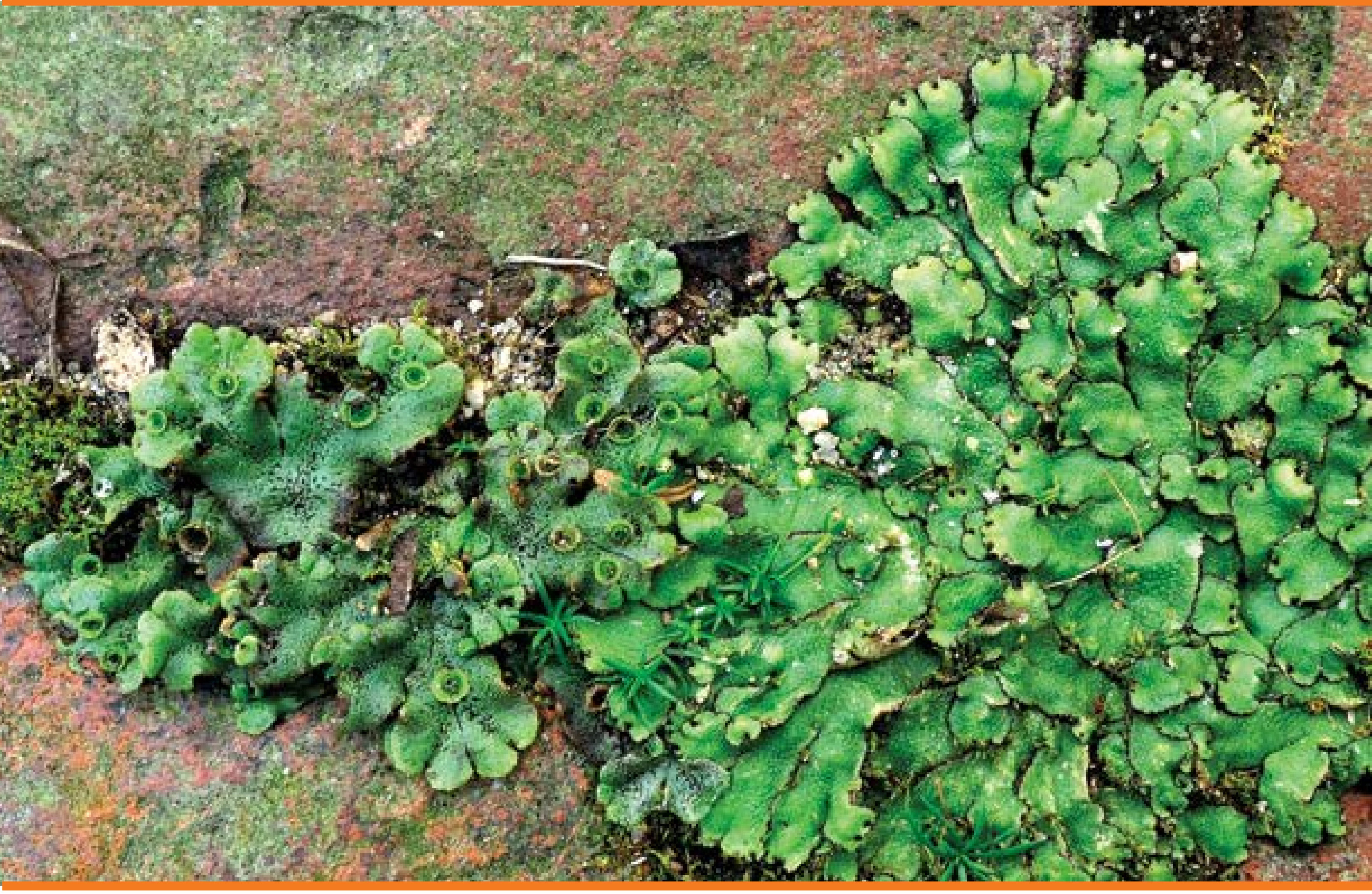
23

LIVERWORT

(*Reboulia hemisphaerica*)



A liverwort known to favor habitats in wild areas has established colonies on brick walkways in Center City.

