

CHAPTER 1-22

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CYATHODIACEAE, DUMORTIERACEAE

TABLE OF CONTENTS

Marchantiidae – Marchantiales	1-22-2
Cyathodiaceae	1-22-2
<i>Cyathodium bischlerianum</i>	1-22-4
Distribution	1-22-4
Aquatic and Wet Habitats.....	1-22-4
Reproduction	1-22-5
Biochemistry	1-22-5
<i>Cyathodium cavernarum</i>	1-22-5
Distribution	1-22-5
Aquatic and Wet Habitats.....	1-22-6
Adaptations	1-22-7
Reproduction	1-22-8
Interactions.....	1-22-9
Biochemistry	1-22-9
<i>Cyathodium foetidissimum</i>	1-22-9
Distribution	1-22-9
Aquatic and Wet Habitats.....	1-22-9
Adaptations	1-22-11
Reproduction	1-22-11
Interactions.....	1-22-12
Biochemistry	1-22-12
<i>Cyathodium spruceanum</i>	1-22-13
Distribution	1-22-13
Aquatic and Wet Habitats.....	1-22-13
Adaptations	1-22-13
Reproduction	1-22-13
Fungal Interactions.....	1-22-14
Biochemistry	1-22-14
Dumortieraceae	1-22-14
<i>Dumortiera hirsuta</i>	1-22-14
Distribution	1-22-15
Aquatic and Wet Habitats.....	1-22-27
Physiology.....	1-22-17
Adaptations	1-22-19
Reproduction	1-22-20
Role.....	1-22-23
Interactions.....	1-22-23
Fungal Interactions.....	1-22-23
Animal Interactions.....	1-22-23
Biochemistry	1-22-25
<i>Dumortiera hirsuta</i> ssp. <i>nepalensis</i>	1-22-27
Distribution	1-22-27
Aquatic and Wet Habitats.....	1-22-27
Biochemistry	1-22-27
Summary	1-22-27
Acknowledgments	1-22-28
Literature Cited	1-22-28

CHAPTER 1-22

AQUATIC AND WETLAND

MARCHANTIOPHYTA, CLASS

MARCHANTIOPSIDA – CYATHODIACEAE, DUMORTIERACEAE



Figure 1. *Dumortiera hirsuta* habitat in Europe. Photo by Michael Lüth, with permission

Marchantiidae – Marchantiales

Cyathodiaceae

There have been several taxonomic considerations of the genus *Cyathodium* (Schiffner 1938; Srivastava & Dixit 1996; Salazar Allen & Korpelainen 2006).

This family often occurs in moist habitats such as caves and stream banks. *Cyathodium* habitats are typically shaded and include river banks on soil or rocks, in waterfalls, caves, cement floors, stairs, and flowerpots, with some occurring as epiphytes (Salazar Allen & Korpelainen 2006). Large communities can occur on

unstable river banks where they can become submerged and sometimes become detached by flooding or drying. They are often associated with filamentous *Cyanobacteria* (Figure 32), but these are not endophytic. Endophytic fungi are known from wild populations of *C. spruceanum* (Figure 2) and *C. cavernarum* (Figure 3) in Panama (Salazar Allen unpublished data). Riverbank plants often provide substrate for diatoms, including *Surirella* (Figure 4), *Nitzschia* (Figure 5), *Amphora* (Figure 6), *Rhopalodia* (Figure 7), *Eunotia* (Figure 8), and possibly *Diploneis* (Figure 9) (Allen & Korpelainen 2006). The most aquatic of *Cyathodium* species is *Cyathodium bischlerianum* (Figure 10).



Figure 2. *Cyathodium spruceanum* males. Photo by José Gudiño L., courtesy of Noris Salazar Allen.



Figure 3. *Cyathodium cavernarum*, a species that grows on river and streambanks with *Cyathodium bischlerianum*. Photo by Renjusplace, through Creative Commons.

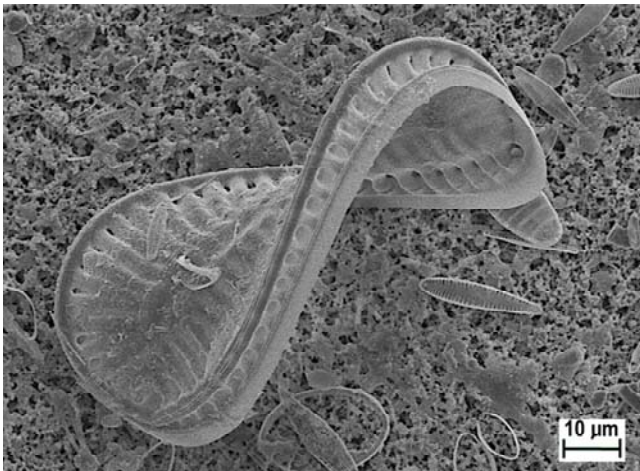


Figure 4. *Surirella spiralis*, in a genus of diatoms that often grows on species of *Cyathodium*. Photo by Nicola Angeli, through Creative Commons.

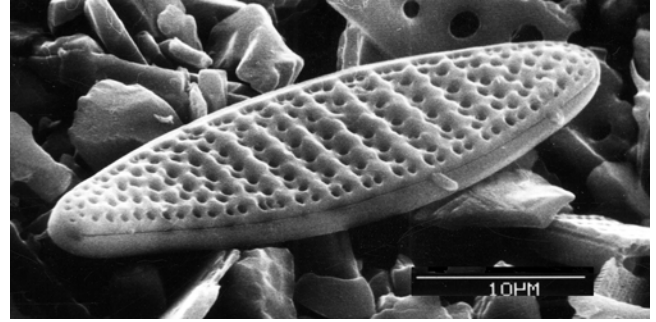


Figure 5. *Nitzschia kerguelensis*, in a genus of diatoms that often grows on species of *Cyathodium*. Photo by Hans Grobe, through Creative Commons.

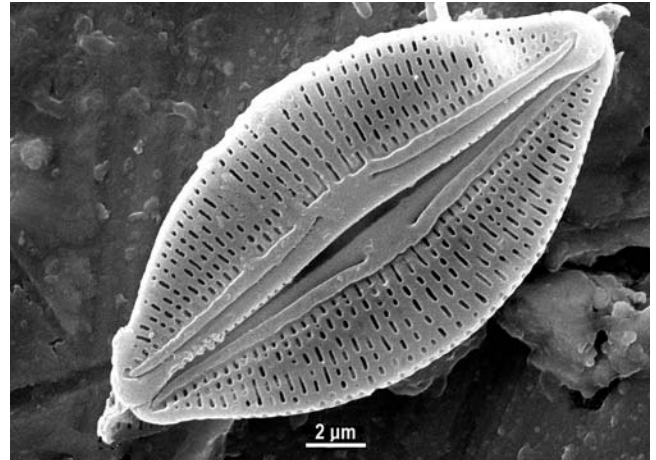


Figure 6. *Amphora* sp, in a genus of diatoms that often grows on species of *Cyathodium*. Photo by Berezovska, through Creative Commons.

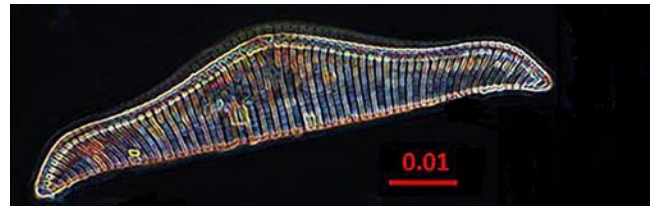


Figure 7. *Rhopalodia gibba*, in a genus of diatoms that often grows on species of *Cyathodium*. Photo by Leena Virta and Alf Norkko, through Creative Commons.



Figure 8. *Eunotia*, in a genus of diatoms that often grows on species of *Cyathodium*. Photo by National Museum of Natural History, through Creative Commons.

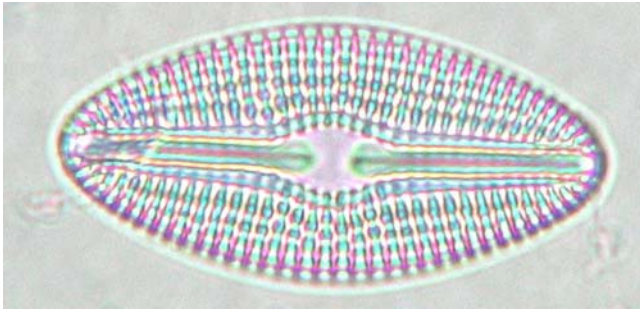


Figure 9. *Diploneis ovalis*, in a genus of diatoms that often grows on species of *Cyathodium*. Photo by Kristian Peters, through Creative Commons.

Members of *Cyathodium* prefer moist, shady habitats (Daniels 1998). Large communities of *Cyathodium* occur on unstable river banks in Costa Rica and Panama, and here they often experience submergence or become detached by floods. In other locations they are subject to drying on soil along cement road ditches in humid areas (Salazar Allen & Korpelainen 2006). The genus endures weak light intensities where it is able to grow on rock, soil, or in two species on bark. *Cyathodium* sp. (Figure 10) occurs over (overhanging?) water and in waterfalls in the tropics (Ruttner 1955). Although there are several semi-aquatic species in *Cyathodium*, Cavers (1910), citing Lang (1905) regarded it as a genus primarily adapted to shade, rather than as a hygrophyte.

Daniels (1998) noted that *Cyathodium* species lack the complex structure of many thallose liverworts, such as well-defined assimilatory and storage zones or scales.

Tiwari (1929a,b, 1935) studied the spore germination of *Cyathodium* spores. Crum (1976) noted that some of the species have spores that emit a yellowish luminescence. There are few spores in *Cyathodium* species, numbering 20-100 per capsule (Bischler-Causse *et al.* 2005).

Cyathodium bischlerianum (Figure 10)

Distribution

Cyathodium bischlerianum (Figure 10) is a Neotropical species known only from Panama (Salazar Allen 2001). Because of its small size and association with other *Cyathodium* species, it can easily be overlooked, and Salazar Allen suspects that it is more widely distributed in the Neotropics. For these reasons, information on it is also rather scant.



Figure 10. *Cyathodium bischlerianum* habit on tree near water. Photo by José Gudiño L., courtesy of Noris Salazar Allen.

Members of *Cyathodium* have a simple, slender, dichotomously branched thallus with no purple coloring (Figure 2-Figure 3). The pores are simple with a single ring of cells and no hyaline inner ring (Salazar Allen 2001; Bischler-Causse *et al.* 2005). The air chambers are empty. Most rhizoids are smooth, but some may be tuberculate. It has 2 rows of ventral scales, often restricted to the apex. Its asexual reproduction includes fragmentation of thallus segments and ventral tubers in some.

Aquatic and Wet Habitats

Cyathodium bischlerianum (Figure 10) is one of two species that can be corticolous (Salazar Allen & Korpelainen 2006). It typically grows mixed with other species of *Cyathodium* in very moist, shaded locations, particularly on rocks near or even in creeks, along eroding river banks, and in other locations subject to partial submergence during high water levels (Bischler-Causse *et al.* 2005). It is more mesic than *C. spruceanum* (Figure 2).

Cyathodium bischlerianum (Figure 10) occurs on stream and river banks, along with *C. cavernarum* (Figure 3), in the shaded, more moist habitats close to the rivers and seepage, whereas *C. spruceanum* (Figure 2) occurs on more upper slopes (Salazar Allen & Korpelainen 2006). *Cyathodium bischlerianum* also can occur on bark (Figure 11-Figure 12) near streams and rivers and in seepages and on moist rocks.



Figure 11. *Cyathodium bischlerianum* habit on bark. Photo by José Gudiño L., courtesy of Noris Salazar Allen.



Figure 12. *Cyathodium bischlerianum* on bark. Photo by José Gudiño L., courtesy of Noris Salazar Allen.

Reproduction

Cyathodium bischlerianum (Figure 10) is **monoicous** (Salazar Allen 2001; Bischler-Causse *et al.* 2005). The involucre can have 1 or 2 archegonia and sporophytes (Figure 13); male receptacles occur on the sides of the thallus. The species lacks any specialized asexual reproductive structures, with no tumors as found in dioicous members of the genus (Salazar Allen & Korpelainen 2006).



Figure 13. *Cyathodium bischleriana* thallus with sporangia. Photo by Noris Salazar Allen, with permission.

Cyathodium bischlerianum (Figure 10) is an **r-selected** species (Salazar Allen & Korpelainen 2006). This means that it has a high reproductive rate, its population size varies through time, and recolonization occurs every year, creating competition with itself and other species (Pianka 1970).

Biochemistry

Despite the newness of the species and its limited distribution, the biochemistry of *Cyathodium bischlerianum* (Figure 10) has been evaluated. It is unique among the *Cyathodium* species, containing mostly aromatic monoterpenes (Salazar Allen *et al.* 2017). It has less than 3% of the sesquiterpenes germacrene D and bicyclogermacrene.

Nerolidol is the main compound among these (Salazar Allen *et al.* 2017). This compound has a floral and woody fragrance (Padalia *et al.* 2015). Already known from other plants, it has been approved for use in fine fragrances, cosmetics, shampoo, soaps, detergents, and cleaning products (Padalia *et al.* 2015; Boskabady *et al.* 2014). The industry level consumption is 10-100 tons per year (Queiroga *et al.* 2014).

Cyathodium cavernarum (Figure 14-Figure 15)

syn. = *Cyathodium africanum*, *C. barodae*, *C. mexicanum*

Distribution

Cyathodium cavernarum (Figure 14-Figure 15) is a widespread pantropical species (Lye & Pócs 1997) and is the most widespread species in the genus (Bischler-Causse *et al.* 2005). It is known from China (Zhang *et al.* 2004a), Japan (Furuki *et al.* 2012), India, Java, Africa, Madagascar (Srivastava & Dixit 1996; Reeb *et al.* 2018), western Australia (Meagher 2002), and the American tropics in Colombia (Winkler 1976), Mexico, Costa Rica, Panama, Cuba, and Brazil (Srivastava & Dixit 1996; Salazar Allen 2005; Salazar Allen & Korpelainen 2006; Gradstein *et al.* 2016; Reeb *et al.* 2018). Shah and Gujar (2016) reported that *Cyathodium cavernarum* was the most widely distributed liverwort species in Gujarat, India.



Figure 14. *Cyathodium cavernarum* on roof of cave. Photo by Célio Moura Neto, through Creative Commons.



