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CHAPTER 1-21
AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CONOCEPHALACEAE, PART 2

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CHAPTER 1-21 AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CONOCEPHALACEAE, PART 2

Figure 1. ***Conocephalum*** *cf.* ***salebrosum*** at water's edge, Wahkeena Historical Preserve, Ohio, USA. Photo by Janice Glime.

Conocephalum purpureorubrum (Figure 2-Figure 14)

Conocephalum purpureorubrum (Figure 2-Figure 14) was previously designated as ***Conocephalum conicum*** F type (Akiyama 2022). The lower surface of the thallus is reddish purple (Figure 2-Figure 4) even in summer, although this coloration may be confined to the midrib (Figure 5). The upper surface of the thallus mat is yellowish green (Figure 6-Figure 9) in western Japan or slightly shiny and blackish green (Figure 10-Figure 11) in eastern Japan. Upper epidermal cells of thalli can have thin or thick walls. The grooves outlining the **areolae** (air chambers) are deep and distinct (Figure 12-Figure 13). These air chambers do not differ in size between the margins and central portions (Figure 14).

Figure 2. ***Conocephalum purpureorubrum*** from Japan, showing partially purple underside. Photo courtesy of Hiroyuki Akiyama.

Figure 3. ***Conocephalum purpureorubrum*** ventral side showing a large portion with purplish coloration. Photo courtesy of Hiroyuki Akiyama.

Figure 4. ***Conocephalum purpureorubrum*** from Toyama Prefecture, Japan, showing form with entire underside purplish in color. Photo courtesy of Hiroyuki Akiyama.

Figure 5. ***Conocephalum purpureorubrum*** ventral surface not purple except along midrib. Photo courtesy of Hiroyuki Akiyama.

Figure 6. ***Conocephalum purpureorubrum*** from Japan, showing thallus grooves and pores. Photo courtesy of Hiroyuki Akiyama.

Figure 7. ***Conocephalum purpureorubrum*** from Japan. Photo courtesy of Hiroyuki Akiyama.

Figure 8. ***Conocephalum purpureorubrum*** light form typical of western Japan. Photo courtesy of Hiroyuki Akiyama.

Figure 9. ***Conocephalum purpureorubrum*** pale form typical in western Japan. Photo courtesy of Hiroyuki Akiyama.

Figure 10. ***Conocephalum purpureorubrum*** showing dark green and blackish form typical of populations in eastern Japan. Photo courtesy of Hiroyuki Akiyama.

Figure 11. ***Conocephalum purpureorubrum*** showing dark thalli mixed with lighter ones. Photo courtesy of Hiroyuki Akiyama.

Figure 12. ***Conocephalum purpureorubrum*** from Japan, showing distinct polygons formed by thallus grooves and yellowish green color typical of populations in western Japan. Photo courtesy of Hiroyuki Akiyama.

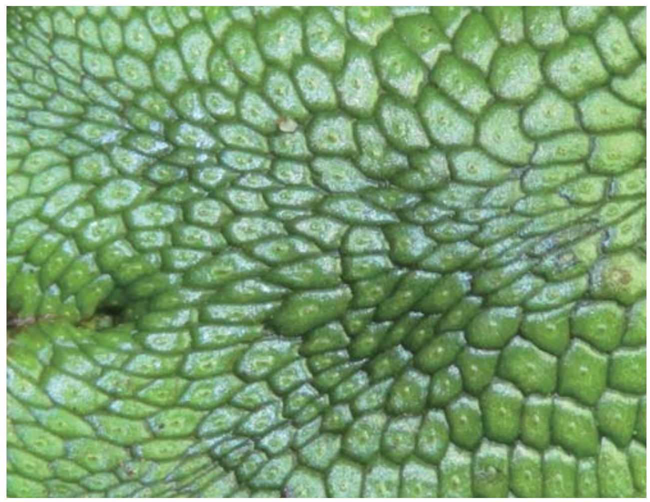

Figure 13. ***Conocephalum purpureorubrum*** from Japan, showing thallus grooves and pores. Photo courtesy of Hiroyuki Akiyama.

Figure 14. ***Conocephalum purpureorubrum*** from Japan, showing pores and distinct thallus grooves. Photo courtesy of Hiroyuki Akiyama.

Distribution

Conocephalum purpureorubrum (Figure 2-Figure 14) is known from southern China, South Korea, Taiwan, and Japan (Akiyama 2022).

Aquatic and Wet Habitats

Conocephalum purpureorubrum (Figure 2-Figure 14) can grow in drier habitats than those of ***C. orientalis*** (Figure 15), but it can also grow intermixed with that species (Figure 16). It occurs at some waterfall sites. It tends to grow in more humid habitats when it grows with ***C. salebrosum*** (Figure 1, Figure 30-Figure 49) (Akiyama 2022), a behavior suggesting possible **indirect facilitation** as discussed in the previous subchapter under ***C. conicum*** (Figure 17). It is also possible that these behavioral differences in habitat preference relate to differences in genetic races (see Akiyama & Hiraoka 1994).

Figure 17. ***Conocephalum conicum*** from Scotland, with distinct thallus grooves. Photo courtesy of David Long.

Figure 15. ***Conocephalum orientalis*** type J2 with wavy margin. Photo courtesy of Hiroyuki Akiyama.

Figure 16. ***Conocephalum purpureorubrum*** (**FW**) and ***C. orientalis*** (**J**) growing intermixed in Japan. Photo courtesy of Hiroyumi Akiyama.

