

# CHAPTER 1-20

## AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CONOCEPHALACEAE, PART 1

---

### TABLE OF CONTENTS

Conocephalaceae.....	1-20-2
<i>Conocephalum conicum</i> .....	1-20-2
Distribution.....	1-20-5
Aquatic and Wet Habitats.....	1-20-5
Stream and River Banks.....	1-20-7
Springs.....	1-20-10
Waterfalls.....	1-20-10
Non-Aquatic Habitats.....	1-20-10
Physiology.....	1-20-10
Adaptations.....	1-20-13
Reproduction.....	1-20-16
Fungal Interactions.....	1-20-18
Animal Interactions.....	1-20-19
Biochemistry.....	1-20-30
<i>Conocephalum orientale</i> .....	1-20-22
Distribution.....	1-20-25
Aquatic and Wet Habitats.....	1-20-25
Physiology.....	1-20-26
Adaptations.....	1-20-27
Reproduction.....	1-20-28
Biochemistry.....	1-20-30
Summary.....	1-20-30
Acknowledgments.....	1-20-31
Literature Cited.....	1-20-31

# CHAPTER 1-20

## AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CONOCEPHALACEAE, PART 1

---



Figure 1. *Conocephalum conicum* s.l. habitat on emergent rock. Photo from <[www.aphotofauna.com](http://www.aphotofauna.com)>, with permission.

### Conocephalaceae

#### *Conocephalum conicum* (Figure 1-Figure 11)

Recently, genetic determinations and usable morphological characters have led to the division of *Conocephalum conicum* (Figure 1-Figure 2-Figure 11) into several species (Szweykowski *et al.* 2005; Akiyama 2022). Therefore, one must read the research attributed to this species with caution because it might actually refer to

*Conocephalum salebrosum* (Figure 12-Figure 13) in North America, or several species in Japan. When I can't be sure which species it is, I shall denote the species as *Conocephalum conicum* s.l. (the abbreviation s.l. refers to *sensu lato* and means in the broad sense; s.s. refers to *sensu stricto* and means in the narrow sense) (Figure 1-Figure 2-Figure 11).

*Conocephalum conicum* s.s. (Figure 1-Figure 11) is a smaller plant than *C. salebrosum* (Figure 12); *C. salebrosum* plants are dull, with more conspicuous thallus grooves that are more conspicuous than the air pores (Figure 13) (Stotler & Crandall-Stotler 2017).





Figure 2. *Conocephalum conicum* showing conspicuous pores. Photo by Li Zhang, with permission.



Figure 3. *Conocephalum conicum* from Scotland, showing conspicuous pores. Photo courtesy of David Long.



Figure 4. *Conocephalum conicum* showing distinct pores and weaker thallus sections. Photo by Hermann Schachner, through Creative Commons.



Figure 5. *Conocephalum conicum* with conspicuous pores. Photo by Ralf Wagner, with permission.



Figure 6. *Conocephalum conicum* from Wales, showing distinct pores. Photo courtesy of Jonathan Sleath.

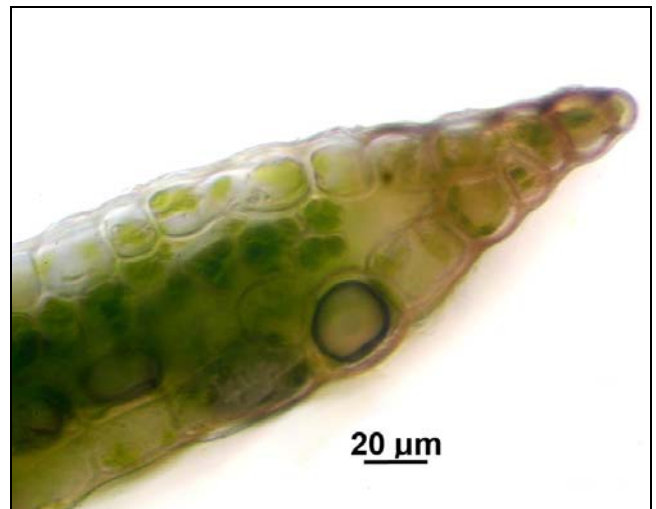


Figure 7. *Conocephalum conicum* thallus margin section, from Céret, France. Photo courtesy of Louis Thouvenot.





Figure 8. *Conocephalum conicum* s.l. showing conspicuous pores. Photo by Li Zhang, with permission.

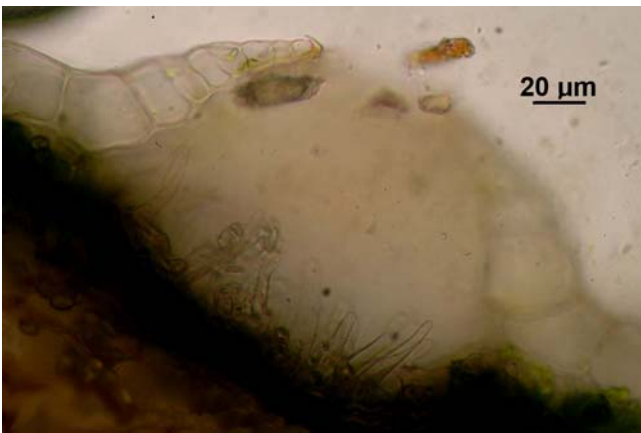


Figure 9. *Conocephalum conicum* from Céret, France, showing pore section. Photo courtesy of Louis Thouvenot.

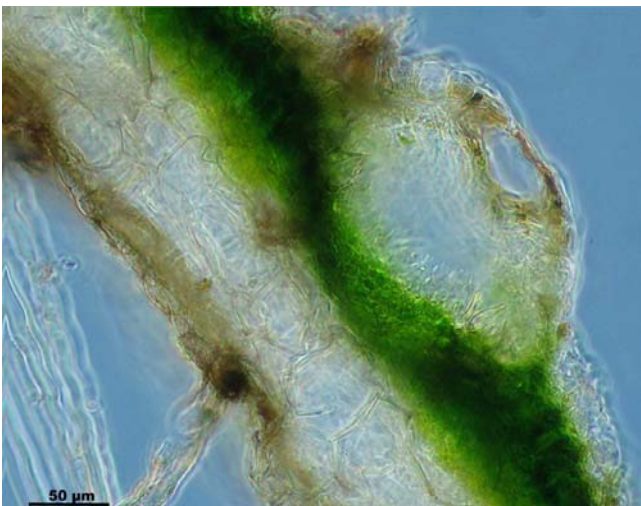


Figure 10. *Conocephalum conicum* showing pore section. Photo by Ralf Wagner at <[www.dr-ralf-wagner.de](http://www.dr-ralf-wagner.de)>, with permission.



Figure 11. *Conocephalum conicum* s.l. pore wall. Photo by Ralf Wagner at <[www.dr-ralf-wagner.de](http://www.dr-ralf-wagner.de)>, with permission.



Figure 12. *Conocephalum salebrosum* on left with conspicuous thallus grooves and dull thallus and *C. conicum* on right and center with conspicuous pores and shiny thallus. Photo courtesy of Jonathan Sleath.



Figure 13. *Conocephalum salebrosum* showing dull thallus, conspicuous grooves, and pores less conspicuous than thallus grooves. Photo by Jouko Rikkinen, through Creative Commons.



### Distribution

Sérgio *et al.* (2011) surmised that *Conocephalum salebrosum* (Figure 12-Figure 13) has a more scattered and wider distribution than does *C. conicum* (Figure 1-Figure 11). Stotler and Crandall-Stotler (2017) concluded that *Conocephalum conicum* does not occur in North America and that all of the specimens previously identified as *C. conicum* are instead aligned with *C. salebrosum*. In Russia Borovichev *et al.* (2009) found *C. conicum* to be more widespread than *C. salebrosum*. The overall distribution of *C. conicum* appears to be restricted to Europe. The photos below illustrate its presence in a number of European countries (Figure 14-Figure 18).



Figure 14. *Conocephalum conicum*, Wales. Photo courtesy of David Long.



Figure 15. *Conocephalum conicum*, Scotland. Photo courtesy of David Long.



Figure 16. *Conocephalum conicum*, Céret, France. Photo courtesy of Louis Thouvenot.



Figure 17. *Conocephalum conicum*, Sardoia, Italy. Photo courtesy of Michael Lüth.



Figure 18. *Conocephalum conicum*, Czech Republic. Photo by Vita Plasek, with permission.

### Aquatic and Wet Habitats

Borovichev *et al.* (2009) found that *Conocephalum conicum* (Figure 1-Figure 11) and *C. salebrosum* (Figure 12-Figure 13) have similar ecological preferences and that they can even grow intermingled (Figure 19). Both form extensive mats on streambanks and at the bases of moist rocks and cliffs. *Conocephalum conicum* tends to be more hygrophytic than *C. salebrosum*. Both species seem to specialize in colonizing spring and river micro-habitats close to running or standing water. The photographs below illustrate some of the habitats where *Conocephalum conicum* has been found in Europe (Figure 20-Figure 22).





Figure 19. *Conocephalum conicum* (left) and *C. salebrosum* (right). Photo courtesy of Michael Lüth.

*Conocephalum conicum* s.l. (Figure 1-Figure 11) occurs in wet places around lakes, especially in shade in Scotland (West 1910); in ground, rock, spring, and water communities associated with streams near Lacko, Western Carpathians (Mamczarz 1970); in association with the River Wear, England (Birch *et al.* 1988); associated with rivers (Ferreira *et al.* 2008). Its habitat seems to be primarily from rivers, streams, and stream banks (Figure 26). Nevertheless, it occurs often on rocky walls above streams (Figure 20) and in caves (Figure 21-Figure 22).



Figure 20. *Conocephalum conicum* growth habit on wall s.l. Photo by Allen Norcross, with permission.



Figure 21. *Conocephalum conicum* in wet limestone cave, Traeth Glaslyn Nature Reserve, Wales. Photo by Janice Glime.



Figure 22. *Conocephalum conicum* in wet, limestone cave, Traeth Glaslyn Nature Reserve, Wales. Photo by Janice Glime.

There are many reports of *Conocephalum conicum* (Figure 1-Figure 11) from streams and rivers. It is among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006). It is among the most common bryophytes in the River Tweed, UK (Holmes & Whitton 1975) and occurs throughout the River Swale, Yorkshire, UK (Holmes & Whitton 1977b). In the River Tyne, UK, it occurs mostly in mid to lower reaches (Holmes & Whitton 1981). It is part of the *Platyhypnidium-Fontinalis antipyretica* (Figure 23-Figure 24) association in Thuringia, Germany (Marstaller 1987). It occurs both in the Iskur River, Bulgaria, and its main tributaries (Papp *et al.* 2006). In Greece it is common in streams (Papp 1998). It occurs on moist stones and rocks in the streambed (Figure 1, Figure 25) in streams of Gory Stolowe Mountains, Poland (Szweykowski 1951). It is also found in mountain streams of northwestern Portugal (Vieira *et al.* 2005) and in mountainous streams on Madeira Island (Luis *et al.* 2015).





Figure 23. *Platyhypnidium riparioides* of the *Platyhypnidium-Fontinalis antipyretica* association that may also include *Conocephalum conicum*. Photo by Hermann Schachner, through Creative Commons.



Figure 24. *Fontinalis antipyretica* of the *Platyhypnidium-Fontinalis antipyretica* association that may also include *Conocephalum conicum*. Photo from Botany Website, UBC, with permission.



Figure 25. *Conocephalum conicum* s.l. on emergent rock in stream. Photo from <www.aphotofauna.com>, with permission.