Figure 15. *Cyathodium cavernarum* showing young and old thalli. Photo by Eric Hough, through Creative Commons.

Aquatic and Wet Habitats

Lye and Pócs (1997) reported *Cyathodium cavernarum* (Figure 14-Figure 15) growing on overhanging, dripping, or sprayed rocks as well as temporarily inundated muddy forest floor low areas of Uganda. On river banks, it occupies lower positions than does *C. spruceanum* (Figure 2), preferring more shaded, damper sites or those with seepage (Bischler-Causse *et al.* 2005; Salazar Allen & Korpelainen 2006). In the Northern Western Ghats it is usually found in low altitudes where there is human habitation or shaded disturbed areas (Nair & Prajitha 2016). Glenny (2002) similarly reported it from stream and river banks in Australia.

Cyathodium cavernarum (Figure 14-Figure 15) usually occurs on calcareous substrata but it can also occupy slightly acidic substrates with underlying calcareous bedrock (Bischler-Causse *et al.* 2005). Its substrata include soil, wet rocks, walls, and termite mounds in moist deciduous, semi-evergreen, or evergreen forests (Nair & Prajitha 2016). In exposed habitats it is typically associated with members of the **Pottiaceae** (Figure 16); in ravines and river banks with species of *Philonotis* (Figure 17), *Fissidens* (Figure 18), *Notothylas* (Figure 19), *Racopilum tomentosum* (Figure 20), *Cyathodium spruceanum* (Figure 2), and **Lejeuneaceae** (Figure 21) (Bischler-Causse *et al.* 2005).



Figure 16. *Syntrichia ruralis*, a member of the **Pottiaceae**, a family that often occurs with *Cyathodium cavernarum*. Photo by Alexis Orion, through Creative Commons.



Figure 17. *Philonotis*, member of a genus that is often associated with *Cyathodium cavernarum*. Photo by A. Neuman, through Creative Commons.



Figure 18. *Fissidens fontanus*, member of a genus that is often associated with *Cyathodium cavernarum*. Photo by Bob Klips, with permission.



Figure 19. *Notothylas orbicularis*, member of a genus that is often associated with *Cyathodium cavernarum*. Photo by Christian , through Creative Commons.



Figure 20. *Racopilum tomentosum*, a species that is often associated with *Cyathodium cavernarum*. Photo by David Tng, with permission.



Figure 21. *Lejeunea flava*, member of a family that is often associated with *Cyathodium cavernarum*. Photo by Scott Zona, through Creative Commons.

Although caves are not aquatic habitats, they are often wet and at least damp, providing suitable habitat for *Cyathodium cavernarum* (Figure 22-Figure 25) including the Birds'-Nest Cave near Niah, Sarawak, Borneo (Holtum 1938). Reeb *et al.* (2018) likewise found this species at cave entrances in Madagascar, occupying naked, compact soils that were shady. And Furuki *et al.* (2012) found it on soil of a limestone cave in Japan and Zhang *et al.* (2004a,b) in karst caves of China.



Figure 22. *Cyathodium cavernarum* iridescence on wall of ruins in Bombay. Photo ©Patrick Blanc, with permission.



Figure 23. *Cyathodium cavernarum* on rock in cave. Photo by Cédric de Foucault, through Creative Commons.



Figure 24. *Cyathodium cavernarum* in cave. Photo by Cédric de Foucault, through Creative Commons.



Figure 25. *Cyathodium cavernarum* on cave ceiling. Photo by Célio Moura Neto, through Creative Commons.

Adaptations

Cyathodium cavernarum (Figure 14-Figure 15) exhibits a bright metallic-green color (Figure 26-Figure 27) (Bischler-Causse *et al.* 2005). Reeb *et al.* (2018) described it as iridescent, with colors that change when viewed from various angles. Zhang *et al.* (2004b) described it as luminous with a "peculiar light-reflecting power which produces a kind of starry effect, so that the plants seem to flood the dark caves where they grow with a luminous, golden-green light."



Figure 26. *Cyathodium cavernarum* iridescence in Bombay. Photo ©Patrick Blanc, with permission.



Figure 27. *Cyathodium cavernarum* showing iridescent colors. Photo by Jan-Peter Frahm, with permission.

But what does this peculiar light reflection mean for the liverwort? Does it increase the ability to capture light for photosynthesis? Does it attract some sort of invertebrate that henceforth carries sperm or fragments, thus aiding in dispersal? This is a mystery that needs to be investigated.

Water can collect on the thallus and remain there for some time (Figure 28), helping the plant to remain hydrated. This may be the mechanism that permits it to live in caves where it doesn't rain.



Figure 28. *Cyathodium cavernarum* with accumulated water droplets. Photo from Idleggraphics, through Creative Commons.

Cyathodium cavernarum has pores in the thallus that increase the loss of water (Figure 29). As with many liverworts, *C. cavernarum* (Figure 14-Figure 15) often benefits from the added water retention of living among mosses (Figure 30).

Reproduction

Cyathodium cavernarum (Figure 14-Figure 15) is **monoicous** (Srivastava & Dixit 1996; Bischler-Causse *et al.* 2005). Salazar Allen and Korpelainen (2006) demonstrated that *C. cavernarum* and *C. spruceanum* (Figure 2) have more similar genetics from nearby geographic areas than those from more distant areas, suggesting a role of sexual reproduction. Sporelings in culture develop initial filamentous growth followed by apical development into the thallus.

In addition to sexual reproduction, it can reproduce by fragments and spread by branching (Figure 31) (Bischler-Causse *et al.* 2005). Tubers are unknown in this and other monoicous species (Salazar Allen & Korpelainen 2006).

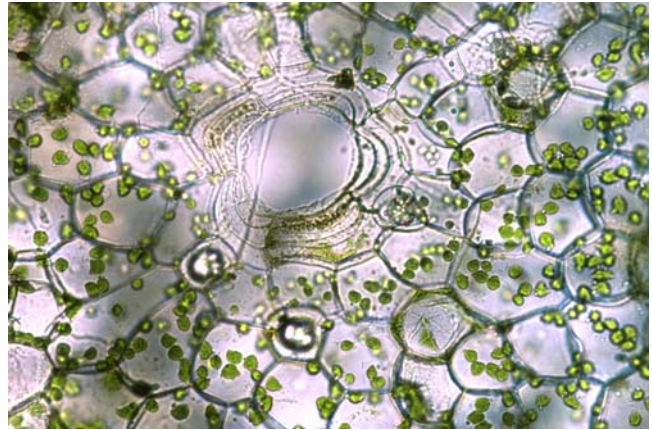


Figure 29. *Cyathodium cavernarum* pore showing layers of cells surrounding it. Photo courtesy of Noris Salazar Allen.



Figure 30. *Cyathodium cavernarum* growing among mosses. Photo by Célio Moura Neto, through Creative Commons.



Figure 31. *Cyathodium cavernarum* showing young thalli mixed with old ones. Some show branching. Others may be derived from fragments or spores. Photo by Eric Hough, through Creative Commons.

Interactions

Cyanobacteria (Figure 32) are common associates of *Cyathodium cavernarum* (Figure 14-Figure 15) (Bischler-Causse *et al.* 2005). Fungal endophytes are known from *Cyathodium cavernarum* in Panama (Salazar Allen & Korpelainen 2006).

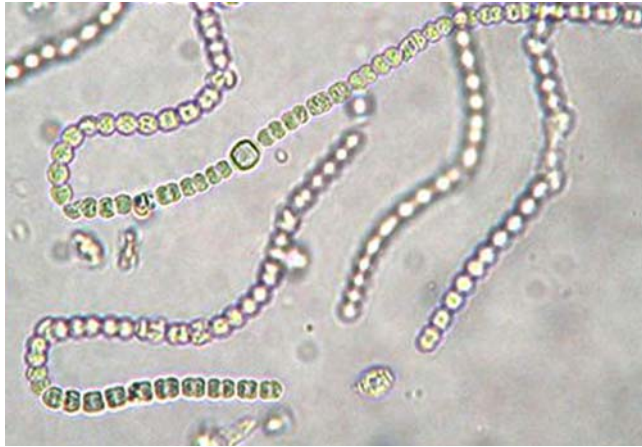


Figure 32. *Nostoc commune*, one of the **Cyanobacteria** often associated with bryophytes. Photo by Kristian Peters, through Creative Commons.

Biochemistry

Salazar Allen *et al.* (2017) found that *Cyathodium cavernarum* (Figure 14-Figure 15) has a distinct chemical composition with an octane derivative as its major compound, suggesting that this could be used as a chemical marker for the species. Nevertheless, Ulka and Karadge (2010) found little antimicrobial activity by extracts of *Cyathodium cavernarum*. Furthermore, Surendra Kumar *et al.* (2014-15) found that extracts of *C. cavernarum* were ineffective, compared to a standard drug, in causing paralysis or death in the Indian earthworm *Pheretima posthuma* (see Figure 33). It is interesting that this widespread species seems to lack the usual liverwort ability to inhibit potentially deadly organisms. Could it be that these other organisms seldom occur where it lives? Or does it have associated bacteria or fungi that accomplish this purpose?



Figure 33. *Pheretima praepinguis* from China; *P. posthuma* is unaffected by extracts of *Cyathodium cavernarum*. Photo by Panzer VI-II, through Creative Commons.

Cyathodium foetidissimum (Figure 34)

Cyathodium foetidissimum (Figure 34) is the largest of the *Cyathodium* species (Lang 1905).



Figure 34. *Cyathodium foetidissimum*. Photo by Philippe Birnbaum, with permission.

Distribution

Cyathodium foetidissimum (Figure 34) is Asiatic with limited records in the Neotropics (Salazar Allen *et al.* 2004). It is known from Java, Sumatra, Tahiti, Nukahiva (Srivastava & Dixit 1996), Cameroon (Wigginton 2002; Wigginton & Grolle 1996), Costa Rica (Salazar Allen *et al.* 2004), Ecuador (Bischler-Causse *et al.* 2005), and Colombia (Gradstein *et al.* 2016). The specimens from Ecuador might represent an error in identification. They have tubers (otherwise unknown in *C. foetidissimum*) and the uppermost thallus cells exceed the size of those found in specimens from Costa Rica (Bischler-Causse *et al.* 2005).

Duckett and Ligrone (2006a) reported the first record of *Cyathodium* in Europe. This they identified as *Cyathodium foetidissimum* (Figure 34). It was located in southern Italy, outside its normal tropical range. They suggested that it was probably a pre-glacial relic rather than a recent arrival from sub-Saharan Africa.

Aquatic and Wet Habitats

Lang (1905) described the habitat of *Cyathodium foetidissimum* (Figure 34) in Perak, Malaysia, as one on rocks in deep forest shade, especially on vertical faces of damp rocks. Salazar Allen and Korpelainen (2006) found that it is more mesic than is *C. spruceanum* (Figure 2). Lang (1905) considers it to be more adapted to shade conditions, rather than being a **hygrophyte** (plant that grows in wet conditions). Angeles *et al.* (2020) described the species as rupestrine, occurring as **chasmophytes** (plants growing in fissures and cracks of limestone) on rock.

In Costa Rica this species forms small patches in depressions in very shady conditions on sandy limestone rock (Bischler-Causse *et al.* 2005); it also occurred in a limestone valley in Italy (Duckett & Ligrone 2006a). Its common associates include *Dumortiera hirsuta* (Figure 35), *Marchantia* (Figure 36), *Fissidens flaccidus* (Figure

37), *Taxiphyllum taxirameum* (Figure 38), and *Lejeuneaceae* (Figure 21).



Figure 35. *Dumortiera hirsuta*, a common associate of *Cyathodium foetidissimum* in Costa Rica. Photo by David T. Holyoak, with permission.



Figure 36. *Marchantia polymorpha* ssp. *montivagans*, in a genus that is a common associate of *Cyathodium foetidissimum* in Costa Rica. Photo by Claire Halpin, with permission.



Figure 37. *Fissidens flaccidus* a common associate of *Cyathodium foetidissimum* in Costa Rica. Photo by Vinod Deora and Deora G.S., through Creative Commons.



Figure 38. *Taxiphyllum taxirameum*, a common associate of *Cyathodium foetidissimum* in Costa Rica. Photo by Bob Klips, with permission.

In Mali, Philippe found it in small caves on rocks (Figure 39-Figure 41).



Figure 39. *Cyathodium foetidissimum* in cave in Mali. Photo by Philippe Birnbaum, with permission.



Figure 40. *Cyathodium foetidissimum* in Mali. Photo by Philippe Birnbaum, with permission.



Figure 41. *Cyathodium foetidissimum* in small cave in Mali. Photo by Philippe Birnbaum, with permission.

Adaptations

Cyathodium foetidissimum (Figure 40) has a multistratose region of cells in the mid region of the thallus (Salazar Allen *et al.* 2004). These could give the thallus greater strength or act as a storage region, but the function needs to be explored. The oil cells have a single oil body. Unlike some species in the genus, this one has strongly dimorphic rhizoids (smooth and pegged) and large ventral scales, both adaptations that could facilitate water movement and uptake.

Srivastava and Dixit (1996) described the thalli as brownish-green and delicate, but usually larger than those of other species in *Cyathodium*. They likewise described large ventral scales, occurring just behind the involucre.

When Duckett and Ligrone (2006a) found this species in Italy, they discovered internal cells in the air chambers, the only report of such internal cells in the genus.

Cyathodium foetidissimum (Figure 40) has a phosphorescent appearance (Figure 42) – another mystery (Lang 1905; Salazar Allen *et al.* 2004). Duckett and Ligrone (2006a) suggested that this might enhance its light interception.

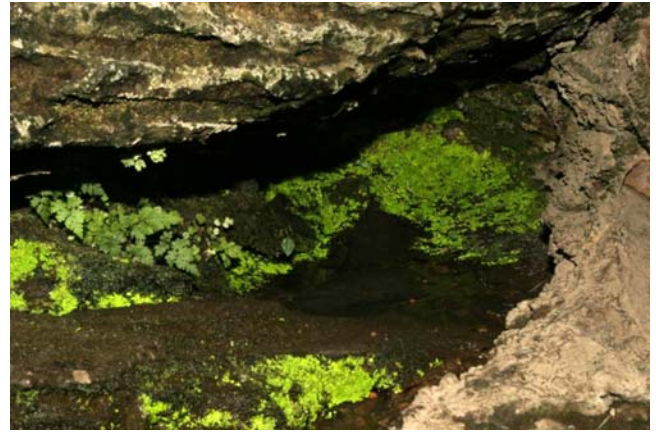


Figure 42. *Cyathodium foetidissimum* in cave in Mali. Photo by Philippe Birnbaum, with permission.

