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MAKING THE MOST OUT OF SMALL THINGS:
TWENTY-FIVE YEARS OF STUDYING
A LITTLE-KNOWN GROUP OF ORGANISMS

by

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THE SERIES

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1. Myxomycetes.



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In addition to his teaching and research, Steve enjoys running, nature study, reading, and photography.

Making the Most Out of Small Things: Twenty-five Years of Studying a Little-known Group of Organisms

by
Steven L. Stephenson

“It is by studying little things that we attain the great knowledge of having as little misery and as much happiness as possible.”
— Samuel Johnson (from Boswell’s London Journal, 1762–63)

The myxomycetes (plasmodial slime molds) are a group of fungus-like organisms usually present and sometimes abundant in terrestrial ecosystems. Because of their life-history strategy and relatively small size, myxomycetes tend to be overlooked in nature; however, careful searching of suitable substrates, especially after a period of rainy weather during summer and autumn, almost invariably will yield a number of their fruiting bodies. Although “slime mold” is not a particularly attractive common name, the fruiting bodies they produce exhibit incredibly diverse forms and colors and are often objects of considerable beauty. Moreover, since those of many of the more common species achieve macroscopic dimensions, they can be collected and preserved for study in much the same way as the fruiting bodies of fungi or even specimens of bryophytes, lichens, and vascular plants. If handled carefully, properly stored myxomycete fruiting bodies will remain suitable for study for many years (Stephenson & Stempen 1994).

There are approximately 875 recognized species of myxomycetes (Lado 2001), and these have been placed in six different taxonomic orders (Ceratiomyxales, Echinosteliales, Liceales, Physarales, Ste-monitales, and Trichiales). Members of the Ceratiomyxales, however, are distinctly different from members of the other orders, and many modern authors have removed these organisms from the myxomycetes and reassigned them to another group of slime molds, the protostelids. The exact evolutionary affinities of the myxomycetes are still debated, but these organisms constitute a well-defined and homogenous group. Evidence from DNA sequence analysis suggests that the myxomycetes

are a very old group. Even what appear to be closely related taxa on the basis of morphological similarity may have diverged from each other a long time ago. The phylogenetic relationships among the orders are not known and the same is true for phylogenetic relationships among the families in each order. Because of their small size and the limited array of morphological characters upon which their taxonomy is based, determination of what constitutes a natural biological species, in the same sense that the concept is used for many of the more familiar groups of organisms, is sometimes rather problematic. Approximately 50% of all described species of myxomycetes are known only from the type locality or fewer than five localities worldwide. It seems likely that many of these "species" are no more than morphologically distinct biotypes present in particular habitats or confined to a certain regions of the world.

The life cycle of a myxomycete involves two very different trophic (or feeding) stages, one consisting of uninucleate amoebae, with or without flagella, and the other consisting of a distinctive multinucleate structure, the plasmodium (Martin et al. 1983). Under favorable conditions, the plasmodium gives rise to one or more fruiting bodies containing spores. The fruiting bodies produced by myxomycetes are somewhat suggestive of those produced by mushrooms, although they are considerably smaller, usually no more than 1–2 mm tall. The spores of myxomycetes are, for most species, apparently wind-dispersed and complete the life cycle by germinating to produce the uninucleate amoeboid flagellate cells. These feed and divide by binary fission to build up large populations in the various microhabitats in which these organisms occur. The transformation from one trophic stage to the other in the myxomycete life cycle is, in most cases, the result of fusion between two compatible haploid amoeboid flagellates, which produces a diploid zygote that feeds, grows, and undergoes repeated mitotic nuclear divisions to develop into the plasmodium. However, some species are known to contain strains that are diploid throughout their entire life cycle. Bacteria represent the primary food resource for both trophic stages, but plasmodia are also known to feed upon yeasts, cyanobacteria, and fungal spores and hyphae.

Under adverse conditions, such as drying out of the immediate environment or low temperatures, a plasmodium may convert into a hardened, resistant structure called a sclerotium, which is capable of reforming the plasmodium upon the return of favorable conditions. More-

over, amoeboflagellate cells can undergo a reversible transformation to dormant structures called microcysts. Both sclerotia and microcysts can remain viable for long periods of time and are probably very important in the continued survival of myxomycetes in some ecological situations and habitats, such as in deserts or on the bark surface of living trees.

