseau de Vau-de-Meu, au pâtis Saint-Lazare, Monfort, France, 10 iv 1872, lectotype here designated, **PC**.
3. B. arcuatoideum C.M.P.Reis (1973: 139). Fontes do rio Liz, Portugal, M. P. Reis, 29 iv 1964, isotype, Reis No. 359 **COI**.
4. B. arcuatum Kylin (1912: 22). Sueciæ in rivulo ad Hör in Scania 4 vi 1896, Wittrock & Norstedt, Algae exsiccatae No. 1356b pro parte, syntype, **S**.

5. B. boryanum Sirodot (1874: 136).

   a. Caniveau de la Trottinais, France, 12 v 1877, lectotype here designated, Herb. Thuret **PC**.

   b. Caniveau de la Trottinais, France, 22 iv 1877, HIS, **PC**.

6. B. carpocontortum Sheath, M.O.Morison, K.M.Cole et VanAlst. (1986: 325). Cascade River, Washington State, U.S.A., 5 vi 1984, R. G. Sheath & M. O. Morison, A 109, holotype, A67724 **UBC**.

7. B. confusum f. spermatoglobcratum C.M.P.Reis (1962: 62). Fonte de Santa Cruz, Braga, Portugal, 29 iii 1960, holotype, P. Reis & A. Nauwerck No. 137 **COI**.

8. B. corbula Sirodot (1884: 226). Ponceau de la Gautrais, St Jacques près Rennes, France, 31 v 1877, lectotype here designated, **PC**.

9. B. corbula var. alcoense C.M.P.Reis (1954: 70). Fontes do rio Alcoa, Alcobaca, Portugal, 19 iv 1954, isotype, **COI**.

10. B. crouanianum Sirodot (1884: 244). Fontaine du Pont Glas près St Pol-de-Léon, France, vii, lectotype here designated, Herb. Thuret **PC**.

11. B. decaisneanum Sirodot (1884: 214). Forêt de Montfort, France, ponceau de la region tourbeuse, 5 vii 1877, lectotype here designated, **PC**.

12. B. densum Sirodot (1884: 228).

   a. Fontaine Cul-de-loup, France, 9 iii 1873 [lectotype of B. gelatinosum var. densum (Sirodot) Compère (1991: 23)], Herb. Thuret **PC**.

   b. Fontaine Cul-de-loup, France, 5 iii 1873, HIS, **PC**.

c. Fontaine de la Taverneraie, commune de la Chapelle-Chaussée, France, 12 iv 1877, HIS, **PC**.

13. B. ectocarpoideum Skuja ex Flint (1949: 552).

a. Turnbridge, Vermont, USA, 20 vi 1946, H. T. Croasdale, lectotype here designated, L. H. Flint collection, **NFLD**.

b. Mud ditch, Childs River, Barnstable Co., Massachusetts, USA, 1942, H. T. Croasdale & W. R. Taylor, HIS, **MICH**.

c. Conestoga Survey, Lititz Run, USA, 6 viii 1948, R. Patrick & J. H. Wallace, HIS, **PH**.

14. B. ectocarpum Sirodot (1884: 222), nom. illeg. [= B. stagnale (Bory) Hassall]

a. Le Meu au dessous de Montfort près Esequil, France, 19 vii 1874, HIS, **PC**.

b. Env. de meu sous le pont de l'Abbaye, France, 29 vi 1869, HIS, **PC**.

c. St Germain Rivière d'Ille, entre le moulin de Fresnais et Ledrem. de fer., France, 12 vii 1877, HIS, **PC**.

d. Ruisseau d'Ille au dessous de moulin de Monery entre Bourgbarré et St Erlon, France, 22 iv 1880, HIS, **PC**.

15. B. filamentosum A.Braun ex Rabenh. (1863: 280). Rabenhorst, Die Algen Sachsens resp. Mitteleuropas No. 360, syntype, **BM**.

16. B. fluitans A.Kerner (1882: 362). Flora Exsiccata Austro-Hungarica No. 397, In fontibus et rivulis rapid fluentifbus in torrentibus et cataractis ad saxa irrigata prope Mühlau in ditione Oenipontana, 800-1000mt, syntype, **BM**.

17. B. fruticulosum K.M.Drew (1946: 340). Chee Dale, Derbyshire, England, 20 vi 1942, isotype, Drew No. 1610b **BM**.

18. B. gelatinosum (L.) deCandolle (1801: 21).

    a. Specimen on which tab. 7 fig. 42 from Dillenius's Historia Muscorum is based, lectotype, [designated by Compère (1991: 22)], **OXF**.

    b. Specimen on which tab. 7 fig. 42 from Dillenius's Historia Muscorum is based, HIS, **BM**.

19. B. godronianum Sirodot (1884: 235). Fontaine de Fayelle, France, viii 1881, holotype, Sirodot collection No. 12 **PC**.

20. B. helminthosum Sirodot (1884: 240), nom. illeg., non Bory 1808.

    a. Ruisseau de Corbière près Chateaubourg, France, 7 v 1882, HIS, **PC**.

    b. Ruiselet affluents du Semnon à Martigné-Ferchaud; Ruisseau de Gallet, France, 22 iv 1869, HIS, **PC**.

21. B. heterocorticum Sheath et K.M.Cole (1990: 556). Mormon Branch at Route 19, Florida, USA 5 v 1989, R. G. Sheath, FL 21, holotype, A70042 **UBC**.

22. B. hybridum Bory (1823: 228). Sur la vase au fond des canaux d'eau pure mais stagnante du parc de St Gratien, France, viii 1815, holotype, Herb. Thuret **PC**.

23. B. japonicum M.Mori (1975: 470). Oomachi Shrine near Ashikaga in Tochigi-Prefecture, Japan, iii 1970, M. Mori, holotype, AL-35555 **TNS**.

24. B. kuehnianum Rabenhorst (1854: 42). In cochleis aquatilibus Germaniae, prop Brunzlau, J. Kühn, No. 379, syntype, **BM**.

25. B. ludibundum var. caerulescens Bory (1808: 324), "Batrachosperma ludibunda caerulescens." Environs de Dax, France, Thore, an V [=1797], holotype, Herb. Thuret **PC**.

26. B. ludibundum var. confusum Bory (1808: 320), "Batrachosperma ludibunda confusa." Environs de Fougerès au Bretagne, France, an VI [= 1798], holotype, Herb. Thuret **PC**.

27. B. ludibundum var. pulcherrimum Bory (1808: 323), "Batrachosperma ludibunda pulcherrima." St Aubin du Cormier entre Rennes et Fougerès, France, an VII [=1799], holotype, Herb. Thuret **PC**.

28. B. ludibundum var. stagnale Bory (1808: 325), "Batrachosperma ludibunda stagnalis." Marais des environs de Bordeaux, Talence, France, an V [= 1797], holotype, Herb. Thuret **PC**.

29. B. moniliforme var. chlorosum Sirodot (1884: 211). Fossé du canal l'Ille et Rance, près de Bélangerais, environs de Rennes, France, 15 iv 1883, lectotype here designated, Herb. Thuret PC.

30. B. moniliforme var. helminthoideum Sirodot (1884: 212). Ruisseau de Corbières, France, v 1882, lectotype here designated, Sirodot collection No. 5 PC.

31. B. moniliforme f. lipsiensis Rabenh. (1868: 405). An Stengeln von Equisetum limosum in einem Sumpfe ad der bei plegwiss Späthebft 185 D. Bulheim. Die Algen Sachens resp. Mittel-Europa No. 418, syntype, **NY**.

32. B. moniliforme var. obtrullatum Kumano et M.Watanabe (1983: 89). Small stream, 3300 m, toward Mt. Albert Edward, central district, Papua New Guinea, 28 ix 1975, holotype, Watanabe 51305a Kobe University, Japan.

33. B. moniliforme var. pisanum Arcang. (1882: 156).

    a.-c. A caldaccoli presso S. Giuliano nel Pisano, Gennajo, Italy, 1882, G. Arcangeli & A. Mori, Erb. Critt. Ital. Ser. II No. 1260, syntype, **NY**.

34. B. moniliforme var. rubescens Sirodot (1884: 212). Fontaine du Pont-Garnier, Morbihan, France, 2 vii 1869, holotype, Herb. Thuret **PC**.

35. B. moniliforme var. scopula Sirodot (1884: 213). Lande du Moulin-Baron, Guipry, France, 29 v 1882, lectotype here designated, Herb. Thuret **PC**.

36. B. moniliforme var. typicum Sirodot (1884: 211), nom. inval. Fontaine de St Pabu à Erquy, Côtes-du-Nord, France, HIS, Herb. Thuret **PC**.

37. B. polycarpum M.Mori (1975: 474). Inoue near Suzaka in Nagan-Pref., Japan, M. Mori, iv 1970, holotype, AL-35594 **TNS**.

38. B. pulchrum Sirodot (1884: 225). Rivière des Écrevisses et l'un de ses petits affluents, à Matouba, Guadeloupe, 15 viii 1868, Maże & Schramm, holotype, Herb. Thuret **PC**.

39. B. pygmaeum Sirodot (1884: 230). Fontaine de la Rifaudais, France, 16 vi 1877, holotype, Herb. Thuret **PC**.

40. B. pyramidale Sirodot (1884: 232) nom. illeg. [= B. caerulescens (Bory) Kützing (1849: 546)].

a. Fontaine de Bourriande, France. 14 ix 1882, [lectotype of B. gelatinosum var. pyramidale (Sirodot) Compère (1991: 23)], Herb. Thuret **PC**.

b. Fontaine de Pauvrette, Beaufort. France 30 iv; Fontaine du Tertre-Huchot, chemin chariter. 30 iv, HIS. **PC**.

c. Fontaine de Hobé, France. 8 vii 1878. HIS. **PC**.

d. Fontaine de Bourrainde, France, 24 vii 1882, HIS, **PC**.

41. B. radians Sirodot (1884: 218). Fontaine de Gaillardon, Monfort, France, 24 iv 1882. lectotype here designated. **PC**.

42. B. reginense Sirodot (1884: 219). Fontaine de St Reine, route de Guichen, France. 20 xi 1880, lectotype here designated. Herb. Thuret **PC**.

43. B. setigerum Rabenh. ex Sirodot (1884: 293). Exsiccata Algen Mitteleuropa No. 854, syntype. **BM**.

44. B. skujae Geitler 1944: 127. No location cited. holotype.

a. No. 93-42/3 **WU**; b. No. 93-42/5 **WU**; c. No. 93-42/6 **WU**.

45. B. sporiferum M.Mori (1975: 472). Tanayama-highland in Aichi-Prefecture, Japan, vi 1961. T. Suzuki. holotype. AL-35575 **TNS**.

46. B. sporulans Sirodot (1884: 216) nom. illeg. [= B. pulcherrimum (Bory) Hassall] Fontaine et doué de Bas-Champs. Betton, France, 2 iv 1882, HIS, **PC**.

Batrachospermum heteromorphum Z.X.Shi. Hu et Kumano (1993), B. nova-guineense Kumano et I.M.Johnstone (1983) and B. szechwanense C.C.Jao (1941) were requested from **HBI**, Kobe University, Japan and **UPNG**, but were unavailable for examination. The type specimens of the following taxa could not be located in any of the pertinent herbaria: B. distensum Kylin (1912) (**LD**, **UPS**, **S**), B. lochmodes Skuja (1938) (**RIG**, **UPS**, **C**, **Z**, **W**) and B. moniliforme var. isoeticola Skuja (1928) (**RIG**, **UPS**, **Z**, **C**, **W**). Measurements from the protologues of these taxa are compared with those obtained for other taxa in this study.

2.2.2 Methods

A portion of the specimen was moistened with distilled water and removed for examination. The morphological characteristics, whorl diameter, carposporophyte diameter, number and cell number, carpogonium diameter, length and form factor, carpogonial branch cell number and carpospoangium diameter and length, were measured (Tables 2.1, 2.2), in replicates of 30 where possible (15 for carpogonia), using an SMI image analysis system. Two additional characteristics, number of carposporophytes per whorl and distance of carposporophyte from the whorl axis, were analysed because these features are considered to be taxonomically important in the section (Mori, 1975; Sheath et al., 1986c). The following qualitative features were noted because they have been used to distinguish species of sect. Batrachospermum: thalli monoecious or dioecious, and presence or absence of the following: irregular cortication, monosporangia, copious secondary fascicles, curled fascicles, contorted carpogonia, spermatangia on the involucral filaments, involucral filaments on one side of the carpogonial branch, brown cortication, exserted carposporophytes and hourglass-shaped cells in the carposporophyte branch (Sirodot, 1884; Mori, 1975; Kumano & Johnstone, 1983; Sheath et al., 1986; Sheath & Cole, 1990).

The Gower similarity coefficient was calculated to incorporate both quantitative and qualitative features in Table 2.1, and the coefficients were subjected to cluster analysis with the unweighted group method (UPGMA) according to the Syntax software package (Podani, 1990) (Fig. 2.1). To compare means of morphometric characteristics measured among all specimens, analysis of variance (ANOVA) and Duncan's multiple-range test were calculated using the SAS statistical package (Anonymous, 1988). Not all specimens examined could be included in the cluster analysis because they were missing one or more morphometric features. These specimens were compared to the cluster analysis groups using ANOVA and Duncan's multiple-range test of means in characteristics present. All following statistical differences are significant at the $p < 0.05$ level.

2.3 Results and discussion

2.3.1 Morphometric Analysis

One of the type specimens examined was found to be misclassified in Batrachospermum sect. Batrachospermum. The syntype of B. filamentosum had few-celled fascicles appressed to the main axis as in sect. Setacea DeToni and closely resembled B. atrum (Hudson) Harvey as analysed by Sheath et al. (1993). Three other type specimens were vegetative only, B. kuehnianum, B. moniliforme var. obtrullatum and B. sporiferum. The specimen of B. kuehnianum was a small immature plant which can be identified only to genus. Even though both B. moniliforme var. obtrullatum and B. sporiferum were vegetative, measurements given in protologues were compared to the analysed specimens.

Numerous qualitative features noted were not incorporated into the analysis because they were found not to be useful in differentiating infrageneric taxa in sect. Batrachospermum, including the following: (1) Shape of the carposporophyte-bearing branch cells was quite variable among carposporophytes of the same plant and even on the same branch (Fig. 2.2). (2) Brown cortication on the main axis varied in intensity from specimen to specimen and may be environmentally influenced (unpubl. data). (3) Exserted carposporophytes were rare and scattered on plants, which may be affected by environmental conditions (Israelson, 1942). (4) No specimens examined had involucral filaments confined to one side of the carpogonial branch as reported for B. nova-guineense by Kumano & Johnstone (1983). The other qualitative features noted, monoecious vs. dioecious, irregular cortication, presence or absence of monosporangia, copious secondary fascicles, curled fascicles, contorted carpogonia, spermatangia on the involucral filaments were employed in the analysis along with the quantitative characteristics (Table 2.1). All the specimens examined had undifferentiated carpogonial branches, a characteristic of sect. Batrachospermum. Additionally, the carposporophytes were all similar, having gonimoblast filaments 2-4 cells long (Table 2.2). Irregular or bulbous cells of the main axis cortical filaments were found in a number of specimens (Fig. 2.3) even though this characteristic has only been reported once (Sheath & Cole 1990). Monosporangia have been reported rarely in sect. Batrachospermum and were only found infrequently in this study (Fig. 2.4). Along with irregular cortication and monosporangia, the present study indicates that qualitative characteristics, such as monoecious vs. dioecious thalli and spermatangia on the involucral filaments, are important diagnostic features.

From the cluster analysis of Batrachospermum sect. Batrachospermum type and historically important specimens, 9 groups of taxa were evident (Fig. 2.1). Group 1 consisted of 1 specimen, B. carpocontortum. This species is characterised by being dioecious and having relatively large, confluent, globose whorls with one to two relatively large carposporophytes in the outer part of the whorl (Fig. 2.5) and contorted trichogynes (Fig. 2.6, Tables 2.1, 2.2). The carposporophyte diameter was significantly larger than in all other groups, but the range overlapped with those of all groups (Table 2.1). Three other groups included only dioecious species and both Groups 4 and 9 were limited to 1-3 carposporophytes per whorl. Therefore, the distinguishing characteristic of B. carpocontortum is the contorted trichogyne and we recognise this species as being distinct.

Group 2 consisting of 3 specimens of Batrachospermum skujae, was characterised by monoecious plants and relatively large, confluent, barrel-shaped whorls with numerous carposporophytes scattered throughout the whorl (Fig. 2.7), lanceolate trichogynes (Fig. 2.8) and monosporangia at the fascicle tips (Fig. 2.4). Group 2 had significantly larger carpogonial and carposporangial dimensions than the other groups (Table 2.1). However, the ranges of these characteristics overlapped with all other groups except Group 8 for carpogonium diameter and Groups 5 and 8 for carpogonium length (Table 2.1). Three other groups were monoecious and, therefore, the distinguishing feature of this group is the presence of monosporangia. One other specimen measured, B. sporulans, had monosporangia and was characterised by globose whorls with one small carposporophyte per whorl (Fig. 2.9) and concave lanceolate trichogynes (Fig. 2.10). In terms of the morphometric features, B. sporulans was significantly smaller than Group 2 in whorl diameter ($\bar{x}$ =554 vs. 747 µm), carposporophyte diameter ($\bar{x}$ = 56 vs. 105 µm) and carposporangial dimensions ($\bar{x}$ = 10 x 9 vs. 14 x 11 µm) and the ranges in whorl diameter and carposporophyte diameter did not overlap (Tables 2.1, 2.2). However, only two carposporophytes were found in the B. sporulans specimen and these structures may have been immature. In addition, neither whorl diameter or carposporphyte diameter have been used in the past to distinguish these species (Geitler, 1944). Therefore, we recognise B. sporulans and B. skujae to be synonymous. B. sporulans is illegitimate and B. skujae is the correct name.

Group 3 contained 26 specimens of 20 infrageneric taxa, Batrachospermum arcuatoideum, B. corbula, B. corbula var. alcoense, B. decaisneanum, B. densum, B. godronianum, B. hybridum, B. japonicum, B. ludibundum var. caerulescens, B.

ludibundum var. stagnale, B. moniliforme var. chlorosum, B. moniliforme var. helminthoideum, B. moniliforme f. lipsiensis, B. moniliforme var. pisanum, B. moniliforme var. rubescens, B. moniliforme var. scopula, B. moniliforme var. typicum, B. polycarpum, B. pyramidale, B. radians (Fig. 2.1). Members of this group are monoecious with globose or barrel-shaped whorls which are confluent (Figs 2.11,2.15,2.16, 2.18, 2.26, 2.31, 2.35, 2.37, 2.38, 2.42, 2.43, 2.45) or at various distances from each other (Figs 2.13, 2.22, 2.24, 2.28, 2.30, 2.33, 2.40, 2.41). Carposporophytes can be exserted from the whorl (Fig. 2.11) or, more commonly, contained within the whorl at various distances from the axis (Figs 2.13, 2.15, 2.16, 2.18, 2.22, 2.24, 2.26, 2.28, 2.29, 2.30, 2.31, 2.33, 2.35, 2.37, 2.38, 2.40, 2.41, 2.42, 2.43, 2.45). Trichogynes vary in shape from short-clavate (Figs 2.12, 2.14, 2.17, 2.19, 2.34), short-lanceolate (Figs 2.36, 2.44) to elongate-lanceolate (Figs 2.20, 2.21, 2.23, 2.25, 2.27, 2.32, 2.39). In terms of morphometry, measurements for this group did not significantly differ from at least three other groups in any feature (Table 2.1). Within the group, there was a continuum among specimens for each of the characteristics (Table 2.2). Specimen b of B. moniliforme var. pisanum had a significantly larger whorl diameter than the group ($\overline{x}$ = 827 vs. 299-786 µm) but the range in this feature overlapped with 12 other specimens (Table 2.2). The carpogonial dimensions for B. japonicum were significantly larger than those of the group ($\overline{x}$ = 15 vs. 6-13 µm in diameter, $\overline{x}$ = 62 vs. 22-55 µm in length), yet the ranges in these measurements overlapped with 8 specimens in diameter and 6 specimens in length (Table 2.2). Even though the carposporangium diameter for B. polycarpum was significantly smaller, the range overlapped with all other specimens (Table 2.2). Six other specimens of Batrachospermum, B. densum, B. gelatinosum, B. ludibundum var. pulcherrimum, B. pygmaeum and B. reginense, could not be included in the multivariate analysis because these specimens lacked some featues used in the cluster analysis, but were similar to those in Group 3, being monoecious and having globose whorls with one to many carposporophytes (Figs 2.47, 2.49, 2.51, 2.53, 2.55) and carpogonia with clavate to lanceolate trichogynes (Figs 2.48, 2.50, 2.52, 2.54, 2.56). In the ANOVA, none of the measurements for these specimens significantly differed from those of the group (Tables 2.1, 2.2). Therefore, we conclude that based on the characteristics analysed here these infrageneric taxa are synonymous and the oldest available specific epithet is B. gelatinosum.

Many of our proposed synonomies are in accord with other taxonomic studies, but typically the infrageneric taxa of Group 3 have been classified in smaller groupings (eg. Sirodot, 1884; Israelson, 1942; Mori, 1975). Sirodot (1884) cited numerous entities described by Bory (1808) as synonymies of his species and later authors have followed his classification of these entities (Reis, 1973; Compère, 1991). Upon detailed examination of the types, we found that many of these combinations are misapplied. Batrachospermum ludibundum var. pulcherrimum was synonymised with B. sporulans (Sirodot, 1884) and they are similar in gross morphology (Fig. 2.51 vs. 2.9, respectively). However, no monosporangia were observed in B. ludibundum var.

pulcherrimum in contrast to B. sporulans. Likewise, B. ludibundum stagnale was synonymised with B. ectocarpum (Group 6), but we did not find B. ludibundum var. stagnale to have irregular cortication (Table 2.2). Mori (1975) developed a new set of criteria to distinguish the infrageneric taxa of the B. gelatinosum group, but most characters, for example the shape of the carposporophyte-bearing branch cells, are not taxonomically useful. Sheath & Burkholder (1983) found that the number of fascicles per pericentral cell could vary from 3-7 on the same specimen and, therefore, this character is not useful in distinguishing among taxa. The validity of carposporophyte position as a taxonomic criterion was investigated in this study. The ratio of carposporophyte distance from the whorl axis to whorl diameter ranged from approximately 0.40 to 0.80 in most specimens (Table 2.2). Thus, most specimens had carposporophytes in both the inner and outer half of the whorl and this criterion is too variable to be diagnostic. Protologues of only four of the infrageneric taxa synonymised included measurements or reported on recent criteria for separation (Reis, 1954; Reis, 1973; Mori, 1975). B. arcuatoideum was originally separated from B. arcuatum because its thalli were monoecious whereas dioecious plants occurred in the latter species, and no other features are given which might distinguish this species from B. gelatinosum (Reis, 1973). B. corbula var. alcoense was separated from the nominate variety based on number of hairs and whorl and carpogonium shape (Reis, 1954). However, our study shows both the whorl and carpogonial measurements of this variety and B. corbula to be very similar (Figs. 2.13 vs. 2.15) (Table 2.2). Mori

(1975) distinguished B. japonicum from other members of the B. gelatinosum group on the basis of barrel-shaped cells of the carposporophyte-bearing branch, the formation of secondary fascicles, and the presence of carpogonia on the lower involucral fasicles of the carpogonial branches. We found that the shape of the carposporophyte-bearing branch cells is variable e.g.cylindrical to hourglass-shaped (Fig. 2.2) and that whorls may be distant with few secondary fascicles or confluent having secondary fascicles within the same specimen (Figs 2.41, 2.42). Also, more than one carpogonial branch off the same primary fascicle was observed in other specimens of this group. Likewise, B. polycarpum was distinguished based on numerous carpogonial branches off the same primary fascicle, placement of carposporophytes within the whorl and curved distal ends of the fascicles (Mori, 1975).

Group 4 contained 1 specimen, Batrachospermum arcuatum (Fig. 2.1). This species is dioecious and has barrel-shaped whorls containing 1-3 carposporophytes (Fig. 2.57) and clavate trichogynes (Fig. 2.58). The specimen had a significantly larger carposporophyte-to-whorl diameter ratio than all other groups (Table 2.1). However, there was much overlap in this feature among all groups (Table 2.1). B. arcuatum is similar to B. gelatinosum in all morphometric characteristics, but differs by being dioecious whereas the latter species is monoecious, and we recognise it as a distinct species. Previously, this species has been synonymised with B. ectocarpum based on morphological similarities of thick mucilage, spermatangia and carposporophytes in the whorl periphery and lack of terminal hairs (Israelson, 1942).

We maintain B. arcuatum separate from B. ectocarpum (Group 6) because of the regular cortication and dioecious plants in the former and the irregular cortication and monoecious plants in the latter species (Tables 2.1, 2.2).

Group 5 was composed of 6 specimens of 4 infrageneric taxa, Batrachospermum crouanianum, B. helminthosum, B. ludibundum var. confusum, B. confusum f. spermatogloberatum (Fig. 2.1). The members of this group are characterised by having irregular, inflated cortication on the main axis (Fig. 2.3), barrel-shaped confluent whorls containing numerous scattered carposporophytes (Figs 2.59, 2.61, 2.63, 2.65) and short-clavate trichogynes (Figs 2.60, 2.62, 2.64, 2.66). In addition, the carpogonial branch of all specimens has involucral filaments with apical spermatangia (Figs 2.60, 2.62, 2.64, 2.66). The mean carpogonium length for this group was significantly smaller, but the range in this feature overlapped with Groups 6-9 (Table 2.1). This group also had significantly smaller carposporangium dimensions than the other groups, but the ranges of these measurements overlapped with all the other groups. In terms of qualitative features, spermatangia on the involucral filaments were observed in Group 8 also and irregular cortication was noted in Groups 6, 7, and 9 (Table 2.1); it is the combination of these two characteristics which makes this group unique. Three other specimens examined but not used in the multivariate analysis, B. alpestre, B. fruticulosum and B. setigerum (Figs 2.67, 2.68, 2.69) possessed these two features. The morphometric features measured for B. fruticulosum did not significantly differ from the other specimens and those in the protologue are also similar (Tables 2.1, 2.2). B. alpestre and B. setigerum had similar carposporangial dimensions and although these were significantly larger than those of the other specimens (Tables 2.1, 2.2), their ranges in these features overlapped among all specimens, and we consider these species to be synonymous. Both B. confusum (Bory) Hassall (= B. ludibundum var. confusum) and B. alpestre were validly published in the same paper (Hassall, 1845) and we have here selected B. confusum to represent the group because it best displays the general characteristics of the species. This synonymy is the first union of B. confusum and B. alpestre. The synonymy of B. helminthosum and B. crouanianum with B. confusum is in accord with other recent taxonomic studies (Compère, 1991; Kumano, 1993). B. fruticulosum was originally distinguished from B. helminthosum and B. crouanianum because its carpogonial branches arose from lower carpogonial branch involucral filaments unlike in B. helminthosum, and because it had spermatangia on the involucral filaments in contrast to B. crouanianum (Drew, 1946). However, both of these characteristics were observed in all three species in this study. Reis (1962) described B. confusum var. spermatogloberatum for plants having short branches with dense spermatangial development, but we found this characteristic to be universal among specimens of this group.

Group 6 contained 5 specimens of 3 species, Batrachospermum anatinum, B. boryanum and B. ectocarpum (Fig. 2.1). This group is characterised by being monoecious and having cortical filaments with irregular, inflated cells (Fig. 2.3), whorls that are relatively large, globose and contain scattered, spherical carposporophytes (Figs 2.70, 2.71, 2.73), and relatively small carpogonia with clavate or lanceolate trichogynes (Figs 2.72, 2.74, 2.75). Although there were significant differences in some measurements among specimens in the group and additional specimens of B. anatinum and B. ectocarpum, the ranges for all characteristics overlapped (Table 2.2). The specimen of B. boryanum was monoecious despite Sirodot's (1884) claim that this species was dioecious; this specimen was probably missclassified and this epithet should not be used for this group. The oldest validly published epithet is B. anatinum, and these specimens are referred to this species. The type specimen of B. fluitans had similar qualitative characteristics to this group, ie. monoecious thalli and irregular cortication (Tables 2.1, 2.2). B. fluitans is characterised by confluent barrel-shaped whorls with scattered, spherical carposporophytes (Fig. 2.76) and lanceolate trichogynes (Fig. 2.77). In terms of the morphometric features measured, B. fluitans had significantly larger carpogonial dimensions than the group and the ranges did not overlap (11-15 vs. 6-10 μm in diameter, 51-65 vs. 17-41 μm in length). Therefore, we recognize B. fluitans as being a distinct entity and distinguishable from B. anatinum by its large carpogonia.

Group 7 contained 4 specimens, 1 of Batrachospermum boryanum and 3 of B. ectocarpoideum (Fig. 2.1). Specimens of this group were characterised by being dioecious and having irregular inflated cortication on the main axis (Fig. 2.3), globose whorls containing numerous carposporophytes (Figs 2.78, 2.80) and relatively small carpogonia with clavate or lanceolate trichogynes (Figs 2.79, 2.81). This group did not significantly differ from the other groups in any of the morphometric features measured. Within the group, the B. boryanum specimen was a larger plant and had significantly greater whorl diameter than the other specimens ($\overline{x}$ = 910 vs. 450-627 µm), but the ranges overlapped (Table 2.2). This specimen was also significantly different from the specimens of B. ectocarpoideum in the following characteristics: number of carposporophytes per whorl, carposporophyte height-to-whorl diameter ratio and carpogonial dimensions (Table 2.2). However, the ranges of B. boryanum for all these characteristics overlapped with at least one other specimen except for number of carposporophytes per whorl (12-30 vs. 1-4) (Table 2.2). This apparent difference may be due to the greater size or reproductive maturity of the B. boryanum specimen. We consider these species to be synonymous and the oldest epithet being B. boryanum. The description of B. ectocarpoideum in the protologue agrees well with the species concept of B. boryanum except that the plants were monoecious (Flint, 1949). We did not observe any spermatangia in any of the specimens.

Group 8 included 1 specimen, Batrachospermum pulchrum (Fig. 2.1) and was characterised by being dioecious and having relatively small, globose whorls composed of well-curled fascicle cells (Fig. 2.82), 1-2 carposporophytes at various distances from the whorl axis (Fig. 2.82, Table 2.1), lanceolate trichogynes (Fig. 2.83), and apical spermatangia on the involucral filaments (Fig. 2.83). This species has significantly smaller diameters than the other groups for whorls and carpogonia, but the ranges of these features overlap with at least 5 other groups (Table 2.1). In terms of qualitative features, both B. pulchrum and B. confusum have spermatangia on the involucral filaments, but B. pulchrum is unique in having well-curled fasicles (Fig. 2.82 vs. Figs 2.59, 2.61, 2.63, 2.65, respectively) while B. confusum has irregular cortication. B. confusum may have as many as 19 carposporophytes per whorl, whereas B. pulchrum was observed to have only 1-2. We recognise B. pulchrum as a distinct species.

Group 9 contained 1 specimen, Batrachospermum heterocorticum (Fig. 2.1). This species is dioecious (Figs 2.84-2.86) with inflated irregular cortication (Fig. 2.3), and it has a main axis made up of distant globose indistinct whorls with abundant secondary fasicles (Figs 2.84, 2.86), 2-8 carposporophytes per whorl (Fig. 2.86) and lanceolate trichogynes (Fig. 2.87). In terms of morphometric characteristics, this species did not significantly differ from the other groups (Table 2.1). The combination of dioecious thalli, irregular cortication and abundant secondary fascicles was unique to this species and we consider B. heterocorticum to be a distinct species. In the protologue of this species, Sheath & Cole (1990) did not observe spermatangia but proposed that the plants are dioecious. In a later collection (June 1993) at the same site, this fact was confirmed. The gross morphology of the male plants closely resembles that of the females (Figs 2.84, 2.86) and the spermatangia are produced apically and subapically on fascicles (Fig. 2.85).

Five species were not examined in the morphometric study but had adequate descriptions to compare with those examined in this study. Batrachospermum lochmodes is similar to B. skujae in having monosporangia but differs by being dioecious (Skuja, 1938) and thus we continue to regard it as a distinct. B. sporiferum is very similar to B. skujae in having monosporangia and the range in morphometric features given in the protologue (whorl diameter, 144-880 vs.586-1003 μm; carposporophyte diameter, 70-137 vs. 77-152 μm; carpogonium length 37-65 vs. 33-59 μm). B. sporiferum was separated from B. sporulans based on appearance of carpogonial branch, structure of the carposporophyte branch, length of involucral filaments and position of carposporophytes (Mori, 1975). Unfortunately, there is not enough information (monoecious or dioecious thalli) given in the protologue to synonymise B. sporiferum with either B. skujae or B. lochmodes. The variety B. moniliforme var. obtrullatum was established because of an obtrullate or inflated trichogyne (Kumano & Watanabe, 1983). However, the carpogonial dimensions are within those given for B. gelatinosum in this study (13-18 x 30-37 μm vs. 5-17 x 20-68 μm), and therefore B. moniliforme var. obtrullatum should not to be separated from B. gelatinosum. The description and illustrations of B. distensum are similar to B. confusum and this species was separated from B. helminthosum on the basis of involucral filaments with carpogonia, spermatangia in clusters on shorter filaments and secondary filaments lacking in B. distensum (Kylin, 1912). However, these features have been observed in B. confusum and hence we consider B. distensum to be synonymous with B. confusum. This synonymy is in disagreement with Israelson (1942) who reduced B. distensum to a variety of B. boryanum based on fascicle cell shape. Skuja (1928) established B. moniliforme var. isoeticola for plants epiphytic Isoetes. From the description and illustrations in the protologue, this variety does not seem to have any characteristics to distinguish it from B. gelatinosum and hence, we propose to include B. moniliforme var. isoeticola in synonymy with B. gelatinosum. B. cylindrocellulare is characterised by cylindrical fascicle cells, spermatangia on short branches and stalked trichogynes (Kumano, 1978), and the combination of these features separates this species from others in sect. Batrachospermum. B. nova-guineense resembles B. pulchrum in gross morphology, but differs from this species in two attributes, unilateral involucral filament development in the former and spermatangia on the involucral filaments in the latter (Kumano & Johnstone, 1983; this study), and can be considered as a distinct species. B. szechwanense is characterised by being dioecious and having curved trichogynes (Jao, 1941) and appears to be distinguished from the other species in this section. Recently, B. heteromorphum has been described by Shi et al. (1993) to have two types of whorls, globose whorls resembling those of Batrachospermum gelatinosum and obconic whorls like B. cayennense of sect. Aristatae. The variation in trichogyne morphology is similar to that shown in B. gelatinosum (Figs 2.19-2.21), but since none of the specimens examined possessed obconic whorls we consider this species to be distinct.

2.3.2 Species and revised descriptions in Batrachospermum sect. Batrachospermum

SPECIES

(1) **B. gelatinosum** (L.) deCandolle (1801: 21).

Basionym: Conferva gelatinosa L. (1753: 1166).

