# A BIOLOGICAL STUDY

# OF

# POLYPODIUM POLYPODIOIDES
(Resurrection Fern)

# AS

# AN AIR PLANT IN MISSISSIPPI

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DISSERTATION

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## I. INTRODUCTION

The only vascular epiphyte found in the northeastern part of Mississippi is Polypodium polypodioides (L) A.S.Hitch.(P.incanum Sw.).It occurs abundantly in the native forests where it inhabits eight or ten different species of trees and is also commonly found growing in large clumps on the trunks of certain planted trees in the city streets. Though widely distributed this polypody seems to be able to grow especially well only on certain species of trees.On these it occurs in very large clumps; on a number of other species it is found only in very small clumps; while on some species the polypody does not grow at all. This restriction of the epiphyte to certain trees led the writer to make a study of the climatic and other conditions influencing both the distribution of this fern on certain individual trees and its degree of development.

## II. GENERAL OBSERVATIONS

In order to determine definitely the causes of the distribution of P.polypodioides actually found, the writer selected seven stations where the epiphyte occurred and kept these under constant observation for one year.

Station #1 was two miles south of A & M College, Mississippi, located about 33° 30' North Latitude. This comprised a woodlot covering several acres and occupied by two distinct forest types, separated by a small pasture. *Ulmus alata*, *Quercus stellata* *Q. falcata*, *Q. velutina*, *Q. rubra*, *Carya ovata*, *C. alba*, and *C. glabra* predominated in the first part. Of the shrubs in this region *Crataegus* sp. and *Rhus* sp. were the most common ones. On the shaded forest floor were also numerous sprouts of oak and many tall herbaceous Compositae. The other part of this woodlot consisted mainly of pine woods where *Pinus taeda*, *P. echinata* and *Juniperus virginiana* predominated with scattered individuals of *Cornus florida* and *Celtis Mississippiensis*. Many parts of the floor of this open forest are exposed to the direct rays of the sun for much of the day and are covered by a thick layer of pine needles.

In the hardwood section of station #1 the epiphytic polypody grows on several species of trees. It was found on the north side of *Carya alba* very close to the ground. A small patch of it was also found growing on the ground itself close to the tree. The epiphyte, however, occurred not only on the north side of the tree but was found also on the northwest and southwest sides of individual trees of the same species, but there it is always close to the ground.

On _Quercus falcata_ it was seen on the southwest side about six centimeters above the soil. On _Q. stellata_, on the contrary, the fern invariably occurred only high in the tree, chiefly on the larger lateral branches and on the north side of the main trunk itself. A similar habit was observed in one instance on _Q. falcata_, while on _Q. rubra_ and _Q. velutina_ the fern never grew more than a few centimeters up the trunk and frequently it was found growing on the very base of the trunk on the northwest side practically imbedded in a mass of mosses and decaying organic matter. The fern was also common on the base of _Carya glabra_ but here it inhabited both the northeast and southeast sides. In a very few cases only has the polypody been found on _Carya ovata_, and there, as on the red oak, it was growing very close to the ground, and generally entangled in a mass of mosses and lichens.

Station #2 was a hardwood area of several acres, located on the campus of the Mississippi Agricultural and Mechanical College. It was a woods consisting mainly of tall specimens of _Populus deltoides_, _Liquidambar Styraciflua_, _Diospyros virginiana_, _Crataegus_ sp. and a few specimens of _Ulmus alata_. In this woodlot the ground between the trees was covered with numerous

weeds and young sprouts of various trees. Like station #1 the floor of these woods was well shaded in the summer. In this region the epiphytic polypody

Fig. 1
A view of Station #2 showing the dense vegetation covering the forest floor.

was abundant though it occurred only on the bases of the tree trunks. On a tree of _Diospyros virginiana_ the fern was found growing on the northwest and norteast sides up to about thirty centimeters from the ground and forming six individual clumps. On _Ulmus alata_ it occurred also on the same exposures but only five centimeters from the ground; on one _Liquidambar Styraciflua_ the polypody inhabited the east side of the tree as high as forty centimeters above ground, while on another individual of the same species it was found on the

southeast side at ten centimeters above ground. The occurrence of the polypody on the stem of Crataegus sp., the diameter of which was only eight centimeters, at sixteen centimeters from the ground, was indeed surprising for the substratum of the stem of so small a tree would seem to furnish no adequate foothold for the epiphyte.