### Stream and River Banks

*Conocephalum conicum* (Figure 1-Figure 11) is able to live on banks with frequent submergence (Figure 26) and slow water, usually on rocks just above water (Figure 27-Figure 31) (Watson 1919). It occurs in a zone above *Cratoneuron filicinum* (Figure 32-Figure 33), up to 0.9 m above the water (Gimingham & Birse 1957). Holmes and Whitton (1977a) found it on the river bank of the River Tees, UK.



Figure 26. *Conocephalum conicum* habitat along a stream in France. Photo courtesy of courtesy of Leica Chavoutier.

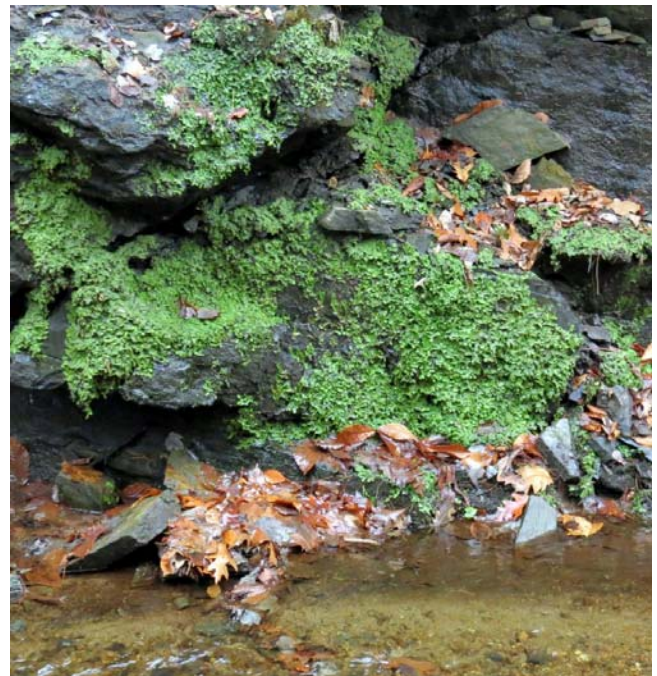


Figure 27. *Conocephalum conicum* s.l. on rock wall at stream edge. Photo by Allen Norcross, with permission.





Figure 28. *Conocephalum conicum* s.l. on rock wall of stream. Photo by Allen Norcross, with permission.



Figure 29. *Conocephalum conicum* s.l. on rock at stream edge. Photo by Allen Norcross, with permission.



Figure 30. *Conocephalum conicum* on wet rock, Sardinia, Italy. Photo courtesy of Michael Lüth.



Figure 31. *Conocephalum conicum* s.l. on rock wall. Photo by Allen Norcross, with permission.



Figure 32. *Cratoneuron filicinum*; *Conocephalum conicum* s.l. lives in a zone above this species in Europe. Photo by Claire Halpin, with permission.



Figure 33. *Cratoneuron filicinum*, a species that lives in a zone closer to the water than that of *Conocephalum conicum* s.l. Photo by Tigrente, through Creative Commons.

Luis *et al.* (2008) reported *Conocephalum conicum* s.s. (Figure 1-Figure 11) along the lower reaches of Ribeira Brava in Madeira in disturbed areas dominated by the great



reed *Arundo donax* (Figure 34). It was associated there with the mosses *Bryum dichotomum* (Figure 35), *Pohlia melanodon* (Figure 36), *Ptychostomum capillare* (Figure 37), and *Scorpiurium circinatum* (Figure 38-Figure 39) and the liverwort *Lunularia cruciata* (Figure 40).



Figure 34. *Arundo donax*, a grass that sometimes is accompanied by *Conocephalum conicum* s.l. along the lower reaches of the Ribeira Brava in Madeira. Photo by Forest and Kim Starr, through public domain.



Figure 37. *Ptychostomum capillare*, an associate of *Conocephalum conicum* along the Ribeira Brava in Madeira. Photo by Michael Becker, through Creative Commons.



Figure 35. *Bryum dichotomum*, an associate of *Conocephalum conicum* along the Ribeira Brava in Madeira. Photo by David T. Holyoak, with permission.



Figure 38. *Scorpiurium circinatum* moist, an associate of *Conocephalum conicum* along the Ribeira Brava in Madeira. Photo by Hugues Tinguy, with permission.



Figure 36. *Pohlia melanodon*, an associate of *Conocephalum conicum* along the Ribeira Brava in Madeira. Photo by David T. Holyoak, with permission.



Figure 39. *Scorpiurium circinatum* dry. Photo by David T. Holyoak, with permission.





Figure 40. *Lunularia cruciata*, an associate of *Conocephalum conicum* along the Ribeira Brava in Madeira. Photo by Michael Langeveld, through Creative Commons.

### Springs

There seem to be few reports of *Conocephalum conicum* (Figure 1-Figure 11) in or around springs. It is known at a spring in the Tara river canyon and Durmitor area, Montenegro (Papp & Erzberger 2011).

### Waterfalls

Watson (1919) reported *Conocephalum conicum* (Figure 1-Figure 11) from waterfalls, but others don't seem to attribute it to this habitat. This is often a lack of detail in reporting, with the splash zone of a waterfall included with "streambank."

### Non-Aquatic Habitats

Although *Conocephalum conicum* (Figure 1-Figure 11) is usually associated closely with water, it can be found on slopes (Figure 41), perhaps getting water from seepage, or occurring on canyon walls where it is shaded and humid (Figure 42).



Figure 41. *Conocephalum conicum* s.l. habitat. Photo by Michael Lüth, with permission.



Figure 42. *Conocephalum conicum* s.l. on rock of stream canyon. Photo by Michael Lüth, with permission.

### Physiology

*Conocephalum conicum* (Figure 1-Figure 11) is more easily stressed by **desiccation** than its sibling species *C. salebrosum* (Figure 12-Figure 13) (Szweykowski *et al.* 2005; Borovichev *et al.* 2009). This explains its more aquatic habitats.

Like *C. salebrosum*, *C. conicum* (Figure 1-Figure 11) has scales (Figure 43-Figure 44) and rhizoids (Figure 45-Figure 46) that provide **capillary spaces** on the ventral surface. We can assume that like the case of *C. salebrosum*, water moves through these spaces along the thallus and is delivered to all points on the thallus where it is taken in and distributed.



Figure 43. *Conocephalum conicum* s.l. from Italy showing scales on the ventral thallus surface. Photo courtesy of Anna di Palma.



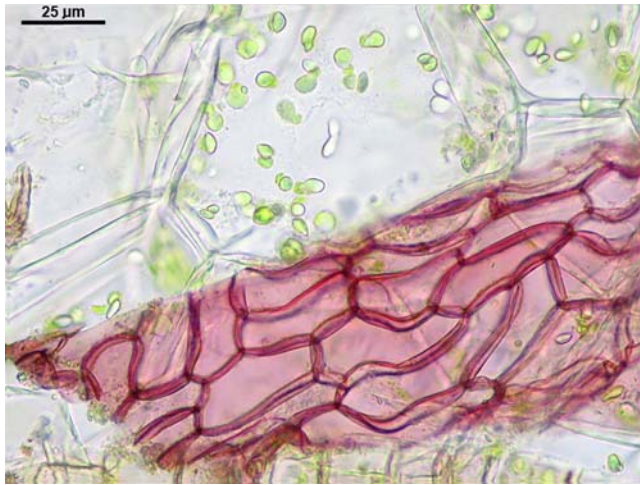


Figure 44. *Conocephalum conicum* s.l. ventral scale that aids in movement of water across the ventral side of thallus. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.



Figure 45. *Conocephalum conicum* s.l. thallus with rhizoids and thallus; rhizoids help to move water across the ventral side of the thallus and facilitate uptake. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.



Figure 46. *Conocephalum conicum* rhizoids showing the capillary spaces where they are massed. Photo by Paul Davison, with permission.

The shade habitat of *Conocephalum conicum* s.l. (Figure 1-Figure 11) is supported by its reaction to supplemented **UV-B radiation** (Ihle & Laasch 1995; Ihle 1997). This radiation causes a drastic decrease in the reaction center proteins D1 and D2 as well as the outer light-harvesting antenna. Streptomycin inhibited the repair process of PS II, indicating that only chloroplastic protein synthesis is needed for recovery. A specimen from India suggests that under the right conditions this species can produce protective pigments (Figure 47).



Figure 47. *Conocephalum conicum* from India showing brown pigmentation. Photo courtesy of Muhammet Ören.

At the other end of the light intensity range, **low light** causes **etiolation**. Ken Adams (pers. comm.) demonstrated this by growing *Conocephalum conicum* in the dark (Figure 48).



Figure 48. *Conocephalum conicum* etiolation (3 weeks in dark). Photo by Ken Adams, with permission.

The **pH** seems to be important in the distribution of *Conocephalum*, but most reports of preference can only be applied to *Conocephalum conicum* s.l. (Figure 1-Figure 11). Trębacz (1992) found that **pH** is also important within the cells of *Conocephalum conicum* s.l. It responds to the onset of **light** by decreasing its internal **pH** by about 0.15 units, followed by a slow increase. Respiration also can exhibit up to a 100% increase in response to excitation, but



the pH seems not to be involved. Dziubińska *et al.* (1989) found that cutting the thallus or providing an electrical stimulus elicited a transient rise in the rate of respiration. If the stimulation fails to produce any excitation, the respiration does not increase. The differences in response depend on the character of the excitation and the area of the thallus stimulated. Erdtmann and Mueller Stoll (1983) investigated the relationship between respiration and regeneration in *Conocephalum conicum* s.l.

Trębacz and Fensom (1989) found that in *Conocephalum conicum* s.l. (Figure 1-Figure 11) labelled carbon travelled cell to cell at a rate of  $\sim 2.0\text{--}1.7\ \mu\text{m}\ \text{s}^{-1}$ , a rate that is the same as that of cytoplasmic streaming. **Photosynthesis** occurs in the thallus cells (Figure 49);  $\text{CO}_2$  is obtained from the air through the pores on the thallus surface (Figure 50-Figure 51) and oxygen is released there. Below these openings are chambers with chlorophyllous cells where photosynthesis occurs (Figure 51). Starch can be stored in the cells and can be densely clumped in the stalk portion of the archegoniophore (Figure 52).



Figure 49. *Conocephalum conicum* photosynthetic cells in thallus. Photo by Ralf Wagner <[www.dr-ralf-wagner.de](http://www.dr-ralf-wagner.de)>, with permission.



Figure 50. *Conocephalum conicum* s.l. showing pore openings on the thallus surface in the UK. Photo by Dick Haaksma, with permission.

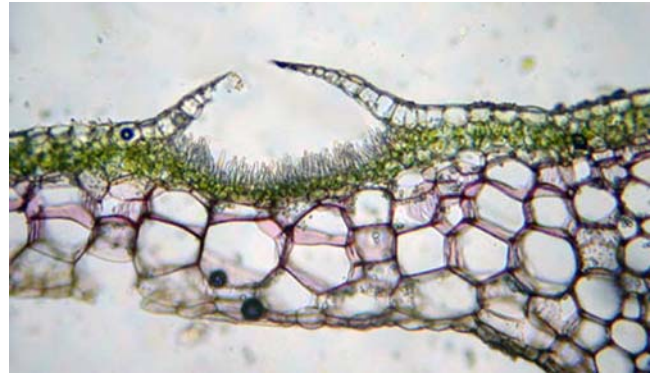


Figure 51. *Conocephalum conicum* s.l. showing longitudinal section of pore. Photo from Botany Website, UBC, with permission.



Figure 52. *Conocephalum conicum* s.l. archegoniophore stalk section showing stained dense starch grains. Photo from Botany Website, UBC, with permission.