Synonyms:
B. arcuatoideum C.M.P.Reis (1973: 139);
B. corbula Sirodot (1884: 226);
B. corbula var. alcoense C.M.P.Reis (1953: 70);
B. decaisneanum Sirodot (1884: 214);
B. densum Sirodot (1884: 228);
B. godronianum Sirodot (1884: 235);
B. hybridum Bory (1823: 222);
B. japonicum M.Mori (1975: 470);
B. ludibundum var. caerulescens Bory (1808: 324);
B. ludibundum var. pulcherrimum Bory (1808: 323);
B. ludibundum var. stagnale Bory (1808: 325);
B. moniliforme var. chlorosum Sirodot (1884: 211);
B. moniliforme var. helminthoideum Sirodot (1884: 212);
B. moniliforme var. isoeticola Skuja (1928: 205);
B. moniliforme f. lipsiensis Rabenh. (1868: 405);
B. moniliforme var. obtrullatum Kumano et M.Watanabe (1983: 91);
B. moniliforme var. pisanum Arcang. (1882: 156);
B. moniliforme var. rubescens Sirodot (1884: 212);
B. moniliforme var. scopula Sirodot (1884: 213);
B. moniliforme var. typicum Sirodot (1884: 211) nom. inval.;
B. polycarpum M.Mori (1975: 474);
B. pygmaeum Sirodot (1884: 230);
B. pyramidale Sirodot (1884: 232) nom. illeg.;
B. radians Sirodot (1884: 218);
B. reginense Sirodot (1884: 219).

Revised description: Monoecious; whorls distant to confluent, sometimes appressed, globose or barrel-shaped, 257-972 µm in diameter with 1-11 carposporophytes exserted or within the whorl at various distances from the axis; main axis with cortication consisting of cylindrical cells only; carposporophytes spherical, pedicellate, 40-139 µm in diameter, gonimoblast filaments of 2-4 cylindrical cells; carpogonia 20-68 µm long with clavate or lanceolate trichogynes 5-17 µm in diameter; carpogonial branch undifferentiated, 3-10 cells long; carposporangia obovoid, 8-16 µm long and 6-12 µm in diameter.

(2) **B. carpocontortum** Sheath, M.O.Morison, K.M.Cole et VanAlsty. (1986: 325).

(3) **B. skujae** Geitler (1944: 127).

Synonym: B. sporulans Sirodot (1884: 216), nom. illeg.

Revised description: Monoecious; whorls confluent or distant, barrel-shaped, 554-1003 µm in diameter with 1-6 carposporophytes scattered within the whorl; main axis with cortication consisting of cylindrical cells only; carposporophytes spherical, pedicellate, 50-152 µm in diameter, gonimoblast filaments of 2-4 cylindrical cells; carpogonia 33-59 µm long with lanceolate or indented lanceolate trichogynes 7-13 µm in diameter; carpogonial branch undifferentiated, 5-10 cells long; carposporangia obovoid, 9-19 µm long and 8-14 µm in diameter; monosporangia 7-10 µm long and 7-10 µm in diameter.

(4) **B. arcuatum** Kylin (1912: 22).

Revised description: Dioecious; whorls confluent, barrel-shaped, 428-727 µm in diameter with 1-3 peripheral carposporophytes; main axis with cortication consisting of cylindrical cells only; carposporophytes spherical, pedicellate, 92-129 µm in diameter, gonimoblast filaments of 2-4 cylindrical cells; carpogonia 28-39 µm long with clavate trichogynes 6-12 μm in diameter; carpogonial branch undifferentiated, 5-9 cells long; carposporangia obovoid, 10-15 long and 7-12 μm in diameter.

(5) **B. confusum** (Bory) Hassall (1845: 105).

Basionym: B. ludibundum var. confusum Bory (1808: 320).

Synonyms: B. alpestre Shuttlew. ex Hassall (1845: 111);
B. confusum f. spermatoglobcratum C.M.P.Reis (1962: 62);
B. crouanianum Sirodot (1884: 244);
B. distensum Kylin (1912: 25);
B. fruticulosum K.M.Drew (1946: 340);
B. helminthosum Sirodot (1884: 240) nom. illeg. non Bory (1808);
B. setigerum Rabenh. ex Sirodot (1884: 293).

Revised description: Monoecious; main axis with inflated irregular cortication; confluent, whorls globose or barrel-shaped, 412-955 μm in diameter with 1-19 carposporophytes scattered within the whorl; carposporophytes spherical, pedicellate, 56-112 μm in diameter, gonimoblast filaments of 2-4 cylindrical cells; carpogonia 14-34 μm long with clavate trichogynes 5-11 μm in diameter; carpogonial branch undifferentiated, 4-9 cells long, with involucral filaments having apical spermatangia; carposporangia obovoid, 8-14 μm long and 6-11 μm in diameter.

(6) **B. anatinum** Sirodot (1884: 249).

Synonym: B. ectocarpum Sirodot (1884: 222) nom. illeg.

Revised description: Monoecious; main axis with inflated irregular cortication; whorls confluent or distant, globose, 479-994 μm in diameter with 1-11 carposporophytes scattered within and exserted from the whorl; carposporophytes spherical, pedicellate, 69-140 µm in diameter, gonimoblast filaments of 2-4 cylindrical cells; carpogonia 17-41 µm long with inflated clavate or lanceolate trichogynes 6-10 µm in diameter; carpogonial branch undifferentiated, 3-8 cells long; carposporangia obovoid, 8-16 µm long and 7-14 µm in diameter.

(7) B. **fluitans** A.Kerner (1882: 362).

Revised description: Monoecious; main axis with inflated irregular cortication; whorls confluent, globose, 488-664 µm in diameter with 1-5 carposporophytes; carposporophytes spherical, pedicellate, 64-93 µm in diameter; carpogonia 52-65 µm long with lanceolate trichogynes 11-15 µm in diameter; carpogonial branch undifferentiated, 4-6 cells long.

(8) B. **boryanum** Sirodot (1874: 136).

Synonym: B. ectocarpoideum Skuja ex Flint (1949: 552).

Revised description: Dioecious; main axis with inflated, irregular cortication; whorls confluent, globose, 337-1034 µm in diameter with 1-30 carposporophytes scattered within the whorl; carposporophytes spherical, pedicellate, 68-139 µm in diameter, gonimoblast filaments of 2-3 cylindrical cells; carpogonia 16-35 µm long with inflated clavate trichogynes 6-10 µm in diameter; carpogonial branch undifferentiated, 4-8 cells long; carposporangia obovoid, 8-17 µm long and 7-14 µm in diameter.

(9) B. **pulchrum** Sirodot (1884: 225).

Revised description: Monoecious; whorls distant, globose, 307-483 μm in diameter composed of few curly fascicles; main axis with cortication consisting of cylindrical cells only; carposporophytes 1-2 per whorl, spherical, pedicellate, 59-108 μm in diameter, gonimoblast filaments of 2-3 cylindrical cells; carpogonia 23-32 μm long with lanceolate trichogynes 6-10 μm in diameter; carpogonial branch undifferentiated, 4-8 cells long, with involucral filaments having apical spermatangia; carposporangia obovoid, 8-17 μm long and 7-14 μm in diameter.

(10) B. **heterocorticum** Sheath et K.M.Cole (1990: 556).

(11) B. **lochmodes** Skuja (1938: 620).

(12) B. **cylindrocellulare** Kumano (1978: 100).

(13) B. **nova-guineense** Kumano et I.M.Johnstone (1983: 66).

(14) B. **szechwanense** C.C.Jao (1941: 264).

(15) B. **heteromorphum** Z.X.Shi, Hu et Kumano (1993: 295).

Table 2.1. Morphometric and qualitative characteristics of Batrachospermum sect. Batrachospermum type and historically important specimen groupings from the cluster analysis. Mean (range).

Group	Whorl	Ratio	Carposporophyte			Carpogonium				Carposporangium		Presence of
No. and name	diameter (µm)	Carposporophyte height: whorl diameter	Number per whorl	Diameter (µm)	Cell number	Diameter (µm)	Length (µm)	Form factor[a]	Branch cell number	Diameter (µm)	Length (µm)	qualitative character[b]
1	796	0.73	1.4	135	2.4	7	34	0.24	5.7	10	13	d, cc, rc
B. carpocontortum	(539-940)	(0.57-1.01)	(1-2)	(87-179)	(2-3)	(6-8)	(28-44)	(0.20-0.30)	(5-10)	(9-12)	(11-15)	
2	747	0.60	2.4	105	2.6	10	41	0.30	6.1	11	14	m, ms,rc
B. skujae	(586-1003)	(0.39-0.90)	(1-6)	(77-152)	(2-4)	(8-12)	(33-59)	(0.21-0.40)	(5-10)	(9-14)	(11-19)	
3	553	0.54	3.4	79	2.4	9	35	0.29	5.6	9	11	m, rc
B. gelatinosum	(257-972)	(0.26-1.10)	(1-11)	(40-139)	(2-4)	(5-17)	(20-68)	(0.16-0.44)	(3-10)	(6-12)	(8-16)	.
4	570	0.80	1.7	106	2.6	9	34	0.28	6.7	9	12	d, rc
B. arcuatum	(428-727)	(0.58-1.00)	(1-3)	(92-129)	(2-4)	(6-12)	(28-39)	(0.23-0.37)	(5-9)	(7-12)	(10-15)	

5	658	0.53	6.4	80	2.4	7	20	0.36	6.1	8	10	m, ir, s
B. confusum	(412-955)	(0.29-0.80)	(1-19)	(56-112)	(2-4)	(5-10)	(14-28)	(0.29-0.44)	(4-9)	(6-10)	(8-12)	
6	735	0.66	4.6	96	2.5	8	28	0.30	6.2	9	11	m, ir
B. anatinum	(479-994)	(0.39-1.13)	(1-11)	(69-140)	(2-4)	(6-10)	(17-40)	(0.22-0.41)	(3-8)	(7-14)	(8-16)	
7	607	0.66	6.6	96	2.5	8	26	0.33	6.3	9	12	d, ir
B. boryanum	(337-1034)	(0.35-0.92)	(1-30)	(68-139)	(2-3)	(6-10)	(16-35)	(0.26-0.40)	(4-8)	(7-14)	(8-17)	
8	390	0.49	1.2	81	2.3	6	25	0.24	4.9	10	12	m, rc, s, cf
B. pulchrum	(307-483)	(0.36-0.83)	(1-2)	(59-108)	(2-3)	(5-7)	(23-32)	(0.23-0.26)	(4-6)	(9-11)	(11-13)	
9	617	0.71	4.1	99	2.6	8	34	[illegible]	4.9	10	12	d, ir, sf
B. heterocorticum	(492-876)	(0.47-0.90)	(2-8)	(71-126)	(2-4)	(6-10)	(27-4[illegible]	[illegible]	(3-9)	(8-11)	(10-15)	

n = 30 except carpogonia where n = 15.

[a] See Sheath et al. (1986b) for description.

[b] d, dioecious; cc, contorted carpogonia; rc, regular cortication; m, monoecious; ms, monosporangia; ir, irregular cortication; s, spermatangia on involucral filaments of carpogonial branch; cf, curled fascicles; sf, secondary fascicles.

Table 2.2. *Morphometric and qualitative characteristics of* Batrachospermum sect. Batrachospermum type and historically important specimens. Mean (range).

Group No. and specimen	Whorl diameter (μm)	Ratio Carposporophyte height. whorl diameter	Carposporophyte Number per whorl	Carposporophyte Diameter (μm)	Carposporophyte Cell number	Carpogonium Diameter (μm)	Carpogonium Length (μm)	Carpogonium Form factor[a]	Carpogonium Branch cell number	Carposporangium Diameter (μm)	Carposporangium Length (μm)	Presence of qualitative character[b]
2												
B. skujae a	803	0.63	2.6	107	2.7	11	44	0.30	5.9	11	14	m, ms, rc
	(708-922)	(0.43-0.85)	(1-6)	(88-134)	(2-4)	(8-12)	(33-59)	(0.21-0.37)	(5-7)	(9-16)	(11-17)	
B. skujae b	721	0.56	2.3	109	2.8	11	39	0.32	5.8	11	15	m, ms, rc
	(586-808)	(0.40-0.86)	(1-5)	(85-152)	(2-4)	(9-12)	(33-43)	(0.25-0.40)	(5-10)	([illegible]-14)	(13-19)	
B. skujae c	718	0.62	2.3	99	2.5	10	38	0.28	6.5	11	14	m, ms, rc
	(590-1003)	(0.39-0.90)	(1-4)	(77-144)	(2-4)	(9-11)	(33-44)	(0.23-0.39)	(5-9)	(10-14)	(12-17)	
B. sporulans[c,d]	564	0.47	1	56	-	10	42	0.29	6.0	9	10	m, ms, rc
	(554-584)	(0.42-0.52)	(1)	(50-62)	-	(7-12)	(34-58)	(0.24-0.32)	(5-7)	(8-10)	(9-12)	

3												
B. arcuatoideum[e]	620	0.80	4.1	99	2.4	7	28	0.34	6.3	9	12	m, rc
	(473-736)	(0.60-1.00)	(2-7)	(79-125)	(2-4)	(6-9)	(21-33)	(0.26-0.44)	(5-7)	(8-11)	(10-13)	
B. corbula[e,f]	682	0.59	5.8	99	2.6	9	28	0.31	5.9	8	11	m, rc
	(540-762)	(0.43-0.90)	(2-10)	(77-120)	(2-3)	(7-10)	(26-34)	(0.25-0.38)	(4-8)	(7-10)	(10-13)	
B. corbula var.	700	0.67	2.6	91	2.5	8	33	0.29	5.3	8	11	m, rc
alcoense[d e,f]	(500-859)	(0.39-0.91)	(1-4)	(76-113)	(2-4)	(8-10)	(32-34)	(0.26-0.32)	(5-6)	(7-10)	(9-13)	
B. decaisneanum[e]	581	0.59	2.3	85	2.4	10	36	0.28	6.0	8	11	m, rc
	(452-709)	(0.37-0.77)	(1-4)	(65-117)	(2-4)	(8-11)	(28-45)	(0.22-0.31)	(5-7)	(7-11)	(9-12)	
B. densum a[e,g,h]	390	0.58	1.4	65	2.4	12	39	0.30	6.4	10	11	m, rc
	(361-411)	(0.50-0.66)	(1-2)	(54-74)	(2-3)	(10-14)	(25-59)	(0.18-0.39)	(5-8)	(8-12)	(9-13)	
B. densum b[h]	431	0.39	2.4	53	2.1	8	30	0.29	3.9	8	10	m, rc
	(360-479)	(0.28-0.52)	(1-4)	(40-94)	(2-3)	(7-10)	(26-34)	(0.23-0.35)	(3-5)	(6-10)	(8-12)	
B. densum c[e,f]	316	0.54	1.5	60	2.3	-	-	-	-	8	10	m, rc
	(271-398)	(0.26-0.84)	(1-2)	(44-75)	(2-3)	-	-	-	-	(7-10)	(9-12)	

B. gelatinosum	337	0.53	3.8	52	-	9	27	0.32	-	8	10	m. .
a[c,d,g]	(289-409)	(0.46-0.62)	(2-5)	(47-53)	-	(8-10)	(24-32)	(0.28-0.38)	-	(7-9)	(9-12)	
B. gelatinosum	632	0.66	4.0	80	-	9	25	0.34	-	-	-	m, rc
b[c,d]	(567-672)	(0.48-0.91)	(1-6)	(66-91)	-	(9)	(25)	(0.34)	-	-	-	
B. godronianum[e]	350	0.54	2.8	56	2.3	10	44	0.25	4.6	9	11	m, rc
	(299-411)	(0.40-0.77)	(1-5)	(42-64)	(2-3)	(9-12)	(37-61)	(0.16-0.30)	(3-6)	(9-11)	(10-12)	
B. hybridum[c,f,h]	483	0.65	1.8	76	2.4	13	47	0.28	5.4	9	12	m, rc
	(350-544)	(0.55-0.76)	(1-3)	(59-88)	(2-3)	(12-14)	(39-54)	(0.23-0.36)	(4-6)	(8-10)	(11-14)	
B. japonicum[d,e]	605	0.42	5.6	89	2.3	15	62	0.24	4.6	10	13	m, rc
	(488-683)	(0.32-0.59)	(3-9)	(72-106)	(2-3)	(11-17)	(49-68)	(0.19-0.29)	(4-5)	(8-12)	(11-16)	
B. ludibundum	465	0.48	3.1	77	2.2	8	31	0.31	8	9	12	m, rc
var. caerulescens[d]	(363-578)	(0.32-0.62)	(1-5)	(64-93)	(2-3)	(8)	(31)	(0.31)	(8)	(7-12)	(9-14)	
B. ludibundum	365	0.54	3.2	50	2.3	11	32	0.38	-	8	10	m, rc
var. pulcherrimum[d,g]	(277-535)	(0.32-0.72)	(1-6)	(33-71)	(2-3)	(11)	(32)	(0.38)	-	(7-9)	(9-12)	

B. ludibundum var. stagnale[d,f]	768 (492-972)	0.68 (0.29-0.85)	4.9 (2-11)	96 (70-139)	2.5 (2-3)	6 (6)	22 (20-28)	0.29 (0.26-0.31)	6.3 (5-8)	8 (7-10)	12 (10-13)	m, rc
B. monilif[illegible] var. chlorosum[d]	509 (405-596)	0.63 (0.46-0.82)	4.6 (1-9)	77 (63-94)	2.2 (2-3)	9 (9-10)	28 (24-32)	0.31 (0.29-0.36)	5.0 (4-6)	8 (6-10)	11 (9-13)	m, rc
B. moniliforme var. helminthoideum[d,e]	563 (506-618)	0.51 (0.33-0.74)	3.8 (2-6)	74 (59-81)	2.3 (2-3)	9 (7-10)	37 (36-38)	0.25 (0.23-0.27)	6 (6)	8 (7-9)	11 (9-13)	m, rc
B. moniliforme f. lipsiensis	591 (513-673)	0.50 (0.37-0.84)	3.8 (1-6)	94 (72-126)	2.3 (2-3)	8 (6-10)	31 (27-34)	0.29 (0.21-0.38)	5.0 (4-7)	10 (8-11)	13 (11-16)	m, rc
B. moniliforme var. pisanum a[d,e]	786 (705-912)	0.52 (0.31-0.72)	5.6 (3-9)	89 (72-106)	2.5 (2-3)	8 (7-8)	29 (28-30)	0.28 [illegible]	7.3 (7-8)	9 (8-10)	11 (9-13)	m, rc
B. moniliforme var. pisanum b[d,e,f]	827 (675-948)	0.58 (0.30-0.78)	5.1 (2-7)	93 (75-116)	2.3 (2-3)	8 (8)	33 (30-35)	0.28 (0.22-0.34)	6.7 (5-9)	10 (8-11)	12 (10-13)	m, rc
B. moniliforme var. pisanum c[c]	773 (619-861)	0.51 (0.39-0.70)	3.4 (2-5)	84 (77-94)	2.5 (2-3)	8 (7-9)	30 (26-37)	0.30 (0.25-0.36)	6.5 (5-10)	9 (8-10)	12 (10-13)	m, rc

B. moniliforme	507	0.47	2.8	69	2.3	9	33	0.29	5.2	9	11	m, rc
var. rubescens[d,e,f]	(350-564)	(0.26-0.65)	(1-6)	(43-86)	(2-3)	(7-10)	(30-41)	(0.25-0.33)	(4-7)	(8-11)	(9-13)	
B. moniliforme	418	0.66	1.0	82	2.4	12	55	0.26	5.8	9	12	m, rc
var. scopula[c,e,f]	(351-493)	(0.42-0.80)	(1)	(59-95)	(2-3)	(11-12)	(48-62)	(0.23-0.31)	(5-7)	(8-11)	(9-13)	
B. moniliforme	524	0.50	3.7	77	2.4	8	28	0.27	5.2	8	10	m, rc
var. typicum[d,e]	(433-568)	(0.40-0.59)	(2-5)	(63-92)	(2-3)	(7-8)	(25-[illegible]	([illegible] 0.29)	(5-6)	(7-10)	(9-13)	
B. pyramidale a[d,e]	412	0.58	2.2	75	2.4	10	39	0.25	4.7	9	10	m, rc
	(324-487)	(0.42-0.72)	(1-4)	(60-91)	(2-3)	(9-10)	(32-46)	(0.22-0.30)	(4-5)	(8-10)	(9-12)	
B. pyramidale b[h]	299	0.57	1.6	54	2.4	9	37	0.29	5.0	9	11	m, rc
	(257-342)	(0.38-0.83)	(1-4)	(40-74)	(2-3)	(8-11)	(30-53)	(0.23-0.37)	(4-7)	(7-11)	(9-13)	
B. pyramidale c[d]	540	0.40	2.9	73	2.5	9	34	0.29	5.2	9	11	m, rc
	(401-673)	(0.30-0.57)	(1-5)	(55-97)	(2-4)	(9-10)	(25-40)	(0.25-0.33)	(4-6)	(7-11)	(9-13)	
B. pyramidale d[h]	364	0.55	1.9	55	2.3	9	35	0.27	5.0	9	12	m, rc
	(332-409)	(0.42-0.93)	(1-3)	(44-70)	(2-4)	(7-10)	(26-42)	(0.22-0.33)	(4-7)	(7-10)	(10-14)	

B. polycarpum[e f h]	650	0.73	3.8	87	2.5	7	23	0.32	7.0	7	10	m, rc
	(498-801)	(0.49-1.10)	(1-10)	(66-122)	(2-3)	(5-8)	(21-27)	(0.26-0.38)	(6-8)	(6-8)	(9-12)	
B. pygmaeum[d e g]	358	0.56	1.7	63	2.4	10	47	0.28	-	10	12	m, rc
	(246-424)	(0.42-0.83)	(1-3)	(40-93)	(2-3)	(9-12)	(32-60)	(0.22-0.37)	-	(9-11)	(11-12)	
B. radians[d]	607	0.42	3.7	96	2.5	9	32	0.30	5.6	9	11	m, rc
	(436-762)	(0.34-0.52)	(2-5)	(72-134)	(2-4)	(7-12)	(27-36)	(0.25-0.36)	(4-8)	(7-11)	(9-14)	
B. reginense[d e f]	418	0.45	3.9	53	2.4	12	36	0.34	-	9	11	m, rc
	(317-514)	(0.34-0.71)	(1-7)	(43-76)	(2-3)	(12)	(36)	(0.34)	-	(7-10)	(10-14)	
5												
B. alpestre[b]	-	-	-	-	2.4	8	24	0.37	5.8	9	11	m, ir, s
	-	-	-	-	(2-3)	(7-11)	(19-29)	(0.32-0.41)	(5-8)	(7-11)	(10-14)	
B. confusum var.	687	0.56	7.6	76	2.5	6	19	0.34	5.3	8	9	m, ir, s
spermato-	(573-795)	(0.36-0.72)	(4-17)	(59-88)	(2-4)	(5-9)	(14-24)	(0.27-0.41)	(4-7)	(7-11)	(8-12)	
globeratum[e]												

B. crouanianum[f,h]	536	0.56	7.6	76	2.5	6	19	0.34	5.3	8	9	m, ir, s
	(412-664)	(0.29-0.80)	(5-19)	(56-109)	(2-3)	(6-8)	(18-27)	(0.28-0.43)	(5-8)	(7-10)	(9-12)	
B. fruticulosum[b]	-	-	-	-	-	8	24	0.36	-	-	-	m, ir, s
	-	-	-	-	-	(7-11)	(18-32)	(0.29-0.46)	-	-	-	
B. helminthosum	596	0.44	4.5	90	2.5	8	27	0.33	8	8	10	m, ir, s
a[d]	(510-713)	(0.34-0.55)	(1-8)	(61-112)	(2-4)	(8)	(27)	(0.33)	(8)	(6-10)	(9-11)	
B. helminthosum	686	0.56	4.3	85	2.6	8	20	0.33	6.2	8	11	m, ir, s
b	(468-799)	(0.31-0.79)	(1-8)	(65-104)	(2-3)	(6-8)	(17-22)	(0.30-0.44)	(4-9)	(7-10)	(9-13)	
B. helminthosum	750	0.62	4.3	81	2.3	8	23	0.38	6.2	8	10	m, ir, s
c[e]	(568-955)	(0.43-0.80)	(1-7)	(61-95)	(2-3)	(6-10)	(18-28)	(0.28-0.43)	(5-8)	(7-10)	(9-12)	
B. ludibundum	749	0.52	6.7	73	2.4	6	17	0.33	8	8	10	m, ir, s
var. confusum[d,a]	(556-901)	(0.36-0.71)	(3-10)	(61-90)	(2-3)	(6-7)	(15-18)	(0.29-0.38)	(8)	(7-10)	(8-12)	
B. setigerum[g]	-	-	-	-	2.3	9	28	0.32	5.4	9	12	m, ir, s
	-	-	-	-	(2-3)	(7-10)	(22-34)	(0.30-0.36)	(4-6)	(8-10)	(9-13)	

6												
B. anatinum a[d,e,f]	695	0.52	3.3	107	2.4	7	20	0.36	7.4	9	10	m, ir
	(599-855)	(0.39-0.70)	(2-5)	(88-136)	(2-3)	(6-8)	(18-22)	(0.33-0.40)	(6-8)	(7-10)	(8-12)	
B. anatinum b	-	-	-	-	-	8	27	0.31	6.4	-	-	m, ir
	-	-	-	-	-	(6-10)	(22-32)	(0.25-0.37)	(5-8)	-	-	
B. boryanum b[d]	708	0.61	4.8	91	2.6	7	20	0.36	7.3	8	10	m, ir
	(543-903)	(0.44-0.76)	(1-10)	(69-114)	(2-3)	(6-8)	(17-22)	(0.31-0.41)	(4-8)	(7-9)	(8-12)	
B. ectocarpum a[b]	779	0.68	7.1	90	2.5	8	34	0.25	7.0	9	11	m, ir
	(633-933)	(0.44-0.85)	(3-11)	(75-114)	(2-4)	(6-10)	(30-41)	(0.23-0.28)	(6-8)	(7-11)	(10-14)	
B. ectocarpum b[d]	658	0.68	3.0	91	2.5	8.4	33	0.26	5.5	10	12	m, ir
	(479-793)	(0.52-0.82)	(1-7)	(76-118)	(2-4)	(8-9)	(28-39)	(0.22-0.32)	(5-6)	(8-14)	(10-16)	
B. ectocarpum c[e]	855	0.75	4.0	111	2.6	8	29	0.30	5.7	9	12	m, ir
	(686-994)	(0.43-1.13)	(1-7)	(95-140)	(2-4)	(6-9)	(26-31)	(0.23-0.37)	(3-8)	(7-10)	(10-13)	
B. ectocarpum d[d]	741	0.70	3.2	110	3.0	9	26	0.31	-	10	12	m, ir
	(612-847)	(0.48-0.90)	(1-6)	(85-133)	(2-4)	(8-10)	(23-29)	(0.30-0.32)	-	(7-12)	(10-15)	

B. fluitans[a]	576	0.54	2.5	76	-	13	56	0.31	5.2	-	-	m, ir
	(488-664)	(0.36-0.92)	(1-5)	(64-93)	-	(11-15)	(51-65)	(0.26-0.37)	(4-6)	-	-	
7												
B. boryanum a[d,e]	910	0.56	20.7	90	2.3	7	20	0.36	7.3	8	10	d, ir
	(789-1034)	(0.35-0.70)	(12-30)	(74-105)	(2-3)	(6-7)	(16-27)	(0.33-0.40)	(7-8)	(7-10)	(8-12)	
B. ecto-	465	0.67	2.3	76	2.4	8	26	0.36	7.3	8	10	d, ir
carpoideum a[c,d,g]	(337-522)	(0.51-0.92)	(1-3)	(68-94)	(2-3)	(7-8)	(23-32)	(0.28-0.40)	(4-6)	(9-14)	(13-17)	
B. ecto-	450	0.70	1.6	90	2.6	9	27	0.33	6.4	9	10	d, ir
carpoideum b[e,f]	(359-536)	(0.48-0.88)	(1-3)	(69-110)	(2-3)	(8-10)	(19-35)	(0.28-0.39)	(4-8)	(7-10)	(9-12)	
B. ecto-	627	0.67	2.4	126	2.6	8	28	0.32	6.2	9	13	d, ir
carpoideum c[g,h]	(467-832)	(0.53-0.83)	(1-4)	(97-139)	(2-3)	(7-9)	(25-30)	(0.26-0.39)	(5-8)	(7-10)	(11-15)	

n = 30 except carpogonia where n = 15. Data for B. arcuatum (Group 4); B. carpocontortum (Group 1), B. heterocorticum (Group 9) and B. pulchrum (Group 8) are in Table 2.1.

[a] See Sheath et al. (1986b) for description.

[b] d, dioecious; cc, contorted carpogonia; rc, regular cortication; m, monoecious; ms, monosporangia; ir, irregular cortication; s, spermatangia on involucral filaments of

carpogonial branch; cf, curled fascicles; sf, secondary fascicles.

[c] 1-14 measurements for whorl diameter, carposporophyte height-to-whorl diameter ratio and carposporophyte number per whorl and diameter.

[d] 1-7 measurements for carpogonium diameter, length, form factor and branch cell number.

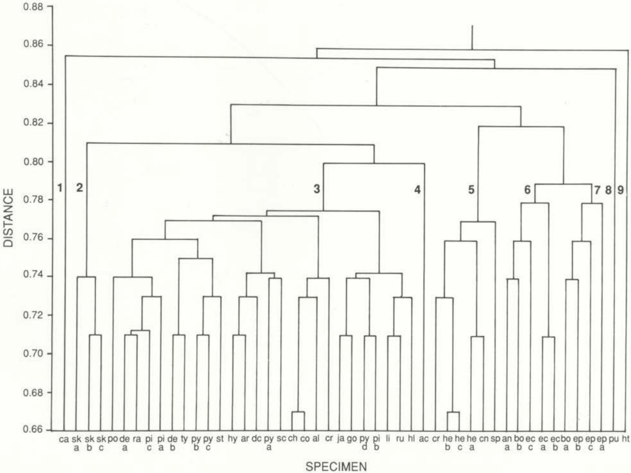
[e] 15-29 measurements for whorl diameter, carposporophyte height-to-whorl diameter ratio and carposporophyte number per whorl and diameter.

[f] 15-29 measurements for carposporophyte cell number and carposporangium diameter and length.

[g] 1-14 measurements for carposporophyte cell number and carposporangium diameter and length.

[h] 8-14 measurements for carpogonium diameter, length, form factor and branch cell number.