Identification of myxomycetes is based almost entirely upon features of the fruiting bodies produced by these organisms. Fruiting bodies (also referred to as “sporophores” or “sporocarps” by some authors) occur in four generally distinguishable forms or types, although there are a number of species that regularly produce what appears to be a combination of two types, apparently in response to certain (as yet undetermined) environmental factors. The most common type of fruiting body is the sporangium, which may be sessile or stalked, with wide variations in color and shape. The actual spore-containing part of the sporangium (as opposed to the entire structure, which also includes a stalk in those forms characterised by this feature) is referred to as a sporotheca. Sporangia usually occur in groups, since they are derived from separate portions of the same plasmodium. A second type of fruiting body, an aethalium, is a cushion-shaped, sessile structure. Aethalia are presumed to be masses of completely fused sporangia and are relatively large, sometimes exceeding several centimeters in extent. A third type is the pseudoaethalium (literally a false aethalium). This type of fruiting body, which is comparatively uncommon, is composed of sporangia closely crowded together. Pseudoaethalia are usually sessile, although a few examples are stalked. The fourth type of fruiting body is called a plasmodiocarp. Almost always sessile, plasmodiocarps take the form of the plasmodial veins from which they were derived. The most commonly encountered combination of two types of fruiting body is represented by those species that produce forms intermediate between sporangia and plasmodiocarps. A few species, though, produce forms intermediate among sporangia or plasmodiocarps and pseudoaethalia.

A typical fruiting body consists of as many as six primary structural components: hypothallus, stalk, peridium, columella, capillitium, and spores. In some fruiting bodies a pseudocolumella or a pseudocapillitium may be present. Not all of these components are present in all fruiting body types. The hypothallus is a plasmodial remnant that forms an extension of the base for one or more fruiting bodies and, in doing so, connects the stalk (if this structure is present) to the substrate. It may be

dull or brightly coloured, thin and delicate or coarse. In some instances, the hypothallus may be composed of calcium carbonate, while in others the hypothallus consists largely of other substances. This structure is not always in evidence and is of limited taxonomic value for most species.

The stalk, on the other hand, is an exceedingly important characteristic for identification. Called a stipe in some texts, the stalk may vary in length, colour, and texture. In some species, the stalk is opaque, while in others it is translucent. The stalk may also be coated with lime or filled with granular or spore-like structures. The peridium is a covering enclosing the spore mass of the fruiting body. It may or may not be evident in a mature fruiting body. In some species, the peridium persists as a calyculus, a cup-like structure holding the bottom of the spore mass. The presence or absence of the calyculus may be used as a diagnostic feature along with the manner in which the fruiting body opens. The peridium may split open along clearly discernible lines of dehiscence, as a pre-formed lid, or in an irregular pattern. In an aethalium, the relatively thick covering over the spore mass is referred to as a cortex rather than a peridium.

The columella appears as an extension of the stalk into the sporotheca, although it may not resemble the stalk. In a sessile fruiting body, the columella may appear as a dome-shaped structure on the inside of the peridium where the latter contacts the substrate. A pseudocolumella is a columella-like structure that does not attach to the stalk. The pseudocolumella is found only in the order Physarales, existing as a lime mass within the spore mass.

Many species of myxomycetes have a capillitium, which consists of a system of thread-like elements, within the spore mass, either as a single interconnected network or as many free elements called elaters. Capillitial elements may be smooth, sculptured or spiny or they may appear to consist of several interwoven strands. Some members of the Physarales have limy capillitial elements (a condition referred to as a badhamioid capillitium), while others have limeless tubules connecting to lime nodes (referred to as a physaroid capillitium). The capillitial elements are separate from the spores within the spore mass and are not connected to them. Capillitial elements, however, may be attached to the columella, pseudocolumella, or, less commonly, the inner surface of the peridium. Some elements may be elastic, allowing for expansion when the peridium opens, while other types are hygroscopic and capable of

dispersing spores by a twisting motion. A pseudocapillitium is present in some aethalia and pseudoaethalia producing species. Pseudocapillitial elements are highly variable in size and shape, and may appear as bristles, threads or perforated plates.