Fig.2
The base of the trunk of Diospyros virginiana showing the epiphytic fern on the northwest and northeast sides.

Station #3 was likewise situated on the campus of the Agricultural and Mechanical College. This area comprised all of the trees growing in the immediate vicinity of the buildings and on the streets of the campus. The predominating trees were Ulmus americana, Quercus stellata and Q. Muehelenbergii. There were also many cultivated shrubs and trees. The epiphyte inhabited

nearly all the elm trees and occurred commonly on the north and northeast sides, Frequently it was found inhabiting the west and south sides also. It seemed so well adapted to grow on the elm that it made very

Fig.3

Trunk of Liquidambar Styraciflua with the epiphyte growing on the east side forty centimeters above ground.

often an enormous mass starting at the very base of the tree and reaching up to the lowermost branches of the crown. On Q.stellata, on the other hand, the fern never occurred lower than three meters above ground and the largest mass of it was usually in the crown on the main trunk and on the old thick branches

Two miles northeast of the campus was station #4. It was a wooded area of several acres. The predominating trees there were Juniperus virginiana (most abundant of all ), Pinus taeda , P. echinata, and among them were

dispersed a few specimens of Ulmus alata, of Celtis Mississippiensis and along the creeks isolated individuals of Populus deltoides. Throughout the woods were scattered impenetrable thickets of Prunus angustifolia (?). The floor of the woods was always shaded by the profusely branched junipers and was covered with old juniper twigs and pine needles.

Fig. 4
Base of Liquidambar Styraciflua bearing the polypody on the southeast side ten centimeters above ground.

In this region the epiphytic polypody occurred on practically all of the junipers. The fern seemed to have no definite distribution on its support. It occurred on all sides of the juniper trunks and at times also on the older branches. About five meters from the very

top of the tree the fern was generally replaced by lichens. Very commonly the fern was found growing in close association with the liverwort Frullania virginica, with the mosses Entodon cladorrhizans, Clasmatodon parvulus and in a few cases also with Orthotrichum ohiense or Leucodon julaceus. Practically the only lichen associated with the polypody was Parmelia centrata.

Fig. 5
Crataegus sp. bearing the epiphytic polypody.

This form was abundant on the lower branches of the tree and was almost imbedded in the mosses. Other lichens occurred on the higher parts of the tree where neither mosses nor ferns were present. The latter forms were: Ramalina calicaris, Sticta sp., Physcia stellaris, Anaptychia speciosa, and Cetraria aurescens. The only algae found on the junipers were Tolypothrix sp.

Pleurococcus sp. and Nostoc sp. and even they were not very abundant. No epiphytic bryophytes or ferns were found on any species of Pinus, but lichens such as Parmelia centrata were abundant on the trunks of many of them.

Fig.6
Typical growth of the fern on the american elm.

Fig.7
A view of the juniper woods of station#4.

Station #5 was located four miles southwest of the campus.Its flora was very similar to that of station #4 as was the distribution of the polypody also.

Station #6 was an open field on the college campus. There a solitary tree of Quercus stellata was located between two low ridges but fully exposed on

all sides. It measured forty eight centimeters in diameter at one and one-half meters from the ground and began to branch out at four meters from the ground. This tree was selected for the ecological study of which further mention will be made below. The epiphytic polypody

Fig. 8
Quercus stellata of station #6.
This also shows the arrangement of the instruments on the tree for ecological study.

together with several species of mosses was abundant on this tree. Wherever the fern and mosses were present

together, they usually were tangled into one huge mass. At the base of the trunk, the mosses inhabited the north side of the tree as well as the northeast and northwest sides. At this height no mosses were present on the south side; higher up into the crown, on the contrary, mosses alone occurred on the south side while the fern inhabited only the northwest, north, and northeast sides. The bryophytes associated with the fern on the oak were Leucodon julaceus, Clasmatodon parvulus rupestris, and Frullania virginica. The lichens were Epra chlorina, Parmelia centrata, and Pertusaria wulfenii. These occurred chiefly on the upper branches where no other green epiphytes were present, while Parmelia perforata inhabited both the upper branches and the parts of the trunk devoid of green epiphytes. At the base Leptogium sp. was common only on the north side of the tree.