Fig. 2.1. Cluster analysis of Batrachospermum sect. Batrachospermum type and historically important specimens. Specimen designations (a, b or c) correspond to those in Table 2.2 and Materials and Methods. Specimen abbreviations are as follows: ca, B. carpocontortum; sk, B. skujae; po, B. polycarpum; de, B. densum; ra, B. radians; pi, B. moniliforme var. pisanum; ty, B. moniliforme var. typicum; py, B. pyramidale; st, B. ludibundum var. stagnale; hy, B. hybridum; ar, B. arcuatoideum; dc, B. decaisneanum; sc, B. moniliforme var. scopula; ch, B. moniliforme var. chlorosum; co, B. ludibundum var. caerulescens; al, B. corbula var. alcoense; cr, B. corbula; ja, B. japonicum; go, B. godronianum; li, B. moniliforme f. lipsiensis; ru, B. moniliforme var. rubescens; hl, B. moniliforme var. helminthoideum; ac, B. arcuatum; cr, B. crouanianum; he, B. helminthosum; cn, B. ludibundum var. confusum; sp, B. confusum f. spermatogloberatum; an, B. anatinum; bo, B. boryanum; ec, B. ectocarpum; ep, B. ectocarpoideum; pu, B. pulchrum; ht, B. heterocorticum.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SPECIMEN

Plate I

Figs 2.2-2.15. Morphological features of Batrachospermum sect. Batrachospermum type specimens. Fig. 2.2. B. ludibundum var. stagnale carposporophyte-bearing branch with both concave or hourglass-shaped cells (arrowheads) and cylindrical cells (large arrowhead). Fig. 2.3. B. anatinum. Cortical cells cylindrical (arrowheads) or irregularly inflated (large arrowheads). Fig. 2.4. B. skujae. Monosporangia (arrowheads) at fascicle apex. Figs. 2.5, 2.6. B. carpocontorum. Fig. 2.5. Barrel-shaped, confluent whorls containing one large carposporophyte (arrowheads) per whorl. Fig. 2.6. Carpogonium with bumped, contorted trichogyne (arrowhead). Figs 2.7, 2.8. B. skujae specimen c. Fig. 2.7. Barrel-shaped, confluent whorls containing many carposporophytes (arrowheads). Fig. 2.8. Fertilized carpogonium with sessile lanceolate trichogyne (arrowhead) on undifferentiated carpogonial branch. Figs 2.9, 2.10. B. sporulans. Fig. 2.9. Main axis with globose, distant whorls containing small carposporophytes (arrowheads). Fig. 2.10. Fertilized carpogonium with concave, lanceolate trichogyne (arrowhead) on undifferentiated carpogonial branch. Figs 2.11, 2.12. B. arcuatoideum. Fig. 2.11. Main axis with confluent, barrel-shaped whorls containing internal carposporophytes (arrowhead) and exserted carposporophytes (large arrowhead). Fig. 2.12. Fertilized carpogonium with sessile, clavate trichogyne (arrowhead) on undifferentiated carpogonial branch. Figs 2.13, 2.14. B. corbula. Fig. 2.13. Main axis with barrel-shaped whorls containing numerous carposporophytes (arrowheads). Fig. 2.14. Fertilized carpogonium with clavate trichogyne (arrowhead) on undifferentiated carpogonial branch. Fig. 2.15. B. corbula var. alcoense. Main axis with confluent, barrel-shaped whorls containing carposporophytes (arrowheads) scattered throughout. (Scale bars represent: Figs 2.2, 2.3, 20 μm; Figs 2.4, 2.6, 2.8, 2.10, 2.12, 2.14, 10 μm; Figs 2.5, 2.7 300 μm; Figs 2.9, 2.15, 250 μm; Figs 2.11, 2.13, 200 μm)

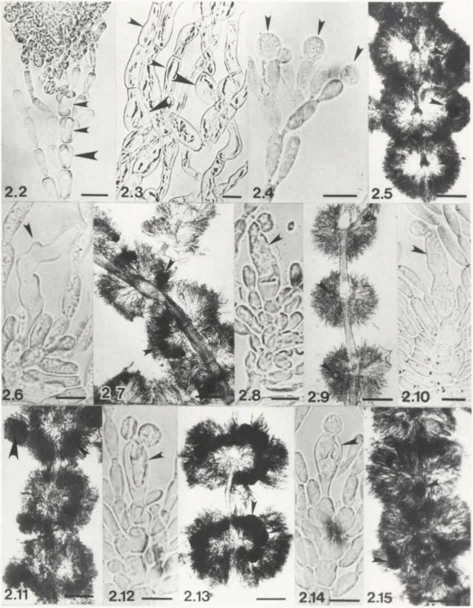
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Plate II

Figs 2.16-2.30. Morphological features of Batrachospermum sect. Batrachospermum type specimens. Figs 2.16, 2.17. B. decaisneanum. Fig. 2.16. Dark corticated main axis with confluent oblong whorls containing carposporophytes (arrowheads). Fig. 2.17. Fertilized carpogonium with trichogyne (arrowhead) on undifferentiated carpogonial branch. Figs 2.18-2.21.B. densum lectotype, specimen a. Fig. 2.18. Main axis with confluent, barrel-shaped whorls containing scattered carposporophytes (arrowheads). Fig. 2.19. Fertilized carpogonium with clavate trichogyne (arrowhead) on undifferentiated carpogonial branch. Fig. 2.20. Fertilized carpogonium with inflated, lanceolate trichogyne (arrowhead) on undifferentiated carpogonial branch. Fig. 2.21. Mature carpogonium with elongate trichogyne (arrowhead). Figs 2.22, 2.23. B. godronianum. Fig. 2.22. Main axis with globose, distant whorls containing numerous carposporophytes (arrowheads). Fig. 2.23. Mature carpogonium with lanceolate trichogyne (arrowhead) on undifferentiated carpogonial branch. Figs 2.24, 2.25.B. hybridum. Fig. 2.24. Main axis with obovoid whorls containing few carposporophytes (arrowhead). Fig. 2.25. Mature carpogonium with inflated, lanceolate trichogyne (arrowhead). Figs 2.26, 2.27.B. japonicum. Fig. 2.26. Main axis with confluent, globose whorls containing numerous carposporophytes (arrowhead). Fig. 2.27. Fertilized carpogonium with inflated clavate trichogyne (arrowhead) on undifferentiated carpogonial branch. Fig. 2.28. B. ludibundum var. caerulescens. Main axis with globose whorls containing carposporophytes (arrowheads). Fig. 2.29.B. ludibundum var. stagnale. Main axis with globose whorls containing numerous carposporophytes (arrowheads). Fig. 2.30.B. moniliforme var. chlorosum. Globose whorl containing numerous carposporophytes (arrowheads). (Scale bars represent: Figs 2.16, 2.18, 2.22, 2.28, 2.30, 150μm; Figs 2.17, 2.19-2.21, 2.23, 2.25, 2.27, 10μm; Fig. 2.24, 250 μm; Fig. 2.26, 200 μm; Fig. 2.29, 350 μm)

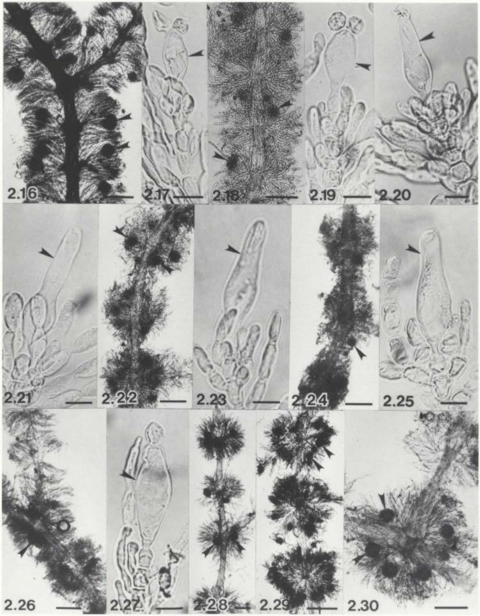

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Plate III

Figs 2.31-2.45. Morphological features of Batrachospermum sect. Batrachospermum type specimens. Figs 2.31, 2.32. B. moniliforme var. helminthoideum. Fig. 2.31. Main axis with confluent, globose whorls containing numerous carposporophytes (arrowheads). Fig. 2.32. Mature carpogonium with inflated clavate trichogyne (arrowhead) on undifferentiated carpogonial branch. Figs 2.33, 2.34.B. moniliforme f. lipsiensis. Fig. 2.33. Main axis with globose whorls containing carposporophytes (arrowheads). Fig. 2.34. Fertilized carpogonium with clavate trichogyne (arrowhead) on undifferentiated carpogonial branch. Figs 2.35, 2.36. B. moniliforme var. pisanum. Fig. 2.35. Main axis with confluent, globose whorls containing numerous carposporophytes (arrowheads). Specimen b. Fig. 2.36. Fertilized carpogonium with lanceolate trichogyne (arrowhead) on undifferentiated carpogonial branch. Specimen c. Fig. 2.37. B. moniliforme var. rubescens. Main axis with confluent, globose whorls containing numerous carposporophytes (arrowheads). Figs 2.38, 2.39.B. moniliforme var. scopula. Fig. 2.38. Somewhat darkly corticated main axis with confluent, globose whorls containing a carposporophyte (arrowhead). Fig. 2.39. Mature carpogonium with inflated, lanceolate trichogyne (arrowhead). Fig. 2.40. B. moniliforme var. typicum. Main axis with globose whorls containing numerous carposporophytes (arrowheads). Figs 2.41, 2.42. B. pyramidale lectotype, specimen a. Fig. 2.41. Main axis with distant, globose whorls containing numerous carposporophytes (arrowheads). Fig. 2.42. Main axis with confluent, ovate whorls containing carposporophytes (arrowhead). Figs 2.43, 2.44.B. polycarpum. Fig. 2.43. Main axis with confluent, barrel-shaped whorls containing numerous scattered carposporophytes (arrowheads). Fig. 2.44. Fertilized carpogonium with lanceolate trichogyne (arrowhead) on undifferentiated carpogonial branch. Fig. 2.45. B. radicans. Main axis with globose whorls containing numerous carposporophytes (arrowheads). (Scale bars represent: Figs 2.31, 2.40, 250μm; Figs 2.32, 2.34, 2.36, 2.39, 10 μm; Fig. 2.33, 150 μm; Figs 2.35, 2.43, 300 μm; Figs 2.37, 2.41, 2.42, 200 μm; Fig. 2.38, 100 μm; Fig. 2.44, 5 μm; Fig. 2.45, 350 μm)

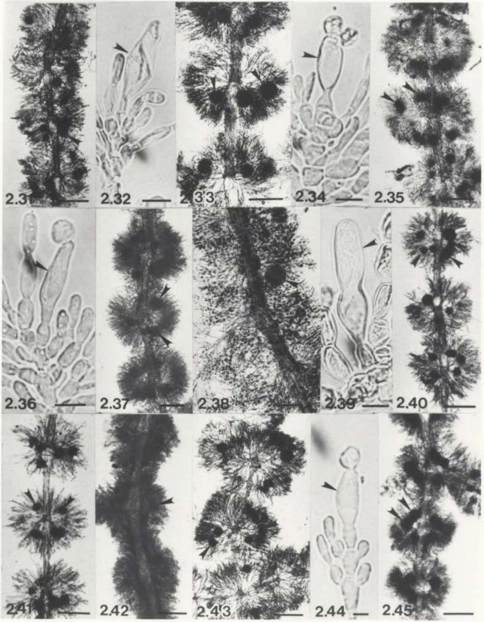
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Plate IV

Figs 2.46-2.60. Morphological features of Batrachospermum sect. Batrachospermum type and historically important specimens. Fig. 2.46. B. radians. Mature carpogonium with clavate trichogyne (arrowhead) on undifferentiated carpogonial branch. Figs 2.47, 2.48. B. gelatinosum lectotype, specimen a. Fig. 2.47. Main axis with globose whorls containing numerous carposporophytes (arrowheads). Fig. 2.48. Fertilized carpogonium with clavate trichogyne (arrowhead). Figs 2.49, 2.50. B. gelatinosum specimen b. Fig. 2.49. Main axis with globose whorls containing numberous carposporophytes (arrowheads). Fig. 2.50. Fertilized carpogonium with clavate trichogyne (arrowhead). Figs 2.51, 2.52. B. ludibundum var. pulcherrimum. Fig. 2.51. Main axis with distant, globose whorls containing carposporophytes (arrowheads). Fig. 2.52. Fertilized carpogonium with clavate trichogyne (arrowheads). Figs 2.53, 2.54. B. pygmaeum. Fig. 2.53. Main axis with confluent, barrel-shaped whorls containing carposporophytes (arrowheads). Fig. 2.54. Fertilized carpogonium with lanceolate trichogyne. Figs 2.55, 2.56. B. reginense. Fig. 2.55. Main axis with confluent, globose whorls containing carposporophytes (arrowheads). Fig. 2.56. Fertilized carpogonium with clavate trichogyne (arrowhead) on undifferentiated carpogonial branch. Figs 2.57, 2.58. B. arcuatum. Fig. 2.57. Main axis with confluent, barrel-shaped whorls containing few carposporophytes (arrowhead). Fig. 2.58. Fertilized carpogonium with inflated clavate trichogyne (arrowhead) on undifferentiated carpogonial branch. Figs 2.59, 2.60. B. crouanianum. Fig. 2.59. Main axis with confluent, barrel-shaped whorls containing carposporophytes (arrowheads) in various stages of developement. Fig. 2.60. Fertilized carpogonium with lanceolate trichogyne (arrowhead). Involucral filaments with apical spermatangia (large arrowhead). (Scale bars represent: Figs 2.46, 2.48, 2.52, 2.54, 2.56, 2.58, 10 μm; Fig. 2.47, 100 μm; Figs 2.49, 2.53, 2.57, 2.59, 200 μm; Fig. 2.50, 5 μm; Figs 2.51, 2.55, 150 μm; Fig. 2.60, 7 μm)

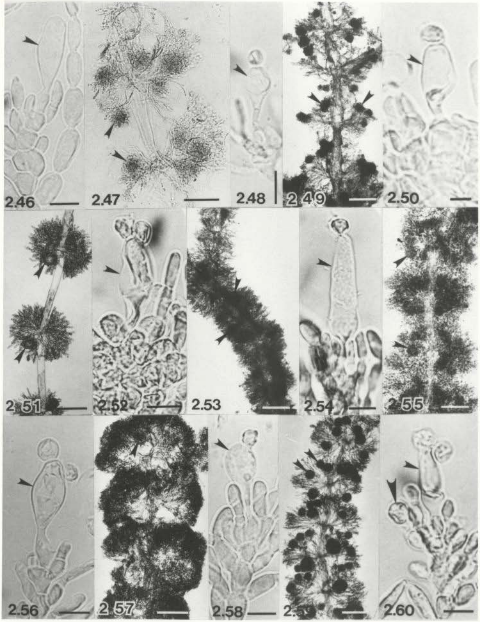
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Plate V

Figs 2.61-2.73. Morphological features of Batrachospermum sect. Batrachospermum type and historically important specimens. Figs 2.61, 2.62. B. confusum var. spermatogloberatum. Fig. 2.61. Main axis with confluent, barrel-shaped whorls containing numerous carposporophytes (arrowheads). Fig. 2.62. Fertilized carpogonium with clavate trichogyne (arrowhead). Dense involucral filaments with apical spermatangia (large arrowheads). Figs 2.63, 2.64. B. ludibundum var. confusum. Fig. 2.63. Main axis with barrel-shaped whorls containing scattered carposporophytes (arrowheads). Fig. 2.64. Fertilized carpogonium with clavate trichogyne (arrowhead). Involucral filaments with apical spermatangia (large arrowhead). Figs 2.65, 2.66. B. helminthosum. Fig. 2.65. Axis with confluent, compressed whorls containing numerous scattered carposporophytes (arrowheads). Specimen a. Fig. 2.66. Mature carpogonium with clavate trichogyne (arrowhead). Involucral filaments with apical spermatangia (large arrowheads). Specimen c. Fig. 2.67. B. alpestre. Mature carpogonium with inflated, lanceolate trichogyne (arrowhead). Involucral filaments with apical spermatangia (large arrowhead). Fig. 2.68. B. fruticulosum. Mature carpogonium with clavate trichogyne (arrowhead). Involucral filaments with apical spermatangia (large arrowhead). Fig. 2.69. B. setigerum. Mature carpogonium with clavate trichogyne (arrowhead). Involucral filaments with apical spermatangia (large arrowheads). Fig. 2.70. B. anatinum specimen a. Main axis with globose whorls containing numerous carposporophytes (arrowheads). Figs 2.71, 2.72. B. boryanum specimen b. Fig. 2.71. Main axis with globose whorls containing numerous, scattered carposporophytes (arrowheads). Fig. 2.72. Fertilized carpogonium with clavate trichogyne (arrowhead). Fig. 2.73. B. ectocarpum specimen a. Main axis with globose whorls containing carposporophytes (arrowheads). (Scale bars represent: Figs 2.61, 2.73, 25 μm; Figs 2.62, 2.64, 2.66-2.69, 10 μm; Figs 2.63, 2.65, 2.70, 200 μm; Fig. 2.71, 350 μm; Fig. 2.72, 5 μm)

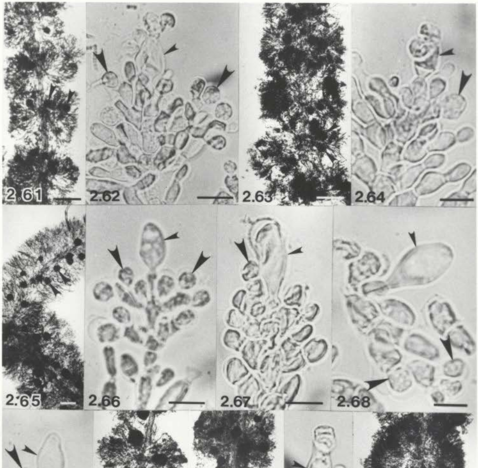

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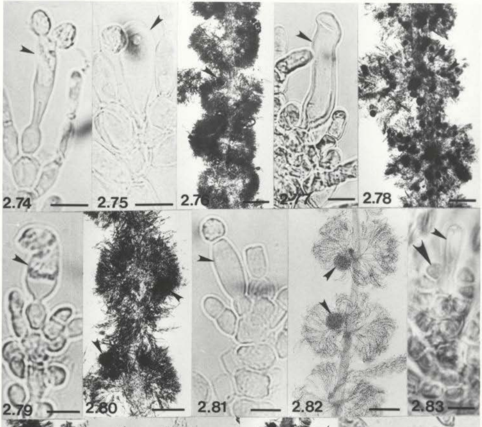
Plate VI

Figs 2.74-2.87. Morphological features of Batrachospermum sect. Batrachospermum type specimens. Figs 2.74, 2.75. B. ectocarpum. Fig. 2.74. Fertilized carpogonium with lanceolate trichogyne (arrowhead) on undifferentiated carpogonial branch. Specimen a. Fig. 2.75. Fertilized carpogonium with inflated, lanceolate trichogyne (arrowhead). Specimen c. Figs. 2.76, 2.77. B. fluitans. Fig. 2.76. Main axis with confluent barrel-shaped whorls containing carposporophytes (arrowheads). Fig. 2.77. Mature carpogonium with clavate trichogyne (arrowhead) on undifferentiated carpogonial branch. Figs 2.78, 2.79. B. boryanum specimen a. Fig. 2.78. Main axis with confluent, barrel-shaped whorls containing numerous scattered carposporophytes (arrowheads). Fig. 2.79. Fertilized carpogonium with clavate trichogyne (arrowhead) on undifferentiated carpogonial branch. Figs 2.80, 2.81. B. ectocarpoideum. Fig. 2.80. Main axis with globose whorls containing carposporophytes (arrowhead). Fig. 2.81. Fertilized carpogonium with lanceolate trichogyne (arrowhead) on undifferentiated carpogonial branch. Figs 2.82, 2.83. B. pulchrum. Fig. 2.82. Main axis with globose whorls composed of few, well-curled fascicles containing one prominent carposporophytes (arrowheads). Fig. 2.83. Carpogonium with lanceolate trichogyne (arrowhead) on undifferentiated carpogonial branch. Involucral filaments with apical spermatangia (large arrowhead). Figs 2.84-2.87. B. heterocorticum. Fig. 2.84. Main axis of male plant with indistinct whorls and abundant secondary fascicle growth (arrowhead). Fig. 2.85. Fascicle with abundant spermatangia development (arrowheads). Fig. 2.86. Main axis of female plant with abundant secondary fascicle growth (arrowhead) and barrel-shaped whorls containing numerous carposporophytes (large arrowhead). Fig. 2.87. Mature carpogonium with lanceolate trichogyne (arrowhead) on undifferentiated carpogonial branch. (Scale bars represent: Figs 2.74, 2.75, 2.77, 2.79, 2.81, 2.83, 2.87, 10 μm; Figs 2.76, 2.80, 200 μm; Figs 2.78, 2.86, 300 μm; Fig. 2.82, 150 μm; Fig. 2.85, 20 μm)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Distribution and systematics of Batrachospermum section Batrachospermum in North America: Description of five new species

3.1 Introduction

Sect. Batrachospermum of the freshwater red algal genus Batrachospermum is generally characterised by undifferentiated, straight carpogonial branches arising from both fascicle and pericentral cells, carpogonia with club- to urn-shaped trichogynes and small, globose, pedicellate carposporophytes at various distances from the whorl axis (Mori, 1975; Starmach, 1977; Kumano, 1993; Chapter 2). Taxa of this section have been reported from Europe, Asia, Australia, South America and North America (e.g. Sirodot, 1884; Reis, 1973; Mori, 1975; Entwisle & Kraft, 1984; Necchi, 1990; Sheath & Cole, 1992). Numerous taxa have been described from this section (Sirodot, 1884). However, in a review of type specimens of 46 species and infraspecific taxa from sect. Batrachospermum, it was concluded that there are 15 well-defined species on the basis of whether they are monoecious or dioecious, carpogonium size and the presence or absence of spermatangia on involucral filaments, irregular cortication, monosporangia, well-curled fascicles and secondary fascicles.

In a survey of 1000 streams from North America (Sheath & Cole, 1992), populations were collected which had previously unreported features and were not referable to any known species. Among these populations, five distinct entities can be seen. Five new species of Batrachospermum sect. Batrachospermum are here described.

3.2 Materials and methods

Nineteen populations which were not attributable to known species of Batrachospermum sect. Batrachospermum were collected from North America (Fig. 3.1). Samples were immediately fixed in 2.5% buffered glutaraldehyde. Maximum depth and width, pH, specific conductance, temperature, and mean current velocity were measured in each stream segment as described by Sheath et al. (1989) (Table 3.1).

Specimens were measured for the morphological characteristics described in Chapter 2 (Table 3.2) in replicates of 30 (15 for carpogonia), using a SMI image analysis system. Qualitative features such as thalli monoecious or dioecious and heterocortication were also noted. Characteristics of each taxon were photographed with an Olympus PM-10 AK camera system. To compare means of morphometric characteristics measured among populations of a species, analysis of variance (ANOVA) and Duncan's multiple-range test were calculated according to the SAS statistical package (Anonymous, 1988). All statistical differences are significant at the $p < 0.05$ level.

3.3 Diagnoses and observations

Batrachospermum spermatoinvolucrum M.L.Vis et Sheath, sp. nov.

Fila monoica cum spermatangis super bracteas involucrorum ab filis carpogonialibus fractis. Verticilli confluentibus et globularis, 239-846 μm lato, 5-18 cellularum fasciculiorum compositae. Spermatangia multi in ramuli, lateralibus terminalia. Carpogonia 8-17 μm lato, 40-86 μm longitudine. Rami carpogonialis 3-11 cellulas longitudine. Carposporangia 6-14 μm diametro, 6-16 μm longitudine. Gonimoblasti orbiculati, 44-158 μm diametro, cum 2-4 cellulis.

Plants are monoecious and have confluent globose whorls (Fig. 3.2). Mature whorls containing carposporophytes range from 239-846 μm in diameter and are composed of 5-18 fascicle cells (Table 3.2). Axial cells are covered by cortical filaments composed of cylindrical cells (Fig. 3.3). Spermatangia are formed at the tips of vegetative fascicles (Fig. 3.4) and on the involucral filaments of the carpogonial branch (Figs 3.5-3.7). Carpogonia are quite variable in size and shape (Figs 3.5-3.7) and the dimensions are 8-17 x 40-86 μm (Table 3.2). Carposporophytes are spherical, 1-10 per whorl and at various distances from the axis (Fig. 3.2) (Table 3.2). At maturity carposporophytes are 44-159 μm in diameter. Carposporangia range from 6-14 μm in diameter and 6-16 μm in length and are produced apically on 2-4-celled gonimoblast filaments (Fig. 3.8) (Table 3.2).

Etymology: Epithet denotes the presence of spermatangia on the involucral filaments of the carpogonial branch.

Holotype: R. G. Sheath LAB 13. Nain (56°30'N, 61°45'W), Labrador, Newfoundland, Canada, 30 viii 1993. Stream characteristics: see Table 3.1. Coll. R. G. Sheath & M. L. Vis. **UBC** A81615.

Specimens examined

AK 5, Route 3N, 4.8 km S of Denali State Park, Alaska, USA [for details see Sheath et al. (1986b)]. AK 58, Toolik Lake headwater, Alaska, USA, 2 viii 1990. Coll. J. A. Hambrook. BC 2, tributary of Cayoosh Creek, southwest of Lillooet, South Cariboo Highway District, British Columbia, Canada, 25 viii 1983. Coll. B. Hymes. BC17a, Thornton Creek, on road to Port Albion, Vancouver Island, British Columbia, Canada, 15 viii 1989. Coll. R. G. Sheath. BC 76, Redroof's Rd. at O'Brian Rd. 0.2 km west of Sunshine Coast Highway, British Columbia, Canada, 1 ix 1991. Coll. R. G. Sheath. BC 86, Angus Creek, Porpoise Bay Provincial Park, British Columbia, Canada, 8 viii 1993. Coll. R. G. Sheath. WA 110, Skagit River, Washington, USA [for details see Sheath et al. (1986a)]. NWT 10, SE head of bay, Pangnirtung, Northwest Territories, Canada, 21 vi 1987. Coll. R. G. Sheath & J. A. Hambrook. NWT 43, below resevoir and down slope of the culvert, Iqaluit, Northwest Territories, Canada, 29 vi 1988. Coll. R. G. Sheath & J. A. Hambrook. NWT 45, stream running behind graveyard on top of the hill behind town, Clyde River, Northwest Territories, Canada, 30 vi 1988. Coll. R. G. Sheath & J. A. Hambrook. NWT 55, third rivlet past the dump road, Pond Inlet, Northwest Territories, 30 vi 1988. Coll. R. G. Sheath & J. A. Hambrook. NWT

61, second stream crossing the road west of the entrance to town, 4 km east of campground, Baker Lake, Northwest Territories, Canada, 29 vi 1989. Coll. R. G. Sheath & J. A. Hambrook. GLD 5, Road to Kellyville, 14 km west of airport, Kangerlussuaq, Greenland, 27 vi 1990. Coll. R. G. Sheath. GLD 20, outflow of river crossing the road to airport, Nuuk, Greenland, 2 vii 1990. Coll. R. G. Sheath. All additional specimens deposited at **NFLD**.

Remarks

The fifteen populations of Batrachospermum spermatoinvolucrum examined represent a continuum in most characteristics. The means for carposporophyte diameter and cell number for NWT 10 are significantly greater than the other populations, but the range overlaps with four other populations. GLD 20 has a significantly larger carpogonium diameter. However, this characteristic is highly variable and the range of GLD 20 overlaps with eight other populations. The mean carpogonium length for AK 58 is significantly larger, but the range overlaps with 11 other populations.

Although spermatangia on the involucral filaments of the carpogonial branch is one of the distinguishing features of Batrachospermum spermatoinvolucrum, not all spermatangia are so restricted (Fig. 3.4). In addition, some carpogonial branches do not have any spermatangia on the involucral filaments. Among the populations examined, number of carpogonial branches per plant with associated spermatangia ranged from 27-67 %. Therefore, this characteristic is consistent for each plant, but multiple carpogonia must be examined.

The haploid chromosome number for Batrachospermum spermatoinvolucrum (GLD 20 and NWT 55) is n = 3, according to Sheath and Cole (1993) (as B. gelatinosum). This number is similar to those reported in the same paper for other members of sect. Batrachospermum in North America, B. boryanum Sirodot and B. gelatinosum.

Within Batrachospermum sect. Batrachospermum, B. spermatoinvolucrum is not unique in possessing spermatangia on the involucral filaments of the carpogonial branch since this characteristic is also found in B. confusum (Chapter 2). However, B. spermatoinvolucrum has cortical filaments composed of cylindrical cells only (Fig. 3.3), whereas B. confusum has heterocortication composed of both cylindrical and bulbous cells (Chapter 2, Fig. 2.3). In addition, the carpogonia of B. spermatoinvolucrum are longer (40-86 µm) and non-overlapping with those of B. confusum (14-34 µm). Spermatangia on the involucral filaments have also been found in B. androinvolucrum Sheath, M.L.Vis et K.M.Cole from sect. Setacea (Sheath et al., 1993b), but the whorls of this species are considerably smaller (70-164 µm diam.) than those of B. spermatoinvolucrum (239-846 µm diam.). They are also present in B. keratophytum Bory from sect. Turfosa (Sheath et al., 1994b), but this species has axial carposporophytes rather than pedicellate ones.

Ecology

Populations of Batrachospermum spermatoinvolucrum were collected in western coniferous forest, boreal forest and tundra regions of North America (Fig. 3.1). Streams tended to be moderate in current velocity ($\bar{x}$ = 34 cm.s^{-1}), maximum width ($\bar{x}$ = 5.8 m), maximum depth ($\bar{x}$ = 48 cm) and temperature ($\bar{x}$ = 9°C) (Table 3.1). The pH was neutral to alkaline except for one acidic stream and the specific conductance in all streams was low ($\bar{x}$ = 26 µS.cm^{-1}) (Table 3.1). Other macroalgal species in these streams included: the rhodophytes, Batrachospermum carpocontortum, Audouinella hermannii (Roth) Duby; the cyanobacteria, Nostoc commune Vaucher, Planktothrix tenue (Thur. ex Gomont) Anagn. & Komárek, Rivularia minutula (Kütz.) Bornet & Flahault, Schizothrix fuscescens Kütz., Scytonema tolypothricoides Kütz., Tolypothrix tenuis Kütz. emend. J.Schmidt.; the chlorophytes, Draparnaldia acuta (C.Agardh) Kütz., Mougeotiopsis calospora Palla, Oedogonium sp., Zygnema spp.; and the diatom, Tabellaria flocculosa (Roth) Kütz.

Batrachospermum trichofurcatum Sheath et M.L.Vis, sp. nov.

Fila monoica cum verticilli confluentibus et globularis, 448-1220 µm lato, 10-14 cellularum fasciculiorum compositae. Spermatangia multi in ramuli, lateralibus terminalia. Carpogonia 5-9 µm lato, 18-27 µm longitudine cum gynopilis furcatis. Rami carpogonialis 3-8 cellulas longitudine. Carposporangia 6-9 µm diametro, 8-12 µm longitudine. Gonimoblasti orbiculati, 78-156 µm diametro, cum 3-4 cellulis.

Plants are monoecious and have confluent, globose whorls (Fig. 3.9). Mature whorls contain carposporophytes and are 448-1220 μm in diameter and composed of 10-14 fascicle cells (Table 3.2). Spermatangia are formed at fascicle tips in abundant clusters (Fig. 3.10). Carpogonia range from 5-9 μm in diameter and 18-27 μm in length (Figs 3.11-3.14) and are on a 3-8-celled, undifferentiated branch (Figs 3.11-3.14) (Table 3.2). The trichogyne forms a slight protrusion (Fig. 3.11) which grows until the mature trichogyne is forked in appearance (Figs 3.12, 3.13). In some cases the furcation of the trichogyne may refork (Fig. 3.14). Carposporophytes are spherical, 1-8 per whorl and at various distances from the axis (Fig. 3.9) (Table 3.2). At maturity carposporophytes are from 78-156 μm in diameter (Table 3.2). Carposporangia are 6-9 μm in diameter and 8-12 μm in length and are formed at the tips of 3-4-celled gonimoblast filaments (Fig. 3.15) (Table 3.2).

Etymology: Epithet denotes the forked trichogyne of the carpogonium.

Holotype: R. G. Sheath CA 18. Route 101 in Redwood National Park at Prairie Creek Pk. (41°15'N, 124°00'W), California, USA, 18 iv 1988. Stream characteristics: see Table 3.1. Coll. R. G. Sheath. **UBC** A81617.

Remarks

The range in morphometric characteristics for Batrachospermum trichofurcatum is similar to other species within sect. Batrachospermum (Chapter 2). Therefore, the forked trichogyne is the distinguishing feature of B. trichofurcatum. Within the sect. Batrachospermum, trichogynes with protrusions have been reported for B. carpocontortum (Sheath et al., 1986b). However, in B. carpocontortum the protrusions are only slight at maturity and the carpogonium can be bent or twisted (Sheath et al., 1986b), whereas in B. trichofurcatum the trichogyne at maturity has a well-developed furcation and the carpogonium is never bent or twisted (Figs 3.12-3.14). Branched trichogynes and ones with protrusions have also been reported for species in sections Virescentia (Sheath et al., 1994a) and Turfosa (Sheath et al., 1994b), but species of these sections have axial carposporophytes, unlike sect. Batrachospermum.

Ecology

Batrachospermum trichofurcatum has only been found at the type locality in California (Fig. 3.1). At the site the temperature was 10°C, current velocity was slow (6 cm.s^{-1}) and the canopy open (Table 3.1). The stream had a maximum width of 3.7 m and depth of 58 cm with clear, yellow-coloured water. The pH was slightly alkaline (7.4) and specific conductance low (50 µS.cm^{-1}) (Table 3.1). Other macroalgae collected at the site were the cyanobacterium Phormidium retzii (C. Ag.) Gom. and the green algae Tetraspora lubrica (Roth) C. Ag. and Spirogyra cf. laxa Kütz.

Batrachospermum carpoinvolucrum Sheath et M.L.Vis, sp. nov.

Fila dioecious cum verticilli confluentibus et doliiformes. Verticilli feminei 489-853 µm lato, 12-14 cellularum fasciculiorum compositae. Spermatangia multi in ramuli, lateralibus terminalia. Carpogonia 6-8 µm lato, 15-26 µm longitudine. Rami carpogonialis 4-10 cellulas longitudine et carpogonia super bractae involucrorum longae. Carposporangia 7-11 µm diametro, 10-14 µm longitudine. Gonimoblasti orbiculati, 128-232 µm diametro, cum 3-4 cellulis.

Male and female plants have barrel-shaped, contiguous whorls (Figs 3.16, 3.20). The main axis is covered by heterocortication composed of cylindrical (Fig. 3.17) to bulbous cells (Figs 3.17, 3.18). Spermatangia are formed at the tips of fasicles (Fig. 3.19). Mature female whorls range from 489-853 µm in diameter and are composed of 12-14 fascicle cells (Fig. 3.20) (Table 3.2). Carpogonial branches are undifferentiated, 4-10 cells long and have long involucral filaments with apical carpogonia (Figs 3.21, 3.22). In addition, after the carpogonium starts to degenerate the carpogonial branch appears to continue to grow and extend beyond it (Fig. 3.22). Carpogonia have dimensions of 6-8 x 15-26 µm with sessile, clavate trichogynes (Fig. 3.23) (Table 3.2). Carposporophytes are spherical, 1-3 per whorl and protrude beyond the whorl (Fig. 3.20) (Table 3.2). At maturity carposporophytes are 128-232 µm in diameter. Carposporangia range from 7-11 µm in diameter and 10-14 µm in length and are formed at the tips of 3-4-celled gonimoblast filaments (Fig. 3.24) (Table 3.2).

Etymology: Epithet denotes the presence of carpogonia on the long involucral filaments of the carpogonial branch.

Holotype: R. G. Sheath AZ 10. Montezuma Well outflow canal (33°06'N, 113°10'W), Arizona, USA, 1 v 1989. Stream characteristics: See Table 3.1. Coll. R. G. Sheath. UBC A81613.

Remarks

Within Batrachospermum sect. Batrachospermum, B. carpoinvolucrum is most comparable to B. boryanum. Both species have similar measurements for all morphometric features with the exception of carposporophyte diameter with the former being larger ($\bar{x}$ = 175 vs. 96 µm, respectively), but the ranges overlap slightly (128-232 vs. 68-139 µm, respectively) (Chapter 2) (Table 3.2). In addition, both species are dioecious and have heterocortication. However, B. carpoinvolucrum is distinguished from B. boryanum in having carpogonia on the involucral filaments, the latter of which extend beyond the main carpogonial branches whereas B. boryanum has only vegetative involucral filaments. Carpogonial branches arising on another carpogonial branch have been reported for B. confusum (Drew 1946, Chapter 2). However, in B. confusum these branches are formed on the lower cells of the carpogonial branch and in B. carpoinvolucrum the carpogonia are on branches arising from the cells immediately subtending the carpogonium.

Ecology

Batrachospermum carpoinvolucrum has been collected only at the type locality in an Arizona spring, Montezuma well (Fig. 3.1). The canal was 1.35 m wide with a depth of 75 cm and moderate current velocity (29 $cm.s^{-1}$). The water was warm (24°C) and alkaline with high conductivity (pH = 7.2, specific conductance = 890 $\mu S.cm^{-1}$) (Table 3.1). Batrachospermum sp. and the chlorophyte Microspora pachyderma (Wille) Lagerh. were also found in the canal.

Batrachospermum involutum Sheath et M.L.Vis, sp. nov.

Fila monoica cum verticilli indistinctes, 627-1405 µm lato, 8-12 cellularum fasciculiorum compositae. Fasciculi apices involuti. Cellulae midi fasciculorum efferens rhizoidea. Carpogonia 7-10 µm lato, 30-54 µm longitudine. Rami carpogonialis 3-8 cellulas longitudine. Spermatangia non nisi super bractae involucrorum ab filis carpogonialibus fractis. Carposporangia 7-11 µm diametro, 12-18 µm longitudine. Gonimoblasti orbiculati, 112-237 µm diametro, cum 3-4 cellulis.

Plants have indistinct whorls ranging from 627-1405 µm in diameter and composed of 8-12 fascicle cells (Fig. 3.25) (Table 3.2). Paired fascicle tips are turned inward towards each other (Fig. 3.26). Mid-fascicle cells may produce rhizoidal outgrowths (Figs 3.27, 3.28). Carpogonial branches are undifferentiated, 3-8 cells long with both long and short involucral filaments and may have more than one carpogonium at the apex (Figs 3.29, 3.33) (Table 3.1). Carpogonium dimensions range from 7-10 μm in diameter and 30-54 μm in length (Table 3.1). Carpogonia have trichogynes which are typically lanceolate but may be curved or branched (Figs 3.30-3.33). Spermatangia were observed only at the apex of one-celled involucral filaments which arise on the subtending cell of the carpogonium (Fig. 3.33). Carposporophytes are spherical, 1-3 per whorl and may be either exerted or within the whorl (Fig. 3.25). At maturity, carposporophytes are from 112-237 μm in diameter (Table 3.2). Carposporangia range from 7-11 μm in diameter and 12-18 μm in length and are formed at the tips of 3-4-celled gonimoblast filaments (Fig. 3.34) (Table 3.2).

Etymology: Epithet denotes the involute tips of the vegetative fascicles.

Holotype: R. G. Sheath TX 7b. San Marcos River at San Marcos (29°54'N, 97°57'W), Texas, USA, 1 xii 1993. Stream characteristics: See Table 3.1. Coll. R. G. Sheath & M. L. Vis. UBC A81614.