Non-Aquatic

The eastern populations of ***Conocephalum purpureorubrum*** (Figure 2-Figure 14) usually occur on soil of valley slopes where they are far from water (Figure 18), but they can sometimes grow along streams (Akiyama 2022).

Figure 18. ***Conocephalum purpureorubrum*** from Mt. Takao, Japan, showing terrestrial habitat. Photo courtesy of Hiroyuki Akiyama.

Physiology

Plants of ***Conocephalum purpureorubrum*** (Figure 2-Figure 14) tend to be thick and pale in sunny conditions (Figure 19) and thin and dark in shaded conditions (Figure 20) (Akiyama 2022). The reddish ventral condition seems to persist all year, but does its intensity relate to low light? In some flowering plants on tropical forest floors this ventral purplish coloring helps in the back-scattering of sunlight to the photosynthetic tissue (Lee *et al*. 1979). Such a role has not been explored in bryophytes. It seems likely that it would mostly work in liverworts among the bryophytes because they have a dorsiventral orientation.

Figure 19. ***Conocephalum purpureorubrum*** pale form typical of populations in western Japan. Photo courtesy of Hiroyuki Akiyama.

Figure 20. ***Conocephalum purpureorubrum*** from Japan, showing dark form typical of shade, with deep thallus grooves. Photo courtesy of Hiroyuki Akiyama.

Rhizoids are abundant on the ventral surface of ***Conocephalum purpureorubrum*** (Figure 21-Figure 23) (Akiyama 2022). These undoubtedly facilitate the movement and uptake of water into the thallus.

Figure 21. ***Conocephalum purpureorubrum*** showing rhizoids along the midrib. Photo courtesy of Hiroyuki Akiyama.

Figure 22. ***Conocephalum purpureorubrum*** showing numerous rhizoids. Photo courtesy of Hiroyuki Akiyama.

Figure 23. ***Conocephalum purpureorubrum*** showing numerous rhizoids. Photo courtesy of Hiroyuki Akiyama.

Conocephalum purpureorubrum (Figure 2-Figure 14) may have mucilage canals (Figure 24), but mucilage cells are often absent (Akiyama 2022). The mucilage may help to keep the cells moist, but experiments are needed to verify this. They are often absent in populations in dry habitats.

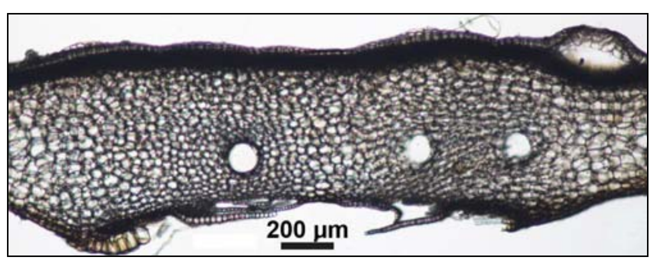

Figure 24. ***Conocephalum purpureorubrum*** from Japan, showing mucilage canals. Photo courtesy of Hiroyuki Akiyama.

Reproduction

Conocephalum purpureorubrum (Figure 2-Figure 14), like other species of ***Conocephalum***, is **dioicous**. The antheridial receptacles form at the apex of the male thallus (Figure 25-Figure 26). Bud scales can often be seen at their margins (Figure 25).

Figure 25. ***Conocephalum purpureorubrum*** young antheridial receptacle. Note the remaining reddish brown bud scales. Photo courtesy of Hiroyuki Akiyama.

Figure 26. ***Conocephalum purpureorubrum*** young antheridial receptacle. Photo courtesy of Hiroyuki Akiyama.

Female plants of ***Conocephalum purpureorubrum*** (Figure 2-Figure 14) form archegoniophores at the apex of the female plants (Figure 27-Figure 28). When sporangia mature, the stalks elongate to 3-6 cm with bluntly conical archegonial heads (Figure 28-Figure 29). The sporangia hang down from the archegonial heads.

Figure 27. ***Conocephalum purpureorubrum*** with young archegoniophore. Photo courtesy of Hiroyuki Akiyama.

Figure 28. ***Conocephalum purpureorubrum*** with young archegoniophores beginning to elongate. Note that the black sporangia are already visible. Photo courtesy of Hiroyuki Akiyama.

Figure 29. ***Conocephalum purpureorubrum*** with mature archegoniophores and sporangia. Photo courtesy of Hiroyuki Akiyama.

Biochemistry

Biochemical analysis may reveal some interesting compounds in ***Conocephalum purpureorubrum*** (Figure 2-

Figure 14). This species has a fresh, earthy odor, usually not a mushroom odor (Akiyama 2022).

Conocephalum salebrosum (Figure 1, Figure 30-Figure 49)

Conocephalum salebrosum (Figure 1, Figure 30-Figure 49) is a relatively recently described species and is a segregate of ***Conocephalum conicum*** (Figure 17) (Szweykowski *et al*. 2005). It appears that many of the North American records of ***Conocephalum conicum*** should be placed here (Stotler & Crandall-Stotler 2017), with populations in California (Figure 50) being potential exceptions (see Shevock *et al*. 2021). The latter, for now, are best designated as ***Conocephalum conicum*** *s.l.*

In Europe, the distinction of the species in older literature is not so simple, if even possible without checking voucher specimens. Both species occur there. For example, Poponessi *et al*. (2014) have reported ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) from Italy. Sérgio *et al*. (2011) reported it from Portugal and Madeira and Azores Islands. Other records are documented in Figure 30-Figure 36. Figure 37 shows the similarities of a British Columbia, Canada, population to ***Conocephalum salebrosum***.