Station #7 was situated in Starkville, Mississippi one and one-half miles from A & M College. There the distribution of the polypody was studied on the trees along the city streets. It was found that Ulmus americana was the only tree thickly inhabited by the fern which was always associated with various mosses. On this elm the polypody was not limited to any particular exposure, nor to any particular height. On individual trees of Quercus stellata in this region the polypody was confined only to the upper part of the tree, inhabiting the thick lateral branches and the trunk

itself. The fern was never found on the oak in this region at an altitude less than five meters. The elm and the oak are the only trees on which the polypody occurs abundantly in this region. Only one specimen of Celtis mississippiensis was found bearing a small clump of the polypody. This was an unusual case since on no other specimen of Celtis, of any diameter, was the fern ever found. It is quite possible that on

Fig. 9
The characteristic habit of P. polypodiodes on Quercus stellata at station #7.

this tree the fern was able to take a good hold beacause there was much decaying vegetable matter accumulated on a projecting piece of bark where the epiphyte anchored itself. It may be added that

on a specimen of Carya pecan ( a cultivated variety) growing close to a residence, on a side street, at Starkville, the polypody occurred abundantly in numerous small clumps. This is of interest since no other Carya bore this polypody, perhaps because no other offered as good a support to the fern as did this pecan.

An analysis of the data at hand indicates that where the light is weak this epiphytic fern is restricted to no definite exposure; it occurs now on the north side, now on the south, or east side and frequently on the west side of the tree. On one tree it is very close to the ground, on another somewhat higher, while on some trees it gets far above the ground. On the other hand, where the light is intense the polypody is either not present at all or when it does occur it is found only on the north side of the tree. It appears, therefore, that the light plays an important rôle in the distribution of the epiphyte. That the light is not the only factor affecting the occurrence of Polypodium polypodioides as an epiphyte is evident from the fact that even when such trees as Pinus echinata, Pinus taeda, and Carya ovata are exposed to weak light, they do not bear the fern.

Another condition that appears to be responsible for the presence of the epiphyte on some trees and its absence from others is the character of the substratum This is evident from a study of a young fern plant which the writer succeeded in removing together with the bark on which it grew without injuring the fern or the bark to which it was attached. The piece of bark bearing the young fern measured eight centimeters in length, four centimeters in width and one centimeter in thickness. The fern grew on the edge of the bark pushing its young roots into the interlaminar spaces so that the youngest roots branched out luxuriantly about two centimeters beneath the surface of the bark.

Fig. 10
Upper surface of bark of elm bearing the polypody on its edge.

Fig. 11
Lower surface of bark with the polypody showing the root system.

In this manner the fern roots were really concealed in the bark half way through its thickness. In this position the young absorbing roots were covered by a thickness of bark sufficient to serve as an excellent protection against desiccation Even when the fern on the outside was apparently dried up, shriveled and

curled up, as it always does in dry weather, its roots beneath the bark were perfectly turgid and showed no apparent suffering from lack of moisture. This observation suggests at once that the character of the bark is as important a factor in the distribution of the epiphyte as is the light. Even when the light conditions are favorable, a tree possessing a horny, a stony, or a flaky bark does not furnish the proper support for the polypody, since its roots can not penetrate into the stony or horny bark, while on a flaky bark that sheds frequently, such as of the pine or the sycamore, the young epiphyte has hardly time to develop strong anchoring roots when the bark is shed carrying with it the young plant to the ground. In most cases, however, the spore fails to germinate, for no prothallium has ever been found on either the pine or sycamore in the northeastern part of Mississippi.

It seems possible that both light and the character of the substratum might be responsible for the diversity in the distribution of the epiphytic fern as it appears from a field study of the seven stations. To determine this definitely the writer was led to carry on quantitative physiological and ecological experiments in two of the observed stations for a definite period of time. It was thought

possible to establish the actual causes underlying the influence of the climatic conditions and of the character of the substratum on the distribution of the epiphyte. Before presenting the data obtained from the physiological, ecological and morphological study of this epiphyte indigenous to the Southeastern United States, it is perhaps well to give a brief review of the literature on epiphytes in general so as to follow up the ideas on epiphytism as conceived by the earlier botanists and particularly to show how little is actually known about this interesting group of plants.