Figure 23.1 Two colonies of liverwort growing from soil in a brick walkway. *Reboulia hemisphaerica* is on the right, and *Marchantia polymorpha* is on the left. The species on the right is reported to favor "wild" habitats; the species on the left can be weedy. The site of all photos of liverworts illustrated in this chapter is the alley in figure 23.7 unless stated otherwise.

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In 1799 the American Philosophical Society of Philadelphia published a list of liverworts found within a mile of the city of Lancaster, 93 kilometers west of Philadelphia. It was the first systematic account of liverworts published in North America. The author, Henrico Muhlenberg, credited his identifications to many authorities, all European. One of the liverworts he found is *Reboulia hemisphaerica*, which has no common name.[1]

Reboulia hemisphaerica in Center City

Reboulia hemisphaerica is shaped like a ribbon about 0.5 centimeter wide and 1–3 centimeters long. In Center City it anchors itself on soil in spaces between brick pavers. The ribbon, or *thallus,* grows flat along the top of the brick and bifurcates once or twice as it grows. If the surface of the soil is below the top of the brick, it grows up the side of the brick. Sometimes many thalli radiate from a sliver of soil between bricks.

For the past five years I have followed two colonies, each occupying less than a square meter on brick walkways, one a residential alley and the other a brick sidewalk along a narrow street (Naudain Street) of two-story row houses. Positioned away from foot traffic, the plants have completed their reproductive cycles, annually sending up spore-filled capsules on slender stalks.

Typical of liverworts and mosses, *R. hemisphaerica* produces male and female structures but no flowers or roots. Fertilization requires that sperm swim in rainwater, dew, or meltwater from male to female organs,[2] both of which are located on each plant.[3] The species is presumably named after the hemispherical shape of its female reproductive organ (archegonium).

Figure 23.2 Reboulia hemisphaerica behind a penny.

Figure 23.3 *Reboulia hemaesphaerica* between brick pavers.

Figure 23.4 Hemispherical structures that presumably inspired the name *hemisphaerica*. Each is a female reproductive organ (archegonium). The dark structure above each hemisphere is the male reproductive organ (antheridium). To fertilize eggs, sperm must swim from male to female organs in rainwater, dew, or meltwater. Photographed January 12, 2008.

Figure 23.5 Spore capsules in heads elevated on stalks of *Reboulia hemisphaerica*. Spores are products of sexual reproduction. Photographed April 26, 2009.

Figure 23.6 Liverwort heads elevated on stalks within a crack between brick pavers. The crack protects them from trampling, but impedes dispersal of spores.

Figure 23.7 Alley with liverworts, mosses, *Mazus,* and *Sagina*—which grow on soil between bricks on the right. The alley is located off Delancey Place near 25th Street. A locked gate has since been installed.

Figure 23.8 Japanese mazus (*Mazus pumilus*) in bloom, with liverwort (*Marchantia polymorpha*), birdseye pearl-wort (*Sagina procumbens*), and moss. Here Japanese mazus grows upright just off the beaten path. In areas where it is subjected to more trampling, its flowers stay almost flush with the bricks, as shown in the photo on page 318.

Figure 23.9 Ornately patterned elevated discs from the liverwort *Marchantia polymorpha* in May. They are stalked male organs (antheridea) that produce sperm. Other plants here are *Reboulia hemisphaerica*, birdseye pearlwort (*Sagina procumbens*), Japanese mazus (*Mazus pumilus*), and moss.

Figure 23.10 Star-shaped heads of female reproductive organs containing spore capsules of *Marchantia polymorpha* in July. Like the male sex organs, these female organs are elevated on stalks, but in May when the males are releasing sperm, the female organs are globular and flush with the ground. Photographed on a brick sidewalk near Fitler Square.