Remarks

Within Batrachospermum, B. involutum is unique in having involute fascicle tips. B.

pulchrum Sirodot also has curled fascicles but they all curve in the same direction (Chapter 2). Rhizoidal growth from mid-fascicle cells has never been reported in any taxon of Batrachospermum. However, this attribute has been found in another species described below. B. involutum is similar to B. androinvolucrum of the sect. Setacea in having spermatangia formed exclusively on a one-celled involucral branch (Fig. 3.33) (Sheath et al., 1993b, Figs 5, 6), but the whorl diameters are significantly different and non-overlapping (627-1405 vs. 70-164 μm, respectively).

Ecology

Batrachospermum involutum has been collected only at the type locality in spring-fed river in Texas, the San Marcos River (Fig. 3.1). The river was relatively wide (20 m) and deep (>100 cm) with a high current velocity (97 cm. s^{-1}) (Table 3.1). The water was warm (21°C), clear, colourless and alkaline with high conductivity (pH = 8.0, specific conductivity = 560 $\mu S.cm^{-1}$) (Table 3.1). Other macroalgae found included the rhodophytes Hildenbrandia angolensis Welw. ex W. et G. S. West, Sirodotia huillensis (Welw. ex W. et G.S.West) Skuja and Thorea violacea Bory, the chrysophyte Terpsinoe musica A.Ehrlich and the chlorophytes Cladophora glomerata (L.) Kütz., Dichotomosiphon tuberosus (A.Braun) Ernst., Nitella furcata (Roxb. ex Bruzelius) C.Agardh and Pithophora mooreana Collins. This is the second report of Sirodotia huillensis in North America and the first was from a stream in Arizona (Necchi et al., 1993).

Batrachospermum trichocontortum Sheath et M.L.Vis, sp. nov.

Fila dioecious cum verticilli globularis separati fascicularis secundariis. Verticilli feminei 1110-1970 μm lato, 12-18 cellularum fasciculiorum compositae. Cellulae midi fasciculorum efferens rhizoidea. Spermatangia multi in ramuli, lateralibus terminalia. Carpogonia 7-10 μm lato, 23-39 μm longitudine. Rami carpogonialis 4-8 cellulas longitudine. Carposporangia 5-9 μm diametro, 9-14 μm longitudine. Gonimoblasti orbiculati, 135-304 μm diametro, cum 2-4 celluli.

Male and female plants with globose whorls separated by abundant secondary fascicles (Figs 3.35, 3.39). The mid fascicle cells form rhizoidal outgrowths (Figs 3.36, 3.37) which can become quite long (Fig. 3.37). The spermatangia are in dense clusters at the tips of vegetative fascicles (Fig. 3.38). Mature female whorls are relatively large ranging from 1110-1970 μm in diameter and are composed of 12-18 fascicle cells (Fig. 3.39) (Table 3.2). Carpogonial branches are undifferentiated and 4-8-celled with both long and short involucral filaments (Fig. 3.40) (Table 3.2). Carpogonium dimensions range from 7-10 μm in diameter and 23-39 μm in length (Figs 3.41-3.43) (Table 3.2). The trichogyne tip may be undulated, capitate or helically twisted (Figs 3.41-3.43). Carposporophytes are spherical, 1-4 per whorl and at various distances from the axis (Fig. 3.39) (Table 3.2). At maturity carposporophytes are spherical and range from 135-304 μm in diameter. Carposporangia range from 5-9 μm in diameter and 9-14 μm in length and are formed at the tips of 2-4-celled gonimoblast filaments (Fig. 3.44) (Table 3.2).

Etymology: Epithet denotes a carpogonium with a consistently contorted trichogyne tip.

Holotype: R. G. Sheath SC 2. Route 121 5 km north of Route 76 and outskirts of Newbury (34°16'N, 81°37'W), South Carolina, USA, 21 iii 1989. Stream characteristics: See Table 3.1. Coll. R. G. Sheath & D. Kaczmarczyk. UBC A81616.

Remarks

Most morphometric characteristics of Batrachospermum trichocontortum are similar to those reported for other species in sect. Batrachospermum (Chapter 2) (Table 3.2). However, the whorl diameter of B. trichocontortum is larger than other species such as B. arcuatum Kylin and B. gelatinosum (> 1110 vs. < 974 μm, respectively) (Chapter 2) (Table 3.2). B. trichocontortum is similar to B. heterocorticum, with both species producing abundant secondary fascicles, but the former species has larger and non-overlapping whorl diameter (1110-1970 vs. 492-876 μm, respectively) and the former lacks heterocortication (Sheath & Cole, 1990; Chapter 2) (Table 3.2). Rhizoidal outgrowths from mid-fascicle cells have been reported for the first time in this paper for B. trichocontortum and B. involutum. Although these two species share this attribute, they differ in fascicle tip and carpogonium morphology. In addition, B. trichocontortum is dioecious and B. involutum is monoecious. B. trichocontortum has the twisting or contortion of the trichogyne restricted to the tip which distingushes it from B. carpocontortum which has bends and twists at various points along the trichogyne (Sheath et al., 1986b) (Figs 3.41-3.43).

Ecology

Batrachospermum trichocontortum has been collected only at the type locality in South Carolina (Fig. 3.1). The stream was relatively small, being 2.5 m wide and 31 cm depth, partly shaded by the canopy and had a moderate flow (30 $cm.s^{-1}$) and temperature (15°C) (Table 3.1). The water was clear, brown coloured with a slightly alkaline pH and low conductance (50 $\mu S.cm^{-1}$) (Table 3.1). Another species of Batrachospermum belonging to the sect. Virescentia, B. helminthosum Bory was collected at the same location. In addition, the cyanophyte Phormidium subfuscum Kütz. and the tribophyte Vaucheria sp. were identified from this site.

3.4 Discussion

Even though 1000 stream segments from throughout North America were surveyed and all relevant type specimens and collections from every major North American herbaria were examined, four of the new species, Batrachospermum trichofurcatum, B. carpoinvolucrum, B. involutum and B. trichocontortum, were found in only the type location. B. carpoinvolucrum and B. involutum from desert springs are geographically isolated and may have undergone speciation analygous to that of the desert pupfish (Miller, 1981). These four species are distinguished from the other species of Batrachospermum sect. Batrachospermum on the basis of distinct features and they exhibit some characteristics, such as rhizoidal outgrowths from mid portions of fascicles, carpogonia on the involucral filaments of carpogonial branches of other carpogonia, involute fascicles and furcate trichogynes, which have not been described previously for any taxon of Batrachospermum. Hence, based on extensive collection and analysis of specimens and the uniqueness of the features of these four species, we conclude that they are not just local variant populations but well distinguished yet rare species.

Table 3.1. Physical and chemical characteristics of stream segments containing new species of Batrachospermum sect. Batrachospermum in North America.

Population number[a]	Location[b]	Maximum width (m)	Maximum depth (cm)	Mean current velocity ($cm.s^{-1}$)	Temperature (°C)	pH	Specific conductance ($\mu S.cm^{-1}$)	Water colour[c]
1	AK 5	9.9	67	39	13	-	27	1
2	AK 58	1.2	11	4	9	7.8	60	0
3	BC 2	-	-	-	-	-	-	-
4	BC 17a	8	60	58	12	8.3	40	0
5	BC 76	5	>100	10	10	7.9	20	-
6	BC 86	7	43	32	14	7.9	30	0
7	WA 110	20	>100	30	10	5.0	-	1
8	NWT 10	1.2	33	8	3	6.0	10	0

9	NWT 43	2.3	17	63	5	7.4	5	0
10	NWT 45	8	18	50	7	6.6	10	0
11	NWT 55	0.9	23	24	2	-	30	0
12	NWT 61	4	30	35	16	7.4	34	0
13	LAB 13	5	>100	96	6	7.3	12.5	0
14	GLD 5	3.5	45	80	13	8.1	90	0
15	GLD 20	3.3	27	2	17	7.3	60	0
16	CA 18	3.7	58	6	10	7.4	50	1
17	AZ 10	1.2	75	29	24	7.2	890	-
18	TX 7b	20	>100	97	21	8.0	560	0
19	SC 2	2.5	31	30	15	7.3	50	1

[a] Populations as indicated on Fig. 3.1.

[b] AK, Alaska; BC, British Columbia; WA, Washington; NWT, Northwest Territiories; LAB, Labrador; GLD, Greenland;

CA, California; AZ. Arizona: TX. Texas: SC. South Carolina.

[c] 0. colourless; 1. yellow coloured.

Table 3.2. Morphometric characteristics of new species of Batrachospermum sect. Batrachospermum from North America. Mean (range).

Taxon	Whorl diameter (µm)	Fascicle length (cells)	Carposporophyte height-to whorl diameter	Carposporophyte: Number per whorl	Carposporophyte: Diameter (µm)	Carposporophyte: Cell number	Carpogonium: Diameter (µm)	Carpogonium: Length (µm)	Carpogonium: Form factor[a]	Carpogonium: Branch cell number	Carposporangium: Diameter (µm)	Carposporangium: Length (µm)
B. spermato-involucrum	514 (239-846)	8.3 (5-18)	0.76 (0.37-1.30)	3.8 (1-10)	79 (44-158)	2.4 (2-4)	10.9 (8-17)	56.7 (40-86)	0.22 (0.14-0.33)	6.3 (3-11)	8.8 (6-14)	11.1 (6-16)
B. tricho-furcatum	841 (448-1220)	11.7 (10-14)	0.72 (0.58-1.03)	3.1 (1-8)	108 (78-156)	3.5 (3-4)	6.9 (5-9)	23.2 (18-27)	0.34 (0.26-0.45)	5.5 (3-8)	7.7 (6-9)	10.4 (8-12)
B. carpo-involucrum	648 (489-853)	13.0 (12-14)	0.83 (0.71-1.09)	1.9 (1-3)	175 (128-232)	3.3 (3-4)	7.5 (6-8)	21.0 (15-26)	0.40 (0.30-0.47)	6.4 (4-10)	8.1 (7-11)	11.8 (10-14)
B. involutum	999 (627-1405)	10.1 (8-12)	0.81 (0.65-1.04)	2.1 (1-3)	161 (112-237)	2.3 (2-3)	8.4 (7-10)	40.9 (30-54)	0.30 (0.18-0.35)	[illegible] (3-8)	9.1 (7-11)	14.9 (12-18)
B. tricho-contortum	1510 (1110-1970)	13.9 (12-18)	0.48 (0.26-0.60)	2.5 (1-4)	184 (135-304)	3.0 (2-4)	8.5 (7-10)	28.6 (23-39)	0.32 (0.20-0.39)	6.3 (4-8)	7.2 (5-9)	11.3 (9-14)

n = 30 except carpogonia where n = 15.

[a] See Sheath et al. (1986b) for description.

Fig. 3.1. Location of North American stream sites from which newly described species of Batrachospermum sect. Batrachospermum were collected. The numbers correspond to the stream numbers in Table 3.1. Dark lines indicate major drainage basins.

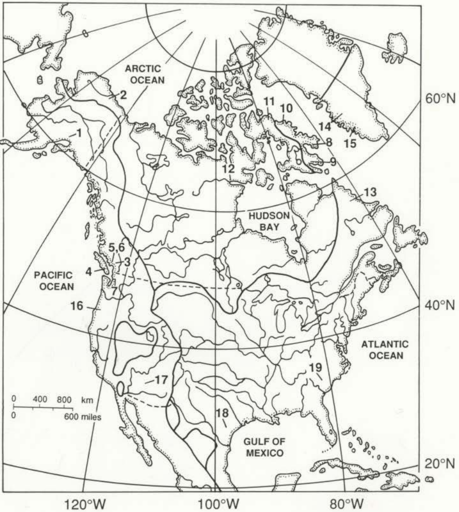
ARCTIC OCEAN
HUDSON BAY
PACIFIC OCEAN
ATLANTIC OCEAN
GULF OF MEXICO
60°N
40°N
20°N
120°W
100°W
80°W
0 400 800 km
0 600 miles
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Plate VII

Figs 3.2-3.15. Morphological characteristics of Batrachospermum spermatoinvolucrum and B. trichofurcatum. Figs 3.2-3.8. B. spermatoinvolucrum holotype and other specimens. Fig. 3.2. Main axis with confluent, globose whorls containing numerous spherical carposporophytes (arrowheads) at various distances from the axis (BC 86). Fig. 3.3. Axial cells covered by cortical filaments composed of regular, cylindrical cells (arrowhead) (LAB 13). Fig. 3.4. Fascicle tips with abundant spermatangia (arrowheads) (NWT 55). Fig. 3.5. Fertilized carpogonium with clavate trichogyne (small arrowhead) and carpogonial branch with involucral filaments some of which have apical spermatangia (large arrowhead) (BC 76). Fig. 3.6. Fertilized carpogonium with elongate trichogyne (small arrowhead) and base surrounded by involucral filaments which have spermatangia (large arrowheads) at their tips (LAB 13). Fig. 3.7. Carpogonium with elongate, concave, lanceolate trichogyne (small arrowhead) and base surrounded by dense involucral filaments with apical spermatangia (large arrowheads) (LAB 13). Fig. 3.8. Carposporophyte with short, dense 2-3-celled gonimoblast filaments having apical carposporangia (arrowheads) (AK 5). Figs 3.9-3.15. B. trichofurcatum holotype. Fig. 3.9. Main axis with globose whorls containing spherical carposporophytes (arrowheads) at various distances from the axis. Fig. 3.10. Fascicle tips with abundant spermatangia (arrowhead). Fig. 3.11. Carpogonium with trichogyne forming a slight protrusion (arrowhead). Fig. 3.12. Carpogonium with forked trichogyne (arrowheads) having a spermatium attached to each fork. Fig. 3.13. Fertilized carpogonium with well-forked trichogyne (arrowheads). Fig. 3.14. Carpogonium with forked trichogyne with one of the furcations reforked (arrowhead). Fig. 3.15. Carposporophyte composed of dense 2-3-celled gonimoblast filaments with apical carposporangia (arrowheads). (Scale bars represent: Fig. 3.2, 200 μm; Fig. 3.3, 100 μm; Figs 3.4, 3.5, 3.8, 3.10, and 3.15, 10 μm; Figs 3.6 and 3.7, 15 μm; Fig. 3.9, 350 μm; Fig. 3.11, 5 μm; Figs 3.12, 3.13 and 3.14, 7 μm)

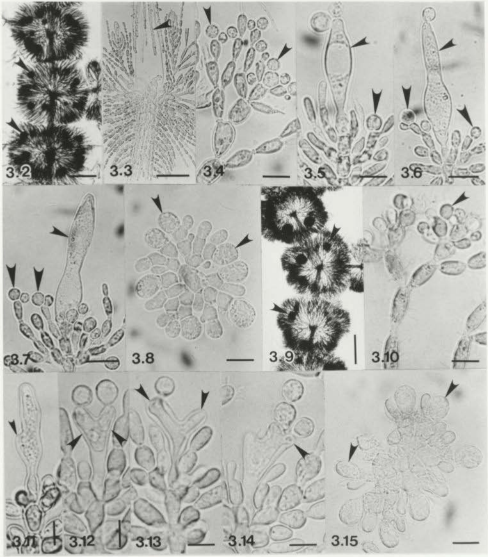

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Plate VIII

Figs 3.16-3.24. Morphological characteristics of Batrachospermum carpoinvolucrum holotype. Fig. 3.16. Male plant main axis with confluent, barrel-shaped whorls. Fig. 3.17. Cortication of main axis with cylindrical (large arrowhead) to bulbous (small arrowhead) cells. Fig. 3.18. Bulbous, clavate cortical cells. Fig. 3.19. Fascicle tip with abundant spermatangia (arrowheads). Fig. 3.20. Female plant main axis with confluent, barrel-shaped whorls having large spherical exserted carposporophytes (arrowhead). Fig. 3.21. Carpogonia (arrowheads) with long involucral filaments having carpogonia (large arrowheads) at their tips. Fig. 3.22. Degenerating carpogonium pushed aside (small arrowhead) by elongating carpogonial branch and involucral filaments with apical carpogonia (large arrowheads). Fig. 3.23. Fertilized carpogonium with ovoid trichogyne (arrowhead). Fig. 3.24. Carposporophyte with dense 2-4-celled gonimoblast filaments having apical carposporangia (arrowheads). (Scale bars represent: Figs 3.16 and 3.20, 350 μm; Fig. 3.17, 100 μm; Figs 3.18, 3.19, 3.21, 3.22 and 3.24, 20 μm; Fig. 3.23, 10 μm)

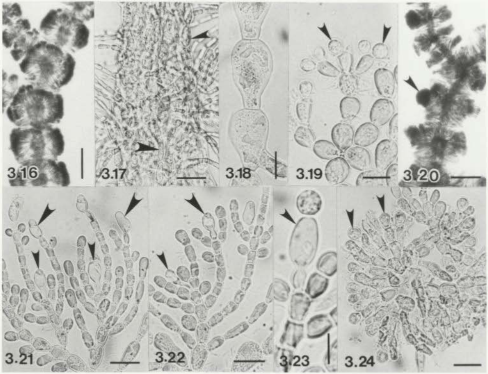
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Plate IX

Figs 3.25-3.34. Morphological characteristics of Batrachospermum involutum holotype. Fig. 3.25. Main axis with indistinct whorls having small spherical peripheral to exserted carposporophytes (arrowheads). Fig. 3.26. Fascicles with dicotomous involute tips (arrowheads). Fig. 3.27. Mid fascicle cell with developing rhizoidal outgrowth (arrowhead). Fig. 3.28. Mid fascicle cell producing a relatively long rhizoidal outgrowth (arrowhead). Fig. 3.29. Carpogonial branch with three carpogonia (arrowhead). short involucral filaments (large arrowhead) and long involucral filaments (double arrowhead). Fig. 3.30. Carpogonium with lanceolate trichogyne (arrowhead). Fig. 3.31. Carpogonium with curved laceolate trichogyne (arrowhead). Fig. 3.32. Carpogonium with branched, lanceolate trichogyne (arrowhead). Fig. 3.33. Carpogonial branch with two carpogonia (arrowheads) and a one-celled branch having a spermatangium (large arrowhead) at its tip. Fig. 3.34. Carposporophyte with short gonimoblast filaments having apical carposporangia (arrowheads). (Scale bars represent: Fig. 3.25, 450 μm; Fig. 3.26, 25 μm; Figs 3.27, 3.28, 3.29, 3.30, 3.31, 3.32, 3.33 and 3.34, 10 μm)

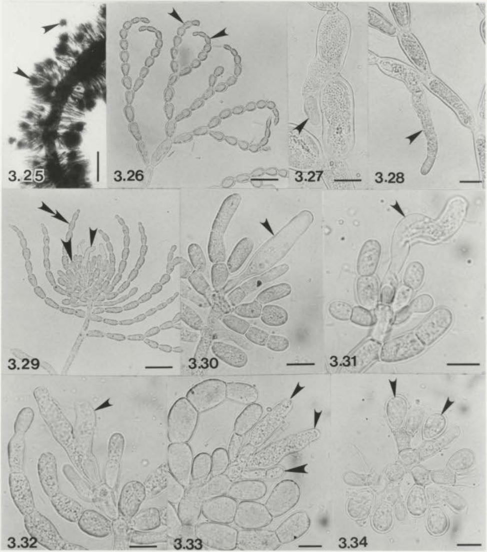
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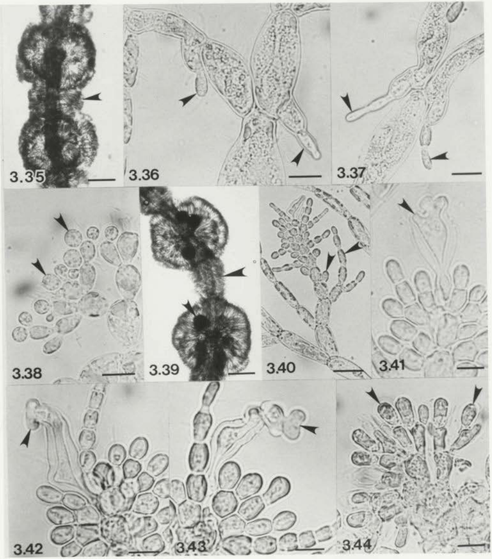
Plate X

Figs 3.35-3.44. Morphological characteristics of Batrachospermum trichocontortum holotype. Fig. 3.35. Male plant main axis globose whorls separated by dense secondary fascicle growth (arrowhead). Fig. 3.36. Mid fascicle cells with rhizoidal outgrowths (arrowheads). Fig. 3.37. Mid fascicle cells with well developed rhizoidal outgrowths (arrowheads). Fig. 3.38. Fascicle tips with abundant spermatangia (arrowheads). Fig. 3.39. Female plant main axis with globose whorls containing spherical carposporophytes (small arrowhead) separated dense secondary fascicle growth (large arrowhead). Fig. 3.40. Carpogonium on seven-celled undifferentiated branch with dense involucral filaments of various lengths (arrowheads). Fig. 3.41. Carpogonium with trichogyne undulate tip (arrowhead) and base surrounded by dense involucral filaments. Fig. 3.42. Carpogonium with trichogyne capitate tip (arrowhead) and base surrounded by dense involucral filaments. Fig. 3.43. Carpogonium with trichogyne helical twisted tip (arrowhead) and base surrounded by dense involucral filaments. Fig. 3.44. Carposporophyte with short gonimoblast filaments having apical carposporangia (arrowheads). (Scale bars represent: Figs 3.35 and 3.39, 550 μm; Figs 3.36, 3.37, 3.38 and 3.44, 10 μm; Fig. 3.40, 30 μm; Figs 3.41, 3.42 and 3.43, 7 μm)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Distribution and systematics of Batrachospermum section Batrachospermum in North America: Previously described species excluding Batrachospermum gelatinosum

4.1. Introduction

Sect. Batrachospermum of the freshwater red algal genus Batrachospermum is generally characterised by the following features: well-developed whorls, undifferentiated and straight carpogonial branches arising from both fascicle and pericentral cells, nonpedicellate carpogonia with club- to urn-shaped trichogynes and relatively small, globose, pedicellate carposporophytes at various distances from the whorl axis (Mori, 1975; Starmach, 1977; Kumano, 1993). Within the section, species have been distinguished on the basis of monoecious or dioecious thalli, carpogonium size and the presence or absence of contorted carpogonia, spermatangia on involucral filaments, irregular cortication, monosporangia, well-curled fascicles and abundant secondary fascicles (Chapter 2). In a review of the type specimens from sect. Batrachospermum, it was concluded that there are 15 well-defined species worldwide.

Taxa of Batrachospermum sect. Batrachospermum have been reported from Europe, Asia, Australia, South America and North America (e.g. Sirodot, 1884; Reis, 1974; Mori, 1975; Entwisle & Kraft, 1984; Necchi, 1990; Sheath & Cole, 1992). Although sect. Batrachospermum is the most widespread infrageneric taxon of the freshwater Rhodophyta (Sheath & Hambrook, 1990; Sheath & Cole, 1992), there has been no summary of the known species distribution or morphological variation. Therefore, an examination of the distribution and systematics of this section is warranted.

In North America, eight species from Batrachospermum sect. Batrachospermum have been previously reported, including B. anatinum, B. boryanum, B. carpocontortum. B. confusum (as B. crouanianum nom. illeg.), B. gelatinosum (often as B. moniliforme nom. illeg.), B. heterocorticum, B. pulchrum Sirodot and B. skujae (as B. sporulans nom. illeg.) (e.g. Hylander, 1928; Vinyard, 1966; Sheath & Burkholder, 1983; Sheath & Cole, 1992). B. gelatinosum, the type species of the genus, is one of the five most widespread macroalgae in North America and has been collected from numerous locations in all biomes except the tropical rain forest and desert/chaparral (Sheath & Cole, 1992). Therefore, a separate chapter has been devoted to this species. The present study examines morphological variation and distribution of other previously described species of Batrachospermum sect. Batrachospermum collected in a survey of 1000 stream segments from North America (Sheath & Cole, 1992) and compares these specimens to relevant type specimens from the analysis (Chapter 2).

4.2. Materials and methods

Sixty-two populations of Batrachospermum sect. Batrachospermum excluding B. gelatinosum were collected from south central Alaska (64°N) and Greenland (66°N) in the north to Louisiana (30°N) in the south (Fig. 4.1). Samples were immediately fixed in 2.5% calcium carbonate-buffered glutaraldehyde. Maximum depth and width, pH, specific conductance, temperature, and mean current velocity were measured in each stream segment in a similar manner to that described in Chapter 3 (Table 4.1).

Specimens were measured for the morphological characteristics as described in Chapter 2 (Table 4.2) in replicates of 30 (15 for carpogonia), using a SMI image analysis system. Qualitative features, monoecious or dioecious thalli, heterocortication, and spermatangia on the involucral filaments of the carpogonial branch, were also noted since these characteristics have been used to differentiate taxa in sect. Batrachospermum (Chapter 2). Characteristics of each taxon were photographed with an Olympus PM-10 AK camera system. To compare means of morphometric characteristics measured among populations of a species and the type specimens from Chapter 2, analysis of variance (ANOVA) and Duncan's multiple-range test were calculated according to the SAS statistical package (Anonymous, 1988). All statistical differences are significant at the $p < 0.05$ level.

4.3. Results and discussion

Five populations referable to B. anatinum were collected in North America (Fig. 4.1) (Table 4.1). These populations are similar to the type specimen in the two distinguishing qualitative features, monoecious thalli and the presence of heterocortication, in addition to most morphometric measurements (Table 4.2). The type specimen means for whorl diameter, carpogonium length and carpogonial branch number were significantly different from the North American populations. However, the range in all these characteristics overlapped between the type specimen and North American populations (Table 4.2). Therefore, the North American populations are considered to be B. anatinum.

The North American populations of B. anatinum are monoecious and have confluent globose whorls (Fig. 4.2). Mature whorls, containing carposporophytes, range from 416-1085 μm in diameter and are composed of 6-13 fascicle cells (Table 4.2). The main axis is covered by heterocortication, which consists of both bulbous and cylindrical cells (Fig. 4.3). Ovoid spermatangia are formed at the tips of vegetative fascicles (Fig. 4.4). The carpogonial branch is composed of 3-7 undifferentiated cells (Fig. 4.5) (Table 4.2). Carpogonia are 17-36 μm in length and have clavate to lanceolate trichogynes with a diameter of 7-11 μm (Figs 4.5, 4.6) (Table 4.2). Carposporophytes are spherical, 1-14 per whorl and at various distances from the axis (Fig. 4.2) (Table 4.2). At maturity, carposporophytes range from 66-173 μm in diameter. Carposporangia are obovoid, 7-10 μm in diameter and 8-15 μm in length, and they are produced apically on 2-4-celled gonimoblast filaments (Fig. 4.7) (Table 4.2).

In North America, collections of B. anatinum are localised in five streams, three in Missouri, and one in both Arkansas and Virginia (Fig. 4.1) (Table 4.1). These streams are in the deciduous forest and coastal plain biomes. The two locations with physical and chemical measurements tended to vary in terms of current velocity ($\bar{x}$ = 6, 57 $cm.s^{-1}$) and be moderate in maximum width (1.0, 4.5 m), maximum depth (33, 65 cm) and temperature (9, 13 °C). The pH was neutral to alkaline (7.5, 8.0) and specific conductance was relatively high (240, 280 $\mu S.cm^{-1}$) (Table 4.1). This species has been previously reported in North America from Connecticut (Hylander, 1928). In addition, herbarium specimens of B. anatinum from California, Indiana, Missouri, Montana, Ohio, Ontario and Pennsylvania exist (see Appendix 1). Worldwide, B. anatinum is known from Europe, including the type locality in France (Sirodot, 1884) and sites in Belgium (Van Meel, 1939a), Latvia (Skuja, 1928), Portugal (Reis, 1962, 1974) and Sweden (Kylin, 1912). Therefore, the range of this species extends further north in Europe (64°N) than in North America (50°N) (this study; Kylin, 1912). This trend is similar to that found for other freshwater red algae, such as Thorea (Sheath et al., 1993c) and Hildenbrandia (Sheath et al., 1993a). In Portugal, Reis (1974) described B. anatinum from habitats with similar temperatures (10-12°C), but lower pH (6.5) than the North American stream sites (Table 4.1).

B. anatinum may be more widespread than the literature would suggest. Sirodot (1884) separated this species from B. boryanum on the basis of monoecious thalli in the former and dioecious plants in the latter species. Other authors (e.g. Israelson, 1942; Kumano, 1993) have chosen to synonymise vegetatively similar monoecious and dioecious species, such as B. anatinum with B. boryanum. Therefore, B. anatinum per se may be under-reported.

Six populations from North America were similar to B. arcuatum (Fig. 4.1), having separate male and female plants and the main axis covered by cortical cells which are strictly cylindrical (Figs 4.8, 4.10) (Chapter 2). In addition, the means of morphometric features measured from the type specimen do not significantly differ from those of the North American populations and the ranges in characteristics are similar (Table 4.2). Therefore, the North American populations are not morphologically distinct and represent B. arcuatum.

The North American populations of B. arcuatum are dioecious and have globose to barrel-shaped whorls, composed of 7-16 celled fascicles (Figs 4.8, 4.10). Male thalli have ovoid spermatangia formed at the tips of the vegetative fascicles (Fig. 4.9). Mature female whorls range from 333-1089 μm in diameter and contain 1-7 spherical carposporophytes (Fig. 4.10) (Table 4.2). Carpogonial branches are 3-11-celled and undifferentiated. Carpogonia are 21-43 μm in length and have clavate trichogynes that are 5-14 μm in diameter (Fig. 4.11) (Table 4.2). Carposporophytes are 68-217 μm in diameter and are composed of 2-3-celled gonimoblast filaments with apical, obovoid carposporangia (Fig. 4.12) (Table 4.2). Carposporangia dimensions are 7-11 μm in diameter and 9-13 μm in length (Table 4.2).

B. arcuatum was collected from six stream sites in western North America, two in the boreal forest, three in western coniferous forest and one in dessert-chaparral (Fig. 4.1) (Table 4.1). Streams tended to be moderate in maximum width ($\bar{x}$ = 8.5 m), maximum depth ($\bar{x}$ = 60 cm) and temperature ($\bar{x}$ = 9°C) (Table 4.1). The water was clear and current velocity was moderate to high (32-93 $cm.s^{-1}$). The pH was slightly alkaline ($\bar{x}$ = 7.6) and specific conductance was low ($\bar{x}$ = 60 $\mu S.cm^{-1}$). Additional herbarium specimens from California and Utah were determined to be B. arcuatum (see Appendix 1). Therefore, it appears that this species has a western distribution in North America which ranges from Alaska to central Mexico. Worldwide, this species has been reported only in Europe from Belgium (Compère, 1991), Crimea (Moshkova, 1960), Poland (Starmach, 1984, 1989; Siemińska, 1992), Portugal (Reis, 1974) and Sweden (Kylin, 1912). In Portugal, this species inhabits waters with similar pH (7.2) and temperatures (12-15°C) (Reis, 1974) as those from North America (Table 4.1). However, in Poland Starmach (1989) collected B. arcuatum from streams with lower pH (5.5-6.5) and temperature (7-8°C).

Thirty-four populations referable to B. boryanum were collected throughout temperate North America (Fig. 4.1) (Table 4.1). These populations are dioecious (Figs 4.13, 4.16) and have heterocortication (Fig. 4.14) similar to the type specimen of this species (Chapter 2, Figs 2.3, 2.71). Only 17 of these populations examined were mature, having carposporophytes. A distinct attribute observed in all the North American populations is curled branch tips (Figs 4.13, 4.16), previously noted by Sheath and Burkholder (1983). This characteristic was not reported in the type specimen (Chapter 2). However, curled branch tips may not be readily distinguishable in dried herbarium specimens. The means of the morphometric measurements varied greatly among populations and were in a continuum among populations. They did not significantly differ from the means of at least three other population means with the exception of CT 7 for whorl diameter and NC 104 for carposporangium length.

However, the ranges in these two features for CT 7 and NC 104 overlapped with the other populations. Means in morphometric characteristics for the type specimen of B. boryanum did not significantly differ from the North American populations except for larger whorl diameter and number of carposporophytes per whorl (Table 4.2). The range in whorl diameter for the North American populations encompasses that for B. boryanum (Table 4.2). In contrast, the range in carposporophyte number for the type specimen does not overlap with that of the North American populations (12-30 vs. 1-10, respectively). This apparent difference may be due to the greater size or reproductive maturity of the B. boryanum type specimen.

The North American populations of B. boryanum are dioecious and have globose whorls composed of 5-13-celled fascicles (Figs 4.13, 4.16). The main axis of both male and female thalli is covered by heterocortication, consisting of both cylindrical and inflated cells (Fig. 4.14). Male plants have abundant ovoid spermatangia at the tips of vegetative fascicles (Fig. 4.15). Mature female whorls, containing 1-10 spherical carposporophytes, range from 320-1360 μm (Fig. 4.16) (Table 4.2). Carpogonia are formed on a 3-10-celled, undifferentiated carpogonial branch (Table 4.2). Carpogonia are 17-39 μm in length and have clavate (Fig. 4.17) to lanceolate (Fig. 4.18) trichogynes which are 5-11 μm in diameter. At maturity, carposporophytes are 61-167 μm in diameter. Carposporangia are obovoid, 6-10 μm in diameter and 7-13 μm in length, and are produced apically on 2-4-celled gonimoblast filaments (Fig. 4.19) (Table 4.2).

The thirty-four populations of B. boryanum collected appear to be concentrated in eastern North America from Newfoundland through Georgia, but this alga was also found in isolated streams of Michigan and British Columbia (Fig. 4.1) (Table 4.1). B. boryanum has been reported in numerous locations throughout North America from Arkansas, Connecticut, Georgia, Illinois, Massachusetts, Michigan, Missouri, Newfoundland, New Hampshire, New York, North Carolina, Quebec, Rhode Island, Tennessee, Vermont, Virginia, West Virginia and Wisconsin (Hylander, 1928; Drouet, 1933; Croasdale, 1935; Britton, 1944; Flint, 1948, 1949, 1957a, 1957b; Prescott, 1962; Whitford & Schumacher, 1968, 1973; Woelkerling, 1975; Sheath & Burkholder, 1983, 1985; Sheath & Cole, 1993). Additional herbarium specimens from locations in California, Indiana, Nevada, New Brunswick, New Jersey, South Carolina, South Dakota, Washington and Wyoming extend the confirmed range of this species (see Appendix 1). In North America, B. boryanum seems to have a broad temperate distribution, but it is not found in the tundra or tropical rain forest. Streams containing this species tend to be moderate in size (maximum width, $\bar{x}$ = 4.7 m; maximum depth $\bar{x}$ = 36 cm), flow (mean current velocity, $\bar{x}$ = 53 $cm.s^{-1}$) and temperature ($\bar{x}$ = 10.5°C) (Table 4.1). The pH is slightly acidic to neutral ($\bar{x}$ = 6.9) with a correspondingly low specific conductance ($\bar{x}$ = 104 μS.cm). The water colour varies from clear to yellow-coloured (Table 4.1). B. boryanum seems equally widespread in Europe, being collected from Belgium (Van Meel, 1939a; Compère, 1991), Crimea (Moshkova, 1960), France (Sirodot, 1884), Poland (Starmach, 1984, 1989; Siemińska, 1992), Portugal (Reis, 1972), Romania (Lungu, 1969) and Sweden (Kylin, 1912; Israelson, 1942). In addition, this alga has been reported from Australia (Entwisle, 1989) and South America (Necchi, 1989, 1990). In Poland, B. boryanum occurs in streams with similar pH (6.5-7.5) and temperatures (2-12°C) as those in North America.