Reproduction

Cyathodium foetidissimum (Figure 40) is **monoicous**, but can also produce unisexual male plants in the same population (Salazar Allen *et al.* 2004). The male receptacle is apical with archegonia, wrapped in undulate laminar involucre, flanking it. It is **protandrous** (antheridia appear before archegonia).

The antheridia occur on short, disc-shaped antheridiophores (Srivastava & Dixit 1996). Archegonia are enclosed by an involucre that sits below the apex at the base of a sinus. Like those in *Targionia hypophylla* (Figure 43), antheridial receptacles occur not only on ventral shoots, but also on the main shoot along the midrib (Kashyap 1914).



Figure 43. *Targionia hypophylla*, a species that, like *Cyathodium foetidissimum*, has antheridial receptacles arising from both ventral shoots and main shoots. Photo by Ken-Ichi Ueda, through Creative Commons.

The capsule has an operculum of only 12 cells. Spores are verrucose (Salazar Allen *et al.* 2004). The spores initially germinate into a filamentous phase in culture (Salazar Allen & Korpelainen 2006). This is followed by apical development of thalli.

Cyathodium foetidissimum (Figure 40) grows in the rainy season, dying back when the dry season begins (Salazar Allen & Korpelainen 2006). Where the habitat is wetter and shaded on the banks of creeks and rivers, it is able to persist for more than one year.

Interactions

Cyanobacteria (Figure 32) are known associates of all species of *Cyathodium* (Salazar Allen & Korpelainen 2006).

Fungi are known to associate with *Cyathodium foetidissimum* (Figure 40) in the Malay Peninsula (Lang 1905) and in Italy (Duckett & Ligrone 2006a).

Biochemistry

Many liverworts have distinctive odors. As its name suggests, *Cyathodium foetidissimum* (Figure 40) is recognizable by its bad smell (Gradstein 2011). Sakurai *et al.* (2018) described it as the smell of an old person or old chest of drawers, but also called it a nostalgic odor. Collections from Tahiti were described as having a pleasant odor, whereas those in the Marquesas Islands smelled like urine and feces.

Ludwiczuk *et al.* (2009) found skatole, a well known compound produced by biodegradation of tryptophan and responsible for the fecal odor of *Cyathodium foetidissimum* (Figure 40). This species also biosynthesized izolepidozene (3.1%) and lunularin (2.4%). Izolepidozene is the main volatile component of *Conocephalum japonicum* (Figure 44) and *Marchantia emarginata* ssp. *tosana* (Figure 45). Among the six species of Polynesian liverworts tested, Ludwiczuk *et al.* (2010) found that each had a unique combination of volatile compounds.



Figure 44. *Conocephalum japonicum*, a species that, like *Cyathodium foetidissimum*, has the compound izolepidozene. Photo by David Long, with permission.



Figure 45. *Marchantia emarginata* ssp. *tosana*, a species that, like *Cyathodium foetidissimum*, has the compound izolepidozene. Photo by Lin Shanxiong, through Creative Commons.

Sakurai *et al.* (2018) identified three volatile components [4-methoxystyrene (24.4%), 3,4-dimethoxystyrene (28.7%), and skatole (15.9%)], as well as several aliphatic aldehydes [n-octanal, n-nonanal, and n-decanal] from Tahitian specimens. However, they did not find (E)-2-nonenal, a recognized compound causing an aged foul odor. Sakurai *et al.* (2018) found that a methanol extract ($100 \mu\text{g mL}^{-1}$) showed no activity against *Bacillus subtilis* (Figure 46), *Staphylococcus aureus* (Figure 47), *Escherichia coli* (Figure 48), or *Klebsiella pneumoniae* (Figure 49), although a number of bryophytes do show activity against these. Perhaps the volatile compounds have a role in antiherbivory?

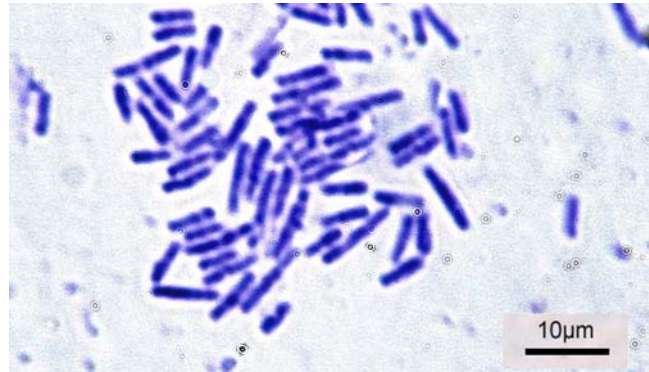


Figure 46. *Bacillus subtilis*, a bacterium that is not inhibited by methanol extracts of *Cyathodium spruceanum*. Photo by Graham Beards, through Creative Commons.

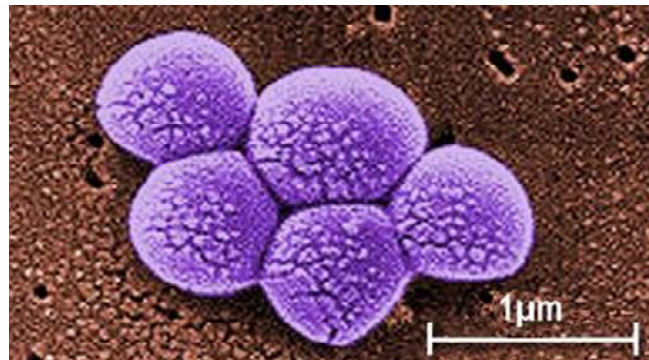


Figure 47. *Staphylococcus aureus*, a bacterium that is not inhibited by methanol extracts of *Cyathodium spruceanum*. Photo by Janice Haney Carr, through public domain.

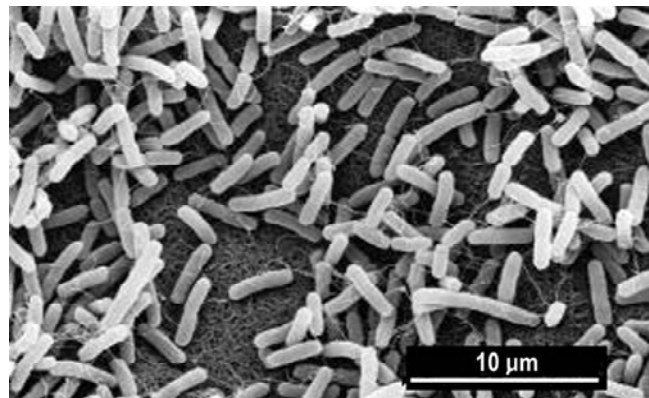


Figure 48. *Escherichia coli*, a bacterium that is not inhibited by methanol extracts of *Cyathodium spruceanum*. Photo by David Gregory & Debbie Marshall, through Creative Commons.



Figure 49. *Klebsiella pneumoniae*, a bacterium that is not inhibited by methanol extracts of *Cyathodium spruceanum*. Photo by NIAID, through Creative Commons.

Of four species of *Cyathodium*, Salazar Allen *et al.* (2017) found indole compounds only in *C. foetidissimum*. The researchers suggested that indole compounds could be used as species markers.

***Cyathodium spruceanum* (Figure 50)**

Among four Neotropical species they examined, Salazar Allen and Korpelainen (2006) found the greatest genetic differences between *Cyathodium foetidissimum* and *C. spruceanum* (Figure 50).



Figure 50. *Cyathodium spruceanum*. Photo by Jose De Gracia, through Creative Commons.

Distribution

Cyathodium spruceanum (Figure 50) is endemic to South America (Srivastava & Dixit 1996) in the Neotropics (Salazar Allen & Korpelainen 2006).

Aquatic and Wet Habitats

Cyathodium spruceanum (Figure 50) typically grows in homogeneous patches on exposed places (Salazar Allen & Korpelainen 2006). Proskauer (1951) reported the original *C. spruceanum* at the edge of a forest stream. The populations are usually rather large in years experiencing high rainfall. The species is less mesic than *C. cavernarum* (Figure 3) or *C. bischlerianum* (Figure 10), with *C. spruceanum* growing farther up the banks in less shaded, less damp habitats that are less mesic. At the Ratu Boko temple in Java, *Cyathodium spruceanum* occurs on limestone (Aryani 2014).

Adaptations

Cyathodium spruceanum (Figure 50) has a thallus that is light-green to whitish-green (Srivastava & Dixit 1996). However, Proskauer (1951) described it as iridescent with light-reflecting lens cells in the roofs of the air chambers. Other than the dark colors that protect against bright sun, little seems to be known about the adaptive values, if any, of some of the colors in bryophytes.

The thalli are overlapping (Srivastava & Dixit 1996), potentially helping to conserve water. Scales provide protection of the growing points (Proskauer 1951).

This species has numerous rhizoids, but the straight, smooth ones predominate (Proskauer 1951; Srivastava & Dixit 1996).

Reproduction

Cyathodium spruceanum (Figure 50) is **dioicous** (Srivastava & Dixit 1996). The female receptacles are ventral pouches. Male (Figure 51) and female plants can grow close to each other, permitting frequent fertilization success (Salazar Allen & Korpelainen 2006). Salazar Allen *et al.* (2017) found that the chemical composition of males and females was very similar, with three compounds found only in females [12-norcyercene-B, longifolenaldehyde and 1(5)-3-aromadenedraidene were found only in female plants].



Figure 51. *Cyathodium spruceanum* males. Photo by José Gudiño L., courtesy of Noris Salazar Allen.

Sporophytes are produced in abundance (Salazar Allen & Korpelainen 2006). Spores are numerous (>400 in a capsule). In culture, these can produce males and female gametophytes in the same year as produced, but there are no field observations to demonstrate germination in the same year as production. Salazar Allen and Korpelainen suggested that this delay in germination is due to soil dryness when the spores are released, a phenomenon that occurs because they are released at the onset of the dry season.



Figure 52. *Cyathodium spruceanum* with sporangia (S). Photo courtesy of Noris Salazar Allen.

The species of *Cyathodium* are **r-selected species** (Salazar Allen & Korpelainen 2006). **R-selected species** generally have high growth rates, produce many offspring, but have a low probability of survival to adulthood. The numerous offspring are able to exploit niches that are less crowded. The abundant sporophytes and spores permit *C. spruceanum* (Figure 50) to be among the better of the *Cyathodium* species at achieving high levels of reproduction. Long-term studies on individual populations are lacking.

The spores of *Cyathodium spruceanum* (Figure 50) are lamellate-reticulate (Salazar Allen *et al.* 2004). The sporeling initially produces a budlike protonema (Salazar Allen & Korpelainen 2006). From this structure, a thallus develops.

Cyathodium spruceanum (Figure 50) is one of the species in the genus to produce ventral tubers (Salazar Allen & Korpelainen 2006). These generally develop in the middle of the rainy season and remain attached to the parent thallus until the thallus decays. In culture, tubers are produced in abundance when nutrients are depleted. The tubers produce numerous rhizoids on their distal portion.

They germinate on agar, but germination in the field has thus far not been observed. Salazar Allen and Korpelainen suggest that when the tubers are covered by mud, they may remain dormant until the next season or become part of the diaspore bank to recolonize if the population is destroyed or if the growing season is extended with plentiful water.

Fungal Interactions

In Panama, fungal endophytes are known from *Cyathodium spruceanum* (Figure 50) (Salazar Allen & Korpelainen 2006). These interactions have barely been explored by bryologists, but mycological literature is not so scarce.

Biochemistry

As in *Cyathodium bischlerianum* (Figure 10), *C. spruceanum* (Figure 50) has less than 3% of the sesquiterpenes germacrene D and bicyclogermacrene (Salazar Allen *et al.* 2017). Oil bodies are present in all cells with the chloroplasts in this species, but the odor is not as offensive as that of *C. foetidissimum*. Nevertheless, the researchers identified far more volatile compounds in *C. spruceanum* than in the other four *Cyathodium* species assessed. Salazar Allen and coworkers identified 12-norcyercene B (70.2%), germacrene D (1.6%), and longifolinaldehyde (1.4%).

Dumortieraceae

Dumortiera hirsuta (Figure 53-Figure 55)

Most bryologists seem to recognize only one species of *Dumortiera* (Figure 53-Figure 55). However, Forrest *et al.* (2011) found two very distinct lineages, represented by ssp *hirsuta* (Figure 53-Figure 55) and ssp *nepalensis* (Figure 102-Figure 103). One (ssp. *hirsuta*) is restricted to Central America and the other (ssp. *nepalensis*) is more widely distributed throughout the range of the genus. See also the discussion of Taiwan populations (Akiyama *et al.* 2003). Forrest and coworkers concluded that there are at least two distinct species, a conclusion reached by O'Hanlon in 1934, but that the molecular basis for naming these is not known for much of the distribution. Therefore, in this chapter I will treat all as *Dumortiera hirsuta* (Figure 53-Figure 55) since most of the publications cited here do not distinguish these.



Figure 53. *Dumortiera hirsuta* mature colony. Photo through Creative Commons.



Figure 54. *Dumortiera hirsuta* s.l. Photo by Nicola van Berkel, through Creative Commons.



Figure 55. *Dumortiera hirsuta* on soil. Photo by Cheong Weei Gan, through Creative Commons.

More recently, the chloroplasts (Kwon *et al.* 2019a) and mitochondria (Kwon *et al.* 2019b) of Korean populations of this liverwort have been sequenced.

Distribution

Dumortiera hirsuta (Figure 53-Figure 55) is widely distributed in tropical and subtropical regions, extending into some temperate regions (O'Hanlon 1934; Forrest *et al.* 2011). It is rare in Europe (Aleffi *et al.* 1998), reaching its northernmost distribution in the UK (Callaghan 2020). In the same year Gaston (2020) found it in France.

This distribution includes more humid and warmer regions of the temperate zones of India, Nepal, Japan, Brazil, México, Jamaica, North and South America, Europe, British Isles, New Zealand, Hawaii, and Africa (O'Hanlon 1934; Nair *et al.* 2005). In the USA it is found in southeastern states, including Arkansas (Timme & Redfearn 1997).

Aquatic and Wet Habitats

Reeb *et al.* (2018) describe the habitat of *Dumortiera hirsuta* (Figure 53-Figure 55) as a shady, humid environment. Tosun *et al.* (2015) considered it to be a large thalloid on wet rocks. Gaston (2020) described it as a pantropical hydrophile.