R. hemisphaerica is one of an estimated 7,500 species of liverwort worldwide.[4] Centuries ago the shape of some of these species was thought to resemble liver, which led to the vernacular name *liverwort*. *Wort* is from an archaic suffix that means "herb."[5]

R. hemisphaerica is distributed in temperate regions worldwide, including all continents except Antarctica.[6] It has been reported from eighteen of Pennsylvania's sixty-seven counties.[7] It tolerates human disturbance and drought, including several months of desiccation.[8]

Scarcity in "civilized" habitats in the North

R. hemisphaerica is not as common as one might expect considering its global distribution and tolerance of harsh conditions. A monograph on the liverworts and hornworts of eastern North America details its distinctive distribution. Written by Rudolf M. Schuster and published in six volumes from 1966 to 1992, the monograph spans nearly 6,000 pages. Schuster observed that *R. hemisphaerica* inhabits highly disturbed habitats in the North but not in the South:

> In the northern portion of our area one soon gets the impression that *R. hemisphaerica* is a "wild" species, rarely persisting after disturbance. Occasionally it occurs over calcareous cement on old stone walls in long-abandoned areas, but such close associations with "civilization" are rare.
>
> By contrast, in the southeast, it becomes abundant in "civilized," i.e., strongly disturbed, areas. For instance, the old brickwork of Fort Clinch, at Fernandina Fla., is absolutely covered by *Reboulia*. The soil peripheral to the old Biology building at Duke University (Durham, N.C.) supported extensive and luxuriant growths…Similarly, the species is common in lawns and on banks along city streets in Oxford, Miss., and at the edges of old fields in the surrounding country. Southward the tolerance of the species for disturbance is evidently much higher than it is northward. Furthermore, southward (and south-westward) its distribution rarely appears to show any correlation with the occurrence of calcareous soil or rocks.[9]

What might account for the establishment of thriving colonies of *R. hemisphaerica* in downtown Philadelphia—just the kind of "civilized" northern habitat where Schuster found it rarely persisted? One possibility is that global warming and Philadelphia's urban heat island displaced to the north the geographic zone where this liverwort tolerates disturbance. Another possibility is that reduction in air pollution expanded this plant's acceptance of "civilization."

Air pollution a century ago

In the nineteenth and first half of the twentieth century, soot blanketed northern cities, as described in a pamphlet published by the American Civic Association in 1908:

> The dweller in a town burning bituminous coal needs no definition of the smoke nuisance. The great cloud that hangs over the city like a pall can be seen from any neighboring hilltop, and the dweller within is only too well aware of the splotches of soot that settle on every object in the city, bedimming buildings, spoiling curtains, injuring books, and increasing the laundry bill. The direct menace to the public health in fostering tuberculous conditions by loading the air with carbon particles to lodge in the lungs, and by causing housekeepers to keep the windows shut for fear of the soot that floats in when they are open, is equaled only by the mentally and physically depressing effect of the pall which shuts out the life-giving and germ-destroying sunshine. Our city parks have mostly lost their evergreen character,

where it existed, as conifers cannot long endure city smoke. Thus one treatment of the most pleasing variations in landscape is made impossible.[10]

Figure 23.11 B & O (Baltimore and Ohio) passenger train billowing smoke as it chugs south at Spruce Street along the Schuylkill River, 1912. (Photo courtesy of PhillyHistory.org, a project of the Department of Records of the City of Philadelphia)