Spores range in size from slightly less than 5 to occasionally more than 15 μm in diameter. Nearly all of them appear to be round and most are ornamented to some degree. In fact, entirely smooth spores may not exist. Spore ornamentation can range from almost smooth to distinctly warted (with short blunt projections), spiny (with sharp pointed projections), or reticulate (covered by a network of ridges). Warts or spines vary in size from small (minutely warted or spiny) to relatively large (coarsely warted or spiny) and may be scattered uniformly over the surface of the spore or occur in groups. Some spores are characterised by a variant of one or more of these morphological expressions. Spore shape (for those examples that are not round) and size are very important in identification. Spore color in mass can be classified as either dark (found in the orders Stemonitales and Physarales) or light to brightly colored (all of the other orders). Dark spores include the colors black, violet, brown, and purplish brown. Brightly colored spores may be red, yellow, orange, white, pale grey, pink, light or rusty brown. In a few species, the spores occur in clusters.

Myxomycetes have been known from their fruiting bodies since at least the middle of the seventeenth century, but because they spend most of their life cycle as true eukaryotic microorganisms (when they cannot be observed directly in the field), relatively little is known about their distribution and ecology. As a result, however, of studies centered at Fairmont State College but carried out at various localities throughout the world over the past twenty-five years, a considerable body of information on myxomycete distribution, ecology, and biodiversity has been accumulated. The availability of this information has allowed us to develop a much better understanding of these truly fascinating organisms, including such things as their global patterns of occurrence, the various microhabitats they occupy, and the roles they play in nature.

First of all, the majority of species of myxomycetes are probably cosmopolitan, and at least some species apparently occur in any terrestrial ecosystem with plants (and, thus, plant detritus) present. For example, I have collected specimens from areas of tundra near the edge of the Arctic Ocean at 71 degrees north latitude, and studies car-

ried out on Macquarie Island and Campbell Island in the south polar region yielded a surprising number of species. A few species, however, do appear to be confined to the tropics or subtropics, and others have been collected only in temperate regions. Compared to most other organisms, myxomycetes show very little evidence of endemism, with the same species likely to be encountered in any habitat on earth where the environmental conditions suitable for its growth and development apparently exist. Nevertheless, a certain degree of distinctiveness for the floras of arctic, subarctic, temperate, tropical, and subtropical regions of the world may be recognized. For example, in the tropics and subtropics, members of the Physarales tend to make up a much greater proportion of both collections and species than elsewhere, whereas members of the Liceales tend to be conspicuously underrepresented.

Temperature and moisture are thought to be the main limiting factors for myxomycetes, and species richness and biodiversity tend to increase with increasing biodiversity and biomass of the vascular plants providing the resources (various types of detritus) that support the bacteria and other microorganisms upon which the two trophic stages in the myxomycete life cycle feed. The pH of the substrates potentially available to myxomycetes in a particular habitat also represents an important factor influencing the distribution of these organisms. Although many myxomycetes appear to have a relatively wide pH tolerance, this is not the case for all species. Härkönen (1977), who measured the pH of substrates upon which fruitings occurred in a study of the distribution patterns of myxomycetes associated with the bark of living trees in southern Finland, concluded that species of myxomycetes have different pH optima and amplitudes. In her study, some species seemed to prefer an acidic substrate, whereas others never developed under low pH conditions. I found the same to be true for both bark and forest floor litter in a study carried out in the Mountain Lake region of southwestern Virginia (Stephenson 1989). In general, members of the Stemonitales developed under more acidic conditions than did members of the Physarales and the Trichiales.

Although the ability of a plasmodium to migrate some distance from the substrate within which it developed has the potential of obscuring myxomycete-substrate relationships, field observations and collections by numerous workers indicate that the fruiting bodies of particular species of myxomycetes tend to be rather consistently as-

sociated with certain types of substrates. For example, some species almost always occur on wood or bark, whereas others are more often found on dead leaves and other plant debris and only rarely occur on wood or bark. The reasons for substrate specificity in myxomycetes are not known but probably involve the interaction of a number of physical and biotic factors.