The writer wishes to express his thanks to Professor C.C.Plitt for the determination of several of the lichens and to Mr.R.S.Williams of the New York Botanic Gardens for the determination of some of the epiphytic mosses.

## III. SUMMARY OF LITERATURE ON BIOLOGY OF EPIPHYTES

Practically nothing was known to the early botanists about the ecological group of plants now known as epiphytes. It was late in the nineteenth century when the first papers dealing with these air plants began to appear. As early as 1881 the question of the source of the mineral elements necessary for the growth and development of the epiphytes interested botanists. It was then that Dixon (4) analyzed chemically the ash of living and dead fronds as well as roots of Platycerium grande, P. alicorne and Asplenium nidus. He likewise analyzed the ash of the humus of the substratum on which these epiphytes were growing. His results indicate that there was no similarity between the composition of the ash of the living epiphyte and that of the substratum to which it was attached. He concluded from this that the epiphytes obtained most of their inorganic matter from the dust of the air. Although these plants generally require "quantities of alkalies", they frequently obtain these substances from decaying fronds and from the humus.

The foremost student of epiphytes was Schimper. His paper (24), the results of his travels in the southern part of the United States and the West Indies, aroused a great deal of enthusiasm over epiphytes

among many European botanists. In his first paper on epiphytes he classified the air plants into four groups according to their anatomical structure and their adaptation to the environment. Those epiphytes which derive their nutrient material mainly from the surface of the substratum to which they are attached he placed into the first group. In this group are the orchids and the aroids which get their mineral nutrients and water through the velamen of the roots. The plants of the second group are those that send roots, which are both anchoring and absorbing, down into the substratum. Clusia and Anthurium pelmatum belong to this group. In the third group are those epiphytes which form root mats and which may also have both anchoring and absorbing roots. Polypodium phyllitidis and Oncidium altissimum are examples of this group. In the fourth group belong those epiphytes which secure their nutrient materials entirely through leaves and lose their roots altogether. A striking example of this group is Tillandsia usneoides.

Schimper's classic work on epiphytes appeared several years later. It was then that the complete results of his study of the tropical epiphytes were first published (25). It is safe to say that this paper stimulated all the work on European "epiphytes" that was carried on during the next several years.

According to Schimper, the condition which enables a plant to become an epiphyte is the adaptibility of the seeds to be transported to branches and trunks of trees and be able to germinate there. Only certain seeds are adopted for such a mode of distribution. He classified the seeds into three categories according to their special adaptations: Seeds which are fleshy, seeds which are very light, and seeds which posses special mechanical devices for dissemination. The seeds of the first category are carried to the trees by animals; those of the second category are transported by the wind due to their lightness; the seeds of the third category are brought to the trees by means of their special flying apparatus and the agency of the wind.

Although a seed may have those special adaptations for dissemination and be able to germinate on the branch or on the trunk of the tree, the young plant may not be able to stand the new conditions and may require new adaptations which frequently result in special modifications of the plant body in order to meet the new conditions. The most marked modifications are evident among those plants which are adapted to resist drought. Some forms such as Polypodium polypodioides are especially adapted to withsatnd the strong sunlight in Trinidad by curling up, thus reducing its transpiring surface. Other plants produce special structures which

store water in the wet season for their later use, when the supply of water is not so abundant. This is especially true for Utricularia and some of the aroids. Still others form special tissues which are capable of absorbing water rapidly as is evident in the orchids. In these plants the velamen, which is so common in epiphytic orchids, is capable of absorbing water rapidly and storing it for some time. Moreover, the aerial roots of the epiphytic orchids in addition to the velamen also have considerable chlorophyll tissue in the cortex. They are thus capable of photosynthetic work.

Schimper further showed that in some bromeliads the leaves and not the roots assume the function of water absorption. In such forms as Tillandsia usneoides, scales which cover the entire body of the plant function as absorbing organs. The structure of such scales was later worked out in detail by Mez (18). Schimper's experiments with the leaves of Caraguata lingulata, Brocinia, and Vresia sp. prove conclusively that in these forms the leaves are the chief organs of absorption.

Concerning the distribution of epiphytic species, Schimper regards light and humidity as the chief condition affecting the occurrence of the epiphytes in special localities. He states (p.90): " Licht, feuchte Luft, reichliche Thaubildung, haufige Regenguesse stellen die

wessentlichen Bedingungen eines üppigen epiphytischen Pflanzenlebens dar."