Figure 30. ***Conocephalum salebrosum*** from Europe, showing distinct thallus grooves. Photo courtesy of Michael Lüth.

Figure 31. ***Conocephalum salebrosum*** showing distinct thallus divisions. Photo by Jouko Rikkinen, through Creative Commons.

Figure 32. ***Conocephalum salebrosum*** showing thallus section grooves, in Wales. Photo courtesy of Jonathan Sleath.

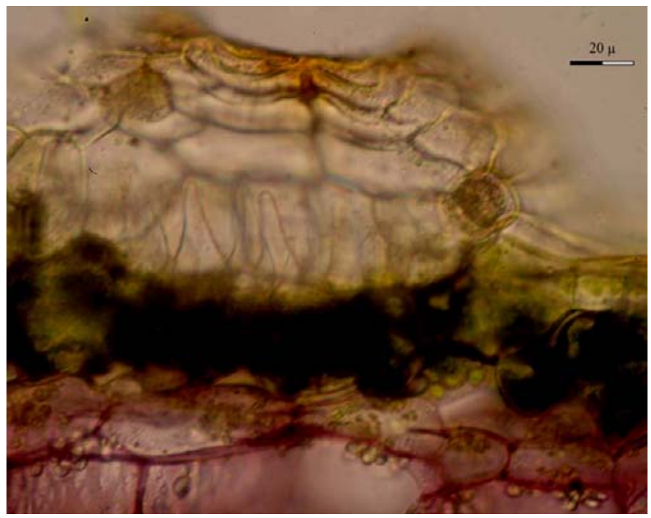

Figure 33. ***Conocephalum salebrosum*** from Corsavy, France, showing pore section. Photo courtesy of Louis Thouvenot.

Figure 34. ***Conocephalum salebrosum*** from Europe, showing pore section. Photo by Norbert J. Stapper, with permission.

Figure 35. ***Conocephalum salebrosum*** from Corsavy, France, showing thallus margin section. Photo courtesy of Louis Thouvenot.

Figure 36. ***Conocephalum salebrosum*** from Wales, showing distinct section grooves. Photo courtesy of Jonathan Sleath.

Figure 37. ***Conocephalum conicum*** *s.l.* showing distinct thallus grooves and less distinct pores. These thallus grooves of a western North American population fit more closely with those of ***C. salebrosum***. Photo from Botany Website, UBC, with permission.

Distribution

The distribution of ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) remains sketchy because of the long treatment of the species as part of ***Conocephalum conicum*** (Figure 17) (Szweykowski *et al*. 2005). It is definitely known from North America (Figure 38-Figure 41), but can also be found in Europe (Figure 42-Figure 43) (*e.g.* Tacchi *et al*. 2009) and eastern Asia (Figure 44-Figure 49) (Sérgio *et al*. 2011). Sérgio and coworkers consider it to be Holarctic.

Figure 38. ***Conocephalum*** *cf.* ***salebrosum*** habitat in Quebec, Canada. Photo by Martine Lapointe, with permission.

Figure 39. ***Conocephalum salebrosum*** in New York, USA. Photo courtesy of Jerry Jenkins.

Figure 40. ***Conocephalum*** *cf.* ***salebrosum*** from Ohio, USA. Photo by Bob Klips, with permission.

Figure 41. ***Conocephalum*** *cf.* ***salebrosum***, Grand Ledge Park, Michigan, USA. Photo by Janice Glime.

Figure 42. ***Conocephalum salebrosum*** from the UK. Photo by Barry Stewart, with permission.

Figure 43. ***Conocephalum salebrosum*** from Chauderon, France. Photo courtesy of David Long.

Figure 44. ***Conocephalum salebrosum*** in Yunnan, China. Photo by David Long, with permission.

Figure 45. ***Conocephalum salebrosum*** from Sichuan, China. Photo courtesy of David Long.

Figure 46. ***Conocephalum salebrosum*** from Japan. Photo courtesy of Hiroyuki Akiyama.

Figure 47. ***Conocephalum*** males, Mt. Hiei, Japan. The prominent thallus grooves suggest this is now in the species ***Conocephalum salebrosum***. The thallus sections do not get larger in the center of the thallus, as they do in ***Conocephalum orientalis***. Photo by Janice Glime.

Figure 48. ***Conocephalum salebrosum*** thallus from Japan, showing grooves and pores. Photo courtesy of Hiroyuki Akiyama.

Figure 49. ***Conocephalum salebrosum*** thallus from Japan, showing pores and distinct grooves. Photo courtesy of Hiroyuki Akiyama.

Populations in California (Figure 50), however, are similar, but not identical, to ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) (Shevock *et al*. 2021).

Figure 50. **Conocephalum conicum** *s.l.* from California, USA. Photo by R. L. Fleming, Jr., courtesy of David Wagner.

Aquatic and Wet Habitats

Conocephalum, presumably ***C. salebrosum*** (Figure 1, Figure 30-Figure 49), occurs on wet, sandy streambanks and on moist rock surfaces (Figure 51-Figure 53) or springy banks of ravines in Connecticut, USA (Nichols 1916). On Cape Breton Island, Canada it also occurs on streambanks (Nichols 1918).

Figure 51. ***Conocephalum*** *cf.* ***salebrosum*** with archegoniophores on canyon wall at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 52. ***Conocephalum*** *cf.* ***salebrosum*** at Scott Falls, Michigan, USA. Photo by Janice Glime.