In addition to whatever benefit may be derived from neighbors, *Conocephalum conicum* s.l. (Figure 1-Figure 11) has anatomical adaptations that may permit it to live where it can become inundated with water. The **air pores** (Figure 50), which are quite large in this genus, have hydrophobic cuticular ridges (Figure 51) surrounding them (Schönherr & Ziegler 1975). This allows only liquids with a contact angle of zero degrees with the ledges to enter the air pore. This presumably permits the internal air chambers of the species to maintain the air space needed to obtain  $\text{CO}_2$ . One would assume that this is necessary for rapid recovery once the water recedes and to allow continued photosynthesis when kept wet on the exterior by splash.

Dilks and Proctor (1975) found that *Conocephalum conicum* s.l. (Figure 1-Figure 11) was killed by **rapid cooling** to  $-5^\circ\text{C}$ , whereas many of the bryophytes tested could withstand such rapid cooling. Nevertheless, it certainly can survive freezing temperatures in caves, where the temperature is not likely to drop suddenly (Figure 53). Dilks and Proctor surmised that the ability to survive long periods at low temperatures, as exhibited by many species, seems to relate to desiccation resistance.





Figure 53. *Conocephalum conicum* s.l. on wet cave roof with ice. Photo by Allen Norcross, with permission.

Krol *et al.* (2003) found that *Conocephalum conicum* (Figure 1-Figure 11) s.l. exhibits all-or-none action potentials in response to **sudden temperature drops**. Calcium is important in these potentials, with its inhibition or decrease resulting in the inhibition of voltage transients. The researchers concluded that the temperature drop causes a change in membrane potential due to calcium influx from both internal and external stores.

*Conocephalum conicum* s.l. (Figure 1-Figure 11) produces **Heat Shock Protein 70** in response to atmospheric pollution (Basile *et al.* 2013). The **heavy metals** accumulate in cell walls, accompanied by a strong increment in the Heat Shock Protein 70. Cadmium and lead accumulate in the parenchyma and are absorbed to cell walls or concentrated in vacuoles. The pollutants result in severe alterations to the organelles. The researchers concluded that *C. conicum* s.l. is tolerant of heavy metals and can serve as a bioindicator (see also Maresca *et al.* 2020). Nevertheless, Iqbal *et al.* (2011b) expressed concern that it was threatened by changes in the environment in Bhaderwah as well as in the Kumaon Himalaya.

Trębacz *et al.* (1994) compared the activities of  $\text{Ca}^{2+}$ ,  $\text{K}^+$ ,  $\text{Cl}^-$ , and  $\text{NO}_3^-$  in *Conocephalum conicum* (Figure 1-Figure 11). The free cytosolic  $\text{Ca}^{2+}$  did not exhibit any light-dependent changes when no action potential was triggered. However, action potentials typically caused a 2-fold increase in free cytoplasmic  $\text{Ca}^{2+}$  concentration. Action potentials cause little change in  $\text{K}^+$  activity. For both  $\text{Cl}^-$  and  $\text{NO}_3^-$  the vacuolar activity was 5 to 6 times that of the cytoplasmic activity. Changes in illumination had little effect on the concentrations of the two ions.

Samecka-Cymerman *et al.* (1997) found that the ecological differentiation between the liverwort species *Conocephalum conicum* (Figure 1-Figure 11), *Marchantia polymorpha* (Figure 54), and *Pellia epiphylla* (Figure 55) correlates closely with the soil chemistry. They found a high correlation between the soil concentrations of heavy metals as well as macroelements and the thalli of these liverworts. *Conocephalum conicum* s.l. proved to be a good biomonitor of chromium and cobalt.



Figure 54. *Marchantia polymorpha* with gemmae cups. Photo by Hermann Schachner, through Creative Commons.



Figure 55. *Pellia epiphylla*, a species of similar locations near stream water, but differs in soil chemistry from that of *Conocephalum conicum*. Photo by Hermann Schachner, with permission.

### Adaptations

Gimingham and Birse (1957) concluded that thalloid mats such as those in *Conocephalum* occur at the most moist end of the spectrum. *Conocephalum conicum* s.l. (Figure 1-Figure 11) often occurs in **association** with other liverworts, such as *Chiloscyphus kashyapii*, *Dumortiera hirsuta* (Figure 56), *Marchantia* spp. (Figure 54), *Pellia endiviifolia* (Figure 57), *Preissia quadrata* (Figure 58), *Reboulia hemispherica* (Figure 59), and occasionally with *Aneura pinguis* (Figure 60), *Clevea hyalina* (Figure 61), *Mannia triandra* (Figure 62), and as well as the mosses *Myurella sibirica* (Figure 63) and *Thuidium delicatulum* (Figure 64) (Iqbal *et al.* 2011a). *Conocephalum conicum* is also associated with fungi, ferns, flowering plants, and even insects. These associations might prove to be beneficial, perhaps by maintaining moisture or in helping the liverworts to obtain it. They could also result in competition.





Figure 56. *Dumortiera hirsuta*, a liverwort that often occurs in association with *Conocephalum conicum* s.l. Photo by George Shepherd, through Creative Commons.



Figure 57. *Pellia endiviifolia*, a liverwort that often occurs in association with *Conocephalum conicum* s.l. Photo by Hermann Schachner, through Creative Commons.



Figure 58. *Preissia quadrata*, a liverwort that often occurs in association with *Conocephalum conicum* s.l. Photo by Bernd Haynold, through Creative Commons.



Figure 59. *Reboulia hemisphaerica*, a liverwort that often occurs in association with *Conocephalum conicum* s.l. Photo by Michael Lüth, with permission.



Figure 60. *Aneura pinguis*, a liverwort that often occurs in association with *Conocephalum conicum* s.l. Photo by Hermann Schachner, through Creative Commons.



Figure 61. *Clevea hyalina*, a liverwort that sometimes occurs in association with *Conocephalum conicum* s.l. Photo by Hugues Tinguy, with permission.





Figure 62. *Mannia triandra*, a liverwort that sometimes occurs in association with *Conocephalum conicum* s.l. Photo courtesy of Guido Brusa.



Figure 63. *Myurella sibirica*, a moss that often occurs in association with *Conocephalum conicum* s.l. Photo by Dick Haaksma, with permission.



Figure 64. *Thuidium delicatulum*, a moss that often occurs in association with *Conocephalum conicum* s.l. Photo by Blanka Agüero, with permission.

Levine (1999) explored the "indirect facilitation" in a riparian community where *Conocephalum conicum* s.l. (Figure 1-Figure 11) (see Shevock *et al.* 2021) was a member. "Indirect facilitation occurs when the indirect positive effect of one species on another, via the suppression of a shared competitor, is stronger than the direct competitive effect." In a northern California, USA, riparian community, Levine conducted field experiments. Using a factorial design, he found three qualitatively different interactions between *Carex nudata* (Figure 65) and three target species. The *Carex* facilitated *Conocephalum conicum* s.l. in the presence of *Mimulus guttatus* (Figure 66) by suppressing the latter. On the other hand, when *M. guttatus* was absent, *Carex nudata* was a competitor with *Conocephalum conicum* s.l.



Figure 65. *Carex nudata*, a species that interacts with *Conocephalum conicum* s.l. by suppressing *Mimulus guttatus*, or to compete when *M. guttatus* is absent. Photo by Paul Slichter, with permission.

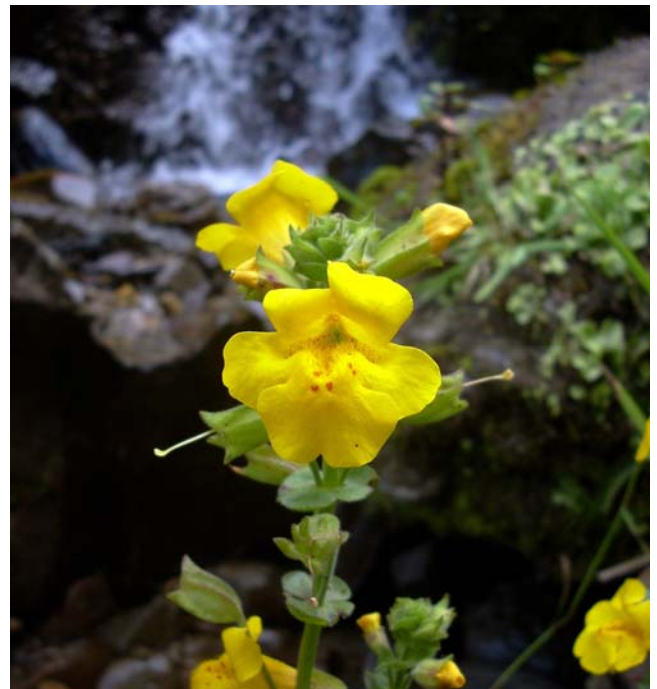


Figure 66. *Mimulus guttatus*, a species that competes with *Conocephalum conicum* s.l. Photo by Christopher M. Luna, through Creative Commons.



## Reproduction

*Conocephalum conicum* s.l. (Figure 1-Figure 11) has been of interest to bryologists in a number of studies related to reproduction. However, some of these have been done in North America, so I must assume they actually refer to *Conocephalum salebrosum* (Figure 12-Figure 13). Thus, I have discussed them under that species in the next subchapter.

One of the mechanisms of spread of *Conocephalum* species is its ability to **overwinter** and produce new growth in spring. The overwintering buds are protected by scales (Figure 67-Figure 69). But young plants (Figure 70-Figure 71) also arise with no apparent connection to plants from a previous year.



Figure 67. *Conocephalum conicum* s.l. overwintering bud scales. Photo from Botany Website, UBC, with permission.



Figure 69. *Conocephalum conicum* s.l. overwintering bud scales. Photo by Dick Haaksma, with permission.



Figure 70. *Conocephalum conicum* s.l. young. Photo by Dick Haaksma, with permission.



Figure 68. *Conocephalum conicum* s.l. with scales covering winter buds. Photo by Allen Norcross, with permission.



Figure 71. *Conocephalum conicum* s.l. young plants. Photo by Dick Haaksma, with permission.

Benson-Evans (1964) found that *Conocephalum conicum* s.l. (Figure 1-Figure 11) from Wales grew best and produced **gametangia** (Figure 72-Figure 75) at 21°C, but not at 10°C. It grew and produced gametangia best in long days (18 hours), but not in short days (6 hours).



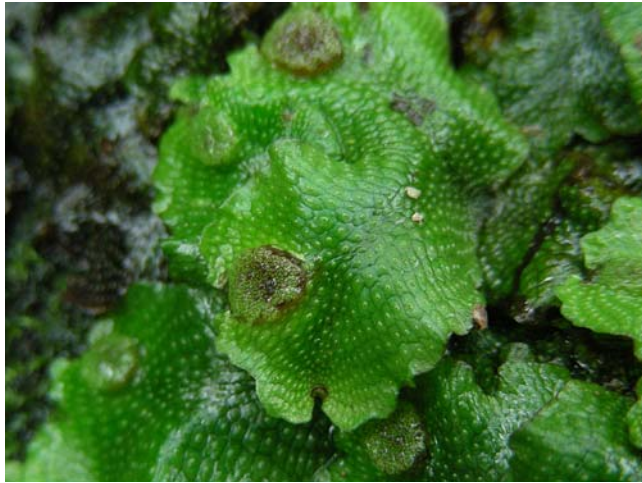


Figure 72. *Conocephalum conicum* with immature antheridial receptacles, Sardoia, Italy. Photo courtesy of Michael Lüth.



Figure 73. *Conocephalum conicum* s.l. antheridial receptacles. Photo by Malcolm Storey through Creative Commons.



Figure 74. *Conocephalum conicum* s.l. males with mature antheridial receptacles, Nichinan, Japan, June 1983. Photo by Janice Glime.