Goebel (7) studying some species of Polypodium and Asplenium nidus conludes that the Polypodium can grow on the ground as well as on trees. The Asplenium, however, builds a substratum about its roots by means of the basal leaves which collect humus therby allowing the creeping stem to penetrate and the roots to thrive within the substratum thus formed. Later Goebel (8) observed that when the seed of an epiphyte lodges on the bark of a tree and succeeds in germinating there, its main root, in the course of time, flattens out and numerous side roots are developed which anchor the plant to its substratum. He found that on the smooth stem of Bambusa only crustaceous lichens occur. He also found that higher up epiphytes do not inhabit the tall smooth barked palms, while on the persisting lower portions of the leaf bases of the sugar palm many epiphytes thrive in the accumulated humus. He concluded that the character of the substratum plays an important rôle in the distribution of the epiphytes. According to this investigator, the ability to be anchored to the substratum, an abundant suppl1y of water, and an accumulation of humus within the reach of the roots as well as protection for the roots against dessication are necessary conditions for the epiphytic mode of life.

The appearance of Schimper's and Goebel's published works on the epiphytes created an interest in this group of plants among other European botanists. Loew (15) studied the "epiphytes" inhabiting the willows of North Germany and found that fifty three percent of the "epiphytes" were brought to the tree by the agency of the wind due to the lightness of their seeds. Twenty three percent of the "epiphytes" originated from seeds brought by animals. The remainder of the "epiphytes" found their way to their supporting trees by unknown means. As a result of his study of the "epiphytes" he concludes that those plants which assume the epiphytic mode of life become associated with mycorhiza on the tree which they inhabit. This is merely an assumption, for he presents no evidence in support of his view. He regards plants which are able to secure substances from humus by means of mycorhiza as better fitted to live as epiphytes than those which do not have that ability. It is probable that Loew's interest in this problem was inspired by Goebel's work rather than by Schimper's.

Loew's view on the mycorhizal association in epiphytes was later disputed by other workers. Willis and Burkill (32) pointed out that a mycorhizal association is not necessary for epiphytic development. They found "epiphytes" occurring on the pollard willows near Cambridge, Englad, in old and fully decayed humus

and no mycorhiza was found in the roots of the "epiphyte". Hoeveler (12) claims that plants may make use of humus without the aid of mycorhiza. Beyer (1) also failed to find mycorhiza in the "epiphytes" that he studied. Stahl (28) studying several epiphytic ferns including Polypodium vulgare confirmed Beyer's results, for he found no mycorhiza in any of the plants studied. Staeger (27) likewise failed to confirm Loew's view regarding the presence of mycorhiza in epiphytes. Czapek (3) in his study of the physiology of epiphytic orchids found no mycorhiza associated with the roots of those plants. Johnson (13), on the other hand, in his study of Polypodium vulgare states (p.239): "Many of these root hairs (of the polypody) had one or more fungus hyphae running lengthwise through them. These hyphae could often be seen enetering at the tip of the root hairs." He has not determined , however, whether these hyphae formed a mycorhizal association or not.

Beyer (1) found that the "epiphytes" belonged to groups of plants whose fruits or seeds are stone-like, bur-like, or have a flying apparatus, or are very small and light. He concludes that the wind and the tree-inhabiting animals aid in the distribution of the "epiphytes". Geisenheyner's observations (5) confirm those of Beyer. In another paper Beyer (2) states: "only those plants can live as epiphytes which can

survive on the meager fertility of the substratum and which can stand the hot sun and the drying of the winds." Karsten (14) found that in Polypodium imbricatum and P. sinuosum scales were present which functioned as water absorbing organs as well as for the distribution of the water drops which settle on the stem. He assumes, however, that the scales are not the sole water absorbers, for he found long, slightly thickened root hairs which he believed to function as the main organs of absorption. Wittrock (33) found no true epiphytes in Sweden. He suggests that in order to assume the epiphytic mode of life the plant must be able to withstand much shade; it must be able to form roots which could thrive in a thin layer of soil, and it must be able to withstand dessication. He agrees with Schimper, Beyer and the others on the characeter of the seed which enables a plant to make its start as an epiphyte. Went (30) made observations on epiphytes in Java and found that the aerial roots of epiphytes vary in form and behavior even in the same species. Some roots may function only for anchorage, others for absorption only and some for both anchorage and absorption. He distinguishes two groups of epiphytes: True epiphytes and Hemiepiphytes. The true epiphytes derive their inorganic substances from the air or from the dust accumulated on the bark; the hemiepiphytes are similar to true epiphytes in their first stages of development