In North America, six populations attributable to B. confusum were collected (Fig. 4.1) (Table 4.1). In comparison with the type specimen, the North American populations are similar in having the distinguishing qualitative characteristics of heterocortication and spermatangia on the involucral filaments of the carpogonial branch (Figs 4.21, 4.23, 4.24) (Chapter 2). In terms of morphometric characteristics, the type specimen of B. confusum has significantly larger mean carposporophyte number and carpogonial branch cell number and significantly smaller mean carposporophyte diameter, carpogonial dimensions and carposporangium length than the North American populations (Table 4.2). Even though the type specimen means differ from those of the North American populations in many characteristics, all of the ranges overlap (Table 4.2). Thus, the North American populations represent a continuum with the type specimen and are considered to be synonymous with B. confusum.

The North American populations of B. confusum have monoecious thalli with barrel-shaped whorls composed of 6-13-celled fascicles (Fig. 4.20) (Table 4.2). Mature whorls range from 466-1184 μm in diameter and have 1-12 spherical carposporophytes within and protruding from the outer part of the whorl (Fig. 4.20) (Table 4.2). The main axis is covered by heterocortication (Fig. 4.21). Spermatangia are ovoid and formed at both the tips of the vegetative fascicles (Fig. 4.22) and 20-73% of the carpogonial branches (Figs 4.23, 4.24). Carpogonia are 19-46 µm in length and have clavate (Fig. 4.23) to bent, lanceolate (Fig. 4.24) trichogynes 6-10 µm in diameter (Table 4.2). At maturity, carposporophytes are 58-193 µm in diameter. Carposporangia are obovoid and range from 7-13 µm in diameter and 10-19 µm in length and are produced apically on 2-4-celled gonimoblast filaments (Fig. 4.25) (Table 4.2).

The six populations of B. confusum from North America are from the western coniferous, boreal, hemlock-hardwood and deciduous forest biomes. The stream sites were moderate in maximum width ($\bar{x}$ = 5.5 cm), maximum depth ($\bar{x}$ = 42 cm), temperature ($\bar{x}$ = 15°C) and mean current velocity ($\bar{x}$ = 44 $cm.s^{-1}$) (Table 4.1). The pH was slightly acidic to alkaline (6.4-8.5) with a corresponding range in specific conductance (20-490 $\mu S.cm^{-1}$). Most streams were clear with one exception having yellow-coloured water (Table 4.1). B. confusum has been reported previously from North America in Oklahoma (Vinyard, 1966; Blair, 1978). Sheath and Cole (1993) reported B. crouanianum, a synonomy of B. confusum, from the Northwest Territories, but this population has regular cylindrical cortication and cannot be classified as B. confusum. Worldwide, B. confusum has been reported from Portugal (Reis, 1962, 1974) and United Kingdom (Hassall, 1845; Cooke, 1882), as B. crouanianum from

France (Sirodot, 1884), Poland (Starmach, 1984, 1989; Siemińska, 1992), Portugal (Reis, 1969) and Sweden (Israelson, 1942), as B. fruticulosum from England ([illegible]w, 1946) and as B. helminthosum Sirodot from Belgium (Van Meel, 1939a) and Sweden (Kylin, 1912). The populations from Portugal and Poland were collected in streams with similar pH (6.4-6.9, 7.0, respectively) and temperatures (15-16, 11°C, respectively) to those in North America (Reis, 1974; Starmach, 1989).

Five populations were collected in North America corresponding to B. heterocorticum (Fig. 4.1) (Table 4.1). These populations are similar to the type specimen in having abundant secondary fascicle development (Chapter 2). In addition, the type specimen and North American specimens do not significantly differ in any of the morphological measurements except carposporophyte number (Table 4.2). Although the type specimen has more carposporophytes per whorl on average, the range in this characteristic overlaps considerably with those of the other North American populations (2-8 vs. 1-4, respectively). Hence, these populations are attributable to B. heterocorticum.

The North American populations of B. heterocorticum are dioecious and have globose whorls separated by abundant secondary fascicle growth (Figs 4.26, 4.29). The main axis of both the female and male plants is covered by heterocortication (Fig. 4.27). Spermatangia are ovoid and formed at the fascicle tips of the male plants (Fig. 4.28). Mature female whorls, containing 2-8 spherical carposporophytes, are 294-972 µm in diameter and composed of 6-11-celled fascicles (Fig. 4.29) (Table 4.2).

Carpogonia are 21-35 μm in length and have wide lanceolate trichogynes (Fig. 4.30) which are 3-11 μm in diameter (Table 4.2). Mature carposporophytes are 53-165 μm in diameter. Carposporangia are obovoid and formed at the apex of 2-4-celled gonimoblast filaments and range from 7-11 μm in diameter and 8-15 μm in length (Fig. 4.31) (Table 4.2).

The five populations of B. heterocorticum occur in the southeastern and south-central U.S. and two (FL 30 and AZ 9) are from spring fed rivers (Fig. 4.1) (Table 4.1). The stream sites are variable in terms of maximum width (2.9-12 m), maximum depth (27->100 cm) and mean current velocity (19-91 $cm.s^{-1}$). The water temperature is relatively warm ($\bar{x}$ = 15°C) and colour ranges from clear to yellow-coloured (Table 4.1). The pH is neutral to alkaline (6.7-8.5) and specific conductance was from 30-280 $\mu S.cm^{-1}$ (Table 4.1). This species was first described from a Florida spring by Sheath & Cole (1990) and has not been reported since from other locations either in North America or elsewhere. These five new sites extend the range of this species from Florida in the south, north to Arkansas and west to Arizona. It appears that B. heterocorticum is localised and may be confined to a south temperate distribution in North America only.

In North America, two populations referable to B. pulchrum were collected (Fig. 4.1) (Table 4.1). These populations have the distinguishing features of this species, spermatangia on the involucral filaments of the carpogonial branch and well-curled fascicles (Chapter 2). The type specimen of B. pulchrum is not significantly different from these populations in all morphological characteristics measured except carposporangium diameter ($\overline{x}$ = 9.9 vs. 8.3 μm, respectively). However, the range in this feature for the populations encompassed that of the type specimen (6-11 μm and 9-11 μm, respectively). Hence, the North American populations are classified as B. pulchrum.

The North American populations of B. pulchrum are monoecious and have barrel-shaped whorls 296-474 μm in diameter and composed of 5-14-celled fascicles (Fig. 4.32) (Table 4.2). Mature whorls contain 1-3 spherical carposporophytes (Fig. 4.32) (Table 4.2). The fascicles are distinctly curved in one direction (Fig. 4.33). Spermatangia are ovoid and formed at the tips of both vegetative fascicles and the involucral filaments of 27-67% of the carpogonial branches (Figs 4.34, 4.35, 4.36). Carpogonial branches are undifferentiated and 3-8-celled with short involucral filaments (Figs 4.35, 4.36). Carpogonia are 17-29 μm in length and have lanceolate trichogynes (Figs 4.35, 4.36) which are 4-7 μm in diameter. At maturity, carposporophytes are 61-144 μm in diameter. Carposporangia are obovoid and range from 6-11 μm in diameter and 9-15 μm in length. They are formed at the tips of 2-4-celled gonimoblast filaments (Fig. 4.37) (Table 4.2).

The two North American populations of B. pulchrum are from the Caribbean islands of Martinique and Grenada in the tropics (Table 4.1). The stream channels were small (1, 2 m wide), shallow (17, 30 cm depth) and slow flowing (10, 16 $cm.s^{-1}$ mean current velocity) (Table 4.1). The water was colourless and warm (Table 4.1).

The pH was alkaline in each stream but the specific conductance varied (50, 180 μS.cm^{-1}). This species was first described from Guadeloupe by Sirodot (1884). Since then this species has not been reported from North America or other continents. In addition, no herbarium specimensof B. pulchrum from North America were identified. From the three localities, it would appear that this species is restricted to the lesser Antilles of the Caribbean Islands. Seven other Caribbean Islands were surveyed in detail by Sheath & Cole (1992) including three Greater Antillean islands, but this taxon was not collected.

Four populations similar to B. skujae were collected from North America (Fig. 4.1) (Table 4.1). The type specimen of B. skujae and the North American populations are monoecious and have monosporangia (Chapter 2). The means in morphometric characteristics of the type specimen do not significantly differ from those of the populations except in whorl, carpogonium and monosporangium diameter (Table 4.2). Although the means in these characteristics differ among specimens, the ranges overlap between the type specimen and the North American populations (Table 4.2). Therefore, the North American populations are referable to B. skujae.

The North American populations of B. skujae are monoecious with globose whorls containing 1-6 spherical carposporophytes (Fig. 4.38). Mature whorls range from 457-956 μm in diameter and are composed of 6-11-celled fascicles (Table 4.2). Monosporangia are obovoid, formed at the fascicle tips and have dimensions of 8-10 x 9-12 μm (Fig. 4.39). Spermatangia are ovoid and apical on the fascicles (Fig. 4.40).

Carpogonial branches are undifferentiated and composed of 4-10 cells (Fig. 4.41) (Table 4.2). Carpogonia are 35-83 μm in length and have clavate trichogynes (Fig. 4.41) which are 10-18 μm in diameter (Table 4.2). At maturity, carposporophytes are 69-173 μm in diameter. Carposporangia are obovoid and range from 7-13 μm in diameter and 10-18 μm in length and are formed at the tips of 2-5-celled gonimoblast filaments (Fig. 4.42) (Table 4.2).

The four populations of B. skujae in North America are from the western coniferous forest and tundra biomes (Fig. 4.1) (Table 4.1). The streams are relatively small in maximum width ($\bar{x}$ = 2.6 m) and maximum depth ($\bar{x}$ = 44 cm) (Table 4.1). Mean current velocity varied among streams (1-50 cm $\cdot s^{-1}$). The water in each stream was colourless and ranged from (0-12°C) in temperature (Table 4.1). The pH was neutral to alkaline ($\bar{x}$ = 8.1) and the specific conductance varied from 47-630 μS cm^{-1}. B. skujae has been previously reported in North America from California (Sheath & Cole, 1993) as B. sporulans Sirodot. However, the monosporangia of this population do not appear to be characteristic of B. skujae. Worldwide, B. skujae has been reported from Poland (Starmach, 1980, 1984) and as B. sporulans from Crimea (Moshkova, 1960), Japan (Mori, 1975), Latvia (Skuja, 1928), Poland (Starmach, 1981, 1984, 1989; Siemińska, 1992) and Sweden (Kylin, 1912; Israelson, 1942). In Poland, B. skujae was collected in streams with similar pH (7.3-8.2) and water temperatures (8-11°C) (Starmach, 1989). In contrast, Reis (1974) reports this alga from a habitat with lower pH (6.6) and higher temperature (17°C).

B. carpocontortum from this section has been described from two streams in Washington state (Sheath et al., 1986b). This species is distinguished from other taxa of sect. Batrachospermum on the basis of contorted carpogonia (for details see Chapter 2). B. carpocontortum appears to be localised and no new populations were found in this study.

Table 4.1. Physical and chemical characteristics of stream segments containing populations of Batrachospermum sect. Batrachospermum in North America

Population number[a]	Location[b]	Biome[c]	Species[d]	Maximum width (cm)	Maximum depth (m)	Mean current velocity (cm s^{-1})	Temperature (°C)	pH	Specific conductance (μS cm^{-1})	Water colour[e]
1	MO 1	df	ana	-	-	-	-	-	-	-
2	MO 3	df	ana	-	-	-	-	-	-	-
3	MO 4	df	ana	-	-	-	-	-	-	-
4	AR 8	df	ana	4.5	65	57	13	7.5	280	0
5	VA 23	cp	ana	1	33	6	9	8.0	240	0
6	AK 104	bf	arc	13.8	85	82	16	-	85	1
7	AK 139	bf	arc	7	>100	93	13	-	68	0
8	OR 118	wc	arc	8	47	74	10	7.4	50	0
9	CA 19	wc	arc	15	76	32	13	-	40	0

10	NV 1	wc	arc	2.6	17	57	3	7.9	30	0
11	MEX 18	dc	arc	5	40	69	15	7.6	90	0
12	MI 103	hh	bor	6.7	37	39	14	-	140	1
13	PA 4	hh	bor	4	40		11	7.7	80	0
14	PA 5	hh	bor	4.1	20	[illegible]	5	7.4	110	0
15	NY 1	df	bor	2.3	35	42	5	7.9	300	0
16	NY 106	hh	bor	1.7	37	63	17	-	55	1
17	NH 5	hh	bor	6.8	41	60	15	7.7	210	0
18	MA 1	df	bor	-	-	-	-	-	-	-
19	MA 111	df	bor	1.8	50	28	15	6.8	60	1
20	RI A	df	bor	8.7	53	69	15	5.5	95	0
21	RI B	df	bor	1.7	19	34	9	5.0	-	1
22	RI E	df	bor	5.6	46	81	16	5.7	108	0

23	CT 7	df	bor	4	16	26	4	7.3	20	0
24	CT 9	df	bor	2.5	25	33	3	7.7	60	0
25	CT 13	df	bor	2.5	45	36	15	7.0	50	0
26	CT 14	df	bor	3	50	27	14	6.4	30	1
27	CT 15	df	bor	3.5	30	51	18	6.8	20	0
28	CT 18	df	bor	2	15	31	11	7.7	40	0
29	CT 20	df	bor	5	18	33	11	6.8	50	0
30	CT 24	df	bor	3.5	30	25	12	7.4	60	0
31	MD 6	df	bor	2	20	31	16	7.2	100	0
32	VA 10	df	bor	3	38	17	8	7.9	130	0
33	VA 11	df	bor	3	36	14	9	8.3	36	0
34	VA 101	df	bor	-	-	-	-	-	-	-
35	VA 200	hh	bor	3	40	30	12	5.1	73	1

36	VA 203	hh	bor	1.1	15	11	5	6.4	106	0
37	WV 9	hh	bor	4.3	75	76	10	8.0	640	0
38	NC 103	hh	bor	2.2	26	19	8	7.3	85	0
39	NC 104	hh	bor	3.5	39	63	7	7.0	56	0
40	NC 106	hh	bor	1.3	15	40	8	6.5	37	0
41	TN 4	hh	bor	2.2	33	36	5	6.1	52	0
42	TN 5	hh	bor	19	44	51	5	6.2	34	0
43	GA 1	hh	bor	6	60	46	9	6.0	84	1
44	BC 18	wc	bor	8	60	27	13	8.2	140	0
45	NF 22	bf	bor	5.5	49	49	11	6.3	63.5	1
46	AB 43	wc	con	5	34	74	17	8.5	490	0
47	AB 49	wc	con	3	36	33	13	8.1	450	0
48	MO 2	df	con	-	-	-	-	-	-	-

49	ME 13	hh	con	6	>100	24	15	6.4	36	1
50	PQ 1	bf	con	5	30	66	24	6.4	80	-
51	NF 207	bf	con	8.4	11	25	10	7.2	20	0
52	AZ 9	dc	het	5	48	20	19	8.5	175	0
53	AR 3	df	het	2.9	*40*	*19*	*15*	7.4	50	0
54	LA 3	cp	het	5.5	27	55	11	6.7	30	1
55	*AL RH*	*cp*	het	-	-	-	-	-	-	-
56	FL 30	cp	het	12	>100	91	15	7.7	280	1
57	GREN 10	tf	pul	2	30	10	23	7.9	180	0
58	MAR 4	tf	pul	1	17	16	21	8.2	50	0
59	MAN 10	t	sku	3.5	52	13	12	7.7	630	0
60	CO 11	wc	sku	2	51	50	0	8.0	150	0
61	CO 14	wc	sku	3	50	9	0	8.5	47	0

62	GLD 3	t	sku	2	23	1	7	8 3	130	0

[a] Populations as indicated on Fig. 4.1.

[b] MO, Missouri; AR, Arkansas; VA, Virginia; AK, Alaska; OR, Oregon; CA, California; NV, Nevada; MEX, Mexico; MI, Michigan; PA, Pennsylvania; NY, New York; NH, New Hampshire; MA, Massachusetts; RI, Rhode Island; CT, Connecticut; MD, Maryland; WV, West Virginia; NC, North Carolina; TN, Tennessee; GA, Georgia; BC, British Columbia; AB, Alberta; ME, Maine; PQ, Quebec; NF, Newfoundland; AZ, Arizona; LA, Louisiana; AL, Alabama; FL, Florida; GREN, Grenada; MAR, Martinque; MAN, Manitoba; CO, Colorado; GLD, Greenland.

[c] df, deciduous forest; cp, coastal plain; bf, boreal forest; wc, western coniferous forest; dc, desert/chaparral; hh, hemlock-hardwood forest; tf, tropical forest; t, tundra.

[d] ana, B. anatinum; arc, B. arcuatum; bor, B. boryanum; con, B. confusum; het, B. heterocorticum; pul, B. pulchrum; sku, B. skujae.

[e] 0, colourless; 1, yellow coloured.

Table 4.2. Morphometric characteristics of Batrachospermum sect. Batrachospermum North American populations and type specimens[a]. Mean (range)

Taxon	Whorl diameter (µm)	Fascicle length (cells)	Carposporophyte height-to-whorl diameter	Carposporophyte			Carpogonium				Carposporangium	
				Number per whorl	Diameter (µm)	Cell number	Diameter (µm)	Length (µm)	Form factor[b]	Branch cell number	Diameter (µm)	Length (µm)
B. anatinum	737 (416-1085)	9.6 (6-13)	0.66 (0.36-1.08)	4.4 (1-14)	108 (66-173)	2.5 (2-4)	8.1 (7-11)	26.4 (17-36)	0.32 (0.22-0.43)	5.1 (3-7)	8.7 (7-10)	11.6 (8-15)
B. anatinum type	695 (599-855)	-	0.52 (0.39-0.70)	3.3 (2-5)	107 (88-136)	2.4 (2-3)	7.2 (6-9)	20.4 (18-22)	0.36 (0.33-0.40)	7.4 (6-8)	8.6 (7-10)	10.4 (8-12)
B. arcuatum	693 (333-1089)	9.4 (7-16)	0.52 (0.33-0.85)	2.2 (1-7)	118 (68-217)	2.3 (2-3)	8.1 (5-14)	31.0 (21-43)	0.29 (0.21-0.38)	5.4 (3-11)	8.9 (7-11)	11.3 (9-13)
B. arcuatum type	570 (428-727)	-	0.80 (0.58-1.00)	1.7 (1-3)	106 (87-179)	2.6 (2-4)	8.8 (6-12)	33.9 (28-39)	0.28 (0.23-0.37)	6.7 (5-9)	9.0 (7-12)	11.8 (10-15)
B. boryanum	668 (320-1360)	9.1 (5-13)	0.60 (0.30-1.06)	3.1 (1-10)	98 (61-167)	2.3 (2-4)	7.7 (5-11)	26.0 (17-39)	0.32 (0.19-0.44)	5.4 (3-10)	8.1 (6-10)	10.6 (7-13)
B. boryanum type	910 (789-1034)	-	0.56 (0.35-0.70)	20.7 (12-30)	90 (74-105)	2.3 (2-3)	6.7 (6-7)	19.8 (16-27)	0.36 (0.33-0.40)	7.3 (7-8)	8.5 (7-10)	9.7 (8-12)

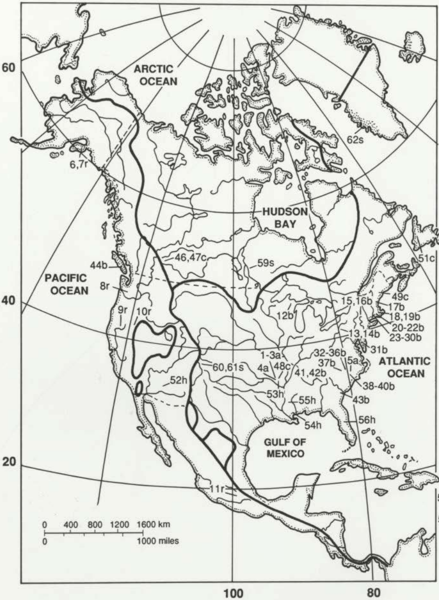
B. confusum	714 (466-1184)	9.4 (6-13)	0.64 (0.41-1.19)	3.5 (1-12)	111 (58-193)	2.5 (2-4)	7.8 (6-10)	31.2 (19-48)	0.30 (0.20-0.42)	5.4 (3-10)	9.4 (7-13)	12.5 (10-19)
B. confusum type	749 (556-901)	- -	0.52 (0.36-0.71)	6.7 (3-10)	73 (61-90)	2.4 (2-3)	6.1 (6-7)	17.2 (15-18)	0.33 (0.29-0.38)	8.0 (8)	8.2 (7-10)	10.2 (8-12)
B. heterocorticum	515 (294-972)	8.4 (6-11)	0.71 (0.42-1.13)	1.6 (1-4)	105 (53-165)	2.5 (2-4)	7.4 (3-11)	29.7 (21-35)	0.29 (0.23-0.38)	4.7 (3-6)	8.8 (7-11)	11.4 (8-15)
B. heterocorticum type	617 (492-876)	8.9 (7-11)	0.71 (0.47-0.90)	4.1 (2-8)	99 (71-120)	2.6 (2-4)	8.1 (6-10)	33.8 (27-40)	0.29 (0.22-0.35)	4.9 (3-9)	9.6 (8-11)	12.2 (10-15)
B. pulchrum	378 (296-474)	9.4 (5-14)	0.60 (0.35-1.18)	1.3 (1-3)	89 (61-144)	2.6 (2-4)	5.2 (4-7)	22.4 (17-29)	0.29 (0.22-0.41)	4.7 (3-8)	8.3 (6-11)	11.9 (9-15)
B. pulchrum type	390 (307-483)	- -	0.49 (0.36-0.83)	1.2 (1-2)	81 (59-108)	2.3 (2-3)	5.6 (5-7)	25.3 (23-32)	0.24 (0.23-0.26)	4.9 (4-6)	9.9 (9-11)	11.7 (10-13)
B. skujae	640 (457-956)	8.3 (6-11)	0.69 (0.37-1.22)	3.2 (1-6)	116 (69-1[illegible])	2.8 (2-5)	13.9 (10-18)	54.0 (35-83)	0.26 (0.18-0.39)	6.0 (4-10)	9.9 (7-13)	14.0 (10-18)
B. skujae type	803 (708-922)	- -	0.63 (0.43-0.85)	2.6 (1-6)	107 (88-134)	2.7 (2-4)	10.8 (8-12)	44.2 (33-59)	0.30 (0.21-0.37)	5.9 (5-7)	11.1 (9-14)	14.3 (11-17)

n = 30 except carpogonia where n = 15.

[a] Measurements from Chapter 2.

[b] See Sheath et al. (1986b) for description.

Fig. 4.1. Location of North American stream sites from which Batrachospermum sect. Batrachospermum species were collected. The numbers correspond to the stream numbers in Table 4.1. a, B. anatinum, r, B. arcuatum, b, B. boryanum, c, B. confusum, h, B. heterocorticum, p, B. pulchrum, s, B. skujae. Dark lines indicate major drainage basins.



ARCTIC OCEAN
HUDSON BAY
PACIFIC OCEAN
ATLANTIC OCEAN
GULF OF MEXICO
60
60
40
20
100
80
6,7r
62s
45b
51c
44b
8r
9r
10r
46,47c
59s
49c
15,16b
17b
18,19b
20-22b
23-30b
12b
13,14b
31b
1-3a
32-36b
37b
5a
4a
48c
41,42b
38-40b
60,61s
52h
53h
55h
43b
54h
56h
11r
58p
57p
0 400 800 1200 1600 km
0 1000 miles

Plate XI

Figs 4.2-4. 12. Morphological characteristics of Batrachospermum anatinum and B. arcuatum North American populations. Figs 4.2-4.7. B. anatinum. Fig. 4.2. Main axis with confluent, globose whorls containing numerous spherical carposporophytes (arrowheads) (MO 3). Fig. 4.3. Cortication of main axis with cylindrical (large arrowhead) to bulbous (small arrowhead) cells (MO 3). Fig. 4.4. Fascicle tip with spermatangia (arrowheads) (MO 1). Fig. 4.5. Fertilized carpogonium with clavate trichogyne (small arrowhead) on undifferentiated carpogonial branch (large arrowhead) (AR 8). Fig. 4.6. Fertilized carpogonium with lanceolate trichogyne (arrowhead) (MO 1). Fig. 4.7. Carposporophyte with dense 2-celled gonimoblast filaments having apical carposporangia (arrowheads) (AR 8). Figs 4.8-4.12. B. arcuatum (CA 19). Fig. 4.8. Male plant main axis with confluent, globose whorls. Fig. 4.9. Fascicle tip with spermatangia (arrowheads). Fig. 4.10. Female plant main axis with confluent, barrel-shaped whorls containing numerous spherical carposporophytes (arrowheads). Fig. 4.11. Fertilized carpogonium with clavate trichogyne (arrowhead). Fig. 4.12. Carposporophyte with short, dense 2-3-celled gonimoblast filaments having apical carposporangia (arrowheads). (Scale bars represent: Figs 4.2, 4.8 and 4.10, 300 μm; Fig. 4.3, 50 μm; Figs 4.4, 4.5 4.6, 4.7, 4.9, 4.11 and 4.12, 10 μm)

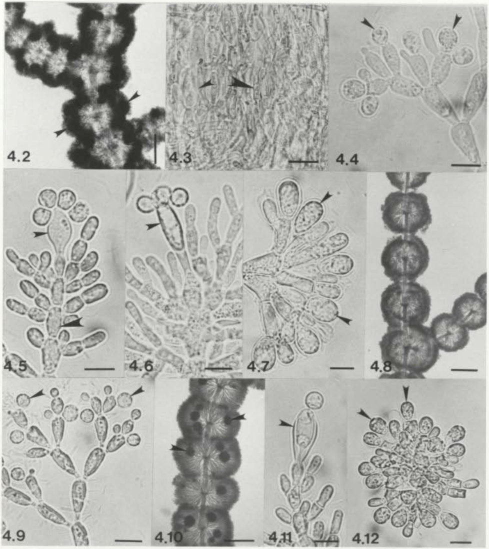

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Plate XII

Figs 4.13-4.25. Morphological characteristics of Batrachospermum boryanum and B. confusum North American populations. Figs 4.13-4.19. B. boryanum Fig. 4.13. Male plant main axis with confluent whorls and secondary branches curled at the tips (arrowheads) (CT 7). Fig. 4.14. Main axis cortication containing bulbous cells (arrowhead) (CT 7). Fig. 4.15. Fascicle tip with spermatangia (arrowheads) (CT 7). Fig. 4.16. Female plant main axis with confluent whorls and secondary branches curled at the tips (arrowheads) (CT 7). Fig. 4.17. Fertilized carpogonium with clavate trichogyne (small arrowhead) on undifferentiated carpogonial branch (large arrowhead) (CT 15). Fig. 4.18. Fertilized carpogonium with inflated, lanceolate trichogyne (arrowhead) (CT 20). Fig. 4.19. Carposporophyte with short, dense 2-3-celled gonimoblast filaments having apical carposporangia (arrowheads) (CT 20). Figs 4.20-4.25. B. confusum. Fig. 4.20. Main axis with confluent whorls containing numerous spherical carposporophytes (arrowheads) (AB 49). Fig. 4.21. Cortication of main axis with cylindrical (large arrowhead) to bulbous (small arrowhead) cells (AB 49). Fig. 4.22. Fascicle tip with spermatangia (arrowheads) (MO 2). Fig. 4.23. Carpogonium with clavate trichogyne (large arrowhead). Involucral filaments with apical spermatangia (small arrowheads) (MO 2). Fig. 4.24. Fertilized carpogonium with bent, lanceolate trichogyne (large arrowhead). Involucral filaments with abundant apical spermatangia (small arrowheads) (AB 49). Fig. 4.25. Carposporophyte with short, dense 3-celled gonimoblast filaments having apical carposporangia (arrowheads) (AB 43). (Scale bars represent: Fig. 4.13, 300μm; Figs 4.14 and 4.21, 50 μm; Figs 4.15, 4.17, 4.18, 4.19, 4.22, 4.23, 4.24 and 4.25, 10μm; Fig. 4.16, 400 μm; Fig. 4.20, 350 μm)

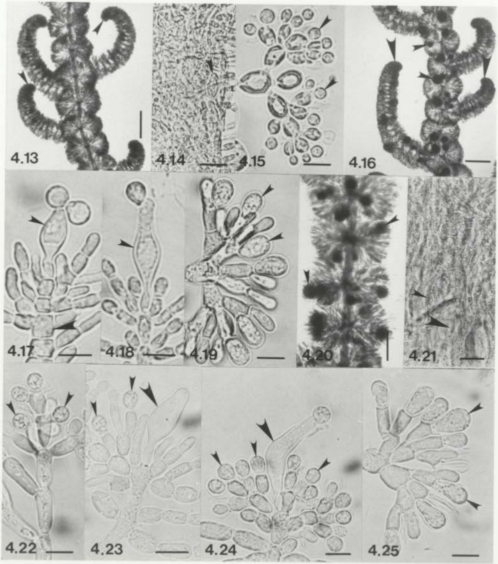

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Plate XIII

Figs 4.26-4.37. Morphological characteristics of Batrachospermum heterocorticum and B. pulchrum North American populations. Figs 4.26-4.31. B. heterocorticum. Fig. 4.26. Male plant with barrel-shaped whorls and abundant secondary fascicle growth (arrowheads) (AR 3). Fig. 4.27. Cortication with bulbous cells (arrowhead) (AL RH). Fig. 4.28. Fascicle tip with spermatangia (arrowheads) (AR 3). Fig. 4.29. Female plant with abundant secondary fascicle growth (small arrowheads) and barrel-shaped whorls containing spherical carposporophytes (large arrowheads) (AR 3). Fig. 4.30. Carposporophyte with lanceolate trichogyne (arrowhead) (AZ 9). Fig. 4.31. Carposporophyte with short, dense 2-3-celled gonimoblast filaments having apical carposporangia (arrowheads) (AZ 9). Figs 4.32-4.37. B. pulchrum. Fig. 4.32. Main axis with barrel-shaped whorls containing spherical carposporophytes (arrowheads) (MAR 4). Fig. 4.33. Fascicles curved in one direction (GREN 10). Fig. 4.34. Fascicle tip with spermatangia (arrowheads) (GREN 10). Fig. 4.35. Carpogonium with lanceolate trichogyne (small arrowhead). Involucral filament with apical spermatangium (large arrowhead) (MAR 4). Fig. 4.36. Fertilized carpogonium with lanceolate trichogyne (arrowhead) (MAR 4). Fig. 4.37. Carposporophyte with short, dense 2-3-celled gonimoblast filaments having apical carposporangia (arrowheads) (MAR 4). (Scale bars represent: Figs 4.26 and 4.29, 350 μm; Fig. 4.27, 100 μm; Figs 4.28, 4.30, 4.31, 4.34, 4.35, 4.36 and 4.37, 10 μm; Fig. 4.32, 200 μm; Fig. 4.33, 150 μm)

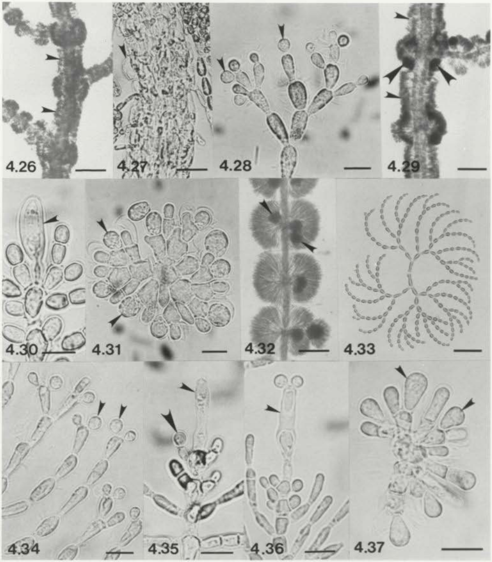
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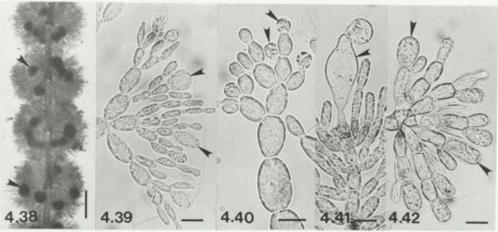
Plate XIV

Figs 4.38-4.42. Morphological characteristics of Batrachospermum skujae North American populations. Fig. 4.38. Main axis with confluent, barrel-shaped whorls containing spherical carposporophytes (arrowheads) (CO 11). Fig. 4.39. Fascicle tip with apical monosporangia (arrowheads) (MAN 10). Fig. 4.40. Fascicle tip with apical spermatangia (arrowheads) (CO 11). Fig. 4.41. Fertilized carpogonium with inflated, clavate trichogyne (arrowhead) (CO 11). Fig. 4.42. Carposporophyte with short, dense 3-4-celled gonimoblast filaments having apical carposporangia (arrowheads) (CO 11). (Scale bars represent: Fig. 4.38, 300 μm: Figs 4.39, 4.40, 4.41 and 4.42, 10 μm)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Distribution and systematics of Batrachospermum section Batrachospermum in North America: Batrachospermum gelatinosum

5.1. Introduction

Sect. Batrachospermum of the freshwater red algal genus Batrachospermum is generally characterised by the following features: well-developed whorls, undifferentiated and straight carpogonial branches arising from both fascicle and pericentral cells, non-pedicellate carpogonia with club- to urn-shaped trichogynes and relatively small globose, pedicellate carposporophytes at various distances from the whorl axis (Mori, 1975; Starmach, 1977; Kumano, 1993). The type species of the genus, B. gelatinosum, is contained within this section and is differentiated from other species on the basis of monoecious thalli and cylindrical cortical cells covering the main axis (Chapter 2).

B. gelatinosum has been collected widely from Asia, Australia, Europe and South America (e.g. Entwisle, 1989; Hu et al., 1981; Necchi, 1990; Reis, 1974). In North America, this species has been reported in numerous locations from the Northwest Territories and Alaska in the north to Mexico in the south (Table 5.1). In a survey of 1000 streams in North America, Sheath and Cole (1992) found B. gelatinosum to be the most common species of freshwater red algae, occurring in 13% of the samples. Additionally, this species can be an important component of stream periphyton, contributing 12% of the total periphyton production in a Quebec stream (Duthie & Hamilton, 1983). In spite of the significance of this alga, little data exist on its morphological variation and there has been no comprehensive study of its biogeography. Therefore, this study examines the distribution and temporal and spatial variation of B. gelatinosum populations from North America.

5.2. Materials and methods

Eighty-six populations of Batrachospermum gelatinosum were collected from the north slope of Alaska (68°N) and northern Baffin Island (73°N) to Texas and Louisiana (37°N) as part of a survey of 1000 streams in North America (Sheath & Cole, 1992) (Fig. 5.1). The samples were immediately fixed in 2.5% calcium-carbonate buffered glutaraldehyde to prevent morphological distortion. Maximum depth and width, mean current velocity, temperature, pH, and specific conductance were measured, and water colour was noted for each stream in a similar manner to that described in Chapter 3 (Table 5.2).