Figure 53. ***Conocephalum*** *cf.* ***salebrosum*** habitat in Quebec, Canada. Photo by Martine Lapointe, with permission.

Figure 54. ***Conocephalum*** *cf.* ***salebrosum*** on canyon wall at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Conocephalum salebrosum (Figure 1, Figure 30-Figure 49) can be found along stream banks in the Appalachian Mountain, USA, streams (Glime 1968). In another humid environment, it is known from the base of the Flume wall and ledges in the flume at Franconia Notch, New Hampshire, USA (Glime 1982). It is likely the species that is a restricted terrestrial species in montane streams and on streambanks in western Canada (Vitt *et al.* 1986; Glime & Vitt 1987). It seems to avoid the submersion that is common for ***C. conicum*** (Figure 17).

Stephenson *et al*. (1995) reported its preferred *p*H as 7.9 in West Virginia, USA, mountain streams. Sérgio *et al*. (2011) considered ***Conocephalum conicum*** (Figure 17) to be less hygrophytic than ***C. salebrosum*** (Figure 1, Figure 30-Figure 49), being more tolerant of desiccation and preferring limestone areas.

Stream and River Banks

In North America, Porter (1933) reported ***Conocephalum*** (now probably ***C. salebrosum*** – Figure 1, Figure 30-Figure 49) from shady streambanks on soil in Wyoming, USA. Little (1936) described its habitat as constantly moist, shaded rock outcrops within a few feet of water in Oklahoma, USA. There it is one of the commonest species on moist, shaded bases of walls near water, occurring on both sandstone and limestone, as well as chert bluffs near water and especially in canyons and by springs.

In Europe, Tacchi *et al*. (2009) found it in ravines in the Apennines of Italy. Antkowiak *et al*. (2008) reported ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) synusia overgrowing high escarpments below the headstream at the River Kamionka in eastern Poland. Borovichev *et al*. (2009) found that ***C. salebrosum*** formed extensive mats on stream banks as well as on the bases of moist rocks and cliffs.

Figure 55. ***Conocephalum*** *cf.* ***salebrosum*** habitat near top of canyon at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Canyon Walls

I have found ***Conocephalum*** *cf.* ***salebrosum*** (Figure 1, Figure 30-Figure 49) in extensive mats on canyon walls (Figure 54-Figure 67). These canyons were sandstone and humid.

Figure 56. ***Conocephalum*** *cf.* ***salebrosum*** on canyon wall at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 57. ***Conocephalum*** *cf.* ***salebrosum*** on canyon walls Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 58. ***Conocephalum*** *cf.* ***salebrosum*** between ledges in damp canyon wall, Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 59. ***Conocephalum*** *cf.* ***salebrosum*** on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 60. ***Conocephalum*** *cf.* ***salebrosum*** and ferns on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 61. ***Conocephalum*** *cf.* ***salebrosum*** and ferns on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 62. ***Conocephalum*** *cf.* ***salebrosum*** and ferns on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 63. ***Conocephalum** cf.* ***salebrosum*** on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 64. ***Conocephalum** cf.* ***salebrosum*** new growth in rock shadow in the canyon at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 65. ***Conocephalum** cf.* ***salebrosum*** with new growth on canyon walls, Hocking Hills, Ohio, USA, on 26 April 2015. Photo by Janice Glime.

Figure 66. ***Conocephalum** cf.* ***salebrosum*** new growth at apices of old thalli on canyon walls, Hocking Hills, Ohio, USA, on 26 April 2015. Photo by Janice Glime.

Figure 67. ***Conocephalum** cf.* ***salebrosum*** young plants on canyon wall at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Floodplains

Because of its need for high humidity and tolerance of submersion, ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) commonly occurs in floodplains of streams and rivers (Figure 69-Figure 68), including periodically flooded bases of canyons (Figure 70-Figure 71).

Figure 68. ***Conocephalum** cf.* ***salebrosum***, floodplain, Rose Lake, Michigan, USA, where the products of sexual reproduction are readily visible (8 May). Photo by Janice Glime.

Figure 69. ***Conocephalum** cf. **salebrosum***, growing on floodplain, Rose Lake, Michigan, USA. Photo by Janice Glime.

Figure 70. ***Conocephalum** cf. **salebrosum*** on mud in the canyon at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 71. ***Conocephalum** cf. **salebrosum*** at base of canyon rock where it is flooded during high water, Hocking Hills, Ohio, USA. Photo by Janice Glime.

Waterfalls

Among its moist habitats, ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) can form large, dense patches on dripping rocks and wet soil where it is in close contact with water (Sérgio *et al*. 2011), including those areas wet by the splash of waterfalls (Figure 72) (personal observation).

Figure 72. ***Conocephalum** cf. **salebrosum*** beside Hungarian Falls at Tamarack City, Michigan, USA. Photo by Janice Glime.

Conocephalum salebrosum (Figure 1, Figure 30-Figure 49) was locally abundant at the entrance to Grotta degli Innamorati in central Italy at the Marmore Waterfalls Regional Park (Poponessi *et al*. 2020). I have seen the species in several locations in Michigan, USA, growing on a rock wall behind a waterfall (Figure 73).

Figure 73. ***Conocephalum salebrosum*** behind waterfall at Scott Cave, Michigan, USA. Photo by Janice Glime.