Yamazaki (1981) discovered that even within a population of *Conocephalum conicum* (Figure 1-Figure 11) the **genetic variation** was abundant, a condition that suggests that sexual reproduction predominates in the natural populations. It is not unusual to see reproductive populations (Figure 76-Figure 78), and for the most part

bryologists have not reported asexual structures. Since *C. conicum* can grow together with *C. salebrosum* (Figure 12-Figure 13), it is possible that some of the variation Yamazaki observed was really that of what we now consider to be two species.



Figure 75. *Conocephalum conicum* s.l. mature antheridial receptacle. Photo by Malcolm Storey, through Creative Commons.



Figure 76. *Conocephalum conicum* s.l. with developing archegoniophore. Photo by Li Zhang, with permission.



Figure 77. *Conocephalum conicum* s.l. mature sporangia in the cone-shaped archegonial head, a relatively frequent sight due to the frequent sexual reproduction. Photo by Hermann Schachner, through Creative Commons.





Figure 78. *Conocephalum conicum* s.l. sporangia ready to release spores. Photo from Botany Website, UBC, with permission.

More recently, **tubers** have been verified on *Conocephalum conicum* s.l. (Figure 1-Figure 11) in Sussex, England (Paton 1993). These were found so uncommonly that their presence was often omitted from descriptions of the species. They may, however, be more common than assumed because they are located on **moribund** (in terminal decline; lacking vitality or vigor; Figure 79) thalli – a part of the plant often overlooked or discarded in the preparation of specimens. Furthermore, they are on the ventral surface, hidden among the rhizoids. Nevertheless, when they become detached, they germinate to produce a new thallus.



Figure 79. *Conocephalum* cf. *salebrosum* dead and new growth on population at Hocking Hills, Ohio, USA. It is on the ventral side of such moribund tissues where tubers have been found in *Conocephalum conicum* s.l. Photo by Janice Glime.

Bhagat *et al.* (2012) suggested that sexual reproduction is a less important means of reproduction in *Conocephalum* than is asexual reproduction. They based this on the relatively constant ratio of spores to elaters (Figure 80) (0.40-0.43:1) over the past 54 years, a ratio that is much lower than that known in other **Marchantiales**.

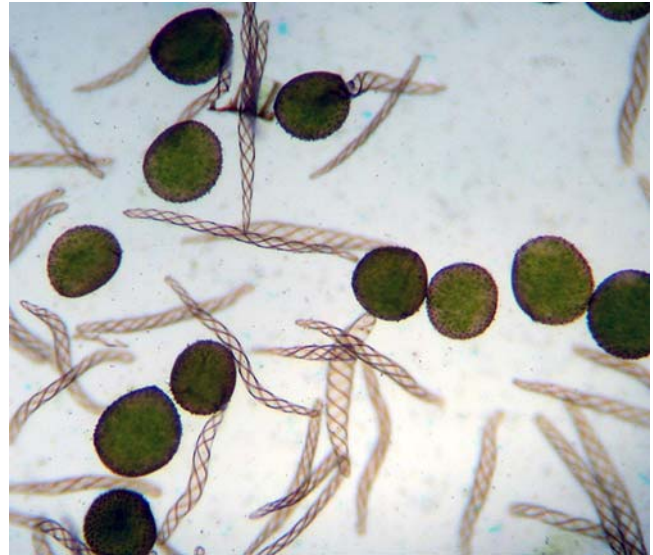


Figure 80. *Conocephalum conicum* s.l. spores and elaters at maturity. Photo from Botany Website, UBC, with permission.

### Fungal Interactions

Carré and Harrison (1961) reported a species of *Pythium* (Figure 81), a parasitic fungus, invading *Conocephalum conicum* s.l. (Figure 1-Figure 11). This endophyte invades the rhizoids (Figure 82) and then the thallus, but is limited to the area adjoining the midrib. A species of *Pythium* was consistently isolated from infected rhizoids and thalli. Other fungal species were in cultures with sterile thalli, but none was able to form the typical **vesicular-arbuscular** (Figure 83) condition. Some were, however, able to penetrate the rhizoids and lower cells of the thallus.

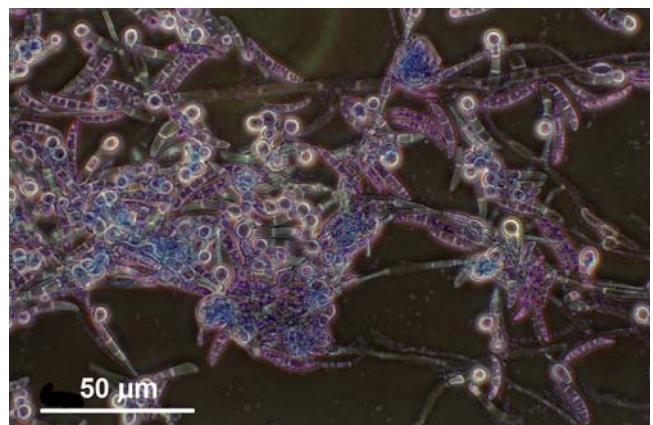


Figure 81. *Pythium* sp.; a species of *Pythium* is endophytic in *Conocephalum conicum* s.l. Photo by Josef Reischig, through Creative Commons.



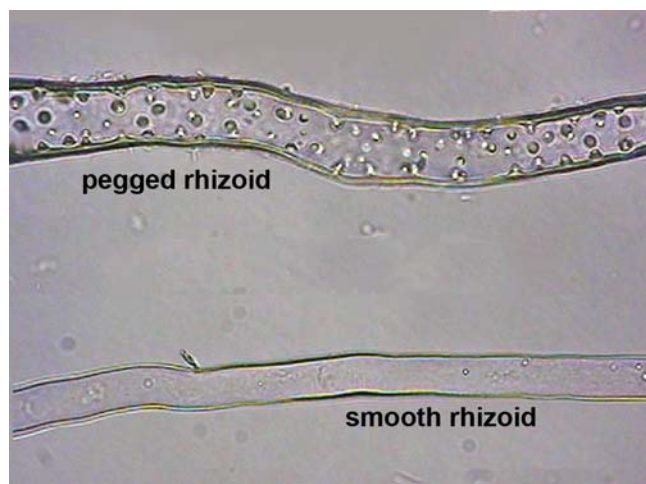


Figure 82. *Conocephalum conicum* s.l. two types of rhizoids. Photo by Paul Davison, with permission.

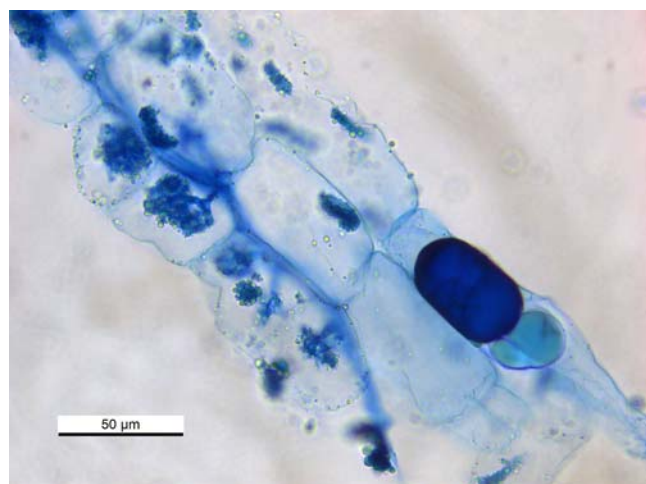


Figure 83. **Vesicular arbuscular mycorrhizae** in root cells, showing the form that might also show up in the thallus of *Conocephalum conicum*. Photo by Rit Rajarshi, through Creative Commons.

Ligrone and Lopes (1989) reported a highly branched fungus that colonizes the smooth-walled rhizoids (Figure 82) of *Conocephalum conicum* s.l. (Figure 1-Figure 11). The fungus is able to enter the thallus through these rhizoids to the parenchyma of the midrib, where it is entirely intracellular. The fungus forms vesicles (see Figure 83) in the rhizoids and a few ventral layers of the parenchyma cells. The fungal hyphae spread from cell to cell. More internal cells have prominent arbuscules (Figure 83) formed by the infecting hyphae. The infected host cells experience proliferation of the ribosomes, plastids, and mitochondria. The arbuscules ultimately degenerate, leaving clumps of collapsed hyphae, and these cells have not been observed to become reinfected.

Later, Ligrone *et al.* (2007) reported **Glomeromycotean** associates in liverworts. *Glomus mosseae* (Figure 84) was identified in axenic thalli of both *Conocephalum conicum* (Figure 1-Figure 11) and *C. salebrosum* (Figure 12-Figure 13) and produced an association with these liverworts similar to that seen in the wild. These fungi suppressed cell wall autofluorescence in Marchantialean liverworts and triggered the deposition of a

new wall layer that specifically bound the monoclonal antibody CCRC-M1 against fucosylated side groups associated with xyloglucan and rhamnogalacturonan I.



Figure 84. *Glomus mosseae* spores cultured with tomato root. Photo by Samson90, through Creative Commons.

Nevertheless, *Conocephalum conicum* s.l. (Figure 1-Figure 11) exhibited some antifungal activity. Asakawa (2007) reported antimicrobial, antifungal, antipyretic, and antidotal activity from *Conocephalum conicum* s.l.. It can be used to cure cuts, burns, scalds, fractures, swollen tissue, poisonous snake bites, and gallstones. We don't know which cryptospecies was used in the study.

### Animal Interactions

Imada *et al.* (2011) found that there are ~25 East Asian endemic members of the micropterigid moths (Figure 85) that occur exclusively on *Conocephalum* (Figure 1-Figure 11, Figure 86). These moth species are separated by geographical isolation. It would be interesting to know if these moth species have any correlations with the chemical differences among cryptospecies of this liverwort.



Figure 85. *Neomicropteryx nipponensis* larva feeding on *Conocephalum conicum* s.l. Note the darkened necrotic areas where the outer cells have been removed. Photo by Yume Imada, with permission.





Figure 86. *Conocephalum conicum* s.l. that has been nibbled. Photo by Allen Norcross, with permission.

### Biochemistry

*Conocephalum conicum* s.l. (Figure 1-Figure 11) has had more than its share of biochemical analyses. Only a few are included here. Unfortunately, most of these predate the breakup of the species into multiple species and cryptospecies.

Markham *et al.* (1976) found that flavonoids differed between a German sample and one from the USA. This difference might be the forerunner of our understanding that the North American populations are actually *Conocephalum salebrosum* (Figure 12-Figure 13). They also found that the flavonoids they identified did not change qualitatively with seasonal changes. Using 280 samples, Toyota *et al.* (1997) compared three chemotypes of *Conocephalum conicum* s.l. (Figure 1-Figure 11).

Ludwiczuk *et al.* (2013) identified cryptic species in *Conocephalum conicum* s.l. using volatile components. Using 13 samples, they identified four cryptic species of *C. conicum* and the species *C. salebrosum* (Figure 12-Figure 13). The chemical differences correlated with the geographic distribution of the samples.

Ghani *et al.* (2016) used Japanese material of Type-II *Conocephalum conicum* s.l. (Figure 1-Figure 11) to release a phenyl propanoid, trans-methyl cinnamate as a stress response. Although they used it to show that this type had this compound, only previously known from Type III, it is interesting ecologically to know that phenyl compounds can be released in response to stress. Are these similar to the herbivory responses known from many tree leaves?

Asakawa and Takemoto (1979) identified tulipinolide as the compound causing the pungency one can sense in the female gametophyte of *Conocephalum conicum* s.l. (Figure 1-Figure 11); the compound and the smell are absent in the males. The guaianolides were inhibitory toward germination and growth of roots of rice in the husk.