Populations were measured for the morphological characteristics described in Chapter 2, using an SMI Microcomp image analysis system. In addition, brown cortication on the main axis was noted and the carposporophyte height-to-whorl diameter ratio was calculated. Associations among populations (Fig. 5.2) and biomes (Fig. 5.3) were determined with cluster analysis using the unweighted method (UPGMA) according to the SAS statistical package (Anonymous, 1988). To compare means of morphometric characteristics measured among populations, analysis of variance (ANOVA) and Duncan's multiple-range test were calculated also using SAS. In addition, correlations among characteristics and with stream physical and chemical parameters were calculated according to Minitab (Ryan et al., 1985). All statistical differences are significant at the $p < 0.05$ level.

Three populations, two from the boreal forest (NF29, NF30) and one from the deciduous forest (RI A), were collected monthly. The monthly samples were measured in the same manner as the other populations in order to assess morphological variation throughout the growing season and among biomes. The means of the morphometric characteristics for each sampling date were compared using the same statistics as the geographic populations.

Specimens of B. gelatinosum from all major North American herbaria were also examined to determine the entire range of this species on the continent.

5.3. Results

The North American populations of B. gelatinosum are monoecious and have either distinct barrel-shaped whorls (Figs 5.4, 5.6) or confluent, indistinct whorls (Fig. 5.5). Mature whorls containing carposporophytes range from 228-1029 µm in diameter and fascicles are 5-13 cells in length. The main axis may or may not have brown cortication. The spherical, colourless spermatangia are formed at the tips of vegetative fascicles (Fig. 5.7). The carpogonial branch is composed of 3-9 undifferentiated cells. Carpogonia are 27-55 µm in length and have fusiform (Fig. 5.8), clavate (Figs 5.9-5.11) or lanceolate (Fig. 5.12) trichogynes with a diameter of 5-16 µm. Carposporophytes are spherical and may be completely contained within the whorl

(Fig. 5.4), protude somewhat (Fig. 5.5) or exserted (Fig. 5.6). At maturity, carposporophytes range from 50-174 μm in diameter. The carposporphyte-bearing branch may be composed of numerous cells of similar size to the fascicle cells (Fig. 5.13) or the cells may become distinctly elongate (Fig. 5.14). Carposporangia are obovoid, 5-12 μm in diameter and 8-17 μm in length and they are produced apically on 2-4-celled gonimoblast filaments.

B. gelatinosum populations were collected from six biomes: tundra, boreal forest, western coniferous forest, hemlock-hardwood forest, deciduous forest and coastal plain (Table 5.2) (Fig. 5.1). Although desert/chaparral and tropical forest biomes were widely sampled, no population of this species was collected. The stream characteristics varied greatly among sites (Table 5.2). The streams ranged from small, gentle flowing rivulets to large, fast flowing rivers (maximum width 0.7-30 m, maximum depth 10->100 cm and mean current velocity 0-106 $cm.s^{-1}$). The waters which this alga inhabits are from 0 to 19°C, acidic to alkaline (pH 5.1-8.5) with a corresponding wide range in specific conductance (0-490 $\mu S.cm^{-1}$) and may be clear or yellow coloured (Table 5.2).

The cluster analysis of the individual B. gelatinosum populations showed several groupings among populations (Fig. 5.2). No geographic trends are evident from the cluster analysis with populations from different biomes and locations associated. In addition, the groupings do not appear to be based on one prominent feature; rather, they are due to a combination of characteristics. For example, populations 41, 43, 74 and 75 are associated (Fig. 5.2) on the basis of large whorls (whorl diameter and fascicle cell number) in conjunction with large carposporophytes.

The cluster analysis of the pooled populations from each biome showed a close association among the hemlock-hardwood, deciduous forest and coastal plain biomes; boreal forest and western coniferous forest were grouped together and the tundra was unassociated (Fig. 5.3). There was no significant difference among the biomes in the means of the following characteristics: carposporophyte diameter and cell number, carposporangium diameter and length and carpogonium form factor (Table 5.3). The mean in whorl diameter for the tundra was significantly smaller than all other biomes except the boreal forest. Likewise, the mean in fascicle cell number for the tundra was the smallest and significantly differed from the hemlock-hardwood forest, deciduous forest and coastal plain biomes. The tundra populations had a significantly greater mean carposporophyte-to-whorl diameter ratio than those of the other biomes. The means in carpogonium diameter for tundra and western coniferous forest populations were not significantly different from each other, but were significantly larger than those of the other biomes. In addition, the mean in carpogonium length for the tundra was significantly greater than those for the hemlock-hardwood forest, deciduous forest and coastal plain. The average carpogonial branch cell number for the tundra was significantly greater than all other biomes except western coniferous forest. Therefore, there appears to be a north-south trend for smaller plant size and larger carpogonium size (Fig. 5.16). However, there is considerable overlap in all morphometric characteristics among biomes (Table 5.3).

Morphological characteristics among populations were compared to biome, latitude, longitude, presence of other red algal taxa and stream physical and chemical parameters. Mean whorl diameter and fascicle length were positively correlated to biome, whereas mean carposporophyte height-to-whorl diameter ratio, carpogonium diameter and length and carpogonial branch length were negatively correlated to biome. However, only mean whorl diameter was negatively correlated to latitude. No morphological characteristics were correlated to either longitude or the presence of other red algal taxa. In terms of stream characteristics, carpogonium diameter and length were negatively correlated to both water temperature and colour and carpogonial branch length was also negatively correlated to water temperature. Brown cortication of the main axis was negatively correlated to the amount of shading a stream received and the combination of water colour and shading but not to water colour alone.

In the monthly study of B. gelatinosum populations, those from Newfoundland (NF 29 & NF30) were observed year round in both streams. However, the Rhode Island population, RI A, was only present from October to June. The range in monthly means of the morphological characteristics for the three populations is similar except for the means in carposporophyte number (Table 5.4). The number of carposporophytes per whorl was significantly higher in RI A than in NF 29 and NF 30 for all sampling dates (Table 5.4) (Fig. 5.18). In all three populations, the number of carposporophytes was negatively correlated to carposporophtye diameter; likewise the carposporophyte height-to-whorl diameter ratio was positively correlated to carposporophyte diameter. In the Newfoundland populations there was considerable monthly variation in mean whorl diameter with no discernable pattern, whereas the Rhode Island population appeared to have a relatively small mean whorl diameter at the begining of the growing season, with an increase in size and then a decline towards the end of the season in June (Fig. 5.17). Similarly, mean fascicle length followed the same trend as the mean whorl diameter in all three populations (Fig. 5.17). There was a spring maximum in mean carposporophyte diameter for the populations (Fig. 5.18). This maximum corresponded to a minimum in carposporophyte number per whorl for RI A, whereas the number of carposporophytes per whorl remained low throughout the year in NF 29 and NF 30 (Fig. 5.18). There were monthly changes in carpogonium diameter for the populations (Fig. 5.19), but this variation was not significant. Mean carpogonium length fluctuated in NF 29 and NF 30 like the mean carpogonium diameter (Fig. 5.19). In population RI A, mean carpogonium length exhibited a March-April maximum which was significantly greater than the length for the other months. The mean carpogonial branch length for each of the populations had a maximum in the late winter-early spring months (Fig. 5.19). Both carpogonium diameter and length fluctuated monthly in all three populations (Fig. 5.20). The monthly variation in the means of the morphological characteristics for all three populations was as great as the variation within and among bioı ɜs (Table

5.3, 5.4). In comparing morphological features with stream characteristics, carpogonial branch length was negatively correlated to water temperature in all three populations. In both NF 29 and NF 30, number of carposporophytes per whorl was positively correlated to water temperature; carpogonial branch length was correlated to pH; and carposporangium length was positively correlated to pH and negatively correlated to water temperature.

The herbarium specimens examined added to confirmed locations for B. gelatinosum as follows: Manitoba, New Brunswick, Oregon, Pennsylvania, Utah, Vermont, Washington and Yukon as well as additional locations in provinces and states collected in this survey (see Appendix). These sites contribute to the overall distribution of this species, but do not extend the range (Fig. 5.1).

5.4. Discussion

5.4.1 Morphological variation

B. gelatinosum has a wide range in variation within and among populations in North America (Tables 5.3, 5.4). In comparison to the type specimen, the North American populations are similar in qualitative features, monoecious thalli and main axis with cylindrical cortical cells and the ranges in morphometric characteristics overlap (Chapter 2). Of the previous studies reporting meaurements for at least a few features, the ranges in morphometric characteristics for the North American populations of this species are similar to those given for populations in Brazil (Necchi, 1990), Japan

(Mori, 1975), Japan and Malaysia (Kumano, 1979) and Sweden (Israelson, 1942). However, Necchi (1990) gives a greater maximum carpogonium length than that observed in the North American populations (75 vs. 55 µm, respectively). One distinguishing characteristic of B. gelatinosum is monoecious plants (Chapter 2). The populations described by Necchi (1990) have dioecious thalli and those of Kumano (1979) are polyoecious so that these populations cannot be referred to B. gelatinosum as circumscribed in Chapter 2.

Geographic trends in morphological characteristics of B. gelatinosum populations were not evident among individual locations. However, a north-south trend in means of some morphological characteristics was observed among the tundra and the more southern hemlock hardwood, deciduous forest and coastal plain biomes. The tundra populations tended to have a smaller mean plant size (whorl diameter and fascicle length) (Fig. 5.16, Table 5.3). A much abbreviated growing season of less than three months in the tundra (Woo, 1991) may partially explain the smaller mean plant for that biome. The carposporophytes for the tundra were localised further out in the whorl than than those of the other biomes (mean CH/WD = 0.83 vs. 0.59-0.70, respectively). However, this phenomenon may be accounted for by the smaller mean whorl diameter in conjunction with longer carpogonial branches. In addition, the mean carpogonium size was larger in the tundra compared with more southern biomes (Fig. 5.16, Table 5.3). Both carpogonium diameter and length were found to be negatively correlated to water temperature which may contribute to the difference in size among the tundra and the more southern biomes. However, these two characteristics were not correlated to water temperature in the populations studied monthly. Therefore, water temperature may not be the only factor influencing carpogonium size. Many of the morphological features measured in the populations throughout North America and those sampled monthly were correlated to physical and chemical stream characteristics. Only carpogonial branch length was correlated to the same factor (water temperature) in both the geographic and the seasonal parts of this study.

5.4.2. Ecology and distribution

The North American populations of B. gelatinosum occur in streams with a wide range in physical and chemical parameters (Table 5.2). Previous accounts of this alga in North America report streams with varying pH and specific conductance, 25-225 $\mu S.cm^{-1}$ in Alaska (Sheath et al., 1986c), 7.8-8.2 in Nevada (LaRivers, 1978), 6.2-8.2, 40-360 $\mu S.cm^{-1}$ in Ontario (Sheath & Hymes, 1980), 5.5 in Quebec (Duthie & Hamilton, 1983), 4.8-6.1, < 50-173 $\mu S.cm^{-1}$ in Rhode Island (Burkholder & Sheath, 1985), 7.0 in Virginia (Woodson & Afzal, 1976) and 6.7-8.4 in Wisconsin (Woelkerling, 1975). B. gelatinosum also inhabits streams with a wide range in water temperature (1-27.5°C) (Woodson & Afzal, 1976; Woelkerling, 1975; Sheath & Hymes, 1980; Burkholder & Sheath, 1985; Sheath et al., 1986c). Current velocity varied greatly in streams containing this alga according to previous studies: 21.8-85.1 $cm.s^{-1}$ in Alaska (Sheath et al. 1986c), 27-79 $cm.s^{-1}$ in Ontario (Sheath & Hymes,

1980) and 1-126 $cm.s^{-1}$ in Rhode Island (Burkholder & Sheath, 1985).

In addition to North America, B. gelatinosum (as B. moniliforme or another synonym) has been reported from locations on four continents: Asia, China (Jao, 1940; Noda, 1963; Hu et al., 1981), India (Balakrishnan & Chaugule (1980), Iraq (Hinton & Maulood, 1980), Japan (Mori, 1975), Korea (Beom-Jun, 1980); Australia (Entwisle & Kraft, 1984, Entwisle, 1989); Europe, Belgium (Van Meel, 1939a, b; Compère, 1991), Crimea (Moshkova, 1960), Czechoslovakia (Skalne, 1973), Finland (Cedercreutz & Fagerström, 1969), France (Sirodot, 1884), Latvia (Skuja, 1928), Poland (Starmach, 1928, 1975, 1984, 1989; Siemińska, 1992), Portugal (Reis, 1962, 1969, 1974), Spain (Sabater et al., 1989), Sweden (Kylin, 1912; Israelson, 1942), United Kingdom (Cooke, 1882; Hassall, 1845); South America, Brazil (Necchi, 1989, 1990). Both water temperature and pH varied greatly for locations in Europe (1.5-20°C, 6.5-8.5, respectively) (Van Meel, 1939a; Skalne, 1973; Reis, 1974; Starmach, 1975, 1984, 1989; Sabater et al., 1989) and in Australia (10-19°C, 6.4-8.3, respectively) (Entwisle & Kraft, 1984; Entwisle, 1989). Therefore, B. gelatinosum appears to be global in its distribution which may be due to its ability to tolerate a wide range in stream chemical and physical characteristics.

Table 5.1. Previous reports of Batrachospermum gelatinosum in North America.

Location	*Reported as*[a]	*References*
Canada		
1. Alberta	Bg	Sheath & Cole (1993)
2. British Columbia	Bm, Bmt, Bg	Stein & Borden (1978), Sheath & Cole (1993)
3. Labrador	Bm	Duthie & Ostrofsky (1975), Sheath et al. (1989)
4. New Brunswick	Bm	Habeeb & Drouet (1948), Hughes (1948)
5. *Newfoundland*	*Bm*	*Sheath et al. (1989)*
6. Northwest Territories	Bg	Sheath & Cole (1993)
7. Nova Scotia	Bm	Roscoe (1931), Hughes (1948)
8. Ontario	Bm	Duthie & Socha (1976), Sheath et al. (1988)
	Bc, Bm	Sheath & Hymes (1980)
9. Quebec	Bm	Dutilly et al. (1958), Duthie & Hamilton (1983), Hamilton & Duthie (1984), Sheath et al. (1989), Sheath & Cole (1993)
Greenland	Bm	Bachmann (1921), Sheath & Cole (1993)

Mexico	Bm	Sánchez-Rodríguez (1974), Ortega (1984)
United States		
1. Alabama	Bm	Harvey (1857), Wood (1872)
2. Alaska	Bm Bg	Sheath et al. (1986b) Sheath & Cole (1993)
3. Connecticut	Bc, Bd, Be, Bm, Bmc, Bmt, Bp	Hylander (1928)
4. Iowa	Be	Roeder & Peck (1977)
5. Louisiana	Bm, Bp	Flint (1949)
6. Massachusetts	Bc, Bd, Bms	Croasdale (1935)
7. Michigan	Bm Be, Bm Bg	Harvey (1857), Wood (1872) Prescott (1962) Sheath & Cole (1993)
8. Minnesota	Bm	Meyer & Brook (1971)
9. Missouri	Bc, Bp Bg	Drouet (1933) Sheath & Cole (1993)
10. Montana	Bm Be	Prescott & Dillard (1979) Wujek & Lee (1984)
11. Nevada	Bm	LaRivers (1978)

12. New Hampshire	Be	Flint (1949)
13. New Jersey	Bm	Wood (1872)
14. New York	Bm	Harvey (1857), Wood (1872)
15. North Carolina	Bm, Bp	Whitford & Schumacher (1973)
16. Ohio	Bm	Rhodes & Terzis (1970), Lillick & Lee (1934)
17. Pennsylvania	Bm	Wood (1872), Rider & Wagner (1972)
18. Rhode Island	Bm	Olney (1871), Bennett (1888), Sheath & Burkholder (1985), Sheath et al. (1986a)
19. South Carolina	Bm Bg	Harvey (1857), Wood (1872) Sheath & Cole (1993)
20. Tennessee	Bm	Steinman et al. (1991)
21. Virginia	Bm	Harvey (1857), Wood (1872), Woodson &Afzal (1976)
22. Vermont	Bg Bm Be	Flint (1916) Joyce (1936) Flint (1949)
23. Wisconsin	Be, Bm Bm	Prescott (1962) Woelkerling (1975)

[a] Bg, Batrachospermum gelatinosum; Bm, B. moniliforme; Bmt, B. moniliforme var. typicum; Be, B. ectocarpum; Bc, B. corbula; Bd, B. densum; Bmc, B. moniliforme

var. chlorosum; Bp, B. pyramidale; Bms, B. moniliforme var. scopula.

Table 5.2. Characteristics of streams containing Batrachospermum gelatinosum populations in North America.

Population number[a]	Location[b]	Biome[c]	Maximum width (m)	Maximum depth (cm)	Mean current velocity ($cm.s^{-1}$)	Temperature (°C)	pH	Specific conductance ($\mu S.cm^{-1}$)	Water colour[d]
1	NWT 5	t	2	45	61	0	7.0	0	0
2	NWT 6	t	0.9	25	35	2	5.9	0	0
3	NWT 7	t	1.6	32	24	1	6.2	0	0
4	NWT 8	t	0.7	37	62	1	6.3	10	0
5	PQ 31	t	4	43	58	10	7.4	40	0
6	PQ 32	t	3	22	34	10	7.2	50	0
7	PQ 33	t	2.8	19	50	12	7.4	70	0
8	PQ 34	t	5	29	0	11	7.2	340	0
9	PQ 35	t	2.6	29	39	10	7.5	350	0

10	NWT 35	t	4	55	25	2	7.6	30	0
11	NWT 37	t	1.2	33	23	3.5	7.8	10	0
12	NWT 39	t	7	80	82	8	7.2	10	0
13	NWT 50	t	7	55	59	6	-	10	0
14	NWT 51	t	2	20	29	6	-	40	0
15	NWT 56	t	1.1	23	15	5	-	50	0
16	AK 43	t	3	51	36	8	6.9	40	0
17	AK 46	t	6.1	30	32	14.5	7.6	40	0
18	AK 47	t	2	18	9	13	7.5	120	0
19	AK 49	t	14	>100	32	9.2	8.4	160	0
20	AK 51	t	2.6	13	26	6	7.8	140	0
21	AK 57	t	2	12	14	7.5	7.6	20	0
22	AK 18	bf	2.1	45	23	11	-	145	1

23	AK 27	bf	2.5	10	42	8	-	200	0
24	AK 28	bf	11.2	>100	88	11	-	120	0
25	PQ 13	bf	20	150	71	8	5.1	19	1
26	PQ 200	bf	12	40	67	7	7.1	40	0
27	LAB 9	bf	25	65	87	12	7.2	60	0
28	LAB 1	bf	22	60	8	9	6.5	10	1
29	LAB 10	bf	1.5	>100	31	7	7.4	14.8	1
30	NF 204	bf	5.1	80	4	14	7.5	160	1
31	NF 208	bf	17	30	94	11	7.0	20	0
32	NF 209	bf	25	60	38	14	7.0	10	0
33	NF 210	bf	4.4	45	23	12	7.3	50	0
34	NF 211	bf	5.2	50	12	12	7.2	40	0
35	NF 215	bf	5.1	60	70	11	8.1	180	1

36	NF 29a	bf	1.3	25	4	14	6.9	52	0
37	NF 30a	bf	6	>100	106	15	6.8	54	0
38	SASK 7	bf	2	44	26	19	7.9	260	1
39	AB 3	bf	3	83	39	8	7.9	130	1
40	NWT 73	bf	20	>100	68	15	7.8	50	0
41	NWT 74	bf	3	10	3	12	7.7	90	0
42	BC 13	wc	10	14	13	12	8.2	50	0
43	BC 16	wc	6	54	22	15	8.2	70	1
44	BC 42	wc	6	85	46	19	8.4	400	0
45	BC 45	wc	2.5	14	3	14	8.5	110	0
46	BC 54	wc	6	71	52	10	8.0	320	0
47	AB 43	wc	5	34	74	17	8.5	490	0
48	AB 49	wc	30	36	33	13	8.1	450	0

49	CA 26	wc	8	55	19	14	-	20	0
50	CA 27	wc	2.7	80	29	12	-	30	0
51	ME 5	hh	8	80	19	14	8.1	17	0
52	ME 11	hh	10	>100	28	14	7.1	29	1
53	ME 12	hh	10	>100	51	15	6.4	25	1
54	ME 13	hh	6	>100	24	15	6.4	36	1
55	ME 16	hh	8	60	33	14	6.5	31	0
56	ME 17	hh	5	>100	26	12	6.9	48	0
57	NY 116	hh	8	70	22	14	8.1	91	0
58	MI 104	hh	11.5	44	29	14	-	80	1
59	MI 105	hh	16.7	37	42	16	-	50	1
60	MI 107	hh	10.5	30	65	15	-	43	1
61	MI 1B	hh	-	-	-	-	-	-	-

62	WI 502	hh	-	-	-	-	-	-	-	
63	ON 102	hh	2.9	51	65	14	5.5	90	1	
64	ON HR	hh	6	>100	32	10	8.0	120	1	
65	NH 10	hh	10	>100	99	15	7.2	70	0	
66	NS 23	hh	15	>100	40	11	8.4	69	1	
67	NS 28	hh	7	>100	51	12	8.2	79	0	
68	MO 12	df	1.9	20	5	12	7.5	230	0	
69	SC 3	df	6	53	10	14	7.4	90	1	
70	MA 112	df	4	>100	71	19	6.5	60	1	
71	RI A	df	8.7	53	69	15	5.5	95	0	
72	RI B	df	1.7	19	34	9	5.0	-	1	
73	RI G	df	1.3	17	34	10	5.6	84	-	
74	RI H	df	4.6	63	32	11	5.7	99	1	

75	RI K	df	2.8	66	77	9	5.5	68	-
76	CT 15	df	3.5	30	51	18	6.8	20	1
77	CT 23	df	.10	60	17	12	7.6	60	1
78	MA 117	df	10	70	34	10	7.4	150	1
79	OH 1	df	-	-	-	-	-	-	-
80	TX 4	cp	3.5	45	47	18	7.7	110	1
81	LA 5	cp	3.5	65	7	12	6.7	50	1
82	GA 4	cp	2.6	71	22	16	7.3	70	1
83	NC 15	cp	3.1	11	-	18	6.1	49	1
84	NC 16	cp	3.4	14	-	19	6.0	69	1
85	VA 16	cp	10	34	6	7	8.0	47	0
86	VA 20	cp	10	65	26	8	7.8	140	0

[a] Populations as indicated on Figs 5.1. 5.2.

[b] NWT, Northwest Territories; PQ, Quebec; AK, Alaska; LAB, Laborador; NF, Newfoundland; SASK, Saskatchewan; AB, Alberta; BC, British Columbia; CA, California; ME, Maine; NY, New York; MI, Michigan; WI, Wisconsin; ON, Ontario; NH, New Hampshire; NS, Nova Scotia; MO, Missouri; SC, South Carolina; MA, Massachusetts; RI, Rhode Island; CT, Connecticut; OH, Ohio; TX, Texas; LA, Louisiana; GA, Georgia; NC, North Carolina; VA, Virginia.

[c] t, tundra; bf, boreal forest; wc, western coniferous forest; hh, hemlock-hardwood forest; df, deciduous forest; cp, coastal plain.

[d] 0, colourless; 1, yellow coloured.

Table 5.3. Morphometric characteristics of Batrachospermum gelatinosum populations in North America. Overall mean, range in means.

Biome	Whorl diameter (μm)	Fascicle cell number	Carposporophyte height-to-whorl diameter	Carposporophyte Diameter (μm)	Carposporophyte Cell number	Carpogonium Diameter (μm)	Carpogonium Length (μm)	Carpogonium Form factor[a]	Carpogonium Branch cell number	Carposporangium Diameter (μm)	Carposporangium Length (μm)
Tundra	449 383-565	7.7 6.7-9.1	0.83 0.72-0.99	84 70-105	2.5 2.3-2.8	11.0 9.6-13.6	40.7 31.7-47.7	0.26 0.23-0.30	6.3 5.2-8.1	8.8 7.2-9.6	11.2 10.5-11.9
Boreal forest	512 331-642	8.4 7.1-9.9	0.70 0.50-1.10	83 67-119	2.5 2.3-3.0	9.1 6.8-10.3	38.1 32.4-42.5	0.25 0.22-0.28	5.3 4.6-6.2	8.9 7.3-10.3	11.2 10.0-12.6
Western coniferous forest	565 482-802	8.0 6.4-9.6	0.65 0.52-0.72	77 65-89	2.5 2.1-2.7	10.4 9.2-12.3	38.6 31.7-44.7	0.27 0.25-0.28	5.7 5.1-6.2	8.8 8.4-9.8	11.2 10.8-12.0
Hemlock-Hardwood forest	562 449-651	8.4 7.3-9.9	0.59 0.48-0.72	80 67-99	2.4 2.1-2.8	9.4 8.0-11.9	36.3 29.9-49.5	0.26 0.24-0.30	5.1 4.5-6.5	8.9 8.2-9.7	11.4 10.4-12.4
Deciduous forest	591 456-658	9.0 7.7-10.5	0.61 0.50-0.84	86 74-108	2.4 2.2-2.6	8.8 7.8-10.1	34.8 29.6-40.6	0.26 0.20-0.28	5.2 4.6-5.9	8.5 7.9-9.3	11.2 10.8-12.9
Southeastern coastal plain	544 466-598	8.6 8.0-8.9	0.61 0.53-0.68	88 81-95	2.5 2.4-2.9	8.6 8.1-9.2	33.6 30.1-40.7	0.26 0.24-0.28	4.7 4.3-5.3	8.7 8.6-8.9	11.1 10.9-11.3

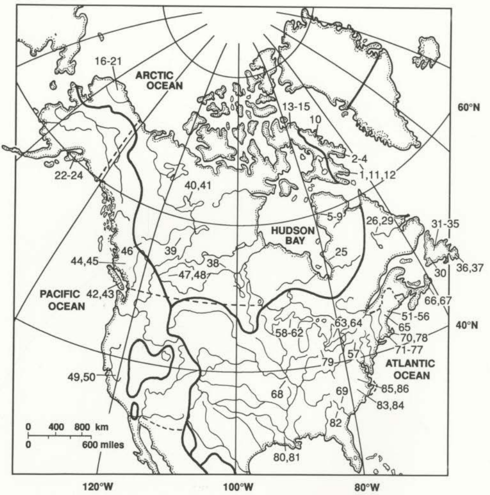
n = 30 except carpogonia where n = 15.
[a] See Sheath et al. (1986b) for description.

Table 5.4. Range in monthly means of morphometric characteristics of *Batrachospermum gelatinosum* populations from Newfoundland and Rhode Island.

Population	Whorl	Fascicle	Carposporophyte	Carposporophyte			Carpogonium				Carposporangium	
	diameter (µm)	cell number	height-to-whorl diameter	Number per whorl	Diameter (µm)	Cell number	Diameter (µm)	Length (µm)	Form factor[a]	Branch cell number	Diameter (µm)	Length (µm)
NF 29	487-741	7.6-8.8	0.56-0.91	1.2-2.3	76-143	2.[illegible]-2.9	8.3-9.9	37.7-42.9	0.22-0.25	4.8-6.1	8.4-10.1	11.1-14.6
NF 30	397-554	7.6-9.3	0.55-0.91	1.2-2.2	71-126	2.2-2.8	9.3-10.9	38.1-48.4	0.23-0.28	4.2-5.3	8.1-9.9	10.6-13.4
RI A	563-746	8.7-9.8	0.57-0.80	3.0-5.8	80-113	2.5-2.7	7.9-9.2	31.2-42.6	0.23-0.28	5.3-6.3	7.6-8.5	10.1-12.4

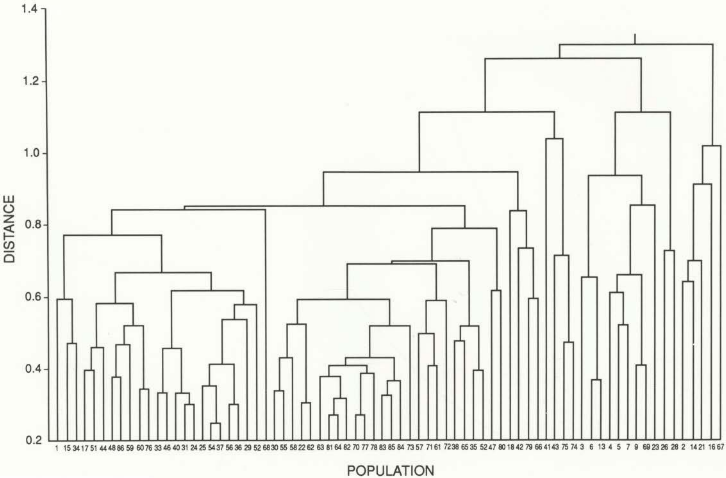
[a] See Sheath et al. (1986b) for description.

Fig. 5.1. Location of North American stream sites from which Batrachospermum gelatinosum populations were collected. The numbers correspond to the stream numbers in Table 5.2. Dark lines indicate major drainage basins.



ARCTIC OCEAN
HUDSON BAY
PACIFIC OCEAN
ATLANTIC OCEAN
60°N
40°N
120°W
100°W
80°W
0 400 800 km
0 600 miles
16-21
13-15
10
2-4
1,11,12
22-24
40,41
5-9
26,29
31-35
36,37
30
25
39
46
44,45
38
47,48
42,43
66,67
51-56
65
70,78
71-77
63,64
58-62
57
79
49,50
68
69
85,86
83,84
82
80,81

Fig. 5.2. Cluster diagram of Batrachospermum gelatinosum populations from North America. The numbers correspond to the stream numbers in Table 5.1.



DISTANCE
1.4
1.2
1.0
0.8
0.6
0.4
0.2
1 15 34 17 51 44 48 86 59 60 76 33 46 40 31 24 25 54 37 56 36 29 52 68 30 55 58 22 62 63 81 64 82 70 77 78 83 85 84 73 57 71 61 72 38 65 35 52 47 80 18 42 79 66 41 43 75 74 3 6 13 4 5 7 9 69 23 26 28 2 14 21 16 67
POPULATION

Fig. 5.3. Cluster diagram of Batrachospermum gelatinosum populations from North America grouped by biome. Biomes are designated as follows: t, tundra; bf, boreal forest; wc, western coniferous forest; hh, hemlock-hardwood forest; df, deciduous forest; cp, coastal plain.

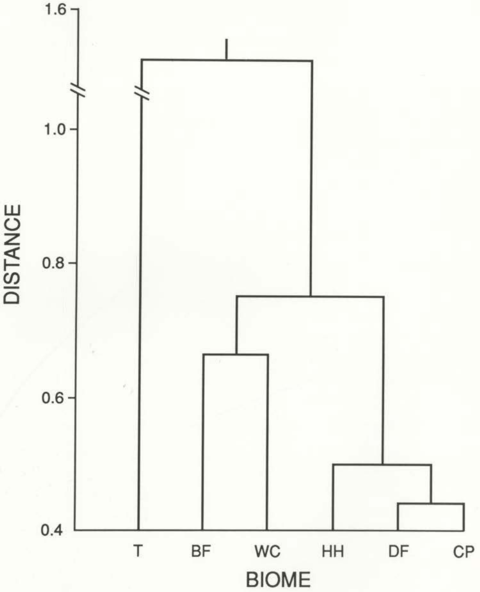

1.6
1.0
0.8
0.6
0.4
DISTANCE
T
BF
WC
HH
DF
CP
BIOME

Plate XV

Figs 5.4-5.15. Morphological characteristics of North American Batrachospermum gelatinosum populations. Fig. 5.4. Main axis with barrel-shaped whorls containing numerous carposporophytes (arrowheads) (CT 15). Fig. 5.5. Main axis with brown cortication. Carposporophytes exserted (large arrowhead) and within (arrowhead) indistinct whorls (NWT 45). Fig. 5.6. Main axis with barrel-shaped whorls and exserted carposporophytes (arrowheads) (MO 12). Fig. 5.7. Fascicle with abundant spermatangia development (arrowheads) (NWT 74). Fig. 5.8. Fertilized carpogonium with fusiform trichogyne (arrowhead) (VA 20). Fig. 5.9. Fertilized carpogonium with clavate trichogyne (arrowhead) (ME 17). Fig. 5.10. Fertilized carpogonium with slightly inflated, clavate trichogyne (arrowhead) (NS 23). Fig. 5.11. Fertilized carpogonium with inflated, ellipsoidal trichogyne (arrowhead) (NWT 6). Fig. 5.12. Fertilized carpogonium with elongate, lanceolate trichogyne (arrowhead) (AK 57). Fig. 5.13. Carposporophyte on branch with cylindrical cells (arrowheads) (MO 12). Fig. 5.14. Carposporophyte on branch with inflated, elongate cell (arrowheads) (MO 12). Fig. 5.15. Compact carposporophyte with obovoid carposporangia (arrowheads) (VA 20). (Scale bars represent: Figs 4 and 5, 300 µm; Fig. 6, 250 µm; Figs 7, 8, 9, 10, 11, 12 and 15, 10 µm; Fig. 13, 20 µm; Fig. 14, 25 µm)

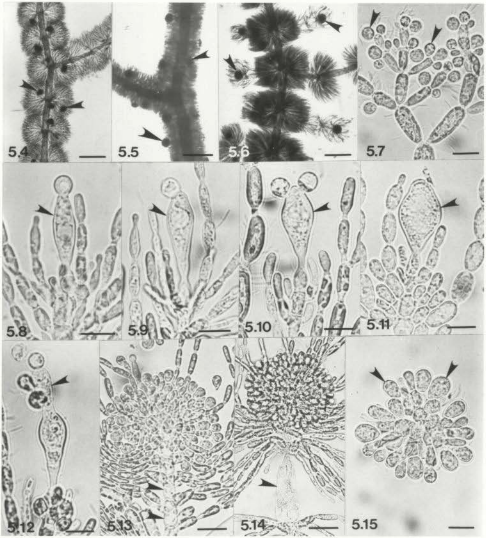

5.4
5.5
5.6
5.7
5.8
5.9
5.10
5.11
5.12
5.13
5.14
5.15

Fig. 5.16. Mean whorl diameter, fascicle length and carpogonium diameter and length for each biome. Error bars, standard error of the mean.

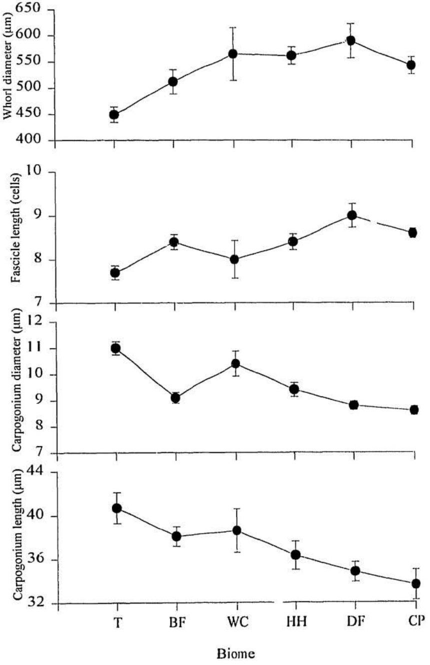

650
600
550
500
450
400
Whorl diameter (µm)
10
9
8
7
Fascicle length (cells)
12
11
10
9
8
7
Carpogonium diameter (µm)
44
40
36
32
Carpogonium length (µm)
T
BF
WC
HH
DF
CP
Biome

Fig. 5.17. Monthly changes in mean whorl diameter and fascicle length for populations NF 29 (●), NF 30 (■) and RI A (▲). Error bar, standard error of the mean.