Non-Aquatic Habitats

Akiyama (2022) considered rather dry habitats (Figure 74) to be included among those of ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49). This fits with my own experience in North America. Other somewhat dry habitats are shown in Figure 75-Figure 79.

Figure 74. ***Conocephalum salebrosum*** from Japan, on limestone boulder. Photo courtesy of Hiroyuki Akiyama.

Figure 75. ***Conocephalum salebrosum*** from Japan, on limestone boulder. Photo courtesy of Hiroyuki Akiyama.

Figure 76. ***Conocephalum salebrosum*** from Japan, dry on thin soil on boulder. Photo courtesy of Hiroyuki Akiyama.

Figure 77. ***Conocephalum salebrosum*** from Japan, on moist limestone soil. Photo courtesy of Hiroyuki Akiyama.

Figure 78. ***Conocephalum salebrosum*** from Japan, on rock. Photo courtesy of Hiroyuki Akiyama.

Figure 79. ***Conocephalum salebrosum*** from Japan, small plants from moist, shaded site. Photo courtesy of Hiroyuki Akiyama.

Physiology

McConaha (1939) determined that the water absorption of ***Conocephalum salebrosum*** is limited to the ventral appendages, which are restricted to the underside of the midrib (Figure 80). The scales (Figure 80) increase the surface area by ~380% and the rhizoids (Figure 80-Figure 83) increase it by 5100%. The rhizoid strands and scales create an extensive capillary system (that is able to move water ventrally along the entire length of the thallus.

Figure 80. ***Conocephalum salebrosum*** showing rhizoids and scales that move water along ventral surfaces by capillarity. Photo by Jouko Rikkinen, through Creative Commons.

Figure 81. ***Conocephalum salebrosum*** from Japan showing rhizoids and purplish coloring restricted to the midrib. Photo courtesy of Hiroyuki Akiyama.

Figure 82. ***Conocephalum salebrosum*** from Japan showing rhizoids and purplish color extending beyond midrib. Photo courtesy of Hiroyuki Akiyama.

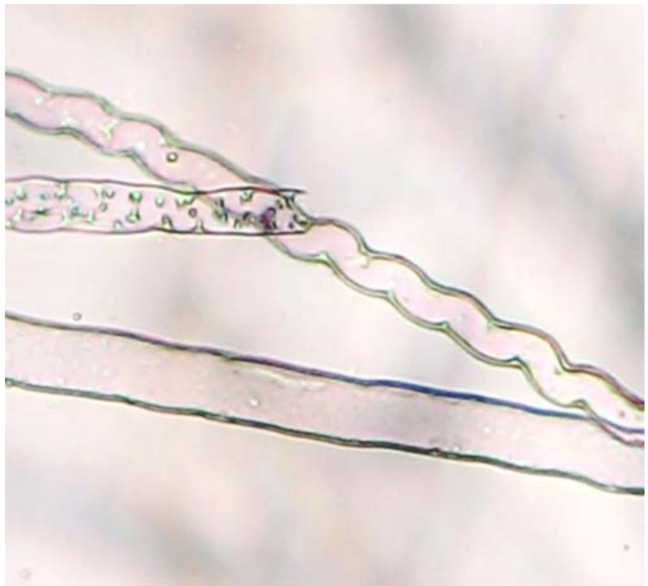

Figure 83. ***Conocephalum conicum*** *s.l.* showing **pegged** (**upper**) and **smooth** (**lower**) rhizoids. Photo from Botany Website, UBC, with permission.

Schott *et al*. (2021) found that ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) from west Germany had ice-nucleating proteins that differed in ice-nucleating temperature and seasonal concentration from those of ***Marchantia polymorpha*** subsp. ***ruderalis*** (Figure 84). Ice formed in the air chambers of both species, and crystals grew out of the air chamber pores (Figure 85). Crystals also formed in various locations on the ventral side of the thallus. This crystal formation resulted in dehydration of the thallus cells and permitted survival of low temperatures and frost (Figure 86). Presumably, this is a means of preventing crystal formation within the cells where it can damage membranes.

Figure 84. ***Marchantia polymorpha*** subsp. ***ruderalis***. Photo by Michel Langeveld, through Creative Commons.

Figure 85. ***Conocephalum*** *cf.* ***salebrosum*** with ice crystals emanating from the thallus. Photo by Allen Norcross, with permission.

Figure 86. ***Conocephalum salebrosum*** and icicles, showing a habitat where it is able to survive the cold of winter with its ice-nucleating proteins, but without sudden cooling. Photo by Allen Norcross, with permission

Adaptations

Although no specific adaptations have been attributed to ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49), it is likely that many are similar to those of ***Conocephalum conicum*** (Figure 17). However, ***C. salebrosum*** does have more conspicuous pores (Akiyama 2022) that could be an advantage is gas exchange and hence, photosynthesis.

Conocephalum salebrosum (Figure 87-Figure 88) from Japan has more mucilage canals and mucilage cells than most other members of the ***Conocephalum conicum*** complex there (Akiyama 2022). These most likely help it to conserve moisture in its drier habitats.