Much of what is known about the distribution and ecology of myxomycetes in terrestrial ecosystems has been derived from studies carried out in temperate forests of the Northern Hemisphere. In such forests, myxomycetes are associated with a number of different microhabitats. (As used herein, the term "microhabitat" simply denotes a specific portion of the total forest habitat, as defined by Stephenson [1989].) These include coarse woody debris (e.g., decaying logs, stumps, and branches) on the forest floor, the bark surface of living trees, forest floor litter, the dung of herbivorous animals, and aerial portions of dead but still standing herbaceous plants. Each of these microhabitats tends to be characterized by a distinct assemblage of species (Stephenson 1988, 1989).

The myxomycetes associated with coarse woody debris are the best known, since the species typically occurring in this microhabitat tend to be among those characteristically producing fruiting bodies of sufficient size to be detected in the field. Many of the more common and widely known myxomycete taxa, including various species of *Arcyria*, *Lycogala*, *Stemonitis*, and *Trichia*, are predominantly found on woody substrates in the field.

Much less is known about the myxomycetes associated with the microhabitats represented by the bark surface of living trees and forest floor litter. The primary reason for this is that many of the species involved are rather inconspicuous or sporadic in their occurrence and thus difficult to detect in the field. However, the moist chamber culture technique as it applies to myxomycetes (as described by Stephenson & Stempen [1994]) provides a convenient and often very productive method of supplementing field collections when studying such microhabitats as bark and litter. Since its introduction, the technique has been used with considerable success by many researchers. More than a hundred species of bark-inhabiting (or corticolous) myxomycetes have been collected from bark in the field or cultured from bark in the laboratory. In some instances, a particular species has been recorded

from bark in the field and in the laboratory. Many of these are also known to occur in other microhabitats, but at least some species seem restricted to bark of living trees. Prominent examples include various species of *Echinostelium*, *Licea*, and *Macbrideola*.

The litter microhabitat of temperate forests is more heterogeneous than the bark microhabitat, since it usually consists of a mixture of leaves from different tree species along with other types of plant debris, such as pieces of bark, fragments of wood, fruits, seeds, inflorescences, and small twigs. Some of the species associated with litter also occur in bark, but others (e.g., various species of *Diderma*, *Didymium*, and *Physarum*) are found predominantly or even exclusively on litter. The assemblage of species associated with litter derived from coniferous trees like spruce, pine, and hemlock tends to be distinctly different from that associated with litter from broadleaf trees such as maple, oak, and birch.

Another microhabitat potentially available for myxomycetes is represented by the dung of herbivorous animals. A few species seem to occur predominantly or even exclusively on dung. Dung is a highly complex substrate, and the exact role of myxomycetes in the communities of organisms associated with its decomposition is not yet known. Dung, however, has several characteristics seemly unusually favorable for myxomycetes: high moisture content, a large microbial population, and nutrient richness. Moreover, dung also has a much higher pH than most of the other substrates upon which myxomycetes are typically found. In moist tropical forests, animal dung decomposes very rapidly and usually does not persist long enough to serve as a potential microhabitat for myxomycetes. In temperate forests, dung also tends to be of minor importance, but in some high-latitude and desert ecosystems, it becomes one of the major substrates on which myxomycetes are encountered.

Myxomycetes also are known to occur in forest soils, but their occurrence in this microhabitat has received very little study. Various species of *Didymium* appear to be the most widespread and abundant myxomycetes present in soil. Interestingly, myxomycetes seem to be relatively more abundant in grassland and agricultural soils than in forest soils, whereas the distribution patterns for the amoeboid cells of dictyostelids (cellular slime molds) are exactly the reverse. Just why this is the case is not yet known. My studies carried out within the Fernow Experimental Forest in eastern West Virginia have indicated that single

genetic strains of particular species of myxomycetes may exist over considerable areas. One such example was recorded from samples collected over a total area of 1.3 square kilometers.