Impact of air pollution on mosses and liverworts

Severe air pollution eliminates populations of bryophytes, which include mosses and liverworts. Oliver S. Gilbert investigated the impact of air pollution from combustion of coal in an urban area in Britain in the 1960s.[11] He found that, approaching a city center from a distance of 17 kilometers, the number of species of bryophytes progressively declined. The number fell by half to sixteen, of which only four were common in the city center. The four common ones were cosmopolitan mosses, such as silvergreen bryum moss (*Bryum argenteum*),[12] which is abundant in Center City, Philadelphia, and may actually benefit from air pollution.[13] One of the uncommon species present in the center of this coal town was a liverwort, *Marchantia polymorpha,* which is present but rare in Center City; it grows in the alley with *Reboulia hemisphaerica,* a liverwort Gilbert did not encounter. Gilbert determined that the primary cause for the drop in diversity of bryophytes in the city center was air pollution, specifically sulfur dioxide.[14] Many other studies have since confirmed the negative impact of air pollution on the diversity of bryophytes.[15]

Figure 23.12 Silvergreen bryum moss (*Bryum argenteum*). It is abundant in Center City and thrives in air pollution.

Abatement of air pollution in Philadelphia

In 1904 the City of Philadelphia took its first steps to control air pollution. It passed an ordinance regulating emission of smoke, measured using a color scale of darkness. The Bureau of Boiler Inspectors enforced the ordinance, based on standards from the color scale. In 1949 the city established an Air Pollution Control Board with powers of enforcement. Implementation of new regulations shut down almost a thousand incinerators. Philadelphia Electric Company (PECO) reduced sulfur and particulate emissions. The sulfur content of heating oil was reduced, and the city banned the burning of coal for heating and cooking. In three decades starting in 1966, sulfur dioxide in the city fell by 94 percent, particulate pollution by 93 percent, and nitrogen oxides by 61 percent.[16] Pollution from sulfur dioxide in the city is now below levels toxic to bryophytes,[17] and particulate air pollution meets standards of air quality established by the U.S. Environmental Protection Agency under the Clean Air Act.[18]

Industrial melanism in Great Britain

Industrial air pollution in Philadelphia declined to levels believed to be safe, but did the decline make a measurable difference to plants and animals in cities? In 1896 James William Tutt, a British lepidopterist, noted that British moths that rested on tree trunks in industrial regions blackened by soot had evolved black, or *melanic,* forms, which camouflaged them better than their previous pale forms. Here is how Tutt described the transformation of the peppered moth (*Amphidasys betularia,* currently named *Biston betularia*):

> The speckled *A. betularia*, as it rests on a trunk in our southern woods, is not at all conspicuous, and looks like a natural splash or scar, or a piece of lichen, and this is its usual appearance and manner of protecting itself. But, near our large towns where there are factories, and

> where vast quantities of soot are day by day poured out from countless chimneys, falling and polluting the atmosphere with noxious vapours and gases, this Peppered Moth has, during the last fifty years, undergone a remarkable change. The white has entirely disappeared, and the wings have become totally black, so black that it has obtained the cognomen "negro" from naturalists. As the manufacturing centres have spread more and more, so the "negro" form of the Peppered Moth has spread at the same time and in the same districts.[19]

Tutt hypothesized that, near industrial centers, natural selection favored the black form, which concealed the moth and protected it from birds.

After passage of the Clean Air Act in Britain in 1956, air pollution in Britain decreased,[20] populations of lichens recovered,[21] and the frequency of black forms in populations of moths reverted toward levels that had existed in the nineteenth century before industrial pollution.[22] Despite controversy,[23] recent studies confirmed Tutt's hypothesis.[24] Industrial melanism is considered a textbook case of evolution in action.[25]

Industrial melanism in Philadelphia

In 1961 Denis F. Owen at the University of Michigan reported finding industrial melanism in moths around Philadelphia, starting in 1922. He also found it around Detroit, New York City, and Pittsburgh around the same time.[26] In 1963 President Lyndon Baines Johnson signed the Clean Air Act, the first of a series of federal legislative steps to reduce air pollution.[27] In 2002, Bruce S. Grant and Lawrence L. Wiseman at the College of William and Mary in Williamsburg, Virginia, reported that the frequency of melanic forms in populations of American peppered moths in Michigan and Pennsylvania declined from more than 90 percent in 1959 to 6 percent by 2001. In Virginia, melanic forms were practically absent throughout this period.[28]

Recovery of tree moss after abatement of pollution

Industrial melanism in moths surfaced in the nineteenth and early twentieth century and has abated over the last half century. It puts into an ecological context the disappearance and return of urban bryophytes vulnerable to air pollution. Examples are tree mosses, which are exquisitely sensitive to sulfur dioxide in the air.[29] In *The Moss Flora of New York City and Vicinity,* published in 1916, Abel Joel Grout noted the absence of *Orthotrichum* tree mosses downtown.