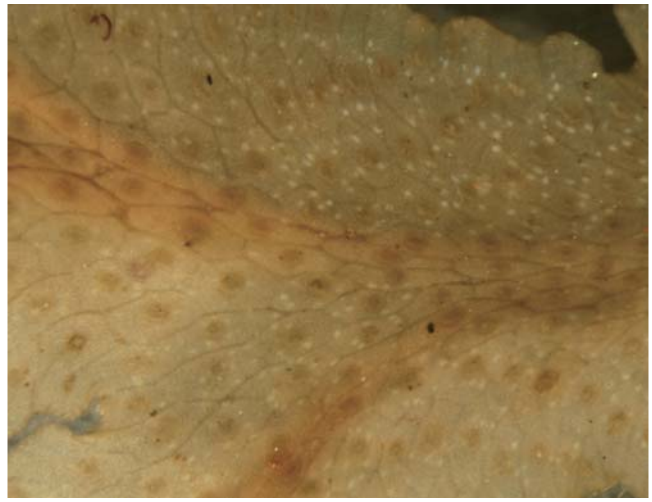

Figure 87. ***Conocephalum salebrosum*** from Japan, showing mucilage cells and canals. Photo courtesy of Hiroyuki Akiyama.

Figure 88. ***Conocephalum salebrosum*** from Japan, showing mucilage cells and canals in thallus cross section. Photo courtesy of Hiroyuki Akiyama.

In addition to its rhizoids and scales (Figure 80-Figure 83) for water movement and uptake, ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) often occurs in large mats (Figure 1) or mixed with other bryophytes (Figure 89-Figure 90) (Akiyama 2022). These closely intermingled plants can help to maintain moisture on the lower side of the plant where uptake occurs.

Figure 89. ***Conocephalum*** *cf.* ***salebrosum*** in Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 90. ***Conocephalum** cf.* ***salebrosum***, ***Mnium hornum***, and ***Atrichum undulatum***. Photo by Bob Klips, with permission.

Reproduction

Showalter (1921) determined that the male and female chromosomes of ***Conocephalum** cf.* ***salebrosum*** (Figure 1, Figure 30-Figure 49) in Wisconsin and New York, USA, and in Copenhagen, Denmark, did not differ as they do in some **dioicous** liverworts, but that 1 of the 9 chromosomes was considerably smaller, a condition that apparently led to some earlier researchers finding only 8.

Antheridia in ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) are borne in receptacles on the thallus surface (Figure 91-Figure 94) and apparently not elevated by an elongated midrib as they are in ***C. orientalis*** (Figure 15) (see Conocephalaceae part 1 subchapter).

Figure 91. ***Conocephalum** cf.* ***salebrosum*** males. Photo by John Hribljan, with permission

Figure 92. ***Conocephalum salebrosum*** males from Canada. Photo by Jean Faubert, with permission.

Figure 93. ***Conocephalum salebrosum*** antheridial receptacle with bud scales at edge. Photo courtesy of Hiroyuki Akiyama.

Figure 94. ***Conocephalum salebrosum*** antheridial receptacle from Japan. Photo courtesy of Hiroyuki Akiyama.

Graham (1909) described the development of both the gametophyte and sporophyte of ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49). In New York, USA, the gametangiophore (Figure 95-Figure 105) begins development early in June. Archegonia are mature by the first of July. The development of the sporangia (Figure 104-Figure 105) is rather slow, with spores and elaters

maturing by the onset of winter. At that time, growth ceases. The stalk of the gametangiophore is still very short, with the conical head appearing to be sessile on the thallus. In the warmth of the following May, this archegoniophore elongates rapidly, lifting the receptacle well above the thallus surface (Figure 100-Figure 103). When the stalk of the sporangium elongates, the spores are released when the capsule ruptures. A surrounding sheath may protect the overwintering capsule from excessive radiation and transpiration.

Figure 95. ***Conocephalum salebrosum*** from Japan, with beginning of archegoniophore. Photo courtesy of Hiroyuki Akiyama.

Figure 96. ***Conocephalum salebrosum*** with young archegoniophore. Photo by Jouko Rikkinen, through Creative Commons.

Figure 97. ***Conocephalum salebrosum*** with beginning archegoniophore, from Pfälzer Wald, Germany. Photo courtesy of Michael Lüth.

Figure 98. ***Conocephalum*** *cf.* ***salebrosum*** developing archegoniophore. Photo from Botany Website, UBC, with permission.

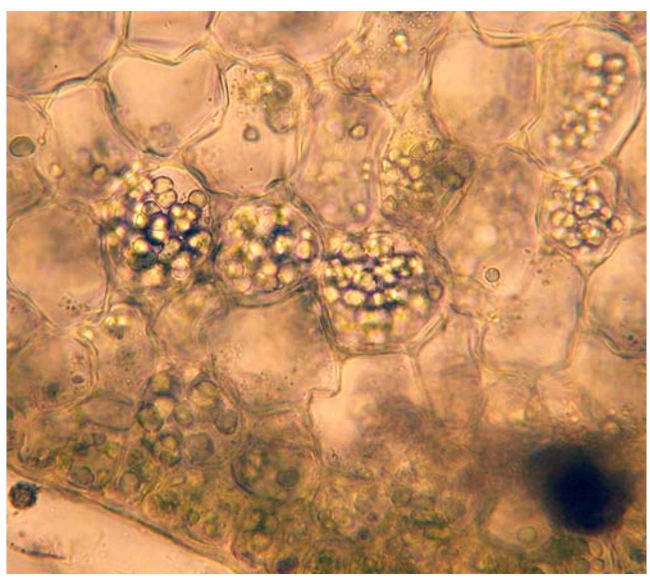

Figure 99. ***Conocephalum salebrosum*** archegoniophore stalk cs showing starch grains. Photo from Botany Website, UBC, with permission.

Figure 100. ***Conocephalum*** *cf.* ***salebrosum*** with elongating archegoniophores, floodplain, Rose Lake, Michigan, USA. Photo by Janice Glime.