Dumortiera hirsuta (Figure 53-Figure 55) occurs on dripping rocks (Watson 1919). Ruttner (1955) reported it in water spray, tuff wall, <40 cm above water level, and waterfalls (Figure 1) in the tropics. McAllister *et al.* (2019) found it to be common on rocks in deep canyons, in riparian habitats, on seepy hillsides, and abundant on shale near seepages. It could occur near tributaries, on slopes near or on the underside of sandstone ravines, and at springs (Figure 56-Figure 60).



Figure 56. *Dumortiera hirsuta* in a wet habitat in the UK. Photo by David T. Holyoak, with permission.

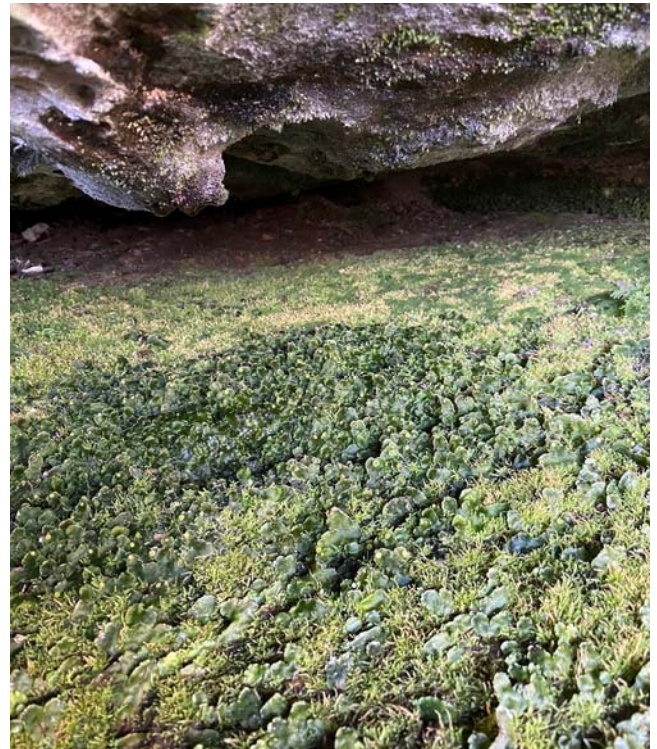


Figure 57. *Dumortiera hirsuta* habitat. Photo by Abel Kinser, through Creative Commons.



Figure 58. *Dumortiera hirsuta* on sandstone. Photo by Vitaly Charny, through Creative Commons.



Figure 59. *Dumortiera hirsuta* where the liverwort can be found on the wet stream banks. Photo by Michael Lüth, with permission.



Figure 60. *Dumortiera hirsuta* habitat on wet soil among rocks. Photo by Luis Funez, through Creative Commons.

Vieira *et al.* (2005) found that in Portugal it was not extensive but seemed stable in steep, water-dripping granite surfaces next to waterfalls. It was also found at the margin of fast flow in a streambed, where it was submerged for long periods and grew associated with *Plagiothecium nemorale* (Figure 61), *Aneura pinguis* (Figure 62), *Pellia epiphylla* (Figure 63), and *Riccardia multifida* (Figure 64), in mountain streams of northwest Portugal (Vieira *et al.* 2005).



Figure 61. *Plagiothecium nemorale*, an associate of *Dumortiera hirsuta* in Portugal. Photo by Hermann Schachner, through Creative Commons.



Figure 62. *Aneura pinguis*, an associate of *Dumortiera hirsuta* in Portugal. Photo by Proyecto Musgo, through Creative Commons.



Figure 63. *Pellia epiphylla*, an associate of *Dumortiera hirsuta* in Portugal. Photo by Bernd Haynold, through Creative Commons.

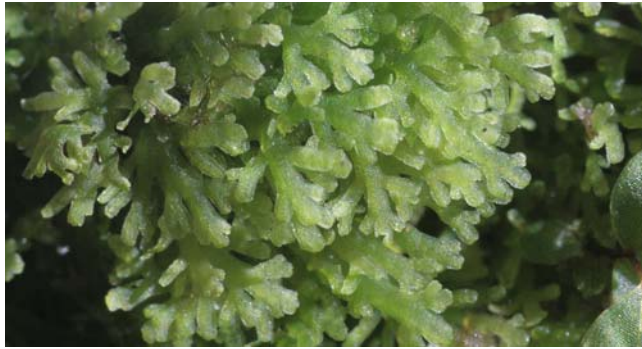


Figure 64. *Riccardia multifida*, an associate of *Dumortiera hirsuta* in Portugal. Photo by Hermann Schachner, through Creative Commons.

In the UK, Callaghan (2020) found all colonies in close association with flowing and moderately alkaline water, including springs, flushes and streams (Figure 56-Figure 60). It never occurred within the **spate zone** (zone suddenly flooded) of larger rivers. It occurs almost entirely on rocks (mudstone, sandstone, slate), predominantly in deciduous woodland and only in lowland sites. In these locations, it occurs with *Thamnobryum alopecurum* (most frequent associate; Figure 65), and *Conocephalum conicum* (Figure 66), as well as *Chrysosplenium oppositifolium* (flowering plant; Figure 67). Ottley (2014) reported a "strong colony" from dripping rocks at Rolvenden in the UK.



Figure 65. *Thamnobryum alopecurum*, the most frequent associate with *Dumortiera hirsuta* in the UK. Photo by Claire Halpin, with permission.



Figure 66. *Conocephalum conicum* on wet rock, a desiccation-intolerant liverwort and frequent associate of *Dumortiera hirsuta* in the UK. Photo by Samaritakis, through Creative Commons.



Figure 67. *Chrysosplenium oppositifolium*, a frequent associate of *Dumortiera hirsuta* in the UK. Photo by Richtid, through Creative Commons.

In the western Himalayas, Pant and Tewari (1984) found *Dumortiera hirsuta* (Figure 53-Figure 55) in tufaceous aquatic habitats, perennial springs, **Gadheras** (small river tributaries; active only during rainy season and stay wet and damp throughout year for growth of bryophytes), and the muddy banks of **Gadhs** (broad rivulets that never dry, resulting from joining of Gadheras). Srinivasan (1968) reported that in India it is often seen in very wet, shady situations where the flow is continuous or at least dripping.

In Java, Indonesia, Nadhifah *et al.* (2018) reported that in the Cibodas Botanical Garden this liverwort occurred on soil in wet areas such as rivers, waterfalls, and ponds. Gradstein (2006) reported that *Dumortiera* sp. was successfully cultivated in association with a small river and pond at the Cibodas Botanical Garden.

In China, *Dumortiera hirsuta* (Figure 53-Figure 55) occurs on brook sides, valleys, or slopes, in wet, mesic, or moist localities, usually in partial or full shade of forested habitats in **orotemperate** (temperate mountain climate) of deciduous and warm temperate evergreen primeval or secondary forests (Piippo & Koponen 2013).

Colon (2000) found it in limestone sinkholes in the karst zone of Puerto Rico, where it had the highest importance value among species in the Empalme Sink.

Not all of its habitats are aquatic. It occurs in oak-hickory forests with shale and sandstone, but still near streams (McAllister *et al.* 2019).

Physiology

Dumortiera hirsuta (Figure 53-Figure 55) is shade adapted (Callaghan 2020). The linear flow of electrons in photosystem II experiences a sharp decline when the photon flux density is greater than $200 \mu\text{mol m}^{-2} \text{s}^{-2}$. The chlorophyll *a:b* ratio was 1.61, contrasting with that of 2.04 in *Phaeoceros carolinianus* (Figure 68), a species of somewhat sunny habitats (Zhang *et al.* 2018). This means that the *D. hirsuta* has more chlorophyll *b*, an adaptation to low light. Duckett and Ligrone (1993, 2006b) reported massive grana and stromal crystals in the chloroplasts and considered it to be a species of extreme shade. The thylakoids in the grana often exceeded 100 (Duckett & Ligrone 2006b). All of these characteristics are consistent with adaptations to shade conditions.



Figure 68. *Phaeoceros carolinianus*, a somewhat sunny species with a higher Chlorophyll *a:b* ratio. Photo by Hermann Schachner, through Creative Commons.

Devi *et al.* (2015) found seasonal variation in the photosynthetic pigments of *Dumortiera hirsuta* (Figure 53-Figure 55). They found that chlorophyll *a* remained higher than chlorophyll *b* in *Dumortiera hirsuta* in all seasons. Chlorophyll *a* is at its lowest levels in winter, whereas there was no seasonal pattern for chlorophyll *b*. Total chlorophyll reaches its greatest levels at the end of the growing season. The carotenoid content was much lower in winter ($0.06 \pm 0.005 \text{ mg g}^{-1}$ fresh weight) than in the rainy season ($0.16 \pm 0.005 \text{ mg g}^{-1}$ fw) or the end of the growing season ($0.15 \pm 0.005 \text{ mg g}^{-1}$ fw).

Bold (1938) demonstrated that the sporophyte is strongly photosynthetic during development in *Dumortiera hirsuta* (Figure 53-Figure 55), exhibiting chloroplasts in the immature foot cells, seta cells, capsule wall cells, and elaters. This photosynthetic ability would provide greater energy for developing spores.

Beckett (1993) found that the turgor of *Dumortiera hirsuta* (Figure 53-Figure 55) correlates well with the other indicators of water stress damage, including photosynthesis, respiration, and potassium loss. The rate of respiration dropped to zero following desiccation and the plants did not recover. This was similar to results of other desiccation-intolerant liverworts such as *Conocephalum conicum* s.l. (Figure 66) (Slavik 1965). However, such measures of intolerance must be reviewed because we now know that the rate of desiccation can have a profound effect on the survival and recovery from desiccation. He developed a successful method, using a thermocouple psychrometer, to correct for apoplastic water. Nevertheless, he found that the error introduced by apoplastic water was negligible.

Loo (2005) noted the difficulties in studying the cytology of *Dumortiera hirsuta* (Figure 53-Figure 55). Nevertheless, Loo *et al.* (2005a) presented a cytological study on this species. In a separate publication (2005b), they reported that *Dumortiera hirsuta* survived at 47-1511 lux, 15-27°C, and relative humidity of 60-95% on Mt. Kinabalu. Frahm *et al.* (1996) considered the minimum light level for photosynthesis to be 400 lux. The numbers presented by Loo and coworkers suggest that this species has a good tolerance range of the physical parameters of the environment.

Proctor *et al.* (1998) found that the full-turgor water content reached 1400% in *Dumortiera hirsuta* (Figure 53-

Figure 55). In a different study it was 1636% (Proctor 1999). These are much higher figures than those in the mosses *Syntrichia ruralis* (Figure 16) or *Andreaea alpina* (Figure 69) (Proctor *et al.* 1998). Beckett (1993) found that *D. hirsuta* was very sensitive to desiccation. The cells lost potassium, and during drying the thallus continued respiration while shutting down photosynthesis, causing the thalli to lose weight. He used this species to show that turgor loss correlated with other indicators of stress-induced damage.



Figure 69. *Andreaea alpina*, a species with a much lower full-turgor water content than that of *Dumortiera hirsuta*. Photo by Stephen Moores, through Creative Commons.

Marschall and Beckett (2005) found that ABA and partial dehydration hardening can increase desiccation tolerance, with *Dumortiera hirsuta* (Figure 53-Figure 55) being much more responsive to ABA treatment than was *Atrichum androgynum* (Figure 70). Furthermore, unlike *A. androgynum*, *D. hirsuta* did not exhibit increased NPQ (non-photochemical quenching) or decreased PSII efficiency with dehydration hardening. It also had little change with partial dehydration hardening before the onset of stress, but following rehydration it displayed a 22% improvement in PSII activity within an hour.



Figure 70. *Atrichum androgynum*, a species that is more resistant to cadmium damage than is *Dumortiera hirsuta*. Photo by Niels Klazenga, through Creative Commons.

Many bryophytes are now known to produce superoxide during rehydration. *Dumortiera hirsuta* (Figure 53-Figure 55) is among those that produce extracellular superoxide rapidly, even when not stressed (Beckett *et al.* 2004). Nevertheless, the production of superoxide increases greatly in this species during rehydration even after a mild desiccation stress. There are indications that this production provides an important protection against invasion of bacteria and fungi during the period of membrane repair. (See Chapter 19 in Volume 2.)

Li *et al.* (2010) determined that cell wall peroxidases are responsible for the extracellular burst of superoxide in *Dumortiera hirsuta* (Figure 53-Figure 55). They also found that this oxidative burst may have roles in formation of protective substances such as suberin, melanin, and lignin, supporting the hypothesis that the burst of superoxide enhances protection against pathogens. These peroxidases might also have a role in signal transduction and protection against abiotic stress and Yadav *et al.* (2022) looked at seasonal changes in chemical constituents of *Dumortiera hirsuta* (Figure 53-Figure 55), particularly changes in oxidative stress responses. In the fruiting season, the plants had their highest level of malondialdehyde (MDA) and H_2O_2 , with the lowest levels occurring during the premonsoon and monsoon seasons. Protein content and pigment concentrations were maximal during the monsoon season and minimal during the fruiting season. On the other hand, the enzymatic activity and content of superoxide dismutase, catalase, and glutathione reductase and non-enzymatic antioxidants were higher during the fruiting season and low during the pre-monsoon and monsoon seasons. During the fruiting season, the temperature is very low and nutrient availability is diminished. Hence these activities provide a defense in neutralizing or suppressing the increased ROS (reactive oxygen species) during the fruiting season. The researchers suggested that the antioxidative defence system may have a role in the adaptation of the species against oxidative stress, mediated by seasonal changes.

Heavy metals are often a component in aquatic and semi-aquatic environments. These are often toxic to plants, including bryophytes, but the latter seem to have at least some coping mechanisms. Heavy metals can interact to provide varying responses in *Dumortiera hirsuta* (Figure 53-Figure 55). It exhibits both internal and external cadmium uptake (Mautsoe & Beckett 1996). The intracellular uptake is linear with time, displaying Michaelis-Menten kinetics, whereas the extracellular uptake exhibits saturation kinetics [$K(m)$ and $V(max)$ $149 \pm 19 \mu M$ & $11.0 \pm 0.8 \mu M g^{-1} h^{-1}$ respectively]. Both are temperature dependent and intracellular uptake is light stimulated, increasing by about 15. Incubation with Cd and equimolar concentrations of Ca, Mg, or Zn reduced both intracellular and extracellular uptake. Pretreating the thalli with KNO_3 stimulated Cd uptake, most likely due to the ability of the K to remove competing ions from the cell walls, a technique used to measure cation exchange. All of this suggests the involvement of cation exchange in the uptake of cadmium. The researchers suggested that such exchange sites might protect the liverworts by securing the heavy metal ions outside the cell.