> As one gets away from the city these mosses begin to appear in normal quantities. For this reason the author is inclined to believe that the gases produced in the city are the cause of this marked absence of arboreal mosses.[30]

A survey of mosses of Philadelphia in 1933 found no *Orthotrichum* tree mosses, and no reports of them since the nineteenth century. It blamed disappearance of mosses in this region on urbanization and smoke.[31] I recently discovered *Orthotrichum pumilum* thriving on tree trunks in Center City five blocks from a municipal power plant. It grows with a second tree moss, *Syntrichia papillosa*. The last published record of these mosses in Philadelphia was by Thomas Potts James,[32] who died in 1882.[33] Except for his specimens, none from Philadelphia is present in collections housed in the Academy of Natural Sciences of Drexel University.

Following reduction of sulfur dioxide pollution, the return of bryophytes on oak trees in London was reported as "spectacular."[34] In Britain, Germany, and Serbia, recent surveys have demonstrated an unprecedented diversity of urban bryophytes, including species that are threatened or endangered.[35] Paradoxically, vehicular traffic may enrich diversity of urban bryophytes by dispersing them[36] and by producing nitrogen and acid pollutants that promote or disrupt their growth, depending on the species and the acid buffering of their substrate.[37]

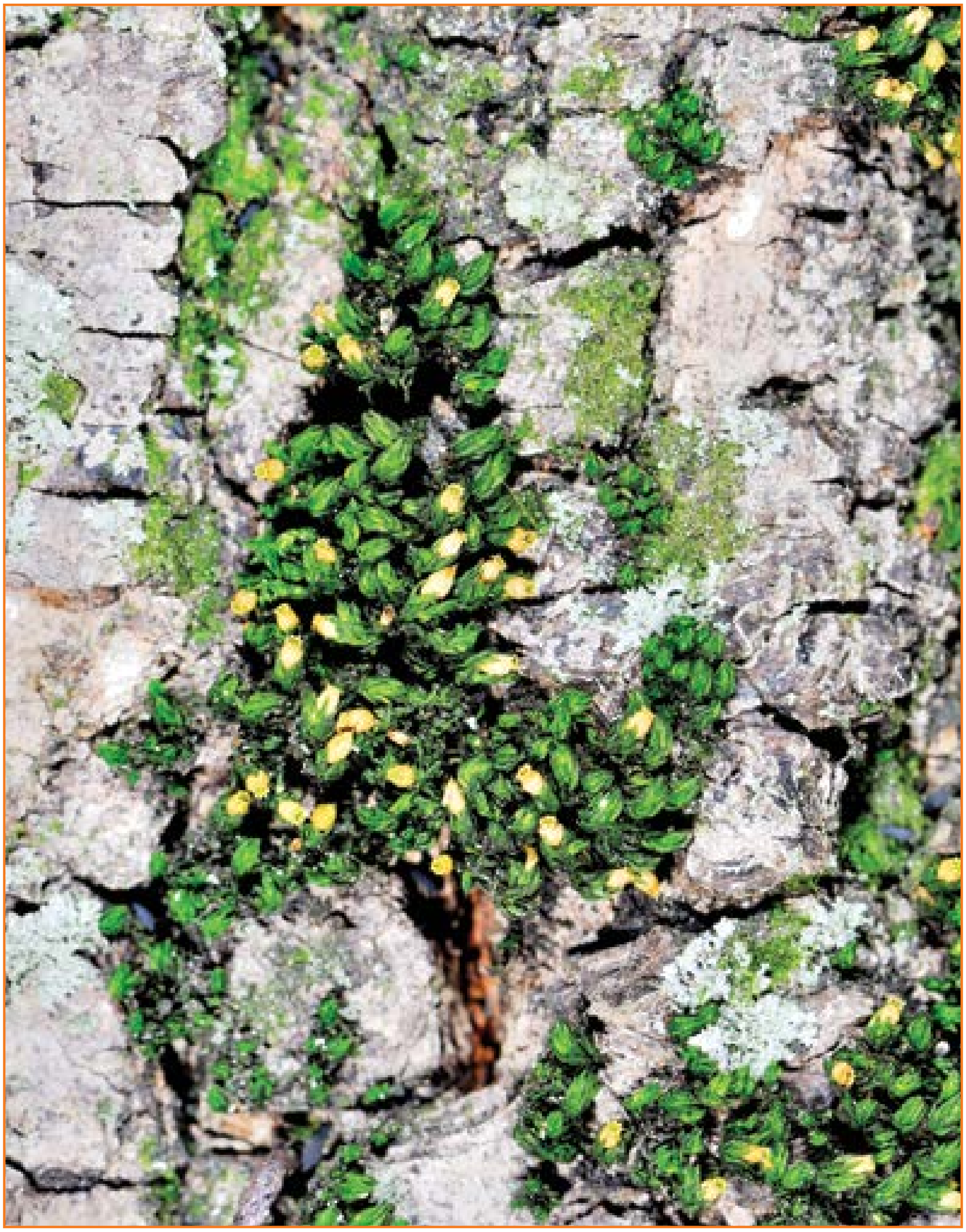

Figure 23.13 Tree moss (*Orthotrichum pumilum*) on bark of a street tree (Norway maple, *Acer platanoides*) in Center City, 2010. By the early twentieth century, sulfur dioxide air pollution had caused local extinction of *Orthotrichum* tree mosses in New York City and Philadelphia. Levels of sulfur dioxide have since declined, allowing the return of tree mosses like this one.