Castaldo-Cobianchi *et al.* (1988) reported antibiotic activity in *Conocephalum conicum* s.l. (Figure 1-Figure 11) against both Gram+ and Gram- bacteria.

Odrzykoski and Szweykowski (1991) described three new sesquiterpenoids from *Conocephalum conicum* s.l. (Figure 1-Figure 11). They found that the compounds varied in their cytotoxicity, but that they could exert immunosuppressive effects on rat splenocytes at lesser concentrations than those that were toxic. Melching and König (1999) identified three new sesquiterpenes from *Conocephalum conicum* s.l. in Germany.

Lu *et al.* (2006) identified four new monoterpene esters and elucidated a number of known compounds in *Conocephalum conicum* s.l. (Figure 1-Figure 11). Two compounds were moderately cytotoxic to human HepG2 cells and one of these also exhibited antibacterial activity against *Pseudomonas aeruginosa* (Figure 87).

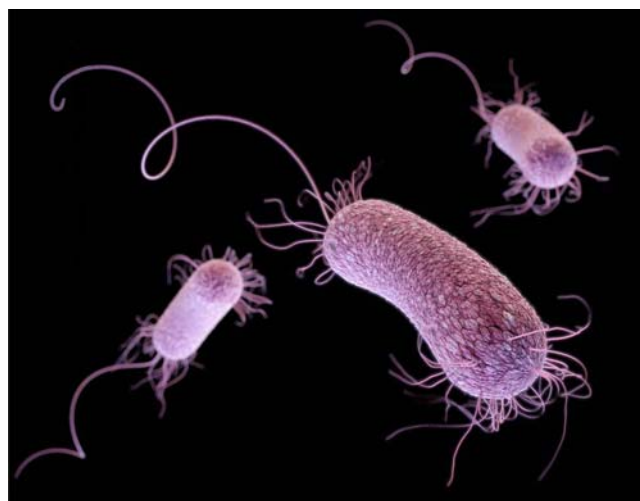


Figure 87. *Pseudomonas aeruginosa*, a bacterium that is inhibited by compounds from *Conocephalum conicum* s.l. Photo from CDC, through public domain.

Himanshu *et al.* (2007) tested several bryophytes, including *Conocephalum conicum* s.l. (Figure 1-Figure 11) for activity against the human pathogens *Escherichia coli* (Figure 88) and *Salmonella typhi* (Figure 89) and two fungi, *Aspergillus niger* (Figure 90), *Candida albicans* (Figure 91). None of the water-soluble extracts was effective on the pathogens. However, the acetone-soluble extract was inhibitory against all the pathogens. *Candida albicans* was strongly inhibited by the extract from *Conocephalum conicum* s.l.



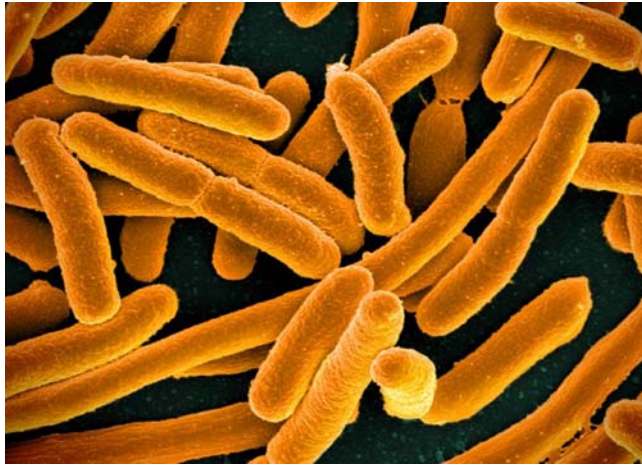


Figure 88. *Escherichia coli*, a human pathogen that is inhibited by extracts of *Conocephalum conicum* s.l. Photo from NIAID, through Creative Commons.

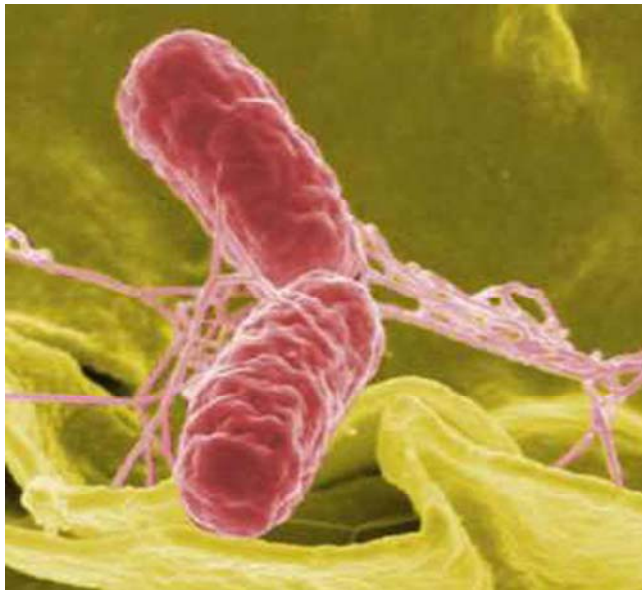


Figure 89. *Salmonella* sp., a human pathogen that is inhibited by extracts of *Conocephalum conicum* s.l. Photo by Elapied, through Creative Commons.

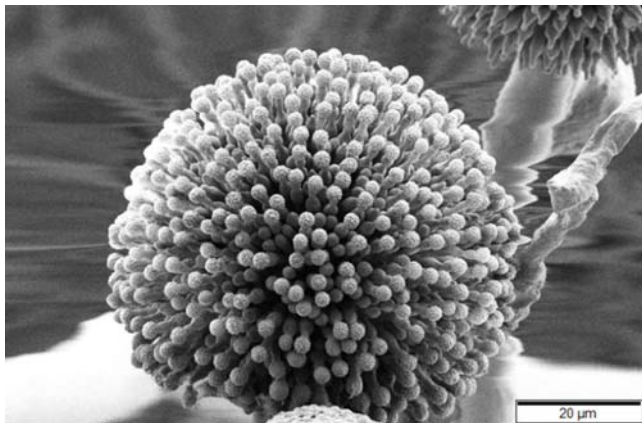


Figure 90. *Aspergillus niger* SEM, a pathogen that is inhibited by extracts of *Conocephalum conicum* s.l. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.



Figure 91. *Candida albicans* pseudohyphae in a fresh and unstained urine sediment. Photo from Controllab, through Creative Commons.

Ivković *et al.* (2021) found that methanol extracts of terpenes, oils, sugars and bis-bibenzylys were absent in *Conocephalum conicum* s.l. (Figure 1-Figure 11), whereas these are present in both *Marchantia polymorpha* (Figure 54) and *Pellia endiviifolia* (Figure 57).

Negi *et al.* (2020) found that *Conocephalum conicum* s.l. (Figure 1-Figure 11) acetone extracts were active against *Aspergillus flavus* (Figure 92) and *A. parasiticus* (Figure 93-Figure 94), with the highest activity coming from populations collected at Mukteshwar (2100 m asl). Negi and Chaturvedi (2021) further evaluated the usefulness of *Conocephalum conicum* s.l. and found that methanol extracts were highly effective against the fungal wilt disease caused by *Fusarium oxysporum* f. *lycopersici* (Figure 95-Figure 96), a disease that makes it unprofitable to grow tomatoes in the tropics. Since *C. conicum* is an "efficient" source of the Riccardin C that is active in inhibiting the fungi on tomatoes, it could be an eco-friendly alternative to the more conventional fungicides.



Figure 92. *Aspergillus flavus*, a fungus that is inhibited by extracts of *Conocephalum conicum* s.l. Photo from Medmyco, through Creative Commons.



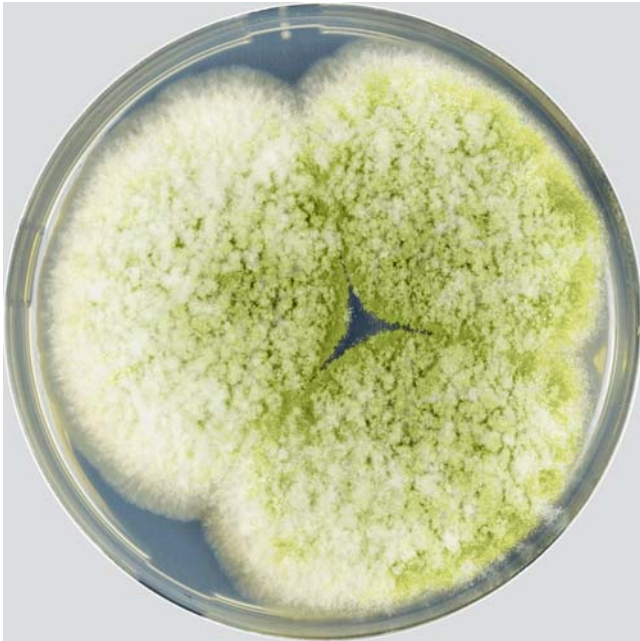


Figure 93. *Aspergillus parasiticus*, a fungus that is inhibited by extracts of *Conocephalum conicum* s.l. Photo by Line Ledsgaard Jensen, Mikael Rørdam Andersen, Ellen Kirstine Lyhne, through public domain.



Figure 95. Tomato plant infected with *Fusarium oxysporum* f. *lycopersici*. Photo by Gerald Holmes, Strawberry Center, Cal Poly San Luis Obispo, with permission.



Figure 94. *Aspergillus parasiticus*. Photo from Medmyco, through Creative Commons.



Figure 96. Culture of *Fusarium oxysporum*, a fungus that is devastating to tomato crops in the tropics; extracts of *Conocephalum conicum* s.l. inhibit its growth. Photo by Keith Weller, through public domain.

#### ***Conocephalum orientalis* (Figure 97-Figure 100)**

In 1994, Akiyama and Hiraoka (1994a, b) noted allozyme variation in the *Conocephalum* in Japan. This



led to later studies on the differences among the Japanese forms. In 2022 Akiyama has published several new species, some of which occur in wet habitats.

One of these new species is *Conocephalum orientalis* (Figure 97-Figure 100), a segregate of *C. conicum* (Figure 1-Figure 11) previously known as J type (Figure 97) (Akiyama 2022). The thallus of *Conocephalum orientalis* is shiny and light green (Figure 98-Figure 99), but becomes yellowish when growing in the shade; the air chambers (visible as polygons at the surface) increase in size toward the center of the thallus (Figure 100) The grooves are deep (Figure 101-Figure 102), like those of *C. salebrosum* (Figure 97). It forms the largest plant bodies of any *Conocephalum* species in Japan.



Figure 99. *Conocephalum orientalis* showing thallus grooves and pores. Photo courtesy of Hiroyuki Akiyama.



Figure 97. *Conocephalum orientalis* (J) and *C. salebrosum* (S). Photo courtesy of Hiroyuki Akiyama.



Figure 100. *Conocephalum orientalis* showing thallus grooves and pores, with polygons larger toward the center. Photo courtesy of Hiroyuki Akiyama.

Thallus variation occurs within as well as between populations of *Conocephalum orientalis* (Figure 97-Figure 100) (Akiyama 2022). These can include differences in thallus size (Figure 101), degree of purplish pigments on ventral surface (Figure 102-Figure 104), wavy margins (type J2; Figure 105), and blackish thallus grooves (type J3; Figure 106-Figure 109).



Figure 98. *Conocephalum orientalis*. Photo courtesy of Hiroyuki Akiyama.



Figure 101. *Conocephalum orientalis* showing variation in single population. Photo courtesy of Hiroyuki Akiyama.





Figure 102. *Conocephalum orientalis* young thallus that is still purplish. Photo courtesy of Hiroyuki Akiyama.