Figure 101. ***Conocephalum salebrosum*** with mature archegoniophores, in Merthyr Tidfil, Wales. Photo by Des Callahan, with permission.

Figure 102. ***Conocephalum*** *c.f.* ***salebrosum*** with archegoniophores on canyon wall, Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 103. ***Conocephalum*** *cf.* ***salebrosum*** with mature archegoniophores. Photo from Botany Website, UBC, with permission.

Figure 104. ***Conocephalum salebrosum*** archegoniophores with capsules.. Photo by Hermann Schachner through Wikimedia Commons.

Figure 105. ***Conocephalum salebrosum*** archegonial receptacle showing black sporangia, from Europe. Photo by Barry Stewart, with permission.

Taylor and Hollensen (1984) elaborated on this cycle for plants of ***Conocephalum** cf.* ***salebrosum*** (Figure 1, Figure 30-Figure 49) in Michigan, USA. Growth is initiated in March. The full reproductive cycle requires 21 months. Archegonia are initiated in August and fertilized the following June. The sporophyte matures in that autumn and spores are shed in the next spring. The thalli are under snow and dormant from December through February.

Ellen (1920) described the germination of the spores of ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) in Sinsinawa, Wisconsin, USA. Here, the spore mother cells are well developed before the beginning of September and the spores are freed from the mother cell walls about mid September. In Early October, growth and a heavy deposit of starch precede the cell division. Each sporeling has up to eight cells that remain in the spore wall (Figure 106). Before winter, the partition cell walls thicken, starch is deposited, and growth occurs by division of the spores. These multicellular sporelings remain through the winter. When warm weather returns, cell division resumes and continues until the stored food is gone. Cell division pauses and the cells expand, accompanied by a rapid development of chlorophyll and starch. This is followed by a second series of cell divisions until the sporelings become a spherical mass of 30-40 cells. As this mass matures, the archegoniophore elongates rapidly in 4-5 days to attain a height of 5-6 cm. At the same time, the seta on each capsule elongates and the capsule emerges through the calyptra and sheath. The capsule wall ruptures and sporelings and elaters are dispersed. Most of the sporelings are short-lived, but some survive up to 38 days of desiccation.

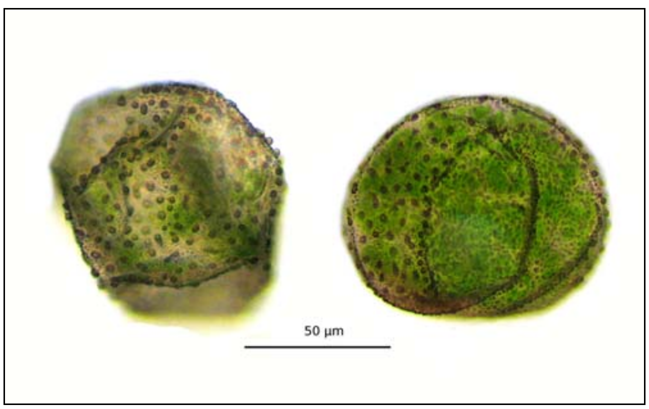

Figure 106. ***Conocephalum salebrosum*** multicellular spores resulting from endosporic development. Photo courtesy of Leica Chavoutier.

It appears that some spores of ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) might be dispersed while they are still small – one-celled (Ellen 1920). This strategy of multicellular spore spheres (sporelings) and single-celled spores would permit achieving a good start in the nearby habitat by dispersed spheres while permitting long-distance dispersal of the one-celled spores.

At the end of the growing season, apical buds form and older portions become moribund (Figure 107). In the spring, these buds expand and develop new plants (Figure 107-Figure 114), increasing the area covered due to branching.

Figure 107. ***Conocephalum salebrosum*** dead (moribund) and new growth at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 108. ***Conocephalum** cf.* ***salebrosum*** showing new growth at tips of older thalli, from Europe. Photo by Michael Lüth, with permission.

Figure 109. ***Conocephalum** cf.* ***salebrosum*** showing new growth and moribund older thalli, from Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 110. ***Conocephalum*** *cf.* ***salebrosum*** new growth, from Hocking Hills, Ohio, USA. Photo by Janice Glime.

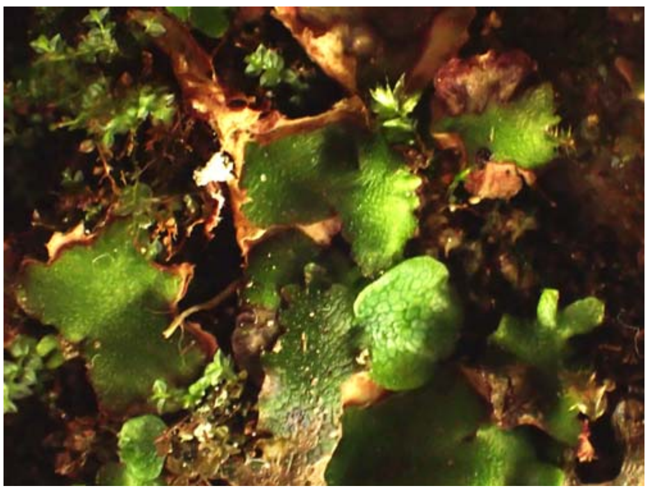

Figure 111. ***Conocephalum*** *cf.* ***salebrosum*** new growth on canyon walls, Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 112. ***Conocephalum*** *cf.* ***salebrosum*** new growth on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 113. ***Conocephalum*** *cf.* ***salebrosum*** new growth and dead thalli at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 114. ***Conocephalum salebrosum*** dead with new growth at Hocking Hills, Ohio, USA, Photo by Janice Glime.