Figure 23.14 Lichens covering stucco on rear wall of South Square Market, which fronts on South Street. Air pollution suppresses the diversity of lichens, but some lichens thrive in it.

Refuges from air pollution

Tree mosses like *Orthotrichum* may be more sensitive to air pollution than other bryophytes, such as *R. hemisphaerica*, which grows on soil over rocks. In 1952, when industrial melanism was documented in Pennsylvania, *R. hemisphaerica* was collected growing on a rocky, shaded bank in Philadelphia.[38] In his classical studies demonstrating the adverse impact of air pollution on bryophytes in Britain, Gilbert noted that shelter and substrate can protect bryophytes from pollution.[39] *R. hemisphaerica* may have survived air pollution in Philadelphia by colonizing protected sites buffered from sulfur dioxide.

Dispersal of *R. hemisphaerica*

R. hemisphaerica is found in less than half as many Pennsylvania counties as the cosmopolitan liverwort *Marchantia polymorpha*,[40] which is regarded as a weed in the northeastern United States.[41] The two species are most easily distinguished by cup-like structures on their surfaces; only *M. polymorpha* has them. The cups contain asexual propagules (gemmae) that are dispersed by rain.[42] Functioning as simple structures for dispersal and reproduction, gemmae endow *M. polymorpha* with efficient mechanisms for colonization of ephemeral, fragmented habitats such as those present downtown. The moss *Bryum argenteum*, abundant in Center City, disperses by spores, but also by plant fragments transported on the soles of shoes.[43]

Figure 23.15 Liverwort *Marchantia polymorpha* with cups containing vegetative propagules (gemmae), minute asexually generated bodies that can disseminate and develop into new plants. When rainwater strikes the cups, it disperses the propagules. *M. polymorpha* can spread quickly and become weedy. It also reproduces sexually, making spores. Unlike this liverwort, *Reboulia hemisphaerica* produces no vegetative propagules.