Our knowledge of the distribution and ecology of myxomycetes in tropical forests is still rather limited, but available data (largely the result of field-based studies centered at Fairmont State College [e.g., Schnittler & Stephenson 2000] and carried out in several areas of Central and South America over the past six years) suggest that the assemblages of species present are associated with microhabitats and exhibit ecological patterns quite different from those found in temperate forests. For example, in tropical forests, myxomycete biodiversity seems to be greatest in aerial microhabitats located above the ground, whereas in temperate and also boreal forests it is greatest in microhabitats associated with the forest floor. Moreover, in tropical forests, myxomycete diversity and abundance appear to be concentrated toward the dry end of the moisture gradient and not toward the moist end as is generally the case in temperate and boreal forests. This is especially true for the species associated with the bark surface of living trees, which tend to support a much lower diversity of corticolous myxomycetes than most trees in temperate forests. Microhabitats seemingly unique to tropical forests and not known to support myxomycetes until very recently are the living inflorescences of large tropical herbs, the cover of epiphyllic liverworts on living leaves of understory plants, and the mantle of dead organic matter (literally a "canopy soil") found at the bases of vascular epiphytes growing on the trunks and larger branches of trees. The first of these appears to be especially rich in myxomycetes, and some species (e.g., *Physarum didermoides*) seem to show a strong preference for this microhabitat.

Boreal forests tend to be characterized by a lower biodiversity of myxomycetes than temperate forests, although certain taxa (*Fuligo septica* and several species of *Trichia*) can be exceedingly common in some situations. The majority of species are associated with wood, and only a few examples (e.g., *Leocarpus fragilis*) are commonly encountered on litter. Most substrates are fairly acidic, which undoubtedly represents a limiting factor. In general, members of the Trichiaceae are the most prominent myxomycetes in boreal forests.

Myxomycetes are even less common in tundra than in boreal forests. Stephenson et al. (2000), who analyzed the data represented

by almost two thousand specimens of myxomycetes collected from areas of tundra and forest-tundra in Iceland, northern Russia, Alaska, and Greenland, recorded a total of 150 species, but only thirty-three of these were widely distributed enough to be regarded as true inhabitants of high-latitude ecosystems. The main factors for the reduction in the number of species of myxomycetes in high-latitude regions are almost certainly the unfavorable temperature conditions and the reduced range and extent of available microhabitats. In typical areas of tundra, the microhabitat represented by coarse woody debris is extremely limited but still exists in the form of small twigs and tiny branchlets of dwarf woody plants such as species of willow and alder. A high proportion of the species present in tundra are associated with litter, especially the litter that accumulates around the base of dwarf woody plants.

Because myxomycetes are almost invariably associated with relatively cool and moist habitats, one might not expect these organisms to occur in deserts. The number of species reported from deserts is surprisingly high, however. The most productive substrates for myxomycetes in deserts include the pith skeletons of decaying cacti in areas of the world where these plants exist, the dead parts of living plants in contact with the ground, animal dung, and the bark of living shrubs and trees. Field collections are usually limited to periods of no more than a few days or weeks immediately following a period significant precipitation, but myxomycetes are exceedingly common in moist chamber cultures prepared with desert plant material.

One group of myxomycetes is restricted to alpine areas of mountains, where its members are found fruiting along the margins of melting snowbanks in late spring and early summer. The species that occupy this rather special and very limited habitat are usually referred to as snowbank or "nivicolous" myxomycetes. They constitute a distinct ecological group, since they usually produce fruiting bodies only during the relatively brief period of time when the special microenvironmental conditions associated with margins of snowbanks and apparently required for their growth and fruiting exist. During the remainder of the summer, the species of myxomycetes found in these alpine areas are very much the same as those collected at lower elevations in the same regions. Interestingly, the majority of species in some genera tend to be predominately alpine in distribution. This is true for *Dianema*, *Lamproderma*, and *Lepidoderma*. Most studies of snowbank myxomycetes

have been limited to the northern hemisphere; the first major study of this group for any region of the southern hemisphere was carried out in the mountains of New Zealand in November and December of 2000. Dawn Black and Maribeth Overking, two undergraduate biology majors from Fairmont State College, participated in this study.

The plasmodia of some species of myxomycetes are known to be capable of feeding upon the mycelia and fruiting bodies of various fungi. For most of these, feeding upon fungi is undoubtedly facultative, but at least a few species (e.g., *Physarum polycephalum*) would seem to have a primary ecological role as that of general fungivores (fungus-feeders). Sometimes the plasmodia of such myxomycetes become rather large. I once observed an example, associated with the fruiting bodies of the oyster mushroom on a decaying beech log in a forest in Ritchie County, West Virginia, that was more than three meters across! Conversely, the fruiting bodies of myxomycetes provide an organic substrate open to colonization by various filamentous fungi. The majority of these fungi also occur on other types of substrates, but a few species appear to be restricted to myxomycetes and thus are obligatory myxomyceticolous (fungus-loving). In some situations, the ecological association of fungi and myxomycetes is likely to be rather important. It has been hypothesized that one of the limiting factors for these organisms in tropical forests is the constant high humidity, which promotes the colonization of their fruiting bodies by filamentous fungi.