By whatever mechanism, when ***Conocephalum*** *cf.* ***salebrosum*** (Figure 1, Figure 30-Figure 49) was growing in my garden room, it managed to appear in new locations around the room. It never had sexual structures. I attributed its dispersal to the movement of my box turtle, but I have no real proof. Unfortunately, I never caught anybody in the act.

Ainsworth (1965) reported bulbils in ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) from New York, USA, that had been kept in the dark for 28 days. These occur anywhere on the ventral surface, but when the midrib has bulbils still attached, these seem to inhibit the production of bulbils elsewhere on the thallus. An average of ~1.3 bulbils can occur in 1 mm² of thallus. This is not the first report of these structures. Karsten (1887) found them on thalli of ***Conocephalum conicum*** *s.l.* (Figure 17) that had been so completely overgrown by other thalli that they too, were in complete darkness.

These "bulbils" have been somewhat controversial. Paton (1993) referred to the tubers of ***Conocephalum conicum*** *s.l* (Figure 17). that occur on the ventral surface of the midrib and become detached to form new plants, as described by MacVicar (1926) and again by Paton from Sussex, England. These likewise occurred on moribund

thalli (Figure 107). Paton noted that these dark-produced structures, termed bulbils by Ainsworth (1965), germinated in ~5 days when placed in moist conditions in the light.

Animal Interactions

When growing in my garden room, ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) had nibbles around its edges. These were triangular and best fit the hypothesis that they were eaten by the Society Finches or the Canary in the room.

In the field I have found evidence of herbivory, but in these cases the removal was not triangular. Instead, it occurred not only on the margins but also mid thallus and the eaten areas were of irregular shape (Figure 115-Figure 117). These could be the product of insects, isopods, or possibly snails.

Figure 115. ***Conocephalum salebrosum*** herbivory in the Upper Peninsula of Michigan. Photo courtesy of John Hribljan.

Figure 116. ***Conocephalum*** *cf.* ***salebrosum*** eaten in Houghton County, Michigan, USA, 6 August 2009. Photo by Janice Glime.

Figure 117. ***Conocephalum*** *cf.* ***salebrosum*** eaten in Houghton County, Michigan, USA. Nibbling on the edges suggests a large arthropod, perhaps an isopod. Photo by Janice Glime.

Fungal Interactions

Liepiņa (2012) reported that both ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) and ***C. conicum*** (Figure 17) were "moderately" mycorrhizal. Both liverworts have Glomeromycotean endophytes and these fungi form nonseptate hyphae, vesicles, and arbuscules (see Figure 118), indicating that they created a functional symbiosis with the liverworts. The hyphae entered through the rhizoids and passed directly through the cell walls of the liverworts.

Figure 118. **Vesicular arbuscular mycorrhizae** in root cells, showing the form that might also show up in the thallus of ***Conocephalum salebrosum***. Photo by Rit Rajarshi, through Creative Commons.

Biochemistry

It is likely that some of the biochemical work attributed to ***Conocephalum conicum*** (Figure 17) actually applies to ***C. salebrosum*** (Figure 1, Figure 30-Figure 49), but unless it is recent or in North America, voucher specimens from the study would need to be verified. Even then, since the two liverworts grow together, the assays might have included both species without having both represented in the voucher specimens.

Craft *et al*. (2016) attempted to demonstrate chemotypes in the ***Conocephalum*** complex in the southern Appalachian Mountains, USA. They used a common garden experiment, but found that the experiment became a common stress experiment that significantly altered the compositions of volatile compounds in ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49). This phenomenon might provide antiherbivory compounds in response to herbivory, as already known from tree leaves (see, for example, Moreira *et al*. 2012). It would also be interesting to know the cost of producing such compounds relative to the cost of herbivory.

Summary

When chemical and genetic analyses were done on the ***Conocephalum conicum*** complex, the researchers decided that division into multiple species was warranted. From that division, ***C. salebrosum*** was identified and determined to be holarctic, seemingly replacing what was known as ***C. conicum*** in North America. Then, in 2022, several Japanese species were segregated from ***C. conicum***, including ***C. purpureorubrum***.

Ecological information on ***Conocephalum purpureorubrum*** is scant due to its recent consideration as a different species. It occurs in both damp habitats and dry ones, sometimes occurring streamside or on steep slopes. Its life cycle seems to be the same as that of ***C. conicum***, with no asexual structures known. It is unusual in always having at least some purplish color present on the ventral surface. It has mucilage canals, but it often lacks mucilage cells.

Conocephalum salebrosum occurs near water, but extends into drier habitats than those typical of ***C. conicum***. Most of the North American populations may belong to this species, often occurring on rock in canyons, near waterfalls, and along stream margins. Scales and rhizoids facilitate water movement and uptake along the ventral surface. The species can suffer from herbivory, but it contains compounds that are potentially antiherbivorous. It also frequently has vesicular arbuscular mycorrhizae.

Acknowledgments

Bryonetters provided a wonderful array of images to illustrate this chapter. Thank you to Masaki Shimamura for providing me with the image of the explosive sperm dispersal in ***Conocephalum cf. orientalis***. And thank you to Hiroyuki Akiyama for sending me his 2022 paper on the new species in Japan and providing me with original images.

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