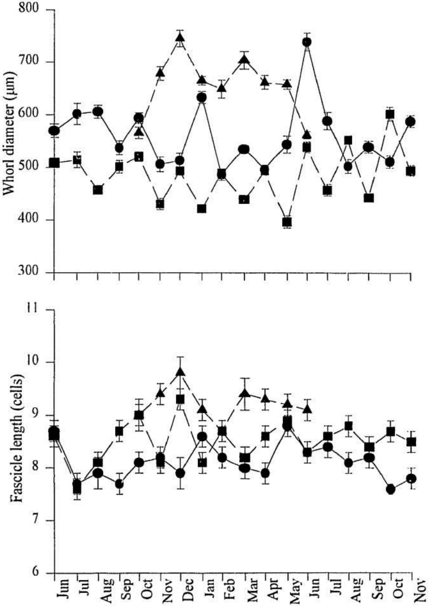

800
700
600
500
400
300
Whorl diameter (μm)
11
10
9
8
7
6
Fascicle length (cells)
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

Fig. 5.18. Monthly changes in mean carposporophyte diameter and carposporophytes per whorl for populations NF 29 (●), NF 30 (■) and RI A (▲). Error bar, standard error of the mean.

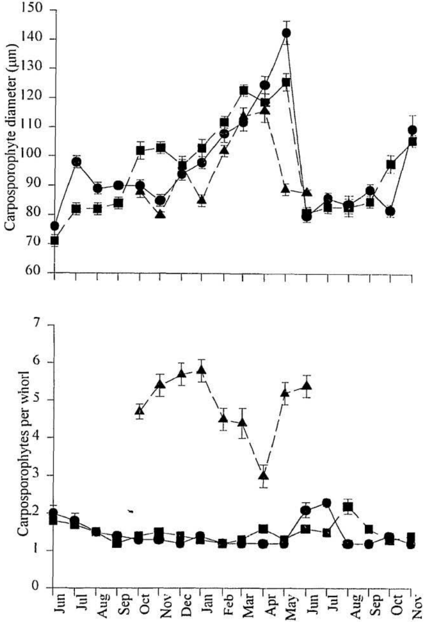
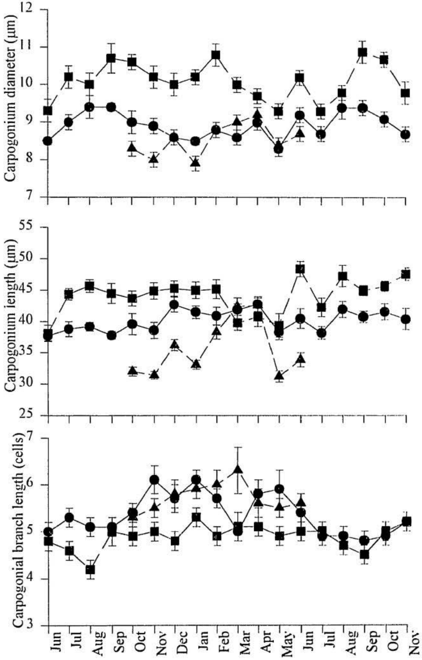
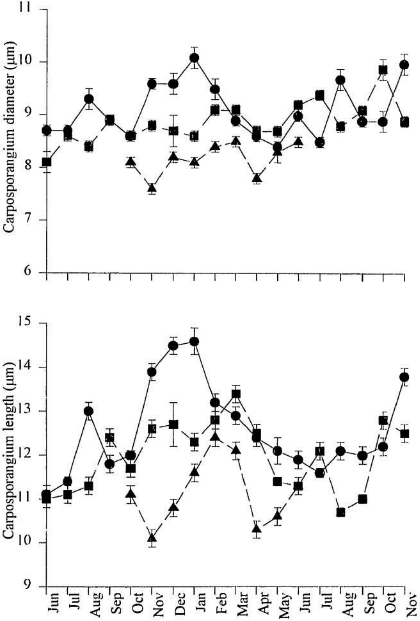

Carposporophyte diameter (µm)
150
140
130
120
110
100
90
80
70
60
Carposporophytes per whorl
7
6
5
4
3
2
1
0
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

Fig. 5.19. Monthly changes in mean carpogonium diameter and length and carpogonial branch length for populations NF 29 (●), NF 30 (■) and RI A (▲). Error bar, standard error of the mean.



Carpogonium diameter (μm)
12
11
10
9
8
7
Carpogonium length (μm)
55
50
45
40
35
30
25
Carpogonial branch length (cells)
7
6
5
4
3
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

Fig. 5.20. Monthly changes in mean carposporangium diameter and length for populations NF 29 (●), NF 30 (■) and RI A (▲). Error bar, standard error of the mean.


Carposporangium diameter (μm)
11
10
9
8
7
6
Carposporangium length (μm)
15
14
13
12
11
10
9
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

General conclusions

6.1 Conclusions

Using type and historically important specimens ten species were recognised: B. anatinum, B. arcuatum, B. boryanum, B. carpocontortum, B. confusum, B. fluitans, B. gelatinosum, B. heterocorticum, B. pulchrum and B. skujae. B. ectocarpum is considered to be synonymous with B. anatinum, rather than with B. boryanum or B. arcuatum as has been proposed by previous authors. The illegitimately named species B. helminthosum Sirodot (non Bory) was referred to B. confusum as were B. crouanianum and B. fruticulosum. No varieties of B. gelatinosum were supported and numerous taxa including B. pyramidale, B. densum and B. decaisneanum were synonymised within this species. B. fluitans was the only species in which a quantitative feature, carpogonium size, was useful in distinguishing it from another species, B. anatinum.

Previously described taxa in sect. Batrachospermum were separated on the basis of the qualitative characteristics: monoecious or dioecious thalli and the presence or absence of spermatangia on the involucral filaments, irregular or bulbous cortical cells, monosporangia, well-curled fascicles and secondary fascicles and quantitative feature, carpogonium size. Other qualitative characteristics previously used to separate taxa in this section, such as carposporophyte position, hourglass-shaped cells of the carposporophyte-bearing branch and brown cortication, were found to be too variable for use as taxonomic criteria.

The five new species, B. spermatoinvolucrum, B. trichofurcatum, B. carpoinvolucrum, B. involutum and B. trichocontortum, were described from North America. B. spermatoinvolucrum had no unusual features, but it was distinguished by the combination of spermatangia on the involucral filaments of the carpogonial branch, relatively long carpogonia and regular, cylindrical cortication. The other four species possessed distinct features previously unreported in any taxon of Batrachospermum. B. trichofurcatum had unique forked or furcate trichogynes. B. carpoinvolutum was distinct having carpogonia at the apex of involucral filaments of other carpogonial branches. The distinguishing feature of B. involutum was involute fascicle tips. B. trichocontortum had a twisted sometime helical trichogyne tip. In addition, B. involutum and B. trichocontortum had distinct rhizoidal outgrowths from the mid portion of the fascicles.

Batrachospermum sect. Batrachospermum is well represented in North America with 14 of 20 species. In addition to the new species described in Chapter 3, three species, B. carpocontortum, B. heterocorticum and B. pulchrum appear to be unique to this continent. B. boryanum and B. gelatinosum are widespread and inhabit in numerous localities; the other species are more localised and/or only occur in a few streams. This trend seems to be true for Europe as well. Most of the species have only been well documented from Europe. However, more intensive sampling of other continents is needed to assess the global distribution of these taxa.

B. gelatinosum exhibits considerable variation in morphological characteristics throughout its range in North America. In addition, seasonal variation within this species in both the boreal forest and deciduous forest biomes is as great as that among and within populations from all biomes. Thus, seasonal variation in populations should be taken into account in systematic and biogeographic analyses. A north-south trend in smaller plant size and larger carpogonium size is evident in this species. More seasonal patterns in morphological characteristics are shown in populations which are present only part of the year than in those present year round. However, there was little correlation among morphological features and stream parameters in either the geographic or seasonal study.

B. gelatinosum has a wide range in North America and appears to be globally distributed. This global distribution is due to its ability to inhabit streams which range widely in physical and chemical parameters. A molecular study of widely dispersed populations would be fruitful in explaining this pattern. In addition, using the morphometric data presented here, molecular and ultrastructure data, this section should be compared to other sections in order to best determine phylogenetic relationships within this genus.

6.2 Synoptic key to Batrachospermum sect. Batrachospermum

1. Monosporangia present 2
1. Monosporangia absent 3

2. Plants dioecious. . . . . .B. lochmodes

3. Spermatangia present on involucral filaments of the carpogonial branch 4

3. Spermatangia absent on involucral filaments of the carpogonial branch 7

4. Fascicles tips involute, rhizoidal outgrowths from mid-fascicle cells present. . . . . . .

. . . . B. involutum

4. Fascicles tips noninvolute, rhizoidal outgrowths from mid-fascicle cells absent. 5

5. Main axis with heterocortication composed of bulbous and cylindrical cells. . . . . . .

. . . . B. confusum

5. Main axis with cortication composed of cylindrical cells only. 6

6. Fascicles well-curled, carpogonium < 33 μm in length. . . . . .B. pulchrum

6. Fascicles straight, carpogonium > 39 μm in length. . . . . B. spermatoinvolucrum

7. Carpogonium contorted. 8

7. Carpogonium symmetrical. 11

8. Carpogonium with a furcated trichogyne. .B. trichofurcatum

8. Carpogonium with unforked trichogyne. 9

9. Twisting or contortion of trichogyne restricted to the tip, monoecious. . . . .

. . . . .B. trichocontortum

9. Bends or contortion at various points along the trichogyne, dioecious. 10

10. Trichogyne with numerous twists and contortions. . . . . B. carpocontortum

10. Trichogyne curved or bent with no twisting . . . . .B. szechwanense

11. Plants monoecious 12

11. Plants dioecious. 16

12. Plants having globose or pear-shaped whorls. . . . . .B. heteromorphum

12. Plants having globose whorls only 13

13. Fascicle cells cylindrical. . . . . .B. cylindrocellulare

13. Fascicle cells obovoid or elliptical. 14

14. Main axis with cortication composed of cylindrical cells . . . . .B. gelatinosum

14. Main axis with heterocortication composed of bulbous and cylindrical cells. 15

15. Carpogonium ≤ 41 μm in length with trichogyne ≤ 10 μm in diameter. . . . .

. . . . .B. anatinum

15. Carpogonium ≥ 51 μm in length with trichogyne ≥ 11 μm in diameter. . . . B. fluitans

16. Carpogonial branch with involucral filaments on one side only. . . . .

. . . . B. nova-guineense

16. Carpogonial branch with involucral filaments not confined to one side. 17

17. Main axis with cortication composed of cylindrical cells . . . . B. arcuatum

17. Main axis with heterocortication composed of bulbous and cylindrical cells. 18

18. Carpogonial branch having involucral filaments with apical carpogonia present. . . .

. . . . B. carpoinvolucrum

18. Carpogonial branches having involucral filaments with apical carpogonia absent. . .

. 19

19. Main axis with distinct whorls and little secondary fascicle growth. . . . . B. boryanum

19. Main axis with indistinct whorls and abundant secondary fascicle growth. . . . .

19. Main axis with indistinct whorls and abundant secondary fascicle growth. . . . .
. . . . .B. heterocorticum

Batrachospermum lochmodes, B. szechwanense, B. heteromorphum, B. cylindrocellulare and B. nova-guineense were not examined by the authors, but were included in the key based on distinguishing characteristics given in the protologues (Skuja, 1938; Jao, 1941; Kumano, 1978; Kumano & Johnstone, 1983; Shi et al., 1993). All morphometric data in this thesis may be obtained from the author or Dr. R.G. Sheath.

References

ANONYMOUS. (1988). SAS/STAT User's Guide, 6.03 Edn. SAS Institute, Cary, North Carolina.

ARCANGELI, G. (1882). Sopra alcune specie di Batrachospermum. Nuovo Giorn. Bot. Ital. 16: 155-167, pl. 5. 6.

BACHMANN, H. (1921). Beiträge zur Algenflora des Süßwassers von Westgrönland. Mitt. Naturforsch. Ges., Luzern 8: 1-181.

BALAKRISHNAN, M.S. & CHAUGULE, B.B. (1980). Indian Batrachospermaceae. In Taxonomy of Algae. (Desikachary,T. V. & Raja Rao, V. N., editors), 225-248. University of Madras, Madras, India.

BENNETT, J.L. (1888). Plants of Rhode Island. Brown University, Providence, Rhode Island.

BEOM-JUN, Y. (1980). Systematic Survey of Brackish and Freshwater Algae of Korea. INHA University Press, Incheon, Korea.

BLAIR, A.P. (1978). New plant distribution records in eastern Oklahoma. Proc. Oklahoma Acad. Sci. 58: 106-107.

BORY [DE ST VINCENT], J.B.G.M. (1808). Mémoire sur le genre Batrachosperma, de la famille des Conferves. Ann. Mus. Hist. Nat. 12: 310-332, pl. 29-31.

BORY [DE ST VINCENT], J.B.G.M. (1823). Ceramiales et Conferves. Dictionaire Classique d'Histoire Naturelle, Vol. 3. Paris.

BRITTON, M.E. (1944). A Catalog of Illinois Algae. Northwestern University, Evanston, Illinois.

BURKHOLDER, J.A. & SHEATH, R.G. (1985). Characteristics of softwater streams in Rhode Island. I. A comparative analysis of physical and chemical variables. Hydrobiologia 128: 97-108.

COMPÈRE, P. (1991a). Taxonomic and nomenclatural notes on some taxa of the genus Batrachospermum (Rhodophyceae). Belg. J. Bot. 124: 21-26.

COMPÈRE, P. (1991b). Flore Pratique des Algues d'Eau Douce de Belgique. Jardin Botanique National de Belgique, Meise, Belgium.

COOKE, M.C. (1882). British Fresh-water Algae. vol. 1. Williams and Norgate, London.

CEDERCREUTZ, C. & FAGERSTRÖM, L. (1969). Freshwater algae of Ostrobottnia Kajanensis, Finland. Acta Soc. Pro Fauna et Flora Fennica 79: 1-34.

CROASDALE, H.T. (1935). The Fresh Water Algae of Woods Hole Massachusetts. Published by the author, Philadelphia, Pennsylvania.

DE CANDOLLE, A.P. (1801). Extrait d'un rapport sur les Conferves. Bull. Sci. Soc. Philomat. Paris 3(51): 17-21.

DE TONI, J.-B. (1897). Sylloge Algarum 4: Florideae, Sectio I: p. XX + LXI + 388 pp. Patavii, Typis Seminarii.

DREW, K.M. (1946). Anatomical observations on a new species of Batrachospermum. Ann. Bot., N.S. 10: 339-352.

DROUET, F. (1933). Algal vegetation of the large Ozark springs. Trans. Am. Micro.

Soc. 52: 83-100.

DUTHIE, H.C. & HAMILTON, P.B. (1983). Studies on periphyton community dynamics of acidic streams using track autoradiography. In Periphyton of Freshwater Ecosystems. (Wetzel, R. G., editor), 185-189. Junk, The Hague.

DUTHIE, H.C. & OSTROFSKY, M.L. (1975). Freshwater algae from western Labrador III. Cyanophyta and Rhodophyta. Nova Hedwigia 26: 555-559.

DUTHIE, H.C. & SOCHA, R. (1976). A checklist of the freshwater algae of Ontario exclusive of the Great Lakes. Nat. Can. 103: 83-109.

DUTILLY, A., LEPAGE, E., DUMAN, M. (1958). Contribution à la Flore des Îles (T. N. O.) et du Versant Oriental (Qué.) de la Baie James. The Catholic University of America Press, Washington D.C.

ENTWISLE, T.J. (1989). Macroalgae in the Yarra River Basin: Flora and distribution. Proc. Roy. Soc. Vic. 101: 1-76.

ENTWISLE, T.J. & KRAFT, G.T. (1984). Survey of freshwater red algae (Rhodophyta) of southeastern Australia. Austr. J. Mar. Freshw. Res. 35: 213-259.

FLINT, L.H. (1916). A First Partial List of the Algae of Vermont. M. S. Thesis, University of Vermont.

FLINT, L.H. (1948). Studies of fresh-water red algae. Amer. J. Bot. 35: 428-433.

FLINT, L.H. (1949). Studies of fresh-water red algae. Amer. J. Bot. 36: 549-552.

FLINT, L.H. (1957a). Notes on algae of Quebec I. Mont Tremblant Park. Nat. Can.

84: 157-160.

FLINT, L.H. (1957b). Notes on algae of Quebec II. Laurentide Park. Nat. Can. 84: 179-181.

GEITLER, L. (1944). Ein neues einheimisches Batrachospermum sowie Beobachtungen an anderen eiheimischen Batrachospermum - Arten. Österr. bot. Zeit. 93: 127-37.

GREUTER, W. ET AL. (1988). International Code of Botanical Nomenclature. Koeltz Scientific Books, Königstein.

HABEEB, H. & DROUET, F. (1948). A list of freshwater algae from New Brunswick. Rhodora 50: 67-71.

HAMILTON, P.B. & DUTHIE, H.C. (1984) Periphyton colonization of rock surfaces in a boreal forest stream studied by scanning electron microscopy and track autoradiography. J. Phycol. 20: 525-532.

HARVEY, W.H. (1857). Nereis Boreali-Americana. Part III. Chlorospermeae. Smithsonian Institute, Washington D. C.

HASSALL, A.H. (1845). A History of the British Freshwater Algae Vols. 1 & 2. Highley and Bailliere, London.

HINTON, G.C.F. & MAULOOD, B.K. (1980). Freshwater red algae, a new addition to the Iraqi flora. Nova Hedw. 33: 487-497.

HOLMGREN, P.K., HOLMGREN, N.H. & BARNETT, L.C. (1990). Index Herbariorum, Part I. The Herbaria of the World. 8th ed. New York Botanical

Garden, Bronx, New York, 643 pp.

HU, H.J., LI, Y.Y., Wei, Y.X., ZHU, H.Z., CHEN, J.Y. & SHI, Z.X. (1981). Freshwater Algae of China. Institute of Aquatic Biology of Chinese Acad. Sinica, Shanghia, China.

HUGHES, E.O. (1948). Fresh-water algae of the maritime provinces. Proc. Nova Scotian Inst. Sci. 22: 1-63.

HYLANDER, J.C. (1928). The algae of Connecticut. State Geo. Nat. Hist. Survey Bull. 42: 1-245.

ISRAELSON, G. (1942). The freshwater Florideae of Sweden. Symb. Bot. Upsal. 6: 1-134.

JAO, C.-C. (1940). Studies on the freshwater algae of China IV. Subaerial and aquatic algae from Nanyoh, Hunan Part II. Sinensia 11: 241-361.

JAO, C.-C. (1941). Studies on the freshwater algae of China VIII. a preliminary account of the Chinese freswater Rhodophyceae. Sinesia 12: 245-289.

JOYCE, R.E. (1936). The Algae of Vermont. M. S. Thesis, Ohio State University, Ohio.

KACŹMARCZYK, D., SHEATH, R.G. & COLE, K.M. (1992). Distribution and systematics of the freshwater genus Tuomeya (Rhodophyta, Batrachospermaceae). J. Phycol. 28: 850-855.

KERNER, A. (1882). Schedae ad Floram exsiccatam Austro-Hungaricum a Museeo botanico Universitatis Vindobonensis anno 1881 editam. Fasc. II 8. Bot.

Centralb. X: 360-362.

KUMANO, S. (1978). Notes on freshwater red algae from West Malaysia. Bot. Mag. (Tokyo) 91: 97-107.

KUMANO, S. (1979). Studies on the Taxonomy and the Phylogenetic Relationships of the Batrachospermaceae of Japan and Malaysia. Doctorate Thesis, Kyoto University.

KUMANO, S. (1993). Taxonomy of the family Batrachospermaceae (Batrachospermales, Rhodophyta). Jpn. J. Phycol. (Sôrui) 41: 253-274.

KUMANO, S. & JOHNSTONE, I.M. (1983). Studies on the freshwater Rhodophyta of Papua New Guinea I. Batrachospermum nova-guineense sp. nov. from the Papuan lowlands. Jpn. J. Phycol. (Sôrui) 31: 65-70.

KUMANO, S. & WATANABE, M. (1983). Two new varieties of Batrachospermum (Rhodophyta) from Mt. Albert Edward, Papua New Guinea. Bull. Nat. Sci. Mus., Tokyo, Ser. B, 9: 85-94.

KÜTZING, F.T. (1849). Species Algarum. F. A. Brockhaus, Lipsiae.

KYLIN, H. (1912). Studien über die schwedischen Arten der Gattungen Batrachospermum Roth und Sirodotia nov. gen. Nova Acta Reg. Soc. Sci. Upsal., Ser. 4, 3: 1-40.

LARIVERS, I. (1978). Algae of the Western Great Basin. University of Nevada, Reno, Nevada.

LILLICK, L.C. & LEE, I.M. (1934). A check-list of Ohio algae with additions from the Cincinnati region. Am. Midl. Nat. 15: 713-751.

LINNAEUS, C. (1753). Species Plantarum, ed. 1, Vol. 2: 561-1200. Stockhom, Imp. Laurentii Salvii.

LUNGU, L. (1969). Batrachospermum boryanum Sirodot în flora algologică a României. Studii si Cerc. Biol. Ser. Bot. (Bucuresti) 21: 13-15.

MEYER, R.L. & BROOK, A.J. (1971). Freshwater algae from the Itasca state park Minnesota. Nova Hedwigia 22: 649-658.

MILLER, R.R. (1981). Coevolution of deserts and pupfishes (genus Cyprinodon) in the American Southwest. In Fishes in North American deserts. (Naiman, R.J. & Soltz, D.L., editors), 39-94, John Wiley & Sons, New York.

MORI, M. (1975). Studies on the genus Batrachospermum in Japan. Jpn. J. Bot. 20: 461-484.

MOSHKOVA, H.O. (1960). Freshwater red algae of the Crimea. Ukrain. bot. Zhu. Kiev. 17: 95-101.

NECCHI, O. Jr. (1989). Geographic distribution of the genus Batrachospermum (Rhodophyta, Batrachospermales) in Brazil. Rev. Brasil. Biol. 49: 663-669.

NECCHI, O. Jr. (1990). Revision of the genus Batrachospermum Roth (Rhodophyta, Batrachospermales) in Brazil. Bibl. Phycologica. 84: III +201p., 264 fig.

NECCHI, O. Jr. & ENTWISLE, T.J. (1990). A reappraisal of generic and subgeneric classification in the Batrachospermaceae (Rhodophyta). Phycologia 29: 478-488.

NECCHI, O. Jr., SHEATH, R.G. & COLE, K.M. (1993). Distribution and systematics of the freshwater genus Sirodotia (Batrachospermales, Rhodophyta) in North America. J. Phycol. 29: 236-243.

NODA, M. (1963). Freshwater algae of North-Eastern China. J. Fac. Sci. Niigata Univ. Ser. 2, Biol., Geol. Mineral. 4: 105-178.

OLNEY, S. (1871). Algae Rhodiaceae. Brown University, Providence, Rhode Island.

ORTEGA, M.M. (1984). Catalogo de Algas Continentales Recientes de Mexico. University Auton de Mexico, Mexico.

PODANI, J. (1990). SYN-TAX IV User's Manual. International Centre for Earth, Environmental and Marine Sciences and Technologies, Trieste, Italy.

PRESCOTT, G.W. (1962). Algae of the Western Great Lakes Area. Wm. C. Brown, Dubuque, Iowa.

PRESCOTT, G.W. & DILLARD, G.E. (1979). A checklist of algal species reported from Montana 1891 to 1977. Proc. Montana Acad. Sci. 38 Suppl. 1: 1-102.

RABENHORST, L. (1854). Batrachospermum kühnianum Rabenh. Hedwigia 1: 42, pl. 7 fig. 1.

RABENHORST, L. (1863). Kryptogamen Flora, Vol. 1, Leipzig.

RABENHORST, L. (1868). Flora Europaea Algarum Aquae Dulcis et Submarinae Vol. 3, Leipzig. 461pp.

REIS, M.P. dos. (1954). Sur le Batrachospermum corbula Sirodot var. alcoense P. Reis n. var. Comm. VIII Congr. Int. Bot. Paris, 17ème Sect.: 70-71.

REIS, M.P. dos. (1962). Subsídios para o conhecimento da Rodofíceas de água doce de Portugal III. Mem. Soc. Brot. 15: 57-71.

REIS, M.P. dos. (1969). Subsídios para o conhecimento das Rodofíceas de agua doce de Portugal VII. Bol. Soc. Brot. 43: 183-192.

REIS, M.P. dos. (1972). Dois taxa do género Batrachospermum Roth novos para a flora portuguesa. Bol. Soc. Portuguesa Cien. Nat. 14: 107-112.

REIS, M.P. dos. (1973). Subsídios para o chohecimento das Rodofíceas de água doce de Portugal VIII. Bol. Soc. Brot. 47: 139-156.

REIS, M.P. dos. (1974). Chaves para a identificação das espécies portuguesas de Batrachospermum Roth. Anuario da Sociedade Broteriana 40: 37-129.

RHODES, R.G. & TERZIS, A.J. (1970). Some algae of the upper Cuyahoga River system in Ohio. Ohio J. Sci. 70: 295-299.

RIDER, D.E. & WAGNER, R.H. (1972). The relationship of light, temperature and current to the seasonal distribution of Batrachospermum (Rhodophyta). J. Phycol. 8: 323-331.

ROEDER, D.R. & PECK, J.H. (1977). Batrachospermum Roth (Rhodophyta), a genus of red algae new to Iowa. Proc. Iowa Acad. Sci. 84: 133-138.

ROTH, A.W. (1797). Bemerkungen über das Studium der Crytoganischen Wassergewachse. Hannover, Germany.

ROTH, A.W. (1800). Tentamen Florae Germanicae. Vol. 3. Leipzig.

RYAN, B.F., JOINER, B.L. & RYAN, T.A. Jr. (1985). Minitab Handbook, 2nd edn.

Duxbury Press, Boston.

ROSCOE, M.V. (1931). The algae of St. Paul Island. Rhodora 33: 127-131.

SABATER, S., ABOAL, M. & CAMBRA, J. (1989). Nuevas observaciones de Rhodofíceas en aguas epicontinentales de NE y SE de España. Limnética 5: 93-100.

SÁNCHEZ-RODRÍGUEZ, E. (1974). Rodofíceas dulceacuícolas de Mexico. Bol. Soc. Brot. México 33: 31-37.

SCHMIDLE, W. (1898). Algologische notizen. Allg. bot. Zeit. für Syst. 5: 2-4.

SHEATH, R.G. & BURKHOLDER, J.M. (1983). Morphometry of Batrachospermum populations intermediate between B. boryanum and B. ectocarpum (Rhodophyta). J. Phycol. 19: 324-331.

SHEATH, R.G. & BURKHOLDER, J.M. (1985). Characteristics of softwater streams in Rhode Island II. Composition and seasonal dynamics of macroalgal communities. Hydrobiologia 128: 109-118.

SHEATH, R.G., BURKHOLDER, J.M., MORISON, M.O., STEINMAN, A.D. & VANALSTYNE, K.L. (1986a). Effect of tree canopy removal by gypsy moth larvae on the macroalgae of a Rhode Island headwater stream. J. Phycol. 22: 567-570.

SHEATH, R.G. & COLE, K.M. (1990). Batrachospermum heterocorticum sp. nov. and Polysiphonia subtilissima (Rhodophyta) from Florida spring-fed streams. J. Phycol. 26: 563-568.

SHEATH, R.G. & COLE, K.M. (1992). Biogeography of stream macroalgae in North America. J. Phycol. 28: 448-460.

SHEATH, R.G. & COLE, K.M. (1993). Distribution and systematics of Batrachospermum (Batrachospermales, Rhodophyta) in North America. 2. Chromosome numbers. Phycologia 32: 304-306.

SHEATH, R.G. & HAMBROOK, J.A. (1990). Freshwater ecology. In Biology of the Red Algae (Cole, K. M. & Sheath, R. G., editors), 423-453. Cambridge University Press, Cambridge.

SHEATH, R.G., HAMBROOK, J.A. & NERONE, C.A. (1988). The benthic macro-algae of Georgian Bay, the North Channel and their drainage basin. Hydrobiologia 163: 141-148.

SHEATH, R.G., HAMILTON, P.B., HAMBROOK, J.A. & COLE, K.M. (1989). Stream macroalgae of the eastern boreal forest region of North America. Can. J. Bot. 67: 3553-3562.

SHEATH, R.G. & HYMES, B.J. (1980). A preliminary investigation of the freshwater red algae in streams of southern Ontario, Canada. Can. J. Bot. 58: 1295-1318.

SHEATH, R.G., KACZMARCZYK, D. & COLE, K.M. (1993a). Distribution and systematics of freshwater Hildenbrandia (Rhodophyta, Hildenbrandiales) in North America. Eur. J. Phycol. 28: 115-121.

SHEATH, R.G., MORISON, M.O., COLE, K.M. & VANALSTYNE, K.L. (1986c). A new species of freshwater Rhodophyta, Batrachospermum carpocontortum.

Phycologia 25: 321-330.

SHEATH, R.G., MORISON, M.O., KORCH, J.E., KACZMARCZYK, D. & COLE, K.M. (1986b). Distribution of stream macroalgae in south-central Alaska. Hydrobiologia 135: 259-269.

SHEATH, R.G., VIS, M.L. & COLE, K.M. (1992). Distribution and systematics of Batrachospermum (Batrachospermales, Rhodophyta) in North America 1. Section Contorta. J. Phycol. 28: 237-246.

SHEATH, R.G., VIS, M.L. & COLE, K.M. (1993b). Distribution and systematics of Batrachospermum (Batrachspermales, Rhodophyta) in North America 3. Section Setacea. J. Phycol. 29: 720-726.

SHEATH, R.G., VIS, M.L. & COLE, K.M. (1993c). Distribution and systematics of the freshwater red algal family Thoreaceae in North America. Eur. J. Phycol. 28: 231-241.

SHEATH, R.G., VIS, M.L. & COLE, K.M. (1994a). Distribution and systematics of Batrachospermum (Batrachospermales, Rhodophyta) in North America. 4. Section Virescentia. J. Phycol. 30: 108-117.

SHEATH, R.G., VIS, M.L. & COLE, K.M. (1994b). Distribution and systematics of Batrachospermum (Batrachospermales, Rhodophyta) in North America. 6. Section Turfosa. J. Phycol. 30: 872-884.

SHEATH, R.G., VIS, M.L. & COLE, K.M. (1994c). Distribution and systematics of Batrachospermum (Batrachospermales, Rhodophyta) in North America 5.

Section Aristata. Phycologia. In press.

SHEATH, R.G. & WHITTICK, A.W. (1995). The unique gonimoblast propagules of Batrachospermum breutelii (Batrachospermales, Rhodophyta). Phycologia 34. In press.

SHI, Z., HU Z. & KUMANO, S. (1993). Batrachospermum heteromorphum, sp. nov. (Rhodophyta) from Hubei Province, China. Jpn. J. Phycol. (Sôrui) 41: 295-302.

SIEMIŃSKA, J. (1992). Red list of threatened algae in Poland. In List of Threatened Plants in Poland. (Zarzycki, K., Wojewoda, W. & Heinrich, Z., editors), 7-19. Polish Academy of Sciences, W. Szafer Institute of Botany, Cracow, Poland.

SIRODOT, S. (1873). Nouvelle classification des algues d'eau douce du genre Batrachospermum; développement; générations alternantes. C. R. Hebd. Acad. Sci. Paris 76: 1216-1220.

SIRODOT, S. (1874). Observations sur les phénomènes essentiels de la fécondation chez les algues d'eau douce du genre Batrachospermum. C. R. Hebd. Acad. Sci. Paris 79: 1366-9.

SIRODOT, S. (1884). Les Batrachospermes, Organisation, Fonctions, Développement, Classification. Librairie de l'Académie de Médicine, Paris, 299 pp.

SKALNE, E. (1973). The algae of the Karst Vaucluse spring at Jerzmanowice (Cracow-Czestochowa Jurassic Region). Frag. Flor. Geobot. 19: 344-348.

SKUJA, H. (1928). Vorarbeiten zu einer Algenflora von Lettland IV. Acta Horti Bot. Univ. Latviensis 3: 103-218, 4 pls.

SKUJA, H. (1931). Einiges zur Kenntnis der brasilianischen Batrachospermen. Hedwigia 71: 78-87, pl. 1-2.

SKUJA, H. (1933). Untersuchungen über die Rhodophyceen des Süsswassers. III. Batrachospermum breutelii Roth und seine Brutkörper. Arch. Protist. 80: 357-366, pl. 12-13.

SKUJA, H. (1938). Die Süsswasserrhodophyceen der Deutschen Limnologischen Suda-Expedition. Arch. Hydrobiol. 15: 603-37.

STARMACH, K. (1928). Beitrag zur Kenntnis der Süsswasser florideen von Polen. Acta Soc. bot. Pol. 5: 367-389.

STARMACH, K. (1975). Algae in the Szopczanski Gorge in the Pieniny Mts. Fragm. Flor. Geobot. 21: 535-549.

STARMACH, K. (1977). Flora Slodkowodna Polski Tom 4: Phaeophyta-Brunatnice and Rhodophyta-Krasnorosty. Polska Academia Nauk, Warszawa.

STARMACH, K. (1980). Eine für Polen neue Art von Batrachospermum skujae Geitler. Frag. Flor. Geobot. 26: 175-180.

STARMACH, K. (1981). Batrachospermum sporulans Sirodot und B. sporulans for. pulvinatum (Bonhomme) Starmach im quellbach "Źródlany" in Krynica. Frag. Flor. Geobot. 27: 545-553.

STARMACH, K. (1984). Red algae in the Kryniczanka stream. Frag. Flor. Geobot. 28: 257-293.

STARMACH, K. (1989). Glony w zlewnipotoku Kryniczanka. Stud. Ośroka

Dokumentacji Fizjogr. 17: 373-400.

STEIN, J.R. & BORDEN, C.A. (1978). Checklist of freshwater algae of British Columbia. Syesis 12: 3-39.

STEINMAN, A.D., MULHOLLAND, P.J. & KIRSCHTEL, D.B. (1991). Interactive effects of nutrient reduction and herbivory on biomass, taxonomic structure, and P uptake in lotic periphyton communities. Can. J. Fish. Aquat. Sci. 48: 1951-1959.

VAN MEEL, L.I.J. (1939a). Quelques récoltes algologiques dans les provinces de Brabant-Hainaut et Namur. Bull. Soc. Roy. Bot. Belg. 62: 41-46.

VAN MEEL, L.I.J. (1939b). Sur la répartition du genre Batrachospermum en Belgique. Bull. Jardin Bot. (Bruxelles) 15: 319-331.