When Mautsoe and Beckett (1996) explored the effects of Cd on *Dumortiera hirsuta* (Figure 53-Figure 55), they

found that intracellular Cd uptake was linear, but extracellular uptake exhibited saturation kinetics. These uptake processes were temperature dependent. Light also stimulated intracellular uptake, but storage for 20 days in the dark did not affect it. Uptake decreased when the plants were incubated with additional Mg, Zn, or Cd, whereas pretreatment with KNO increased uptake, indicating cation exchange with the KNO clearing the exchange sites of cations. Such exchange sites might protect the liverworts by securing the heavy metal ions outside the cell.

Mautsoe (1997) found that photosynthesis of *Dumortiera hirsuta* (Figure 53-Figure 55) was more sensitive to Cd than it was in *Atrichum androgynum* (Figure 70), with differences directly related to intracellular Cd concentrations. These concentrations were considerably higher in *D. hirsuta*. Furthermore, in *D. hirsuta* the Cd caused K loss, but this did not occur in *A. androgynum*. Intracellular uptake in *D. hirsuta* was affected by thallus age, K pretreatment, and site characteristics.

Loo *et al.* (2005b) described the tolerance range of *Dumortiera hirsuta* (Figure 53-Figure 55) to occur within the 480-1740 m asl on Mt. Kinabalu. Here it experienced ranges of 47-1511 lux, 15-27°C, and 60-95% humidity. Hence we should expect it to be adapted to stresses within these ranges.

Adaptations

Butt and Anima (2011) found that *Dumortiera hirsuta* (Figure 53-Figure 55) in Bhaderwah, northwest Himalayas, exhibits great diversity of habitat, pH, and altitude, with accompanying diversity of morpho-anatomical characters of both gametophyte and sporophyte. Piippo and Koponen (2013) noted that this species is likely to include many cryptic taxa.

Although *Dumortiera hirsuta* (Figure 53-Figure 55) occurs in moist habitats, those are not always moist (Figure 71). Thus, the plants need mechanisms to protect vulnerable life cycle stages that coincide with less favorable seasons. Perhaps one such adaptation is that the archegonial head is covered with hairlike appendages (O'Hanlon 1934), suggesting an adaptation that protects the critical archegonia and developing sporophytes from drying out. The adult thallus has no lacunae (unfilled space or interval; gap) and no definite demarcation between the chlorophyllous and colorless cells, the latter being mostly in the central part of the thallus. Does the lack of lacunae suggest faster drying, or does the absence of these air spaces slow it down? Based on movement of water through stomata of tracheophytes, we can hypothesize that the absence of lacunae would slow down water loss. Researchers have demonstrated that stomatal-derived water loss from plants is ~50% of the total terrestrial evaporation and 80-90% of the continental evaporation (Hetherington & Woodward 2003; Jasechko *et al.* 2013).

There are only vestigial ventral scales (Figure 72) (McAllister *et al.* 2019) – structures that usually help in water movement, uptake, and conservation, perhaps causing the restriction of *Dumortiera hirsuta* to moist habitats. Watson (1919) considered that having few or no ventral scales is an adaptation or characteristic of a species from an aquatic habitat.



Figure 71. *Dumortiera hirsuta* with thallus showing signs of drying. Photo by Blanka Aguero, with permission.



Figure 72. *Dumortiera hirsuta* ventral side showing absence of or vestigial scales. Photo by Nicola van Berkel, through Creative Commons.

Adaptations may differ between lineages. The Central American lineage has plants with a light green velvety appearance, caused by abundant papillae on the upper surface (Forrest *et al.* 2011). The role of papillae has been controversial and unproven, including movement of water into cells in some species, scattering light, and reducing water loss. The more widespread lineage is dark green and papillae range from absent to dense; marginal hairs are usually abundant. It appears that these two lineages might have different adaptations to surviving periods of drought and receding water.

Dumortiera hirsuta (Figure 53-Figure 55) is polyploid, with populations exhibiting monoploid or diploid gametophytes (Tatuno 1938, 1939). It is likely that the differences between monoploid and diploid gametophytes of *Dumortiera hirsuta* might confer some differences in adaptations. In some cases, some alleles of diploids were missing among monoploids, but both types shared the character of upright, short hairs scattered on the dorsal surface (Akiyama *et al.* 2003). In Taiwan populations, Akiyama and coworkers found that monoploids could grow on non-calcareous substrata, a single population could have different levels of ploidy, heterozygosity is fixed in diploids, and there are at least four monoploid lineages ("species" according to Akiyama *et al.*). The evidence suggests that these diploids are **allopolyploids** (two or more chromosome sets originating

as complete sets from different species or lineages). The presence of multiple chromosome sets and lineages would provide greater variation, thus permitting the species to survive a wider range of conditions.

Storage compounds can vary with seasons. Kapila *et al.* (2014) compared three liverworts and found that the more hydric *Dumortiera hirsuta* (Figure 53-Figure 55), with a habitat near streams or other hydric locations, exhibits higher carbohydrate and protein content with little seasonal change compared to *Marchantia emarginata* (Figure 73) and *M. paleacea* (Figure 74), both of mesic habitats. All three species experienced a decrease in α -amylase, β -amylase, and invertase near the end of the primary growth season due to carbohydrate accumulation in their tissues. There was an inverse relationship between protein and free amino acids. Protease activity, associated with protein metabolism, peaked in the rainy season.



Figure 73. *Marchantia emarginata*, a species with lower carbohydrate and protein content and more seasonal change compared with *Dumortiera hirsuta*. Photo by Li Zhang, with permission.



Figure 74. *Marchantia paleacea*, a species with lower carbohydrate and protein content and more seasonal change compared with *Dumortiera hirsuta*. Photo by Jan-Peter Frahm, with permission.

Reproduction

Mcallister *et al.* (2019) considered *Dumortiera hirsuta* (Figure 53-Figure 55) to be **monoicous**. But Bischler-Causse *et al.* (2005) considered it to be **monoicous** or **dioicous** (Figure 75-Figure 77). It has no known asexual propagules.



Figure 75. *Dumortiera hirsuta*, with emerging archegoniophores. Photo by Cheng-Tao Lin, through Creative Commons.



Figure 76. *Dumortiera hirsuta* with archegoniophores. Photo by Luis Funez, through Creative Commons.

Shimamura (2015) reported that the sperm possessed four flagella and experienced aerial dispersal. This species was the first to be documented with explosive sperm dispersal. Small droplets with sperm cells are expelled several centimeters into the air from the antheridial disk. Even in monoicous plants, this explosive dispersal facilitates the cross-fertilization between male and female reproductive structures on different individuals.

From South Carolina, USA, Patterson (1933) reported that male receptacles were initiated 11-19 August, with female receptacles (Figure 77) appearing 5-12 September. Fertilization occurred primarily 25 September to 5 October. Young embryos appeared 5 October to 15 October. Sporophytes developed in November and December, with meiosis occurring 26 January to 4 February. Meanwhile, the antheridial branches withered 20 December to 20 January. Spores matured in February. In March, the capsules blackened, fertile thalli were dying, and the receptacles elongated. In April the setae elongated and the spores were dispersed. Precipitation modified this schedule from year to year. Patterson detailed the development of the reproductive structures. One unusual character is that some receptacles have both male and female gametangia,

but these do not occur on the same radii, with radii of the same sex grouped together. These receptacles with both sexes were relatively common in populations from Jamaica, but were rare in the North Carolina populations.



Figure 77. *Dumortiera hirsuta* young archegoniophores. Photo by Lin Kyan, with permission.

All the archegonia within an involucre may experience fertilization, but only one will get beyond the 2-8 cell stage (Patterson 1933).

In the UK the production of sporophytes is rare (Callaghan 2020). Since the seasons there are quite different from those in the tropics, temperature, day length, and rainy season might modify the reproductive timing so that it is unlikely to be successful.

Patterson (1933) reported the species producing sporophytes (Figure 78-Figure 80) on the bank of a small stream near Columbia, South Carolina, USA. O'Hanlon (1934) found that only one or two sporophytes (Figure 81) in each of the typically eight groups of archegonia are able to reach maturity. In Florida, USA, O'Hanlon found ripe spores (Figure 82-Figure 83) in the middle of April. They remain viable for only a short time after dehiscence. In the lab they germinate within 6-7 days on a liquid medium.



Figure 78. *Dumortiera hirsuta* with archegoniophores. Photo by buggi, through Creative Commons.



Figure 79. *Dumortiera hirsuta* with mature sporangia. Photo by Chris Wagner, through Creative Commons.



Figure 82. *Dumortiera hirsuta* archegonial head with dehiscent sporangia, in this case with four sporangia. Photo courtesy of Zen Iwatsuki.



Figure 80. *Dumortiera hirsuta* with maturing sporangia. Photo by Chris Wagner, through Creative Commons.



Figure 83. *Dumortiera hirsuta* with sporangia and ripe spores. Photo by Luis Funez, through Creative Commons.



Figure 81. *Dumortiera hirsuta* with mature sporangia, showing only 1-3 mature sporangia per archegonial head. Photo by tigris 8, through Creative Commons.

The young sporocyte has a single large plastid, but the plastid divides before the nucleus divides, resulting in four plastids (Shimamura *et al.* 2000). These often continue to divide before nuclear division. The cytoplasm forms lobes around the four plastid domains, enclosing at least one plastid. This monoplastidic meiosis is rare among liverworts.

O'Hanlon (1934) found that *Dumortiera hirsuta* (Figure 53-Figure 55) produces 1-2 sporophytes (Figure 82) that reach maturity among the eight groups of archegonia. Spores reach maturity in mid April in Florida, USA. They remain viable only a short time after the capsule dehisces. These spores germinate within 6-7 days after culturing in a liquid medium. The spore first produces a rhizoid; then a bud forms from the spore.

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Miyoshi (1973) described the spore wall structure of *Dumortiera hirsuta* (Figure 53-Figure 55). Kamimura (1973) used the electron microscope to help describe the

fine structure of the spore walls. Pyramidal or rectangular planks or columnar protuberances have irregular patterns on the surfaces of the spore walls. Two-three of these protuberances frequently form lamellae. The foundation of the spore wall is nearly smooth.

Role

This species surely plays a greater role in housing invertebrates than the examples we know (Figure 84). And what might its role be in stabilizing the banks of streams during high water? The ecosystem role of *Dumortiera hirsuta* (Figure 53-Figure 55) remains mostly unexplored.



Figure 84. *Dumortiera hirsuta* with snail, a potential herbivore on this species. Photo by Chaturvedi, with permission.

Interactions

Iqbal *et al.* (2011) enumerated the wide array of organisms associated with *Dumortiera hirsuta* (Figure 85), including fungi, other bryophytes, pteridophytes, gymnosperms, angiosperms, and insects. In Bhaderway in the Doda district of Jammu, India, in the range of 1230-2600 asl *Conocephalum conicum* (Figure 66) formed the most frequent associations, but these researchers found 12 species of plants and one insect that were frequently associated with *D. hirsuta*.



Figure 85. *Dumortiera hirsuta* with the moss *Sematophyllum* sp. in India. Photo by Syamal L, through Creative Commons.

Fungal Interactions

The fungi associated with *Dumortiera hirsuta* (Figure 53-Figure 55) remain unexplored. The species has antifungal properties (Alam *et al.* 2011), but that is not usually enough to deter all fungi. And are those antifungal compounds produced by the liverwort, or by associated bacteria?

Alam *et al.* (2011) found that treatment of *Aspergillus niger* (Figure 86) by extracts from *Dumortiera hirsuta* (Figure 53-Figure 55) caused distinct morphological changes in the fungus. These included anomalies in the hyphae, flaccid cell wall, and cytoplasm leaking through cell wall and becoming granulated.

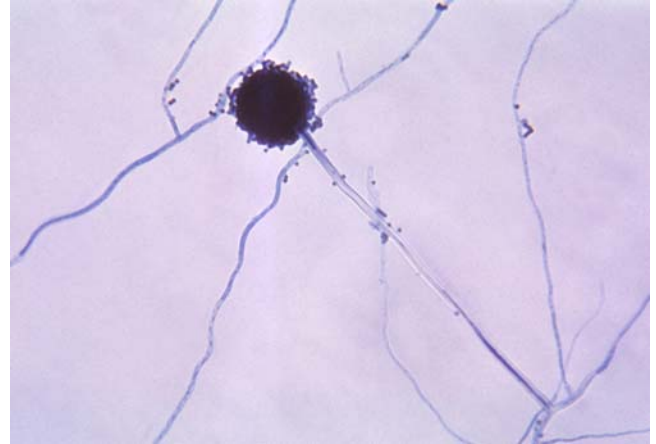


Figure 86. *Aspergillus niger*, a species that exhibits morphological aberrations after exposure to extracts of *Dumortiera hirsuta*. Photo from CDC, through public domain.

Egertová *et al.* (2018) described a new species of Ascomycetes growing on *Dumortiera hirsuta* (Figure 53-Figure 55). *Octosporopsis erinacea* (Figure 87) parasitizes the thallus, exhibiting tiny, light yellow, rimless apothecia. The hyphae develop both on and within the cells of the thallus, especially near a waterfall.



Figure 87. *Octosporopsis erinacea*, a species of Ascomycetes that parasitizes the thallus of *Dumortiera hirsuta*. Photo by Z. Egertová, through Creative Commons.

Animal Interactions

Among the inhabitants of *Dumortiera hirsuta* (Figure 53-Figure 55) is the odonate *Epiophlebia superstes* (Figure

88) (Asahina & Sugimura 1981). This odonate is intermediate between dragonflies and damselflies. It injects its eggs into the thallus of *D. hirsuta*. Later, Carle (2012) described the new species *Epiophlebia diana* from naiads in China. However, Büsse and Ware (2022) have considered it to be a synonym of *Epiophlebia laidlawi* (Figure 89), occurring in Nepal, India, Bhutan, and Vietnam. Members of this genus in China typically choose plants growing in wet and mostly shaded areas less than a meter from a stream.



Figure 88. *Epiophlebia superstes* on bryophytes. Photo by Tom Kompier, with online non-commercial permission.