Dispersal of spores from refuges buffered or sheltered from pollution is a plausible route by which *R. hemisphaerica* colonized brick walkways in Center City. Center City, with its nineteenth-century landscape largely intact, gave this liverwort time to disperse and colonize despite its lack of gemmae.

Springtails as possible agents of dispersal

Insects may have helped *R. hemisphaerica* to disperse in Center City. I watched garden springtails (*Bourletiella hortensis*) climb up stalks of this liverwort to the heads containing spore capsules. They clambered around the heads and climbed down with liverwort fragments stuck to their backs. The fragments were from sticky, breakable filaments that dangle just under the spore capsules; pieces fall off and adhere to the stems. The long filaments are characteristic of the species, and their function has never been described. Spores released from liverwort capsules would strike these filaments and presumably adhere to them, just as the filaments adhere to the springtail and stems. Carrying the filaments, the springtail would disperse these spores. I observed springtails on *R. hemisphaerica* on different days and on spore capsules in different stages of development, including mature capsules ready to release their spores. This arthropod is common and distributed in all continents.[44] The sticky filaments could disperse spores on other carriers, such as birds or people. Dispersal of spores of *R. hemisphaerica* by animals has not been previously reported, but flies disperse spores of dung moss,[45] and ants disperse propagules (gemmae) of aulacomnium moss.[46] In Center City blow flies (Calliphoridae) disperse spores of the stinkhorn mushroom (*Mutinus caninus*), which attracts them.[47]

Figure 23.16 Garden springtail (*Bourletiella hortensis*) on stalked head of *R. hemisphaerica* bearing spore capsules. Sticky, breakable, white filaments dangle below the spore capsules.

Figure 23.17 Garden springtail (*Bourletiella hortensis*) descending stalk of *R. hemisphaerica*. Fragments of adhesive white filaments from below spore capsules have stuck to its back and head. Transported by the springtail, these fragments could disperse the liverwort's spores.

Figure 23.18 Stinkhorn mushroom (*Mutinus caninus*) sprouting in mulch in landscaped border along the Schuylkill River Trail in Center City. It attracts blow flies (Calliphoridae) that disperse its spores.

Continental drift

What advantage would such complex dispersal offer *R. hemisphaerica*, given that the plant has populated all continents but Antarctica? Marie-Catherine Boisselier-Dubayle and her colleagues at the Muséum National d'Histoire Naturelle in Paris investigated the genetics of *R. hemisphaerica* from five continents. They showed that genetically similar populations are found on continents separated by oceans. Doubting the capacity of this liverwort to disperse long distances, they could not account for this wide distribution.[48]

Continental drift has been invoked to explain species of liverworts with populations separated by oceans,[49] but continental drift does not fit with *R. hemisphaerica's* genetic uniformity. Populations separated from one another by oceans since the continents drifted apart almost 100 million years ago would be expected to have undergone genetic divergence.[50] Presumably, *R. hemisphaerica* has somehow managed to disperse across oceans.

The diameter of this liverwort's spores is 70–80 microns,[51] compared to 5–50 microns for most fungal spores,[52] and 22–32 microns for ragweed pollen grains.[53] A single capsule of *R. hemisphaerica* produces around 3,000 spores,[54] which are viable for at least five months.[55] Considered on a scale that encompasses billions of spores over millions of years, the hypothesis that rare meteorological events blew spores of *R. hemisphaerica* into the stratosphere and across oceans seems possible.[56] Mosses experimentally exposed to the stratosphere by a weather balloon survived despite temperatures of -30°C.[57]

Compared to dispersal across oceans, dispersal of *R. hemisphaerica* within Philadelphia seems prosaic. Possible carriers of its spores include wind, water, vehicles, springtails, birds, rodents, and people.