Figure 105. *Conocephalum orientalis* type J2 with wavy margin. Photo courtesy of Hiroyuki Akiyama.



Figure 103. *Conocephalum orientalis* showing purplish midrib on underside. Photo courtesy of Hiroyuki Akiyama.



Figure 106. *Conocephalum orientalis* type J3 showing variation in purplish ventral side. Photo courtesy of Hiroyuki Akiyama.



Figure 104. *Conocephalum orientalis* showing red underside of older tissues. Photo courtesy of Hiroyuki Akiyama.



Figure 107. *Conocephalum orientalis* type J3 with purplish ventral side and dark thallus grooves. Photo courtesy of Hiroyuki Akiyama.





Figure 108. *Conocephalum orientale* type J3 showing blackish thallus grooves. Photo courtesy of Hiroyuki Akiyama.



Figure 109. *Conocephalum orientale* type J3 with purplish ventral side and dark grooves. Photo courtesy of Hiroyuki Akiyama.

Although the separation of the species names is new, some natives of Japan have distinguished them for some time (Akiyama 2022). The plants now known as *Conocephalum orientale* (Figure 97-Figure 100) are heated in oil and eaten like potato chips. The distinctive aroma is lost during heating. They taste similar to the dried seaweed **nori** (Figure 110).



Figure 110. Nori, a red alga used to wrap sushi; fried *Conocephalum orientale* tastes much like this alga. Photo by Kropsoq, through Creative Commons.

### Distribution

*Conocephalum orientale* (Figure 97-Figure 100) is described as a segregate of *C. salebrosum* (Figure 111), another recent segregate from *C. conicum* (Akiyama 2022). *Conocephalum orientale* is known from Japan and Taiwan, where it is the largest of the Japanese species and is the *Conocephalum* species most likely to be encountered on stream banks.



Figure 111. *Conocephalum salebrosum* from Japan. Photo courtesy of Hiroyuki Akiyama.

### Aquatic and Wet Habitats

*Conocephalum orientale* (Figure 97-Figure 100) forms large plants on streamsides (Figure 112) (Akiyama 2022). It occurs in slightly shaded places along streams and seepage slopes along forest trails.





Figure 112. *Conocephalum orientalis* on rock. Photo courtesy of Hiroyuki Akiyama.

*Conocephalum orientalis* (Figure 97-Figure 100) avoids rock surfaces with no soil, except where there is an extreme amount of rainfall (Akiyama 2022). It becomes quite succulent in areas with good moisture conditions. By contrast, populations in direct sunlight, such as concrete retaining walls along sunlit roadways, can become hard and yellowish. The J2 type becomes very thick with wavy margins in dry conditions (Figure 113). The J3 type is more common in mountain areas such as Hokkaido; these thalli can be orange to purplish on the ventral side, even in summer (Figure 114), most likely a response to higher UV light. Thalli in these mountainous areas are also larger than the streamside populations of lower elevations.



Figure 113. *Conocephalum orientalis* type J2 with wavy margin. Photo courtesy of Hiroyuki Akiyama.



Figure 114. *Conocephalum orientalis* type J3 showing variation in orange to purplish ventral side. Photo courtesy of Hiroyuki Akiyama.

### Physiology

Although there has not been time for separate physiological studies to be done on the newly named species *Conocephalum orientalis*, we can infer some of its physiology from its structures and their known functions in other members of the *C. conicum* species complex. In other cases, Akiyama (2022) was able to link earlier studies with the new species through voucher specimens.

The color of *Conocephalum orientalis* (Figure 97-Figure 100) also changes with the seasons. The thallus is pale green in spring through autumn (see Figure 115), although there is a pale reddish purple coloration at the basal part of the midrib. In the shade the thallus can become dark green (Figure 116). However, in late autumn and through winter, the entire under surface becomes reddish purple.



Figure 115. *Conocephalum orientalis* pale color at one location in the sun. Photo courtesy of Hiroyuki Akiyama.





Figure 116. *Conocephalum orientalis* dark color at one location in the shade. Photo courtesy of Hiroyuki Akiyama.

Akiyama (2022) found that plants of *Conocephalum orientalis* (Figure 97-Figure 100) grown in good moisture conditions become succulent and have clear slimy contents of polysaccharides flowing from the cut across mucilage canals (Figure 117). But it often lacks mucilage cells, suggesting that it is best adapted for a wet habitat (Akiyama 2022). It does, however, have abundant rhizoids (Figure 118-Figure 119) that form capillary spaces suitable for movement of water. We can surmise that its rhizoids and scales (Figure 118-Figure 119) move water along the ventral surface, as in other *Conocephalum* species, facilitating the uptake of water. In addition, it often has symbiotic fungi that can help in obtaining nutrients.



Figure 117. *Conocephalum orientalis* from Japan showing leak of mucilage from cross section of mucilage canals. Photo courtesy of Hiroyuki Akiyama.



Figure 118. *Conocephalum orientalis* from Taiwan, ventral side showing rhizoids. Photo courtesy of Hiroyuki Akiyama.



Figure 119. *Conocephalum orientalis* type J3 rhizoids and purplish ventral side. Photo courtesy of Hiroyuki Akiyama.

### Adaptations

Plants of *Conocephalum orientalis* (Figure 97-Figure 100) seem to be quite plastic in nature. When plants grow in darker places, such as the entrance of a cave, thalli become very thin and yellowish (Figure 120), resembling Japanese forms of *C. salebrosum* (Akiyama 2022). Hard, leathery thalli can form in the sun, accompanied by dense ventral scales (Figure 119); their appendages are large and strongly colored reddish purple, a color that is also seen on the upper side of the thalli. These population differences can relate to altitude and shading, but the differences seem not to be linked to any genetic differences.



Figure 120. *Conocephalum orientalis* thin thalli produced under diffuse light. Photo courtesy of Hiroyuki Akiyama.



Akiyama (2022) described the thallus of *Conocephalum orientalis* (Figure 97-Figure 100) as having a light green ventral surface (Figure 118). However, this becomes reddish purple toward late autumn. This is a pattern seen in other bryophytes, including *Sphagnum* (Figure 121) species, presumably in response to the greater light intensity due to loss of canopy leaves, and to the cold nights. The cold nights and warm days are also responsible for the red colors seen on trees in the autumn (Kyne & Diver 2012).



Figure 121. *Sphagnum capillifolium* showing a color transition from green to red. Photo by Bernd Haynold, through Creative Commons.

Akiyama (2022) noticed that smaller plants of *Conocephalum orientalis* (Figure 97-Figure 100) tended to be the most common along the lower elevation streams, whereas at higher elevations they were larger, more "normal" plants.

### Reproduction

*Conocephalum orientalis* (Figure 97-Figure 100) is **dioicous** (Figure 125-Figure 128) and **perennial** (Akiyama 2022). The antheridia appear as clusters in antheridial receptacles on the upper surface of the thallus at the tips of the thallus branches (Figure 122-Figure 124). In the spring, these receptacles appear at tips of newly formed lobes. These antheridial receptacles may appear on stalks created by the midrib because the thallus tissue ceases growth when the receptacle forms (Figure 125). These stalks differ from those of *Marchantia* in which the thallus folds and encloses the rhizoids.



Figure 122. *Conocephalum orientalis* male with antheridial receptacles. Photo courtesy of Hiroyuki Akiyama.



Figure 123. *Conocephalum orientalis* male with immature antheridial receptacle. Photo courtesy of Hiroyuki Akiyama.



Figure 124. *Conocephalum orientalis* male showing antheridial receptacle. Photo courtesy of Hiroyuki Akiyama.



Figure 125. *Conocephalum orientalis* male with stalked thallus, a condition that can sometimes be seen in new growth. Photo courtesy of Hiroyuki Akiyama.



Shimamura *et al.* (2008) described the dispersal of sperm (Figure 126) in *Conocephalum conicum* (Figure 1-Figure 11), providing photographs of their discovery in Japan. Shimamura now considers that the species is probably the newly described *Conocephalum orientalis* (Figure 97-Figure 100). Shimamura and coworkers found that as the sperm were discharged, they became airborne (Figure 126), a phenomenon they were able to verify in the field. They postulated that this explosive behavior, along with the elevated receptacles, would increase the efficiency of fertilization in this (and probably many other) liverwort species, particularly in a drought environment.

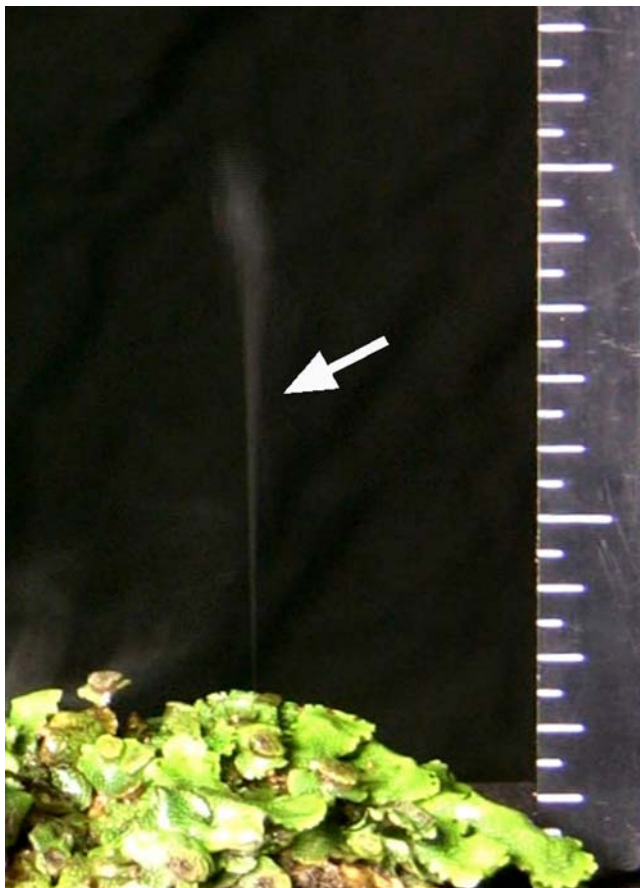


Figure 126. *Conocephalum orientalis* explosive sperm dispersal. Photo courtesy of Masaki Shimamura.

The archegonial heads begin growing near the growing tips (Figure 127). At maturity the archegonial heads are large and are perched on a stalk (Figure 128) up to 9 cm tall (Akiyama 2022).

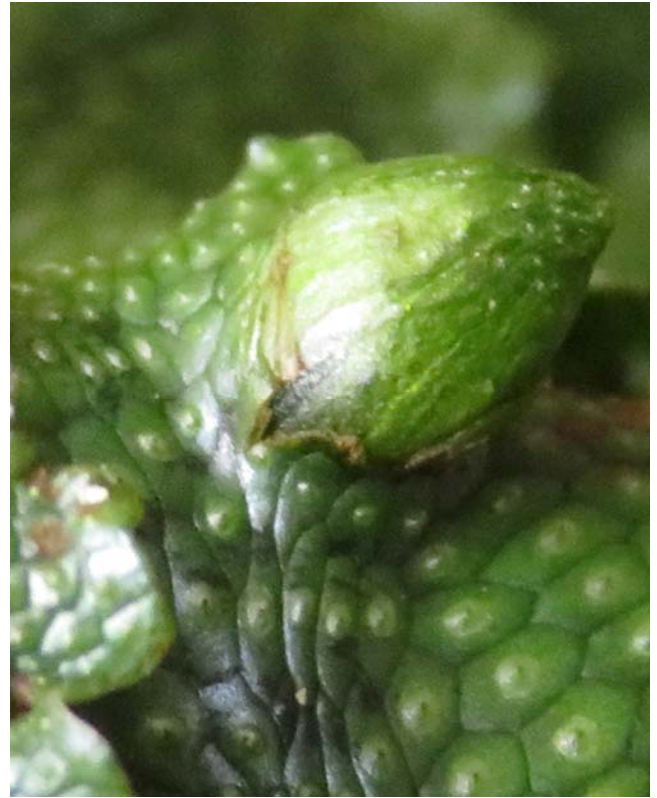


Figure 127. *Conocephalum orientalis* with young archegoniophore. Photo courtesy of Hiroyuki Akiyama.