Figure 89. *Epiophlebia laidlawi* naiad, an inhabitant of *Dumortiera hirsuta* in China. Photo modified from Robert John Tillyard, through public domain.

Lien (1989) suggested that species of biting midges (*Ceratopogonidae*: *Lasiohelea*) that rest on *Dumortiera hirsuta* (Figure 53-Figure 55) and other bryophytes are likely to be feeding on the *Cyanobacteria* (Figure 32) that are growing there. Lien found that *Anabaena* sp. (Figure 90) is especially beneficial for *Forcipomyia anabaenae* (see Figure 91), in a closely related genus.



Figure 90. *Anabaena circinalis*; the genus *Anabaena* is a beneficial food for some biting midges that visit bryophytes. Photo by B D Carl, through Creative Commons.



Figure 91. *Forcipomyia* sp., a genus wherein some members seem to benefit from eating *Anabaena* associated with bryophytes. Photo by XPDA, through Creative Commons.

The fly family *Agromyzidae* (Figure 92-Figure 94) occurs on liverworts throughout the world (Spencer 1990). It is a miner on *Dumortiera hirsuta* in Mexico.



Figure 92. *Phytoliriomyza dorsata* (*Agromyzidae*), in a family that mines thallose liverworts. Photo by Mardon Erbland, through Creative Commons.

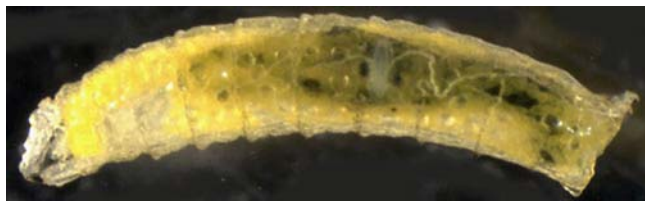


Figure 93. *Phytoliriomyza melampyga* larva (**Agromyzidae**), in a family that mines thallose liverworts. Photo by W. N. Ellis, through Creative Commons.



Figure 94. *Phytomyza* sp. leaf mining (**Agromyzidae**), in a family that mines thallose liverworts. Photo by Beatriz Moisset, through Creative Commons.

Biochemistry

Dumortiera hirsuta (Figure 53-Figure 55) has been the subject of a number of biochemical studies. Matsuo *et al.* (1976) reported 10 sesquiterpene hydrocarbons from *Dumortiera hirsuta*. Toyota *et al.* (1997a,b) reported on a new sesquiterpene compound and 13 additional known compounds from the species and described their structures. Saritas *et al.* (1998) added additional sesquiterpenes to this list, some of which were rare or unusual. To these, Lu *et al.* (2006) added more compounds (terpenoids and bisbibenzyls from Chinese populations, including riccardin D) and described their structure. Some of these were cytotoxic to the human HepG2 cells. One was also active against *Pseudomonas aeruginosa* (Figure 95).

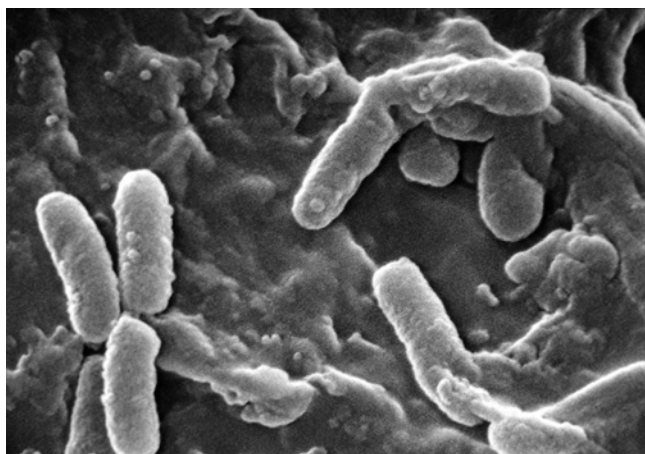


Figure 95. *Pseudomonas aeruginosa*, a species that experiences toxicity from one of the compounds produced by *Dumortiera hirsuta*. Photo by Janice Haney Carr, CDC, through public domain.

Liu *et al.* (2012) found that riccardin D (a macrocyclic bisbibenzyl compound), a product of *Dumortiera hirsuta* and other liverworts, was effective at inhibiting intestinal adenoma from forming in mice. Its effectiveness is through multiple mechanisms, including anti-proliferative, apoptotic, anti-angiogenic, and anti-inflammatory activity. Xue *et al.* (2012) found that the riccardin D also induces apoptosis of human leukemia cells.

Xie and Lou (2008) identified two calamenane-type sesquiterpenoids (5,7-dihydroxycalamenene and 7-hydroxycalamenene) from *Dumortiera hirsuta* (Figure 53-Figure 55). Bardón *et al.* (1999) isolated dumortane sesquiterpenes, four new, from Argentine populations of *Dumortiera hirsuta* (Figure 53-Figure 55). Linde *et al.* (2016) considered that the presence of dumortane-type sesquiterpenoids in *D. hirsuta* from South Africa indicated that this species is similar in chemistry to an Argentinean sample.

Xie *et al.* (2007) reported an unusual phenylethyl cyclohexadienone (dumhirone A) from Chinese populations of *Dumortiera hirsuta* (Figure 53-Figure 55).

Alam *et al.* (2011) found that aqueous extracts of *Dumortiera hirsuta* (Figure 53-Figure 55) were effective against seven plant pathogens. Six of seven plant pathogenic fungi were completely inhibited by the extract at 550-600 ppm. Joshi (1993) also found extracts to be effective against bacteria. Kumar *et al.* (2007) likewise found that extracts of this liverwort in Indian Himalayas were effective in enhancing wound healing due to its antibacterial properties.

Setyati *et al.* (2021) found that extracts from *Dumortiera hirsuta* (Figure 53-Figure 55) were able to prevent infection by pathogenic bacteria, including flavonoids, alkaloids, and steroids. These were able to inhibit the bacteria *Escherichia coli* (Figure 48), *Staphylococcus aureus* (Figure 47), and *Salmonella typhi* (Figure 96), causing weak to moderate responses (see also Luthfiah *et al.* 2021). Junairiah *et al.* (2015) similarly found that ethylacetate extracts of *D. hirsuta* from Indonesia contained flavonoids, alkaloids, and steroids that can inhibit the pathogenic bacteria *Staphylococcus aureus* and *Escherichia coli* and the yeast *Candida albicans* (Figure 97).



Figure 96. *Salmonella typhi*, a species that is inhibited by extracts from *Dumortiera hirsuta*. Photo by CDC, through public domain.

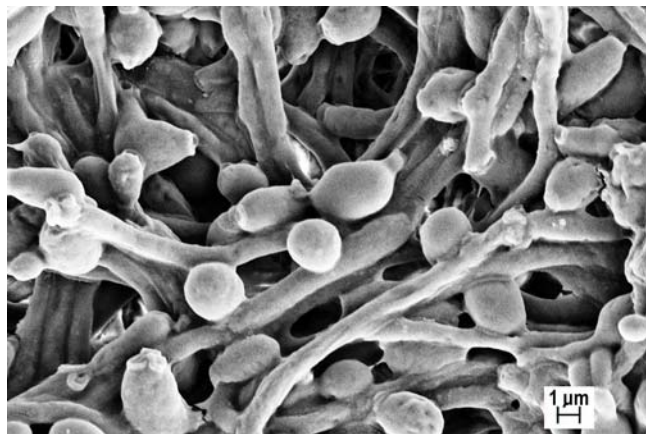


Figure 97. *Candida albicans* SEM, a yeast species that is inhibited by extracts from *Dumortiera hirsuta*. Photo by Vader1941, through Creative Commons.

An aqueous extract from *Dumortiera hirsuta* (Figure 53-Figure 55) exhibited fungitoxicity against seven plant pathogenic fungi, inhibiting their ability to produce germinable spores (Alam *et al.* 2011). Morphological aberrations were present in *Aspergillus niger* (Figure 86) treated with extracts of *Dumortiera hirsuta*.

Mukherjee *et al.* (2012) examined antibacterial activity of *Dumortiera hirsuta* (Figure 53-Figure 55) against *Serratia marcescens* (Figure 98) from various altitudes in the Himalayas. Those plants from higher altitudes exhibited slightly less antibacterial activity than those from lower altitudes. The reproductive thallus extracts exhibited less antibacterial activity than did the vegetative thallus.



Figure 98. *Serratia marcescens* on bread, a bacterial species that is inhibited less by populations of *Dumortiera hirsuta* from higher elevations than by those at lower elevations. Photo by DBM, through Creative Commons.

Noting that *Dumortiera hirsuta* contains the bioactive alkaloids, terpenoids, flavonoids, and saponin, Sari (2014) explored its usefulness in the treatment of malaria. It was effective in treating parasitemia caused by *Plasmodium berghei* (Figure 99) in mice, so its usefulness against *Plasmodium malariae* (Figure 100) was worth exploration. Unfortunately, in their further experiments against *P. berghei* in mice, they found that it damaged microanatomical structures in the liver and kidneys at levels of 300 mg kg⁻¹ BW and above.

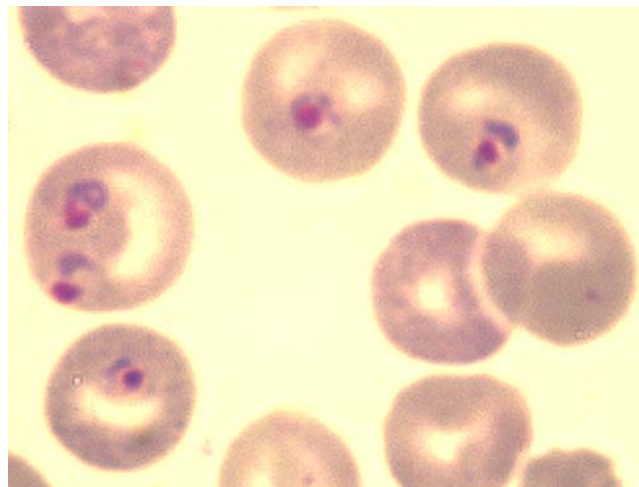


Figure 99. *Plasmodium berghei*, a species that can be inhibited successfully by extracts of *Dumortiera hirsuta*. Photo by C. J. Janse, through Creative Commons.

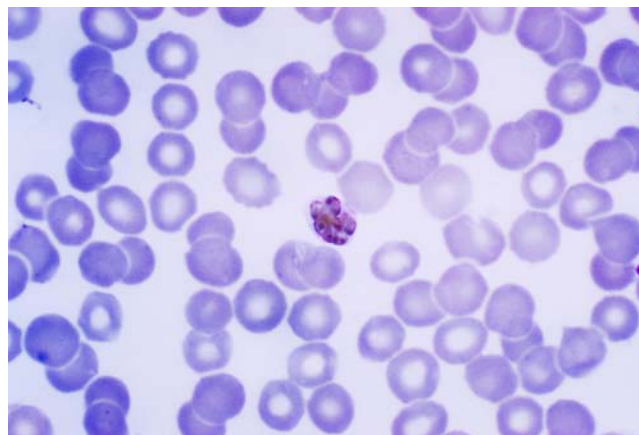


Figure 100. *Plasmodium malariae*, a species that might be inhibited by extracts of *Dumortiera hirsuta*. Photo by Mae Melvin, CDC, through public domain.

Shirzadian *et al.* (2009) found that ethanolic extracts of *Dumortiera hirsuta* (Figure 53-Figure 55) exhibited one of the broadest spectra of antifungal activities shown by the 23 bryophytes tested. Luthfiah *et al.* (2021) noted that this species can be used medically to prevent bacterial infection.

Asakawa (1982) used the terpenoids and aromatic compound differences to argue for separation of *Wiesnerella denudata* (Figure 101) and *Dumortiera hirsuta* (Figure 53-Figure 55) into different families. Those sesquiterpene lactones and monoterpenoids occurring in *W. denudata* appear to be absent in *D. hirsuta*. This supports the morphological differences also known between these two species. Kraut *et al.* (1996) reported several carboxylated α -pyrone derivatives and flavonoids from *Dumortiera hirsuta* and elucidated structures.

In their attempts to distinguish differences in secondary compounds between *D. hirsuta* ssp. *hirsuta* (Figure 53-Figure 55) and *D. hirsuta* ssp. *nepalensis* (Figure 102-Figure 103). Durant-Archibold *et al.* (2018) reported 34 compounds for the first time in the species *Dumortiera hirsuta*. They found that the two subspecies differed biochemically.



Figure 101. *Wiesnerella denudata* in Bhutan, a species wherein chemical differences separate it from *Dumortiera hirsuta*. Photo by David Long, with permission.

Dumortiera hirsuta ssp. *nepalensis* (Figure 102-Figure 103)

(syn. = *Dumortiera trichocephala*)



Figure 102. *Dumortiera hirsuta* ssp. *nepalensis*. Photo courtesy of David Wagner.



Figure 103. *Dumortiera hirsuta* ssp. *nepalensis* from Bhutan. Photo courtesy of David Long.

In most cases, the subspecies *nepalensis* is considered as part of *Dumortiera hirsuta*, but it has been classified as a variety, a subspecies, and even a species. In the foregoing discussion I have considered *Dumortiera hirsuta sensu lato*. However, since I did find some separate information on it, I shall comment on that with the anticipation that it might be officially removed from *D. hirsuta* in the future.

Distribution

In 1919, Evans considered this to be the separate species *Dumortiera nepalensis* (Figure 102-Figure 103). He described its distribution as close to that of *D. hirsuta* (Figure 53-Figure 55), but absent in Europe and Africa. But it is rare in much of its range, especially the southern United States and West Indies, and David Long (pers. comm. 26 June 2022) considers these populations to belong to *Dumortiera hirsuta* ssp. *hirsuta* (Figure 53-Figure 55). *Dumortiera hirsuta* ssp. *nepalensis* (Figure 102-Figure 103) is most abundant in southeastern Asia.

Aquatic and Wet Habitats

Dumortiera hirsuta ssp. *nepalensis* (Figure 102-Figure 103) occurs submersed under water jets, above the water level, and in waterfalls in the tropics (Ruttner 1955). David Long (pers. comm. 26 June 2022) reports the subspecies from the slope of dry rocky side valley and under overhanging dripping rocks by roads in the Tashigang districts south of Tashi Yangtse, Bhutan.