Myxomycetes are known to offer food, shelter, and a breeding place to various species of insects, but the ecological relationships involved are very inadequately known. Among the most commonly encountered insect associates of myxomycetes in temperate forests are beetles. Members of the family Leiodidae, particularly species of *Anisotoma* and *Agathidium*, often referred to as "slime mold beetles," are the predominant taxa involved. A number of these are apparently obligate myxomycete specialists and feed only upon the fruiting bodies or plasmodia of myxomycetes or both. Various species of flies also commonly occur as associates of myxomycetes. The majority of these are species that develop from larvae generally regarded as saprophagous or fungivorous. At least a few species, though, do seem to be restricted to myxomycetes in that they are not known to breed in any other microhabitat. The flies most commonly encountered as myxomycete associates belong to the family Mycetophilidae, with members of the

families Sciaridae and Drosophilidae also represented.

A number of instances are known of apparent ecological associations of myxomycetes and vascular plants. The ultimate basis of these associations relates to the structure of the plants in question. For example, in his studies of the myxomycetes of Hawaii, Eliasson (1991) suggested that the network of supporting tissue within decaying stems of certain cacti (*Opuntia*) and other succulent vascular plants could function as a "natural moist chamber." Such decaying stems may retain moisture for several weeks after the last precipitation and the temperature beneath them may be many degrees below that of the exposed soil surface, thus providing unusually favorable conditions for myxomycetes. The enclosed space formed by the basal sheath of a palm petiole represents yet another example of such a natural moist chamber. The leaves of most palms are rather large, and the base of the petiole is expanded to form a sheath where it is attached to the stem. After abscission occurs and the leaves fall to the forest floor, the edges of the sheath become convoluted, creating a more-or-less enclosed space. Nikau palm (*Rhopalostylis sapida*) is one of the more characteristic small trees of lowland forests of northern New Zealand. The microhabitat represented by the basal sheath of decaying leaves of this plant often yields collections of myxomycetes when all other substrates in the same forest and are non-productive. Moreover, some of the species I collected from nikau palm in New Zealand during the period of 1992 to 2002 were new records for the country.

Although the work I have carried out over the past twenty-five years has provided at least partial answers to many fundamental questions relating to the distribution and ecology of myxomycetes, these same answers have given rise to additional questions that do not as yet have satisfactory answers. As Ann Haywood Zwinger observes, "Questions are beginnings, answers are endings, and . . . all the answers come in the form of questions." I can attest, however, that posing questions and then pursuing answers to those questions can represent an extraordinary experience in itself, even if the object of study is a little-known and, to most people, a rather insignificant group of organisms.



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COLOPHON

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The institution now known as Fairmont State was founded as a private school in 1865. It became Fairmont State Normal School in 1867, serving the north central part of the newly created state of West Virginia. In 1931, its name was changed to Fairmont State Teachers College. In 1943, the school became a four-year college and its name was changed to Fairmont State College. The College has occupied its present location in Fairmont since 1917, when its administration building, Hardway Hall, was opened.

In 1974, Fairmont State Community & Technical College was created. Over the years, FSC's enrollment has grown to more than 4,200 and FSC&TC's enrollment has grown to more than 2,400.

Fairmont State College, a comprehensive, multi-site, selective, four-year institution with an administratively linked community and technical college, offers a quality education in a diverse and supportive learning environment that fosters individual growth, professional and career development, lifelong learning, global understanding, and a commitment to excellence in academic and community pursuits.

The mission of Fairmont State Community & Technical College is to enhance the quality of life for people of north central West Virginia through accessible, affordable, comprehensive, responsive, workforce-related training, and quality higher education opportunities.

Persons desiring further information about the college should write the Director of Public Relations, Fairmont State College, Fairmont, West Virginia 26554, or call (304) 367-4000.

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