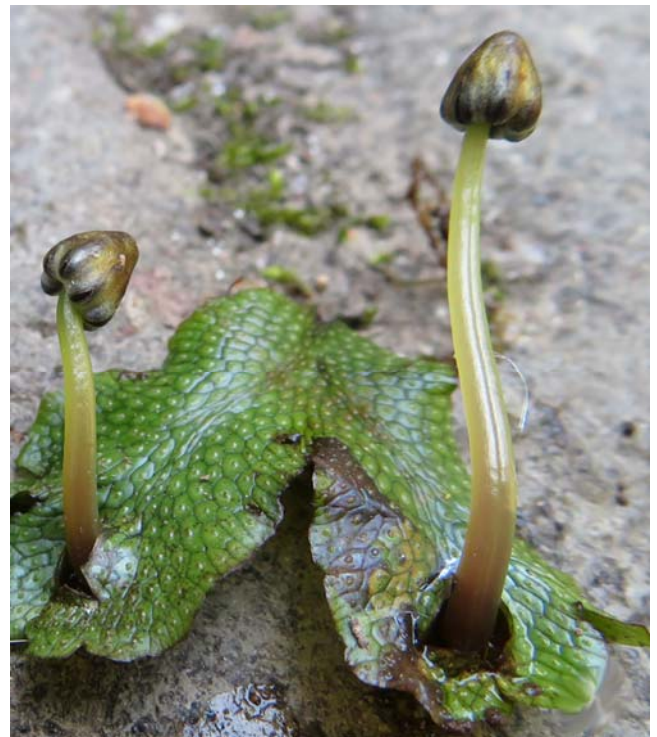


Figure 128. *Conocephalum orientalis* with mature archegoniophore. Photo courtesy of Hiroyuki Akiyama.

*Conocephalum orientalis* (Figure 97-Figure 100) produces spores that may be dispersed while small, or they may remain in the capsule, dividing into **endosporic** sporelings (Akiyama 2022). Spore germinability is 40-100% among the smaller spores. The remaining spores



divide within the spore walls (Figure 129) while still in the sporangium, thus increasing the number of chloroplasts. These larger spores lose their germinability within 30 days under room conditions (Inoue 1966 in Akiyama 2022). Such a two-size strategy permits immediate long distance dispersal of small spores, whereas the larger, short-lived spores have a size advantage that permits them to get a rapid start near the location of their parents. Spore sizes range 65-130  $\mu\text{m}$  in longer diameter (Akiyama 2022).



Figure 129. *Conocephalum conicum* s.l. multicellular spores and elaters. Photo by Hugues Tinguy, with permission.

*Conocephalum orientale* (Figure 97-Figure 100) has no known asexual reproductive structures (Akiyama 2022), but presumably it can reproduce by fragments. It is able to overwinter and produces bud scales (Figure 130-Figure 131) that protect the growing points. The thallus produces winter buds at the tip of the thallus in autumn, developing new shoots in the following spring. It can afford to lose some older cells, with other cells remaining viable, but cells that give rise to new tissue are few in number and vulnerable at the tip of the plant, so the bud scales help to protect them. These scales are absent in tropical populations, where the thallus grows throughout the winter, but a few populations in more northern locations of Japan also lack the buds, and these have been aligned with unique alleles (Isono *et al.* 1999; Akiyama 2022).



Figure 130. *Conocephalum orientale* with young overwintering bud. Photo courtesy of Hiroyuki Akiyama.



Figure 131. *Conocephalum orientale* with overwintering bud. Photo courtesy of Hiroyuki Akiyama.

### Biochemistry

*Conocephalum orientale* (Figure 97-Figure 100) produces large amounts of methyl cinnamate, giving it a pleasant odor (Toyota *et al.* 1997; Toyota 2000; Ab Ghahi *et al.* 2016; Miyatake *et al.*, 2018). It would be interesting to see if this compound has any role in discouraging herbivores.

Other biochemical studies on *Conocephalum orientale* likely exist, but the task remains to link the studies with their current species concept.

### Summary

*Conocephalum conicum* s.l. has recently been divided into multiple species in addition to several cryptospecies. Some studies indicate that *Conocephalum* s.s. does not exist in North America or Asia and is confined to Europe. This reconfiguration of the *Conocephalum conicum* complex has made it difficult to link many published studies with the modern species concepts.

Several of these newly defined species occur in wet habitats. *Conocephalum conicum* tends to be in wetter habitats than those of *C. salebrosum*, a widespread species and possibly the only one in most of North America. Nevertheless, both of these species occur near water (streambanks, springs, splash of waterfalls, canyon walls) and can grow intermixed in Europe. *Conocephalum conicum* prefers shade and can grow in running water or on emergent rocks. It can also occur on slopes where it may get water from seepage.

Members of *Conocephalum* often occur in large mats or mixed with other bryophytes. They have scales and rhizoids on the ventral surface that aid in movement and uptake of water. Air pores have hydrophobic cuticular ridges that prevent water from entering to the internal air chambers through the pores. Rapid cooling kills the cells of *C. conicum* s.l., but apical buds of members of the genus survive winter under the



protection of bud scales. Heat Shock Proteins help to protect the cells from heavy metals, where the latter can accumulate and serve as biomonitors.

*Conocephalum conicum* can experience **indirect facilitation** from other species, in some cases in which another species outcompetes a species that is a strong competitor to the *C. conicum*.

Little is known about the tubers that grow among the rhizoids, but fragmentation occurs as new growth and branching occur and older parts die. Sexual reproduction is common. Gametangia of *C. conicum* s.l. are produced best at 21°C in long days.

*Conocephalum conicum* s.l. is often infected by vesicular-arbuscular fungi and a species of *Glomus*, but benefits and harmful effects need to be evaluated. The species does produce antifungal and antibacterial compounds, some of which could be used commercially.

There are ~25 East Asian micropterigid moths that occur exclusively on species of *Conocephalum*.

*Conocephalum orientalis* is a newly described species from Japan that has deep grooves unlike those of *C. conicum* s.s. It is sometimes eaten in Japan, where it is the most common *Conocephalum*, especially along streams. This species changes color with the seasons, becoming pale reddish purple in late autumn, and becoming dark green in the shade. It becomes succulent in good moisture conditions, but very thin in low light of caves.

*Conocephalum orientalis* expels its sperm explosively, presumably facilitating their dispersal to nearby female plants. Like other species of *Conocephalum*, some spores are small and dispersed early, whereas others are larger due to **endosporic** development.

## Acknowledgments

Bryonettors 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. I appreciate Guido Bursa's notification that one of my images was not the species indicated, and supplying me with a new, correct image.

## Literature Cited

- Ab Ghahi, N., Ludwiczuk, A., Ismail, N. H., and Asakawa, Y. 2016. Volatile components of the stressed liverworts *Conocephalum conicum*. Nat. Prod. Comm. 11: 103-104.
- Akiyama, H. 2022. Morphological and ecological diversification of *Conocephalum conicum* complex in Japan and Taiwan. Humans Nat. 32: 1-45.
- Akiyama, H. and Hiraoka, T. 1994a. Allozyme variability within and divergence among populations of the liverwort *Conocephalum conicum* (Marchantiales: Hepaticae) in Japan. J. Plant Res. 107: 307-320.
- Akiyama, H. and Hiraoka, T. 1994b. Notes on the *Conocephalum conicum* complex in Japan. Bryol. Res. 6: 94-97. (In Japanese).
- Asakawa, Y. 2007. Biologically active compounds from bryophytes. Pure Appl. Chem. 4: 557-580.
- Asakawa, Y. and Takemoto, T. 1979. Sesquiterpene lactones of *Conocephalum conicum*. Phytochemistry 18: 285-288.
- Basile, A., Sorbo, S., Conte, B., Cardi, M., and Esposito, S. 2013. Ultrastructural changes and Heat Shock Proteins 70 induced by atmospheric pollution are similar to the effects observed under *in vitro* heavy metals stress in *Conocephalum conicum* (Marchantiales-Bryophyta). Environ. Pollut. 182: 209-216.
- Benson-Evans, K. 1964. Physiology of the reproduction of bryophytes. Bryologist 67: 431-445.
- Bhagat, M., Sharma, A., and Langer, A. 2012. *Conocephalum conicum* (L.) Dumort: A case of unique reproductive biology. Amer. J. Plant Sci. 3(8): 22194, 4 pp.
- Birch, S. P., Kelly, M. G., and Whitton, B. A. 1988. Macrophytes of the River Wear: 1966- 1976, 1986. Trans. Bot. Soc. Edinb. 45: 203-212.
- Borovichev, E. A., Kalinauskaite, N., and Konstantinova, N. A. 2009. On the distribution of *Conocephalum conicum* and *C. salebrosum* (Marchantiophyta) in Russia. Arctoa 18: 115-120.
- Carré, C. G. and Harrison, R. W. 1961. Studies on vesicular-arbuscular endophytes: III. An endophyte of *Conocephalum conicum* (L.) Dum identified with a strain of *Pythium*. Trans. Brit. Mycol. Soc. 44: 565-572.
- Castaldo-Cobianchi, R., Giordano, S., Basile, A., and Violante, U. 1988. Occurrence of antibiotic activity in *Conocephalum conicum*, *Mnium undulatum* and *Leptodictyum riparium* (Bryophyta). Giorn. Bot. Ital. 122: 303-311.
- Dilks, T. J. K. and Proctor, M. C. F. 1975. Comparative experiments on temperature responses of bryophytes: Assimilation, respiration and freezing damage. J. Bryol. 8: 317-336.
- Dziubińska, H., Trębacz, K., and Zawadzki, T. 1989. The effect of excitation on the rate of respiration in the liverwort *Conocephalum conicum*. Physiol. Plant. 75: 417-423.
- Erdtmann, J. and Mueller Stoll, W. R. 1983. Relations between respiration and regeneration in the liverwort *Conocephalum conicum* (L.) Dum. Biochem. Physiol. Pflanz. 178: 337-345.
- Ferreira, M. T., Aguiar, F. C. F., Rodríguez-González, P., Albuquerque, A., and Sérgio, C. 2008. Manual Para a Avaliação Biológica da Qualidade da Água Em Sistemas Fluviais Segundo a Directiva Quadro da Água. Protocolo de amostragem e análise para os macrófitos. [Manual for Biological Assessment of Water Quality in River Systems under the Water Framework Directive. Sampling and analysis protocol for macrophytes.]. Ministério Do Ambiente, Do Ordenamento Do Território e Do Desenvolvimento Regional, 18 pp.
- Ghani, N. A., Ludwiczuk, A., Ismail, N. H., and Asakawa, Y. 2016. Volatile components of the stressed liverwort *Conocephalum conicum*. Nat. Prod. Comm. 11(1), 1934578X1601100130.
- Gimingham, C. H. and Birse, E. M. 1957. Ecological studies on growth-form in bryophytes: I. Correlations between growth-form and habitat. J. Ecol. 45: 533-545.
- Himanshu, V., Dubey, R. C., and Pandey, N. 2007. Antimicrobial activity of three bryophytes against human pathogens. Curr. Trends Bryol. 2007: 47-59.
- Holmes, N. T. H. and Whitton, B. A. 1975. Macrophytes of the River Tweed. Trans. Bot. Soc. Edinburgh 42: 369-381.