Biochemistry

Durant-Archibold *et al.* (2018) found that the major volatile compounds in *Dumortiera hirsuta* ssp. *nepalensis* (Figure 102-Figure 103) from Panama were ledene, α -gurjunene, β -caryophyllene, and α -guaiene, differing from those of the subspecies *hirsuta*.

Summary

Cyathodium is **r-selected**. It has several species that occupy wet habitats in mostly tropical areas. Several species occur on stream and river banks, with *C. bischlerianum* and *C. cavernarum* typically closer to the water than is *C. spruceanum*. Species often have pungent odors, attesting to their unique secondary compounds. Others, such as *Cyathodium bischlerianum*, have pleasant odors suitable for cosmetics and soaps. Some species, such as *Cyathodium cavernarum*, have iridescent colors, but the function of those, if any, is unknown.

Dumortiera hirsuta has a similar distribution and occurs in splash zones of streams and waterfalls and on otherwise wet rocks. It is a shade-adapted species that otherwise occupies a wide range of habitat conditions, pH, and altitude. There are flies in **Agromyzidae** and **Ceratopogonidae** that are specialists on it. In some cases, the invertebrates occur there to consume associated **Cyanobacteria**. The secondary compounds of *D. hirsuta* possess antibiotic and medicinal properties.

Acknowledgments

Lars Söderström helped me find the current acceptable names for a number of older taxa.

Literature Cited

- Akiyama, H., Kosuge, K., and Yamaguchi, T. 2003. Biosystematic studies of the *Dumortiera hirsuta* complex (Hepaticae). 1 Genetic and morphological diversity found in Taiwanese populations. *Bryol. Res.* 8: 203-213.
- Alam, A., Tripathi, A., Vats, S., Behera, K. K., and Sharma, V. 2011. *In vitro* antifungal efficacies of aqueous extract of *Dumortiera hirsuta* (Swaeagr.) Nees against sporulation and growth of postharvest phytopathogenic fungi. *Arch. Bryol.* 103: 1-9.
- Aleffi, M., Schumacker, R., Puntillo, D., Privatera, M., Bernardo, L., and Raso, C. 1998. *Dumortiera hirsuta* (Sw.) Nees in Calabria (Italy), its southernmost and highest localities in Europe, and additions to the bryophyte flora of this region. *Cryptog. Bryol. Lichénol.* 19: 341-360.
- Angeles, E. J. A., Magat, M. B., and Jalandoni, R. S. D. 2020. Distribution of bryophytes in the University of the Philippines – Diliman, Quezon City, Philippines. *Plant Sci.* 9: 3957-3969.
- Aryani, R. D. 2014. Keanekaragaman Lumut pada Batu Putih di Candi Ratu Boko, Yogyakarta. Ph. D. dissertation, Universitas Gadjah Mada, Indonesia.
- Asahina, S. and Sugimura, M. 1981. Oviposition of *Epiophlebia superstes* into bryophytes. *Tombo* 24(1): 22-23.
- Asakawa, Y. 1982. Terpenoids and aromatic compounds as chemosystematic indicators in Hepaticae and Anthocerotae. *J. Hattori Bot. Lab.* 53: 283-293.
- Bardón, A., Kamiya, N., Toyota, M., and Asakawa, Y. 1999. A 7-nordumortenone and other dumortane derivatives from the Argentine liverwort *Dumortiera hirsuta*. *Phytochemistry* 51(2): 281-287.
- Beckett, R. P. 1993. The effect of water stress on the liverwort *Dumortiera hirsuta* measured using thermocouple psychrometry. *S. Afr. J. Bot.* 59: 462-464.
- Beckett, R. P., Minibayeva, F. V., Lüthje, S., and Böttger, M. 2004. Reactive oxygen species metabolism in desiccation-stressed thalli of the liverwort *Dumortiera hirsuta*. *Physiol. Plant.* 122: 3-10.
- Bischler-Causse, H., Gradstein, S. R., Jovet-Ast, S., Long, D. G., and Salazar Allen, N. (eds.). 2005. Marchantiidae. New York Botanical Garden Press, NY. *Flora Neotropica Monograph* 97: 1-262.
- Bold, H. C. 1938. The nutrition of the sporophyte in the Hepaticae. *Amer. J. Bot.* 25: 551-557.
- Boskabady, M. H., Alitaneh, S., and A. Alavinezhad. 2014. *Carum copticum* L.: A herbal medicine with various pharmacological effects. Review article. *BioMed. Res. Int.* 2014: 1-11.
- Büsse, S. and Ware, J. L. 2022. Taxonomic note on the species status of *Epiophlebia diana* (Insecta, Odonata, Epiophlebiidae), including remarks on biogeography and possible species distribution. *ZooKeys*: 1127: 79-90.
- Butt, F. A. and Anima, L. 2011. Studies on the population status of *Dumortiera hirsuta* (SW) Nees growing in Bhaderwah (North West Himalaya). *Indian J. Forest.* 34(1): 95-98.
- Callaghan, D. A. 2020. Status and ecology of the tropical liverwort *Dumortiera hirsuta* in England. *J. Bryol.* 42: 235-245.
- Carle, F. L. 2012. A new *Epiophlebia* (Odonata: Epiophlebioidae) from China with a review of epiophlebian taxonomy, life history, and biogeography. *Arthropod Syst. Phylog.* 70(2): 75-83.
- Cavers, F. 1910. The inter-relationships of the Bryophyta. *New Phytol.* 9(5): 157-186.
- Colon, C. M. R. 2000. Bryoflora of limestone sinkholes in the north-central karst zone of Puerto Rico. Ph. D. dissertation. University of Puerto Rico, Mayaguez, Puerto Rico, 68 pp.
- Crum, H. 1976. Mosses of the Great Lakes Forest, revised edition. Vol. 10, University Herbarium, University of Michigan, Ann Arbor, pp. 1-404.
- Daniels, A. E. D. 1998. Ecological adaptations of some bryophytes of the Western Ghats. *J. Ecobiol.* 10(4): 261-270.
- Devi, K., Kapila, S., and Rao, A. 2015. Seasonal variations in photosynthetic pigments of three species of Marchantiaceae. *Internat. J. Adv. Pharm. Bio. Chem.* 4: 713-718.
- Duckett, J. G. and Ligrone, R. 1993. Massive grana and stromal crystals in the chloroplasts of an extreme-shade liverwort *Dumortiera hirsuta* (W.) Nees (Marchantiales, Hepaticae). *Giorn. Bot. Ital.* 127: 320-322.
- Duckett, J. G. and Ligrone, T. 2006a. *Cyathodium* Kunze (Cyathodiaceae: Marchantiales), a tropical liverwort genus and family new to Europe, in Southern Italy. *J. Bryol.* 28: 88-96.
- Duckett, J. G. and Ligrone, R. 2006b. Novel features of the plastids in some deep-shade, antipodean thalloid liverworts. *Cryptog. Bryol.* 27: 75-83.
- Durant-Archibald, A. A., Salazar Allen, N., Garrido, A., Ledezma, J. G., and Gupta, M. P. 2018. An analysis of volatile components of the liverworts *Dumortiera hirsuta* subsp. *hirsuta* and *Dumortiera hirsuta* subsp. *nepalensis* (Dumortieraceae) from Panama and taxonomic observations on the species. *Nat. Prod. Comm.* 13: 1031-1034.
- Egertová, Z., Döbbeler, P., and Sochor, M. 2018. *Octosporopsis erinacea* and *Octospora kelabitiana* (Pezizales) – two new hepaticolous Ascomycetes from Borneo. *Mycol. Prog.* 17(1): 103-113.
- Evans, A. W. 1919. A taxonomic study of *Dumortiera*. *Bull. Torrey Bot. Club* 46: 167-182.
- Forrest, L. L., Salazar Allen, N., Gudiño, J. A., Korpelainen, H., and Long, D. G. 2011. Molecular and morphological evidence for distinct species in *Dumortiera* (Dumortieraceae). *Bryologist* 114: 102-115.
- Frahm, J. P., Frey, W., Kurschner, H., and Menzel M. 1996. Mosses and Liverworts of Mount Kinabalu. Natural History Publications, Kota Kinabalu.
- Furuki, T., Kido, M., Shirakawa, J., and Yoshikazu Hoshi, Y. 2012. Rediscovery of *Cyathodium cavernarum* Kunze from Kumamoto Prefecture. *Jap. Bryol. Res.* 8: 255-256.
- Gaston, A. 2020. Contribution à la connaissance de la Bryoflore du Tarn. Découverte de deux Hépatiques, *Dumortiera hirsuta* (Sw.) Nees et *Jubula hutchinsiae* (Hook.) Dumort., en Montagne Noire (Tarn, France). *Carnets Nat.* 7: 95-98.
- Glenny, D. 2002. *Cyathodium cavernarum* in Australia. *Australasian Bryol. Newslett.* 46: 5.
- Gradstein, R. 2006. Bryophyte Garden inaugurated in Cibodas Botanical Garden, Java, Indonesia. *Bryol. Times* 120: 11.
- Gradstein, S. R. 2011. Guide to the Liverworts and Hornworts of Java. In: Tjitrosoedirdjo, S. S. (ed.). *Seameo-Biotrop, Southeast Asian Regional Centre for Tropical Biology*, Bogor, Indonesia, 129 pp.

- Gradstein, R., Morales, C., Negritto, M. A., and Duckett, J. G. 2016. New records of liverworts and hornworts from the Sierra Nevada de Santa Marta, Colombia. *Cryptog. Bryol.* 37(4): 463-475.
- Hetherington, A. M. and Woodward, F. I. 2003. The role of stomata in sensing and driving environmental change. *Nature* 424: 901-908.
- Holttum, R. E. 1938. The ecology of tropical pteridophytes. In: Verdoorn, F. (ed.). *Manual of Pteridology*. Springer, Dordrecht, pp. 420-450.
- Iqbal, M., Butt, F. A., Langer, A., and Alam, A. 2011. Studies on the associates of *Conocephalum conicum* L. (Dumort.) and *Dumortiera hirsuta* Sw. (Nees). *Amer. J. Plant Sci.* 2(3), 283.
- Jasechko, S., Sharp, Z. D., Gibson, J. J., Birks, S. J., Yi, Y., and Fawcett, P. J. 2013. Terrestrial water fluxes dominated by transpiration. *Nature* 496: 347-350.
- Joshi, D. Y. 1993. In pursuit of the antibacterial property of *Lunularia cruciata* Dum. and *Dumortiera hirsuta*. *Adv. Plant Sci.* 6 (Suppl): 66-70.
- Junairiah, J., Sa'diyah, M., and Salamun, S. 2015. Identifikasi Metabolit Sekunder dan Aktivitas Antimikrob Ekstrak Etil Asetat *Dumortiera hirsuta*. *Sains Matemat.* 3(2): 45-49.
- Kamimura, M. 1973. Electron-microscopic studies on the fine structures of spore walls in Marchantiaceae (Hepaticae) I: On the fine structures of spore walls of *Dumortiera hirsuta*. *Bull. Kochi Gakuen College* 4: 15-18 + 1 p. images.
- Kapila, S., Devi, K., Rao, A., and Mahajan, A. 2014. Seasonal variations in carbohydrate, protein, free amino acids and enzyme activities in three species of Marchantiaceae. *Lindbergia* 37: 85-89.
- Kashyap, S. R. 1914. Morphological and biological notes on new and little known West Himalayan liverworts. I. and II. *New Phytol.* 13: 206-236.
- Kraut, L., Mues, R., Speicher, A., Wagmann, M., and Eicher, T. 1996. Carboxylated α -pyrone derivatives and flavonoids from the liverwort *Dumortiera hirsuta*. *Phytochemistry* 42: 1693-1698.
- Kumar, K., Nath, V., and Asthana, A. K. 2007. Concept of bryophytes in classical text of Indian ethnobotanical prospective. In: Nath, V. and Asthana, A. K. (eds.). *Current Trends in Bryology*. Bishen Singh Mahendra Pal Singh. Dehra Dun, India, pp. 215-220.
- Kwon, W., Kim, Y., and Park, J. 2019a. The complete chloroplast genome sequence of *Dumortiera hirsuta* (Sw.) Nees (Marchantiophyta, Dumortieraceae). *Mitochondrial DNA Part B*, 4(1): 318-319.
- Kwon, W., Kim, Y., and Park, J. 2019b. The complete mitochondrial genome of *Dumortiera hirsuta* (Sw.) Nees (Dumortieraceae, Marchantiophyta). *Mitochondrial DNA Part B*, 4(1): 1586-1587.
- Lang, W. H. 1905. On the morphology of *Cyathodium*. *Ann. Bot.* 19: 411-426.
- Li, J. L., Sulaiman, M., Beckett, R. P., and Minibayeva, F. V. 2010. Cell wall peroxidases in the liverwort *Dumortiera hirsuta* are responsible for extracellular superoxide production, and can display tyrosinase activity. *Physiol. Plant.* 138: 474-484.
- Lien, J. C. 1989. Taxonomic and ecological studies on the biting midges of the subgenus *Lasiohelea*, genus *Forcipomyia* from Taiwan. *臺灣省立博物館半年刊* 42(1): 37-77.
- Linde, J., Combrinck, S., Vuuren, S. van, Rooy, J. van, Ludwiczuk, A., and Mokgalaka, N. 2016. Volatile constituents and antimicrobial activities of nine South African liverwort species. *Phytochem. Lett.* 16: 61-69.
- Liu, H.-P., Gao, Z.-H., Cui, S.-X., Sun, D.-F., Wang, Y., Zhao, C.-R., Lou, H.-X., and Qu, X.-J. 2012. Inhibition of intestinal adenoma formation in APC^{Min/+} mice by riccardin D, a natural product derived from liverwort plant *Dumortiera hirsuta*. *PLoS ONE* 7(3): e33243. <<https://doi.org/10.1371/journal.pone.0033243>>.
- Loo, M. J. 2005. Problems and difficulties in studying hepatological cytology with reference to *Dumortiera hirsuta* (Sw.) Nees. *Sepilok Bull.* 4: 49-52.
- Loo, M. J., Suleiman, M., and Abdul Latip, M. 2005a. Cytological study on *Dumortiera hirsuta* (Sw.) Nees (Class Hepaticae). *Sepilok Bull.* 2: 9-16.
- Loo, M. J., Suleiman, M., and Abdul Latip, M. 2005b. A note on the tolerance range of *Dumortiera hirsuta* (Sw.) Nees cytoforms in Mount Kinabalu. *Sepilok Bull.* 3: 51-56.
- 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., Komala, I., Pham, A., Bianchini, J. P., Raharivelomanana, P., and Asakawa, Y. 2009. Volatile components from selected Tahitian liverworts. *Nat. Prod. Comm.* 4(10): 1934578X0900401015.
- Ludwiczuk, A., Raharivelomanana, P., Komala, I., Pham, A., Bianchini, J., and Asakawa, Y. 2010. Chemodiversity of Polynesian liverworts. *Planta Med.* 76(12): P022.
- Luthfiah, L., Setyati, D., and Arimurti, S. 2021. Antibacterial activity of liverworts of *Dumortiera hirsuta* (Sw.) Nees ethyl acetate extract against pathogenic bacteria. *Berkala Sainstek* 9(2): 75-80.
- Lye, K. and Pócs, T. 1997. New records and additions to the hepatic flora of Uganda. *Lidia* 4: 13-36.
- Marschall, M. and Beckett, R. P. 2005. Photosynthetic responses in the inducible mechanisms of desiccation tolerance of a liverwort and a moss. *Acta Biol. Szegediensis* 49: 155-156.
- Matsuo, A., Uto, S., Nakayama, M., and Hayashi, S. 1976. Sesquiterpene hydrocarbons of the liverwort, *Dumortiera hirsuta*. *Zeit. Naturfor. C* 31: 401-402.
- Mautsoe, P. J. 1997. Uptake of Cadmium and its effect on the physiology of the liverwort *Dumortiera hirsuta* (SW) Nees and the moss *Atrichum androgynum* (CM) Jaeg. M.S. thesis, University of Natal, Pietermaritzburg, 99 pp.
- Mautsoe, P. J. and Beckett, R. P. 1996. A preliminary study of the factors affecting the kinetics of cadmium uptake by the liverwort *Dumortiera hirsuta*. *S. Afr. J. Bot.* 62: 332-336.
- McAllister, C. T., Robison, H. W., and Davison, P. G. 2019. Dumortier's liverwort, *Dumortiera hirsuta* (Sw.) Nees (Hepaticophyta: Marchantiales: Dumortieraceae) in Arkansas. *J. Ark. Acad. Sci.* 73: 151-155.
- Meagher, D. 2002. *Cyathodium cavernarum* Kunze in Western Australia. *Hikobia* 13: 633-635.
- Miyoshi, N. 1973. Spore wall structure of *Dumortiera hirsuta* (Hepaticae). *Hikobia* 6: 251-253.
- Mukherjee, S., De, A., Ghosh, P., and Dey, A. 2012. In vitro antibacterial activity of various tissue types of *Dumortiera hirsuta* (Sw.) Nees from different altitudes of eastern Himalaya. *Asian Pacific J. Trop. Dis.* 2(suppl. 1): S285-S290.
- Nadhifah, A., Khujjah, M., Vitara, P. E., and Noviady, I. 2018. Bryophytes in Cibodas Botanical Garden: Diversity and potential uses. *Biosaintifika* 10: 455-463.
- Nair, M. C., Rajesh, K. P., and Madhusoodanan, P. V. 2005. Bryophytes of Wayanad in Western Ghats. *Malabar Natural History Society, Kozhikode*, 284 pp.