VINYARD, W.C. (1966). Additions to the algal flora of Oklahoma. Southwestern Nat. 11: 196-204.

WHITFORD, L.A. & SCHUMACHER, G.J. (1968). Notes on the ecology of some species of fresh-water algae. Hydrobiologia 32: 225-236.

WHITFORD, L.A. & SCHUMACHER, G.J. (1973). A Manual of Fresh-water Algae. Sparks Press, Raleigh, North Carolina.

WOELKERLING, W.J. (1975). Observations on Batrachospermum (Rhodophyta) in southeastern Wisconsin streams. Rhodora 77: 467-477.

WOO, M.-K. (1991). Arctic streamflow. In Arctic Environment: Past, Present and Future. (Woo, M.-K. & Gregor, D.J., editors), 105-111, Department of

Geography, McMaster University, Hamilton, Ontario.

WOOD, H.C. (1872). A contribution to the history of the fresh-water algae of North America. Smithsonian Contrib. Knowledge 19: 1-262.

WOODSON, B.R. & AFZAL, M. (1976). The taxonomy and ecology of algae in the Appomattox River, Chesterfield County, Virginia. Virginia J. Sci. 27: 5-9.

WUJEK, D.E. & LEE, J.L. (1984). New, rare, and unusual algae from Montana. Northwest Sci. 58: 213-221.

Appendix 1 : Additional North American herbarium specimens.

The following specimens can be classified as B. anatinum:

Originally identified as Batrachospermum sp.:

1. California: Santa Barbara, S. P. Cooper, **F** 1206641.
2. Indiana: Monticello, 4 vi 1939, W. A. Daily, **F** 1224235, **FH**, **LAM** 599988, MO in **UC MO** 1178073, **UC** 634347, **UC** 752175.
3. Missouri: Barnhart, 6 i 1931, J. A. Steyermark, **MO** in **UC MO** 1018434, **NY**, **F** 968133; Barnhart, 16 i 1931, J. A. Steyermark, **FH**; Burns, 17 vii 1934, J. A. Steyermark, **F** 1014314.
4. Montana: Flathead Co., 16 v 1942, F. A. Barkley, **F** 1108579.
5. Pennsylvania: Northampton Co., 20 xii 1977, **PH**.
6. Utah: Salt Lake City, 1931, A. O. Garrett, **F** 1223029.

Originally identified as B. anatinum:

7. Michigan: Ann Arbor, 22 iv 1932, W. R. Taylor, **F** 546840, **F** 950915, **F** 950916, **MICH** 16543, **MICH** 16544, **MICH** 16545; Delhi, 21 v 1932, I. Clark, **MICH** 16802.
8. Missouri: Gravois Mills, 4 iv 1931, F. Drouet, **MICH** 16797; Gravois Mills 3 v 1931, F. Drouet, **MICH** 16490; Gravois Mills, 21 vi 1931, F. Drouet, **MICH** 16798, **MICH** 16799; Gravois Mills, 7 xi 1931, F. Drouet, **MICH** 16800.
9. Ohio: Champaign Co., 3 v 1934, W. R. Taylor, **MICH** 16805.

Originally identified as B. boryanum:

10. Pennsylvania: F. Wolle, **UC** 95491, **UC** 95508.

Originally identified as B. depauperatum nom. nud.:

11. Missouri: Bennett Spring State Park, 6 vi 1929, **MICH** 16803; Hahatonka, 27 ii, 1932, **MICH** 16804.

Originally identified as B. ectocarpum:

12. Ontario: Owen Sound, 1871, Mrs. H. Roy, **F** 1206698.

Originally identified as B. hesperatum nom nud.:

13. Missouri: Gravois Spring, 19 viii 1934, F. Drouet, **MICH** 16806.

Originally identified as B. moniliforme:

14. Ontario: Owen Sound, viii 1871, J. Macoun, **F** 1206713; Owen Sound, 1874, **CANA** 5642.

The following specimens can be classified as B. arcuatum:

Originally identified as B. arcuatum:

1. California: Kelseyville, 20 iii 1931, V. Duran, **F** 1068984, **LAM** 599956, **US** 39728.
2. Utah: Unitah, vii 1869, S. Watson, **US** 03616.

Originally identified as B. boryanum:

3. California: Los Angeles (P.B.-A. 1644), v 1908, N. L. Gardner, **CANA** 93, **F** 546114, **F** 1017415, **MICH**, **US** 03624; Placer Co., iv 1928, N. L.

Gardner, **UC** 314992; Santa Cruz, 1933, C. L. Anderson, **NY**, **UC** 95495.

Originally identified as B. moniliforme:

4. California: Shasta Springs, viii 1894, M. A. Howe, **NY**.

The following specimens can be classified as B. boryanum as follows:

Originally identified as Batrachospermum sp.:

1. Connecticut: East Haven, 2 vi 1870, D. C. Eaton, **F** 12006896; Norwich, iv 1885, W. A. Setchell, **F** 1206891.
2. Illinois: Galena, 17 vi 1946, F. Drouet & H. B. Louderback, **F** 1185350, Lemont, 18 x 1938, F. Drouet, P. C. Standley & J. A. Steyermark, **F** 1062823, **FH**, **MICH** 18158.
3. Indiana: Indianapolis, 11 iv 1939, W. A. Daily & F. Kenayer, **FH**, **NY**, **UC** 634349.
4. Michigan: Washtenaw Co., 3 xii 1892, L. N. Johnson, **F** 1159684.
5. Missouri: Steelville, 17 ix 1938, C. Shoop, **F** 947351.
6. New Jersey: Spooky Brook, Somerset, 6 iii 1972, E. T. Moul, **RUT**.
7. Pennsylvania: Conestoga Creek, Lititz Run, 6 viii 1948, R. Patrick & J. Wallace, **PH**.
8. South Carolina: Savannah River, Allendale Co., 26 ix 1961, **PH**; Savannah River, Allendale Co., 30 xi 1972, R. R. Grant Jr., **PH**.

9. Virginia: Bland & Giles Co., 28 vi 1968, C. J. Feller, **US** 60568.

Originally identified as B. boryanum:

10. Arkansas: Imboden, Winter 1924, B. C. Marshall, **NY**.

11. California: Arroyo Seco, v 1908, N. L. Gardner, **F** 947596, **FH**, **NY**, **UC** 39469; Fort Rose, iii 1896, M. A. Howe, **UC** 92625; Los Angeles, 19 iv 1931, G. J. Hollenberg, **US** 63032; Los Angeles, 22 iv 1935, G. J. Hollenberg, **US** 63033; Pasadna [Tilden (1896) American Algae Century II no. 109], 6 xii 1895, A. J. McClachie, **F** 951831, **NY**, **UC** 278173, **UC** 740265, **US** 56083.

12. Connecticut: Bridgeport, 24 iv 1889, I. Holden, **FH**; Bridgeport, 19 v 1889, I. Holden, **FH**; Bridgeport 16 ii 1890, I. Holden, **FH**, **UC** 95500, **UC** 95003; Bridgeport, 20 iv 1890, I. Holden, FH; Bridgeport, 2 iii 1890, I. Holden, **UC** 95502, **UC** 9501; Bridgeport, 16 iii 1890, I. Holden, **UC** 95504, **UC** 95505; Bridgeport, 23 iii 1890, I. Holden, **F**, **FH**; Bridgeport, 10 v 1890, I. Holden, **LAM** 599963, **NY**; Bridgeport, 13 xi 1890, I. Holden, **FH**; Bridgeport, 7 xii 1890, I. Holden, **UC** 95486; Bridgeport & Stratford (P.B.-A. 187a), 15 ii 1891, I. Holden, **CANA** 94, **F** 1017429, **LAM** 599953, **NY**, **US** 69924; Bridgeport & Stratford, 22 iii 1891, I. Holden, **LAM** 599952; East Haven, 10 vi 1885, W. A. Setchell, **NY**, **UC** 95479; Easton, 9 v 1886, I. Holden, **FH**; Norwich, iv 1885, W. A. Setchell, **NY**, **UC** 95478; Stratford, 23 iv 1886, I. Holden, **F** 1208816,

NY, **UC** 95480; Stratford, 23 iii 1890, I. Holden, **FH**; Stratford, 13 iii 1892, I. Holden, **FH**.

13. Illinois: Charleston, 26 iv 1911, E. Franscan, **NY**.

14. Massachusetts: Arlington, 6 iv 1890, J. W. Dewart, **UC** 95476; Arlington 4 iv 1893, B. M. Davis, **MICH**; Arlington, 23 iv 1894, B. M. Davis, **MICH** (in part); Arlington, 11 v 1894, D. M. Davis, **MICH**; Cuttyhunk, 25 vi 1929, W. R. Taylor, **MICH** 15039; Malden, 16 iii 1890, F. S. Collins & W. A. Setchell, **F** 676429, **LAM** 599965, **MICH** 26028, **NY**, **UC** 95471, **UC** 95477, **US** 006533; Malden, 23 iv 1890, F. S. Collins & W. A. Setchell, **F** 1017425, **FH**; Malden, 13iv 1890, F. S. Collins, **UC** 95475; Malden, 14 iv 1890, F. S. Collins, **FH**, **UC** 95474; Manchester, 8 iv 1890, W. C. Sturgis, **UC** 95485; Manchester, 1 v 1891, W. C. Sturgis, **NY**; Manchester, v 1891, Dewart, Keeley & Sturgis, **F** 975658, **F** 1001587, **UC** 92627, **US** 03621; Medford, 16 iii 1890, F. S. Collins, **NY**; Medford, 5 v 1889, F. S. Collins, **NY**; Middlesex Fells (P.B.-A. 187b), 14 iv 1890, F. S. Collins, **CANA** 94, **F** 545526, **LAM** 599957, **LAM** 599960, **LAM** 599962, **LAM** 599964, **NY**, **UC** 693309, **US** 03623, **US** 072427; Middlesex Fells, 1890, F. S. Collins, **NY**, **UC** 759302; Saugus, 16 iv 1890, F. S. Collins, **FH**, **NY**, **UC** 95473, **UC** 777388; Saugus, 23 iv 1890, F. S. Collins, **UC** 777375, **UC** 777385; Sharon, 8 iv 1890, F. S. Collins & W. A. Setchell, **F** 1012125, **FH**, **UC** 95482; Sharon, 24 v

1890, W. A. Setchell, **UC** 95488; Stony Brook, 19 v 1898, **NY**; Wakefield, 6 iv 1890, F. S. Collins, **UC** 95472; Wakefield, 12 iv 1890, F. S. Collins, **NY**; Westford, 5 v 1889, **NY**; Waverley, v 1892, **UC** 92626.

15. Michigan: Ann Arbor, 3 iii 1893, M. A. Howe, **NY**; Ann Arbor (P.B.-A. 187c), xi 1893, L. N. Johnson, **CANA** 94, **F** 1170907, **F** 1171154, **NY**, **UC** 95492, **US** 69925; Delhi, 21 v 1932, I. Clark, **MICH** 16802; Oakland, 1906, J. L. H., **NY**; Saline, 16 iv 1953, J. Blum, **MICH** 26524; Washington, D. D. Cooley, **NY**.

16. Missouri: St. James, 13 iv 1930, F. Drouet, **MICH** 15042.

17. Montana: Great Falls, 28 ix 1885, F. Anderson, **NY**, **UC** 95493, **UC** 95494; Great Falls, vii 1885, F. Anderson, **NY**; Great Falls, viii 1886, F. Anderson, **NY**.

18. Nevada: Albemarle Co. 30 iii, J. C. Strickland, **F** 1099198; Hopewell, 14 iv 1938, E. C. Leonard, **US** 03691; Lincoln Co., 8 iii 1891, F. V. Coville & F. Funston, **FH**, **UC** 95497.

19. New Jersey: New Brunswick, 28 ii 1950, E. T. Moul, **F** 1017427; New Brunswick, 19 ii 1961, E. T. Moul, **NY**, **UC** 107857; Princeton Junction, 6 v 1892, Brown, **FH**, **NY**; Somerset Co. 31 i 1970, E. T. Moul, **RUT**.

20. New York: Bayville, D. G. Banks, **NY**; Bronx River, 30 iv 1906, **NY**;

Cortland Co., W. C. Muenscher, **MICH** 16489; Etna, 23 v (no year given), W. C. Muenscher, **MICH**; Ithaca, 4 iv 1895, G. J. Atkinson, **UC** 95511; Ithaca 5 iv 1919, J. R. Schramm, **MICH** 6496; Jamesville, iv 1887, L. M. Underwood, **NY**; Jerome Station, 2 v 1899, R. Hitchcock, **US** 03622; Springville, 20 xi 1948, J. Blum, **F** 1303617.

21. Ontario: Paris, 1828, C. Fischer, **FH**, **NY**.
22. Pennsylvania: Wolle, **UC** 95508; Broomall, 3 iv 1920, G. E. Jewett & W. R. Taylor, **MICH**; Chester Co., 1860, H. Jackson, **NY**; Chester Co. xii 1890, H. Richards, **F** 1223932, **NY**; Delaware Co., 10 iii 1919, W. R. Taylor, **MICH** 2840; Pomeroy, iv 1890, H. M. Richards, **F** 1015080, **LAM** 599966, **UC** 95484, US 39697.
23. Rhode Island: Lincoln, 19 iv 1906, **NY**; Olneyville, 4 ii 1894, W. J. V. Osterhout, **UC** 273966; Warwick, 20 v 1897, M. R. Clarke, **FH**, **NY**.
24. South Carolina: Columbia, ii 1889, G. F. Atkinson, **UC** 95481.
25. Virginia: Great Falls, 5 iv 1925, R. Dowell Svihla, **NY**.
26. West Virginia: Bayard, 2 vii 1891, W. C. Sturgis, **UC** 95506.
27. Washington: Lyndon, 31 v 1918, W. C. Muenscher, **MICH** 6500.
28. Wyoming: Laramie, 14 vi 1948, H. Habeeb, **F** 1297688.

Originally identified as B. ectocarpoideum:

29. Georgia: Savannah River, Burke Co., 30 xi 1976, R. R. Grant Jr., **PH**; Savannah River, Burke Co., 27 xi 1979, R. R. Grant Jr., **PH**; Savannah

River, Screven Co., 4 xii 1975, R. R. Grant Jr., **PH**; Savannah River, Screven Co., 29 xi 1979, R. R. Grant Jr., **PH**.

30. Massachusetts: Barnstable Co., 26 i 1948, H. T. Croasdale & W. R. Taylor, **MICH** 20844.

Originally identified as B. gelatinosum:

31. South Dakota: Mystic, xi 1895, C. L. Shear, **US** 03642.

Originally identified as B. moniliforme:

32. Massachusetts: Stony Brook, M. C. H. Clarke, **FH**.

33. New Brunswick: Grand Falls, 25 vi 1947, H. Habeeb, **F** 1224860; Grand Falls, 30 vi 1947, H. Habeeb, **NY**: Grand Falls, 14 vi 1948, H. Habeeb, **F** 1297688; Grand Falls, 18 vi 1948, H. Habeeb, **F** 1014277; Grand Falls, 29 vi 1948, H. Habeeb, **F** 1015071; Grand Falls, 2 i 1949, H. Habeeb, **F** 1013402; Grand Falls, 14 vi 1951, H. Habeeb, **F** 1013415; Grand Falls, 17 vi 1951, H. Habeeb, **F** 1013405, **F** 1013406, **F** 1013411; St. Quentin, 29 xiii, R. Crozier, **F** 1014493; Victoria Co., 24 vi 1951, H. Habeeb, **F** 1014923.

34. New York: Astoria, 25 v 1851, J. Walters, **PH**.

35. South Carolina: Savannah River, Allendale Co., 29 iv 1976, R. R. Grant Jr., **PH**.

Originally identified as B. occidentale nom. nud.:

36. California: Sonojua Co., iii 1896, M. A. Howe, **UC** 92625.

Appendix 2: Additional North American herbarium specimens.

The following specimens can be classified as B. gelatinosum:

Originally identified as Batrachospermum sp.:

1. Connecticut: Bridgeport, 8 v 1872, D. C. Eaton, **FH**; Bridgeport, 28 iv 1889, I. Holden, **FH**, Bridgeport, 25 vii 1889, I. Holden, **FH**; Bridgeport, 27 x 1889, I. Holden, **UC** 95440; Bridgeport, 24 xi 1889, I. Holden, **UC** 95438, **UC** 95439, **UC** 95498; Bridgeport, 15 xii 1889, **FH**; Bridgeport, 19 i '890, I. Holden, **FH**; Bridgeport, 2 ii 1890, I. Holden, **NY**, **UC** 95451, **UC** 95452, **UC** 95453; Bridgeport, 16 ii 1890, I. Holden, **UC** 95450, **UC** 95500; Bridgeport, 28 v 1893, **FH**; Stony Creek, 8 v 1872, D. C. Eaton, **F** 1206696.
2. Maine: Cape Rosier, 13 vii 1892, F. S. Collins, **FH**; Mount Desert, 7 viii 1890, I. Holden, **FH**, **NY**.
3. Massachusetts: 19 v 1884, F. S. Collins, **UC** 777371; Barnstable County, 28 vii 1947, E. T. Moul, **RUT** 2434, **RUT** 3298, **RUT** 04904, **RUT** 04908; Malden, 13 iv 1890, F. S. Collins, **UC** 7773577; Malden, 28 iv 1891, F. S. Collins, **UC** 777377; Malden, 8 v 1892, F. S. Collins, **UC** 777373; Melrose, 7 vi 1891, F. S. Collins, **UC** 94120; Wakefield, 14 iv 1892, F. S. Collins, **UC** 777387.
4. Michigan: Levering, 2 vii 1951, W. L. Culberson, **F** 1068296.
5. Missouri: Round Spring State Park, 1 vi 1931, F. Drouet, **MICH**; Yancy

Mills, 31 v 1931, F. Drouet, **MICH**.

6. New Brunswick: Cranberry Lake, 3 v 1951, H. Habeeb, **PH**; Grand Falls, 3 viii 1947, H. Habeeb, **F** 1245173; Upsalquitch, 19 vi 1949, H. Habeeb, **PH**.
7. Nova Scotia: Mahone Bay, C. A. Hamilton, **CANA** 5891, **NY**.
8. Oregon: Fogerty Creek, Lincoln County, 7 viii 1949, W. H. Hansen, **RUT**, **UC** 027125.
9. Pennsylvania: Constoga Creek, Buffalo Springs, 19 viii 1948, J. H. Wallace. **PH**; Slippery Rock Creek, 28 vi 1967, R. Patrick, **PH**.
10. Rhode Island: Providence, W. J. V. Osterhout, **UC** 273898.
11. Tennessee: Holston River, 20 vi 1965, R. R. Grant Jr., **PH**.
12. Utah: Summit County, 16 viii 1936, B. Maguire, **F** 108749.

Originally identified as B. boryanum:

13. Massachusetts: Arlington, 23 iv 1894, B. M. Davis, **MICH** (in part); Middlesex Fells, 14 iv 1890, F. S. Collins, **UBC** A653.

Originally identified as B. corbula:

14. Connecticut: Bridgeport, (P.B.-A. 184), 11 v 1890, I. Holden, **CANA** 97, **LAM** 599968, **LAM** 599970, **NY**, **PH**, **UC** 95469, **US** 03630; Bridgeport, 30 v 1890, I. Holden, **NY**, **UC** 954363, **UC** 95467, **UC** 995468; Bridgeport, 7 xii 1890, I. Holden, **US** 072648; Bridgeport (P.B.-A. 184), 1 iii 1891, I. Holden, **F** 968229, **FH**, **MICH**.

15. Maine: Mount Desert, 7 viii 1890, I. Holden, **MICH** 31563.

16. Massachusetts: Cambridge, 24 v 1891, L. M. Underwood, **NY**; Cuttyhunk, 1 vii 1931, W. R. Taylor, **F** 950836, **FH**, **LAM** 599969, **MICH** 15034, **NY**; Lynnfield, 13 v 1890, F. S. Collins, **UC** 95466; Saugus, 13 v 1890, F. S. Collins, **UC** 95464, **UC** 95465.

17. Yukon: Dawson, vii 1899, R. S. Williams, **NY**.

Originally identified as B. decaisneanum:

18. Massachusetts: Malden, 16 iii 1890, F. S. Collins & W. A. Setchell, **F** 1017430, **FH**, **LAM** 599972, **UC** 95462, **US** 39770; Medford, 13 iv 1890, F. S. Collins, **FH**; Middlesex Fells, 16 iii 1890, **FH**, **NY**; Middlesex Fells (P.B.-A. 181), iii & iv 1890, F. S. Collins, **CANA** 98, **F** 968247, **LAM** 599971, **MICH**, **NY**, **PH**, **US** 03673.

Originally identified as B. densum:

19. Alaska: Awakuak Island, 1889, A. A. Larson & W. A. Setchell, **UC** 93449.

20. Connecticut: Norwich (P.B.-A. 185), 30 vi 1890, W. A. Setchell, **CANA** 99, **F** 968533, **F** 1152146, **LAM** 599974, **MICH**, **NY**, **PH**, **UC** 95456, **US** 03633 (in part); Norwich, 1 vii 1890, W. A. Setchell, **F** 1015021, **LAM** 599975.

21. Maine: Cape Rosier, vii 1897, F. S. Collins, **F** 947423, **FH**, **NY**, **US** 072426; Mount Desert, 14 vii 1899, **F** 1208782, **FH**, **NY**.

22. Massachusetts: Arlington, 11 vi 1890, W. A. Setchell, **FH**, **NY**, **UC** 95461, **US**; Arlington, 14 xii 1890, W. A. Setchell, **UC** 95460; Falmouth, 22 vii 1931, H. T. Croasdale, **MICH**, **NY**; Lynnfield, 13 v 1890, F. S. Collins, **F** 1208988, **F** 1209265, **FH**, **NY**, **UC** 687577, **US** 03632; Sharon, 8 iv 1890, W. A. Setchell, **UC** 95458; Sharon, 4 v 1890, W. A. Setchell, **UC** 95454; Sharon 24 v 1890, W. A. Setchell, **F** 1209204, **FH**, **NY**, **UC** 95459, **US** 03633, **US** 072425.
23. New York: Union Springs, 20 v 1923, W. C. Muenscher, **MICH**.
24. Pennsylvania: Loganton, vii 1890, H. M. Kelley, **UC** 95457.
25. Rhode Island: East Greenwich, 30 v 1918, W. J. V. Osterhout, **UC** 273910.

Originally identified as B. durum:

26. Rhode Island: East Greenwich, 30 v 1893, **UC** 777336.

Originally identified as B. ectocarpum:

27. Alaska: Golofruir Bay, 1900, R. C. McGregor, **UC** 93457.
28. Connecticut: Bridgeport, 27 x 1889, I. Holden, **UC** 95440; Bridgeport, 24 xi 1889, I. Holden, **UC** 95439; Bridgeport, 26 i 1890, I. Holden, **FH**, **MICH**, **NY**; Bridgeport, 2 ii 1890, I. Holden, **LAM** 599977; Bridgeport, 16 ii 1890, I. Holden, **FH**, **MICH** 9744, **MICH** 16172, **MICH** 16216, **MICH** 26030, **MICH** 26029; Bridgeport, 2 iii 1890, I. Holden, **FH**, **UC** 95446, **UC** 95447, **UC** 95448, **UC** 95449; Bridgeport, 6 iv 1890, I.

Holden, **F** 968227, **FH**, **US** 03629; Bridgeport, 22 v 1890, I. Holden, **FH**; Bridgeport 7 xii 1890, I. Holden, **UC** 95441; Brigeport (P.B.-A. 183), Spring 1890 & 1891, I. Holden, **CANA** 100, **MICH** 9744, **NY**, **PH**; Norwich, 1 iv 1890, W. A. Setchell, **F** 676459, **F** 1014278, **FH**, **LAM** 599978, **MICH**, **NY**, **UC** 93458; Norwich, 20 vi 1890, W. A. Setchell, **UC** 93459.

29. Massachusetts: Malden, 29 iii 1891, F. S. Collins, **UC** 777355; Saugus, 20 iv 1890, I. Holden, **FH**.
30. Michigan: Emmett Co. 14 vii 1942, H. K. Phinney, **F** 1138152.

Originally identified as B. moniliforme:

31. British Columbia: Beavermouth, ix 1921, W. R. Taylor, **FH**, **MICH**, **NY**; Revelstoke, 19 viii 1921, W. R. Taylor, **FH**, **MICH**, **NY**, **UC** 211084, **US** 03650; Vancouver Island, vii 1901, Butler & Polley, **NY**; Vancouver Island, 29 vii 1909, J. Macoun, **CANA** 5890.
32. California: Santa Barbara, **FH**; Santa Cruz, iii 1877, **FH** 1118387.
33. Connecticut: Bridgeport, v 1890, I. Holden, **F** 947599; East Haven, 10 vi 1885, W. A. Setchell, **UC** 95479; Easton, 9 v 1886, I. Holden, **UC** 95429.
34. Louisiana: Sabine Parish, 9 iv 1960, L. H. Flint; Union Parish, 15 iv 1960, L. H. Flint; Vernon Parish, 9 iv 1960, L. H. Flint.
35. Manitoba: Churchill, 24 vii 1956, R. Dunbar, **CANA** 5941.

36. Massachusetts: Amherst, 7 vii 1891, J. E. Humphrey, **US** 03701; Arlington Heights, 5 iii 1894, B. Davis, **UC** 93524, **NY**; Malden, **US** 072476; Malden, 3 vi 1883, F. S. Collins, **US** 072478; Malden, 1 vi 1884, F. S. Collins, **US** 072479, **NY**; Middlesex Fells, 6 vi 1958, S. Dick, **FH**, **UC** 099019; Saugus, 3 vii 1883, J. E. Humphrey, **US** 072502, Saugus, 23 iv 1890, F. S. Collins, **FH**, **NY**, **US** 072477; South Natick, v 1883, C. E. Cummings, **F** 1223929; Wakefield, 6 iv 1890, F. S. Collins, **PH**; Weymouth, ix 1883, J. E. Humphrey, **US** 072502.

37. Michigan: Isle Royale, 22 ii 1930, J. L. Lowe, **MICH** 16524; Levering, 8 vii 1940, H. K. Phinney, **F** 1110383.

38. New Brunswick: Blue Bell, 7 vii 1948, H. Habeeb, **F** 1297758; Grand Falls, 3 viii 1947, H. Habeeb, **F** 1245173; Grand Falls, 9 viii 1950, H. Habeeb, **F** 1014475.

39. New Hampshire: Canaan, 1 ix 1962, H. T Croasdale, **MICH** 31151; Plainfield, 10 viii1954, L. H. Flint.

40. New York: Adirondack Mountains, 7 ix 1921, W. C. Muenscher, **MICH** 6499; Shaushau, 7 ix 1910, F. Dobbin, **FH**, **NY**; West Point, **PH**.

41. Nova Scotia: Paul's Island, 7 viii 1929, **MICH** 15043.

42. Pennsylvania: Lititz, 3 x 1948, R. Patrick, **F** 1297339; 2 vii 1922, W. R. Taylor, **MICH** 6510, **PH**.

43. Rhode Island: Kingston, 1 iii 1954, R. D. Wood, **NY**; Kingston, iv 1950,

R. D. Wood, **NY**; Warwick, 20 v 1897, M. R. Clarke, **FH**, **NY**.

44. Virginia: H. Jackson, **PH** 849774; Newport, 3 viii 1939, J. C. Strickland, **F** 991886.

45. Vermont: West Townshend, 3 vii 1912, F. Dobbin, **NY**.

Originally identified as B. moniliforme var. chlorosum:

46. Connecticut: Bridgeport, 27 x 1889, I. Holden, **FH**, **MICH** 26032, **NY**; Brigeport, 9 ii 1890, **MICH**; Bridgeport, 5 x 1890, I. Holden, **FH**; Bridgeport, 16 xi 1890, I. Holden, **FH**; Bridgeport, 7 xii 1890, I. Holden, **FH**, **NY**, **UC** 95441; Bridgeport, 14 xii 1890, I. Holden, **FH**; Bridgeport, 1 ii 1891, I. Holden, **FH**; Brigeport (P.B.-A. 1137), I. Holden, **CANA** 104, **F** 968219, **LAM** 599985, **MICH**, **NY**, **PH**, **US** 03655.

47. Oregon: Forest Grove [Tilden(1898) American Algae Centruy III specimen no. 226], 12 iv 1897, F. E. Lloyd, **F** 951847, **NY**, **UC** 278277, **UC** 763470, **US** 072475.

Originally identified as B. moniliforme var. helminthoideum:

48. Massachusetts: Melrose (P.B.-A. 877a), 5 v 1893, F. S. Collins, **CANA** 105, **F** 545642, **NY**, **US** 03697; Wakefield (P.B.-A. 877b), 6 iv 1890, F. S. Collins & W. A. Setchell, **CANA** 105, **DS** in **US DS** 503706, **F** 676428, **F** 947470, **F** 1005497, **F** 1013407, **FH**, **LAM** 599980, **LAM** 599981, **LAM** 599982, **LAM** 599984, **NY**, **PH**, **US** 03653, **US** 072481.

49. Washington: Orcas Island, vii 1901, N. L. Gardner & W. A. Setchell,

FH, **MO** in **UC** 24417, **NY**, **UC** 93542, **US** 03658.

Originally identified as B. moniliforme var. rubescens:

50. Utah: Garfield Beach [Tilden (1898) American Algae Century III no. 225], 7 vii 1897, **F** 951662, **NY**, **UC** 278276, **UC** 763560, **US** 56084.

Originally identified as B. moniliforme var. scopula:

51. British Columbia: Vancouver Island [Tilden (1900) American Algae Century IV, no. 332], 3 viii 1898, J. E. Tilden, **F** 951718, **NY**, **UC** 763643, **US** 03649.

52. Massachusetts: Falmouth, 5 viii 1931, H. T. Croasdale, **NY**; Malden, 5 v 1889, F. S. Collins, **UC** 777386; Malden, 16 iii 1890, F. S. Collins & W. A. Setchell, **UC** 95430, **UC** 95431; Malden (P.B.-A. 878), 25 iv 1900, F. S. Collins, **CANA** 100, **F** 545643, **NY**, **PH**, **US** 69928.

53. New Hampshire: Enfield, 12 viii 1959, L. H. Flint.

Originally identified as B. moniliforme var. typicum:

54. British Columbia: Vancouver Island (P.B.-A. 876), 14 vii 1901, E. Butler & J. Polley, **CANA** 103, **F** 968117, **MICH** 7683, **NY**, **US** 69926.

55. Connecticut: Bridgeport (P.B.-A. 180), v 1890, I. Holden, **CANA** 102, **F** 967865, **FH**, **LAM** 599987, **MICH** 9746, **NY**, **US** 03656.

Originally identified as B. pyramidale:

56. Connecticut: Bridgeport, 20 x 1889, I. Holden, **UC** 93553; Bridgeport, 30 v 1890, I. Holden, **NY**, **UC** 95432, **UC** 95433, **UC** 95434, **UC** 95435, **UC**

95436; Bridgeport (P.B.-A. 186c), 6 v 1893, I. Holden, **CANA** 107, **F** 546613, **MICH**, **LAM** 599990, **NY**, **US** 03666; Bridgeport, 6 v 1894, I. Holden, **FH**; East Haven, 1 v 1892, W. A. Setchell, **UC** 93554.

57. Maine: Caribou, 24 vi 1898, M. L. Fernald, **NY**; Mount Desert, 7 viii 1890, I. Holden, **UC** 95422, **UC** 95423; Mount Desert, 16 vi 1900, **NY**; Mount Desert, vi 1891, E. Faxon, **UC** 95426; Mount Desert, 30 viii 1920, W. R. Taylor, **MICH**; Southwest Harbor, 2 viii 1890, I. Holden, **FH**, **PH**, **LAM** 599992.

58. Massachusetts: Malden, 5 v 1889, F. S. Collins, **NY**; Malden, 21 v 1890, F. S. Collins, **FH**, **UC** 95427, **UC** 95428; Medford, 7 vi 1894, F. S. Collins, **F** 1209356, **FH**, **NY**, **UC** 687576, **US** 03667; Medford, 15 v 1896, F. S. Collins, **F** 1001602, **US** 03665, **US** 006537; Middlesex Fells (P.B.-A. 186a), 5 v 1889, **CANA** 107, **F** 1005420, **LAM** 599989, **LAM** 599993, **MICH**, **NY**, **PH**, **UC** 95420, **UC** 95421, **US** 69927; Middlesex Fells (P.B.-A. 186b), 21 v 1890, F. S. Collins, **CANA** 107, **F** 1005420, **LAM** 599991, **MICH**, **NY**, **US** 072487.

59. New York: Hamilton Co. 24, 25 viii 1896, I. Holden, **F** 1209217, **NY**, **US** 072480.

60. Rhode Island: Exeter, 30 v 1893, W. J. V. Osterhout, **UC** 273963, **UC** 777334, **UC** 800574; Thornton, 16 iv 1893, W. J. V. Osterhout, **UC** 273907.

61. Washington: Orcas Island, vii 1901, N. L. Gardner, **MICH**, **MO** in **UC** **MO** 25811, **NY**, **UC** 93552, **US** 03668.

Originally identified as B. radians:

62. Connecticut: Woodbridge, vi 1891, A. W. Evans, **UC** 95414.

63. Massachusetts: Medford, F. S. Collins, **F** 1208777; Melrose, 2 v 1890, F. S. Collins, **FH**, **UC** 95411, **UC** 95412; Melrose (P.B.-A. 182), 7 v 1890, F. S. Collins, **CANA** 108, **F** 968130, **LAM** 599994, **MICH**, **NY**, **PH**, **US** 03672; Middlesex Fells, iii & iv 1890, F. S. Collins, **F** 1209263, **F** 1209264, **FH**, **NY**; Saugus, F. S. Collins, **F** 1223773; Saugus, 23 iv 1890, F. S. Collins, **NY**, **UC** 95413, **UC** 687575; Saugus 28 iv 1890, F. S. Collins, **F** 1005430, **FH**, **LAM** 599995, **US** 39721; Wakefield, 30 iv 1894, F. S. Collins, **F** 1005422, **LAM** 599996 (in part); Walden, 23 iii 1890, W. A. Setchell, **NY**.

64. New York: Hamilton Co., 17 viii 1896, I. Holden, **FH**, **NY**, **PH**; Hamilton Co., 24 viii 1896, I. Holden, **F** 1001586, **UC** 93638, **US** 006538; Hamilton Co., 24, 25 viii 1896, I. Holden, **NY**; Westchester Co. 4 vi 1933, R. Weikert, **NY**.

65. Nova Scotia: Mahone Bay, 24 viii 1906, C. A. Hamilton, **CANA** 3324.

66.. Rhode Island: East Greenwich, 30 v 1893, W. J. V. Osterhout, **UC** 95418, **UC** 95419; Providence, 9 v 1893, **UC** 95417, Valley Falls, x 1893, W. J. V. Osterhout, **UC** 95415, **UC** 95416.

Originally identified as B. reginense:

65. Massachusetts: Sharon, 4 v 1890, W. A. Setchell, **F** 676430, **F** 1005425, **LAM** 599997, **LAM** 599998, **MICH**, **NY**, **UC** 94106, **US** 03674.