- Holmes, N. T. H. and Whitton, B. A. 1977a. Macrophytic vegetation of River Tees in 1975 - Observed and predicted changes. *Freshwat. Biol.* 7: 43-60.
- Holmes, N. T. H. and Whitton, B. A. 1977b. Macrophytic vegetation of River Swale, Yorkshire. *Freshwat. Biol.* 7: 545-558.
- Holmes, N. T. H. and Whitton, B. A. 1981. Plants of the River Tyne system before the Kielder water scheme. *Naturalist* 106: 97-107.
- Ihle, C. 1997. Degradation and release from the thylakoid membrane of Photosystem II subunits after UV-B irradiation of the liverwort *Conocephalum conicum*. *Photosyn. Res.* 54: 73-78.
- Ihle, C. and Laasch, H. 1995. Inhibition of photosystem II by ultraviolet-B radiation and the mechanism of recovery in the liverwort *Conocephalum conicum* Dum. *Photosyn. Light Biosphere* 4: 231-234.
- Imada, Y., Kawakita, A., and Kato, M. 2011. Allopatric distribution and diversification without niche shift in a bryophyte-feeding basal moth lineage (Lepidoptera: Micropterigidae). *Proc. Royal Soc. B Biol. Sci.* 278: 3026-3033.
- Iqbal, M., Butt, F. A., Langer, A., and Alam, A. 2011a. Studies on the associates of *Conocephalum conicum* L. (Dumort.) and *Dumortiera hirsuta* Sw. (Nees). *Amer. J. Plant Sci.* 2: 283-286.
- Iqbal, M., Langer, A., and Alam, A. 2011b. *Conocephalum conicum* (L.) Dumort. (snake liverwort) threatened in Bhaderwah (J & K) due to environmental shock. *Amer. J. Plant Sci.* 2: 554.
- Isono, H., Akiyama, H., and Yamaguchi, T. 1999. Allozyme variability and divergence within and among populations of *Conocephalum conicum* (Conocephalaceae, Hepaticae) from Kyushu and the Ryukyu Islands. *Hikobia* 13: 97-112. (In Japanese).
- Ivković, I. M., Bukvički, D. R., Novaković, M. M., Ivanović, S. G., Stanojević, O. J., Nikolić, I. C., and Veljić, M. M. 2021. Antibacterial properties of thalloid liverworts *Marchantia polymorpha* L., *Conocephalum conicum* (L.) Dum. and *Pellia endiviifolia* (Dicks.) Dumort. *J. Serb. Chem. Soc.* 12: 1249-1258.
- Krol, E., Dziubinska, H., and Trębacz, K. 2003. Low-temperature induced transmembrane potential changes in the liverwort *Conocephalum conicum*. *Plant Cell Physiol.* 44: 527-533.
- Kyne, A. and Diver, K. 2012. Climate change and autumn colors in New England's Forests. *Northeast. Geogr.* 4: 34-53.
- Levine, J. M. 1999. Indirect facilitation: evidence and predictions from a riparian community. *Ecology* 80: 1762-1769.
- Ligrone, R. and Lopes, C. 1989. Cytology and development of a mycorrhiza - like infection in the gametophyte of *Conocephalum conicum* (L.) Dum. (Marchantiales, Hepatophyta). *New Phytol.* 111: 423-433.
- Ligrone, R., Carafa, A., Lumini, E., Bianciotto, V., Bonfante, P., and Duckett, J. G. 2007. Glomeromycotan associations in liverworts: A molecular, cellular, and taxonomic analysis. *Amer. J. Bot.* 94: 1756-1777.
- Lu, Z. Q., Fan, P. H., Ji, M., and Lou, H. X. 2006. Terpenoids and bisbibenzyls from Chinese liverworts *Conocephalum conicum* and *Dumortiera hirsuta*. *J. Asian Nat. Prod. Res.* 8: 187-192.
- Ludwiczuk, A., Odrzykoski, I. J., and Asakawa, Y. 2013. Identification of cryptic species within liverwort *Conocephalum conicum* based on the volatile components. *Phytochemistry* 95: 234-241.
- Luís, L., Sim-Sim, M., Fontinha, S., and Holyoak, D. T. 2008. New data on riparian bryophytes of Madeira. *Cryptogamie* 29: 393-396.
- Luís, L., Bergamini, A., and Sim-Sim, M. 2015. Which environmental factors best explain variation of species richness and composition of stream bryophytes? A case study from mountainous streams in Madeira Island. *Aquat. Bot.* 123: 37-46.
- Mamczarz, H. 1970. The bryophyte communities in streams near Lacko in the Sadecki Beskid. *Ann. Univ. Mariae Curie-Skłodowska, Sec. C Biol.* 3. Biol. 25: 105-136.
- Maresca, V., Lettieri, G., Sorbo, S., Piscopo, M., and Basile, A. 2020. Biological responses to cadmium stress in liverwort *Conocephalum conicum* (Marchantiales). *Internat. J. Molec. Sci.* 21: 6485.
- Markham, K. R., Porter, L. J., Mues, R., Zinsmeister, H. D., and Brehm, B. G. 1976. Flavonoid variation in the liverwort *Conocephalum conicum*: Evidence for geographic races. *Phytochemistry* 15: 147-150.
- Marstaller, R. 1987. Die Moosgesellschaften der Klasse *Platyhypnidio-Fontinalietea antipyreticae* Philippi 1956. 30. Beitrag zur Moosvegetation Thüringens. [The moss communities of the class *Platyhypnidio-Fontinalietea antipyreticae* Philippi 1956. 30. Contribution to the Thuringian moss vegetation]. *Phytocoenologia* 15: 85-138.
- Melching, S. and König, W. A. 1999. Sesquiterpenes from the essential oil of the liverwort *Conocephalum conicum*. *Phytochemistry* 51: 517-523.
- Miyatake, H., Akiyama, H., Asakawa, Y., and Okamoto, Y. 2018. Geographical distribution of volatile components in the liverwort, *Conocephalum conicum*. *Proc. 62nd TEAC, Nagasaki University* 62: 25-27.
- Negi, K. and Chaturvedi, P. 2021. Antifungal activity of *Conocephalum conicum* (L) Dumort. (Marchantiophyta) against *Fusarium oxysporum* f. sp. *lycopersici*. *bioRxiv*. <<https://doi.org/10.1101/2021.07.27.454003>>.
- Negi, K., Asthana, A. K., and Chaturvedi, P. 2020. GC-MS analysis and antifungal activity of acetone extract of *Conocephalum conicum* (L) Underw (liverwort) against aflatoxins producing fungi. *S. Afr. J. Bot.* 131: 384-390.
- Odrzykoski, I. J. and Szwejkowski, J. 1991. Genetic differentiation without concordant morphological divergence in the thallose liverwort *Conocephalum conicum*. *Plant Syst. Evol.* 178(3): 135-152.
- Papp, B. 1998. Investigation of the bryoflora of some streams in Greece. *Stud. Bot. Hung.* 29: 59-67.
- Papp, B. and Erzberger, P. 2011. Additions to the bryophyte flora of the Tara River Canyon and Durmitor area, Montenegro. *Stud. Bot. Hung.* 42: 31-39.
- Papp, B., Ganeva, A., and Natcheva, R. 2006. Bryophyte vegetation of Iskur River and its main tributaries. *Phytol. Balcan.* 12: 181-189.
- Paton, J. A. 1993. Tubers on *Conocephalum conicum* (L.) Lindb. thalli. *J. Bryol.* 17: 503-505.
- Samecka-Cymerman, A., Marczonek, A., and Kempers, A. J. 1997. Bioindication of heavy metals in soil by liverworts. *Arch. Environ. Contam. Toxicol.* 33: 162-171.
- Scarlett, P. and O'Hare, M. 2006. Community structure of in-stream bryophytes in English and Welsh rivers. *Hydrobiologia* 553: 143-152.
- Schönherr, J. and Ziegler, H. 1975. Hydrophobic cuticular ledges prevent water entering the air pores of liverwort thalli. *Planta* 124: 51-60.



- Sérgio, C., Vieira, C., Claro, D., and Garcia, C. 2011. *Conocephalum salebrosum* Szweykowski, Buczkowska & Odrzykoski (Marchantiopsida): Modelling the occurrence of a hygrophytic species new to the bryoflora of Portugal, Madeira and Azores. *J. Bryol.* 33: 30-34.
- Shevock, J. R., Toren, D. R., and Wagner, D. H. 2021. Bryoflora of the Russian Wilderness and adjacent slopes of the Salmon Mountains, Klamath National Forest, Siskiyou County, California. *Madroño* 68: 209-256.
- Shimamura, M., Yamaguchi, T., and Deguchi, H. 2008. Airborne sperm of *Conocephalum conicum* (Conocephalaceae). *J. Plant Res.* 121: 69-71.
- Stotler, R. E. and Crandall-Stotler, B. 2017. A Synopsis of the liverwort flora of North America North of Mexico. *Ann. Missouri Bot. Gard.* 102: 574-709.
- Szweykowski, J. 1951. On the distribution of moss-communities in the streams of the Gory Stolowe Mountains (Sudeten). *Poznan Soc. Friends Sci., Dept. Math. Nat. Sci., Publ. Biol. Sec.* 13(3): 41-46.
- Szweykowski, J., Buczkowska, K., and Odrzykoski, I. J. 2005. *Conocephalum salebrosum* (Marchantiopsida, Conocephalaceae) – a new Holarctic liverwort species. *Plant Syst. Evol.* 253: 133-158.
- Toyota, M. 2000. Phytochemical study of liverworts *Conocephalum conicum* and *Chiloscyphus polyanthos*. *J. Pharm. Soc. Japan* 120: 1359-1372.
- Toyota, M., Saito, T., Matsunami, J., and Asakawa, Y. 1997. A comparative study on three chemo-types of the liverwort *Conocephalum conicum* using volatile constituents. *Phytochemistry* 44: 1265-1270.
- Trębacz, K. 1992. Measurements of intra- and extracellular pH in the liverwort *Conocephalum conicum* during action potentials. *Physiol. Plant.* 84: 448-452.
- Trębacz, K. and Fensom, D. 1989. The uptake and transport of  $^{14}\text{C}$  in cells of *Conocephalum conicum* L. in light. *J. Exper. Bot.* 40: 1089-1092.
- Trębacz, K., Simonis, W., and Schonknecht, G. 1994. Cytoplasmic  $\text{Ca}^{2+}$ ,  $\text{K}^+$ ,  $\text{Cl}^-$ , and  $\text{NO}_3^-$  activities in the liverwort *Conocephalum conicum* L. at rest and during action potentials. *Plant Physiol.* 106: 1073-1084.
- Vieira, C., Sérgio, C., and Séneca, A. 2005. Threatened bryophytes occurrence in Portuguese stream habitat. *Bol. Soc. Española Briol.* 26: 103-118.
- Watson, W. 1919. The bryophytes and lichens of fresh water. *J. Ecol.* 7: 71-83.
- West, G. 1910. An epitome of a comparative study of the dominant phanerogamic and higher cryptogamic flora of aquatic habit, in seven lake areas of Scotland. In: Murray, J. 1910, Bathymetrical Survey of the Scottish Fresh-water Locks, Conducted Under The Direction of Sir John Murray... and Laurence Pullar... During The Years 1897 to 1909. Report on the Scientific Results. Edinburgh, Challenger Office, pp. 156-260.
- Yamazaki, T. 1981. Genic variabilities in natural population of haploid plant, *Conocephalum conicum* I. The amount of heterozygosity. *Jap. J. Genetics* 56: 373-383.