- O'Hanlon, M. E. 1934. Comparative morphology of *Dumortiera hirsuta*. Bot. Gaz. 96: 154-164.
- Ottley, T. 2014. BBS Spring Meeting 2014, Rolvenden. Field Bryol. 112: 66-75.
- Padalia, R., Verma, R. S., and Chauhan, A. 2015. The essential oil composition of *Melaleuca leucadendra* L. grown in India: A novel source of (*E*)-nerolidol. Indus. Crops Prod. 69: 224-227.
- Pant, G. B. and Tewari, S. 1984. On some aquatic bryophyte communities of Nainital and its environs (western Himalayas). Geoplytolog 14(2): 137-142.
- Patterson, P. M. 1933. A developmental study of *Dumortiera hirsuta* (Sw.) Nees. J. Elisha Mitchell Sci. Soc. 49: 122-150.
- Pianka, E. R. 1970. On r- and K-selection. Amer. Nat. 104: 592-597.
- Piippo, S. and Koponen, T. 2013. Bryophyte flora of Hunan Province, China. 16.: Complex thalloids (Marchantiopsida, Hepaticae). Polish Bot. J. 58: 179-192.
- Proctor, M. 1999. Water-relations parameters of some bryophytes evaluated by thermocouple psychrometry. J. Bryol. 21: 263-270.
- Proctor, M. C., Nagy, Z., Csintalan, Z., and Takacs, Z. 1998. Water-content components in bryophytes: Analysis of pressure-volume relationships. J. Exper. Bot. 49: 1845-1854.
- Proskauer, J. 1951. Notes on Hepaticae. II. Bryologist 54: 243-266.
- Queiroga, C. L., Cavalcante, M. Q., Ferraz, P. C., Coser, R. N., Sartoratto, A., and Magalhães, P. M. de. 2014. High-speed countercurrent chromatography as a tool to isolate nerolidol from the *Baccharis dracunculifolia* volatile oil. J. Essent. Oil Res. 26: 334-337.
- Reeb, C., Marline, L., Rabeau, L., Andriamanantena, A., Andriamiarisoa, R. L., Ranarijaona, H. L., and Pócs, T. 2018. A survey of Marchantiales from Madagascar. Acta Biol. Plant. Agr. 6(1): 3-72.
- Ruttner, F. 1955. Zur Ökologie tropischer Wassermoose. Arch. Hydrobiol. (Suppl.) 21: 343-381.
- Sakurai, K., Tomiyama, K., Kawakami, Y., Yaguchi, Y., and Asakawa, Y. 2018. Characteristic scent from the Tahitian liverwort, *Cyathodium foetidissimum*. J. Oleo Sci. 67: 1265-1269.
- Salazar Allen, N. 2001. *Cyathodium bischlerianum*, sp. nov. (Marchantiales) a new species from the Neotropics. Bryologist 104: 141-145.
- Salazar Allen, N. 2005. Cyathodiaceae. In: Bischler, H., Gradstein, S. R., Jovet Ast, S., Long, D. G., and Salazar Allen, N. Marchantiidae. Flora Neotrop. Monogr. 97: 131-147.
- Salazar Allen, N. and Korpelainen, H. 2006. Notes on Neotropical *Cyathodium*. Cryptog. Bryol. 27(85): 1-12.
- Salazar Allen, N., Lépiz, E., and Gracia, J. E. de. 2004. *Cyathodium foetidissimum* (Marchantiales), an Asiatic species new to tropical America. Bryologist 107: 41-46.
- Salazar Allen, N., Santana, A. I., Gómez, N., Chung, C., and Prashad Gupta, M. 2017. Identification of volatile compounds from three species of *Cyathodium* (Marchantiophyta: Cyathodiaceae) and *Leiosporoceros dussii* (Anthocerotophyta: Leiosporocerotaceae) from Panama, and *C. foetidissimum* from Costa Rica. Bol. Soc. Argentina Bot. 52: 357-370.
- Sari, P. R. 2014. Pengaruh ekstrak etanolik *Dumortiera hirsuta* (Swaegr.) Nees terhadap struktur mikroanatomi hepar dan ren mencit (*Mus musculus* L.) jantan yang diinfeksi *Plasmodium berghei* Vincke & Lips, 1948. Ph. D. dissertation, Universitas Gadjah Mada.
- Saritas, Y., Bülow, N., Fricke, C., König, W. A., and Muhle, H. 1998. Sesquiterpene hydrocarbons in the liverwort *Dumortiera hirsuta*. Phytochemistry 48: 1019-1023.
- Schiffner, V. 1938. Monographie der Gattung *Cyathodium* I. Ann. Bryol. 11: 131-140.
- Setyati, D., Luthfiah, L., and Arimurti, S. 2021. Antibacterial activity of liverworts of *Dumortiera hirsute* (sic) (Sw.) Nees ethyl acetate extract against pathogenic bacteria. [Aktivitas Antibakteri Ekstrak Etil Asetat Lumut Hati *Dumortiera hirsuta* (Sw.) Nees terhadap Bakteri Patogen]. Berkala Sainstek 9(2): 75-80.
- Shah, D. G. and Gujar, R. 2016. Diversity and distribution of liverworts in Gujarat—Current Status. Plant Sci. Today 3: 124-128.
- Shimamura, M. 2015. Aerial dispersal of tetraflagellated sperm cells in *Dumortiera hirsuta* (Marchantiophyta, Dumortieraceae). Hikobia 17(1): 27-29.
- Shimamura, M., Mineyuki, Y., and Deguchi, H. 2000. Monoplastidic meiosis in *Dumortiera hirsuta* (Bryophyta; Marchantiales). J. Hattori Bot. Lab. 88: 267-270.
- Shirzadian, S., Afshari Azad, H., and Khalghani, J. 2009. Introductory study of antifungal activities of bryophyte extracts. Appl. Entomol. Phytopathol. 77(1): 1-22.
- Slavik, B. 1965. The influence of decreasing hydration level on photosynthetic rate in the thalli of *Conocephalum conicum*. In: Slavik, B. (ed.). Water Stress in Plants. Junk, The Hague, pp. 195-201.
- Spencer, K. A. 1990. Host Specialization in the World Agromyzidae (Diptera). Springer, Netherlands, 444 pp.
- Srinivasan, K. S. 1968. An ecological and distributional resume of the liverworts and mosses of India. Nelumbo 10: 377-380.
- Srivastava, S. C. and Dixit, R. 1996. The genus *Cyathodium* Kunze. J. Hattori Bot. Lab. 80: 149-215.
- Surendra Kumar, M., Astalakshmi, N., Mithra, T., Nikhil, B. R., Zubair, R. P., Muhammed Ameer, V. K., and Babu, G. 2014-15. Evaluation of *Cyathodium cavernarum* Kunze aqueous extract for anthelmintic activity. Internat. J. Pharmacog. Phytochem. Res. 6: 778-779.
- Tatuno, S. 1938. Über Polyploidie und Geographische Verbreitung bei *Dumortiera hirsuta*. Bot. Mag. (Tokyo) 52: 434-441.
- Tatuno, S. 1939. Weitere untersuchungen über die Polyploidie und Geographische Verbreitung bei *Dumortiera hirsuta*. Bot. Mag. 53: 345-350.
- Timme, S. L. and Redfearn, P. L. 1997. Checklist of the liverworts and hornworts of the Interior Highlands of North America in Arkansas, Illinois, Missouri, and Oklahoma. Evansia 14: 89-105.
- Tiwari, N. K. 1929a. The discovery of germination of *Cyathodium* spores. J. Bombay Nat. Hist. Soc. 33: 1001-1002.
- Tiwari, N. K. 1929b. A preliminary note on the germination of the spores of *Cyathodium* sp. J. Indian Bot. Soc. 8: 139-143.
- Tiwari, N. K. 1935. Observations on the artificial germination of *Cyathodium* spores. J. Indian Bot. Soc. 14: 167-171.
- Tosun, A., Nagashima, F., and Asakawa, Y. 2015. Terpenoid and steroid components of selected liverworts. Chem. Nat. Comps. 51: 387-391.
- Toyota, M., Yoshida, T., Matsunami, J., and Asakawa, Y. 1997a. Sesquiterpene and other constituents of the liverwort *Dumortiera hirsuta*. Phytochemistry 44: 293-298.
- Toyota, M., Bardon, A., Kamiya, N., Takaoka, S., and Asakawa, Y. 1997b. Dumortenols, novel skeletal sesquiterpenoids

- from the Argentinian liverwort *Dumortiera hirsuta*. Chem. Pharm. Bull. 45: 2119-2121.
- Ulka J., S. and Karadge, B. A. 2010. Antimicrobial activity of some bryophytes (liverworts and a hornwort) from Kolhapur district. Pharmacog. J. 2(16): 29-32.
- 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.
- Wigginton, M. J. 2002. Checklist and distribution of the liverworts and hornworts of sub-Saharan Africa, including the East African Islands. Trop. Bryol. Res. Rep. 3: 1-88.
- Wigginton, M. J. and Grolle, R. 1996. Catalog of the Hepaticae and Anthocerotae of sub-Saharan Africa. Bryophyt. Biblio. 50: 1-267.
- Winkler, S. 1976. Die Hepaticae der Sierra Nevada de Santa Marta, Kolumbien. 1. Terrestrische, epixyle und epipetrische Arten. Rev. Bryol. Lichénol. 42: 789-827.
- Xie, C. and Lou, H. 2008. Chemical constituents from the Chinese bryophytes and their reversal of fungal resistance. Curr. Org. Chem. 12: 619-628.
- Xie, C.-F., Qu, J.-B., Sun, B., Guo, H.-F., and Lou, H.-X.. 2007. Dumhirone A, an unusual phenylethyl cyclohexadienone from the Chinese liverwort *Dumortiera hirsuta*. Biochem. Syst. Ecol. 35: 162-165.
- Xue, X., Sun, D.-F., Sun, C.-C., Liu, H.-P., Yue, B., Zhao, C.-R., Lou, H.-X., and Qu, X.-J. 2012. Inhibitory effect of riccardin D on growth of human non-small cell lung cancer: In vitro and in vivo studies. Lung Cancer 76: 300-308.
- Yadav, S., Srivastava, A., Biswas, S., Basu, S., Singh, S. K., and Mishra, Y. 2022. Seasonal changes in the antioxidative defence system of a liverwort *Dumortiera hirsuta*. J. Plant Growth Reg. 41: 1265-1275.
- Zhang, W., Gao, X.-D., Ding, X.-L., Sun, L.W., Zhuang, L.-J., Wang, J.-T., Peng, T., Liu, X.-X., and Tang, L.-Y. 2018. Chlorophyll content and photosynthetic efficiency of six thalloid bryophytes. Subtrop. Plant Sci. 47: 312-316.
- Zhang, Z., Li, X. N., Peng, T., and Xhao, C. H. 2004a. New records of luminous liverworts from the karst caves of Guangxi Province, P. R. China: *Cyathodium cavernarum* Kuntze and *C. smaragdium* [sic!] Schiffin.[sic!] ex Keissler (Cyathodiaceae, Hepaticae). Carsol. Sinica 23: 154-157.
- Zhang, Z.-H., Peng, T., Li, X.-N., and Zhao, C.-H. 2004b. A study on the bryophytes of karst cave threshold at Kunming Area in Yunnan Province, PR China. Carsologica Sinica 23: 229-233.