but later develop absorbing roots by means of which they grow as terrestrial plants.He believes that the distribution of the epiphytes depends on the presence or absence of inorganic material.He suggests that epiphytes have been evolved from root climbers which at first possessed only anchoring roots,later absorbing roots were also formed,and so the plant became a "hemiepiphyte"; finally,both the anchoring and the absorbing roots ceased to function and the plant became a"true epiphyte". Nabokisch (20) found that the velamen is not concerned with the condensation of of atmospheric humidity.It serves chiefly as a good protection against dessication and against sudden cooling of the roots.Where the mists are very heavy the velamen may absorb the drops of water which form on the roots.He believes that the velamen can absorb water only in the form of liquid.Lindsbauer (16) found that the typical absorbing roots of the aroids are positively geotropic while the anchoring roots are usually negatively geotropic. Staeger (27) searched for any possible adaptations among the"chance epiphytes" of Switzerland in order to determine any possible relation between the European "epiphytes" and the tropical true epiphytes.He found no special adaptations for the epiphytic mode of life among the European "epiphytes".This investigator applied for the first time the name of "accidental epiphytes" to those forms studied by Loew,Beyer,and the other students

of the European"epiphytes".He regards the factors which help the existence of the "epiphyte" as both external and internal.The external factor is the ability to grow in a shady and humid environment; the internal,the hereditary adaptaion to withstand dessication.These are the only adaptations possessed by the "accidental epiphytes".Czapek (3) studied the morphology and physiology of epiphytic orchids and found that the roots showed positive geotropism.Some orchids,however,possess roots which are negatively heliotropic.When aerial roots were grown in the dark numerous root hairs were developed.Furthermore,he found that only liquid water is absorbed by the roots in appreciable amount.The velamen may condense atmospheric moisture but the quantity of such moisture is so small that the velamen can not be considered chiefly as a condenser of atmospheric humidity, but should be regarded primarily as a water absorbing organ.Through a continual absorption of small quantities of water, the roots really perform the function of supplying the plant with the necessary amount of water.

Of the distribution of the epiphytes in Jamaica, Shreve (26) says (p.189) :"The trees of the upper slopes have the same epiphytic flora that would be found in the upper two-thirds of the trees of the ravines.The trees of the ridges and peaks have only those that are characteristic of the uppermost third and the midheight species are restricted in

these habitats to the sides of prostrate trunks or fallen logs."He found that the Hymenophyllaceae obtain most of their water through the absorbing power of their leaves,though the roots also function as water absorbing organs.The drought-resisting species are capable of absorbing atmospheric humidity when the leaves are placed in an environment of very moist air especially if the surface of the leaves is dry.Miehe (19) found that Polypodium vulgare was confined to the branches of the oak.He also found that Sorbus, Amelanchier, and Sambucus occurring as "epiphytes" were not restiricted to any particular side.Olsen (21) found that epiphytic bryophytes are moar commonly found on the upper side of inclined trunks.This, he thinks,is due to the rain falling vertically in the woods so that the upper side of the inclined trunk gets the most moisture.The conditions which affect the bryophytic vegetation,according to Olsen, are the age of the tree, position in regard to light,position in regard to wind,position in regard to rainfall,the species of the tree, and the chemical composition of the "soil".Of these, the age of the tree is the most important one since it affects the character of the bark.Young trees possessing smooth bark offer no footing for epiphytic growth.When the tree becomes older fissures appear in the bark in

which sufficient soil accumulates to allow the bryophytes to appear. He found the epiphytic bryophytes to be xerophyllous in character. They possess high osmotic pressure in the cells and their leaves in dry weather can fold and hug the stem. He also found that most of the epiphytic bryophytes can endure a high degree of shade."

In recent years the physiological and ecological aspects of the epiphytic mode of life began to interst botanists. Harris (10) after studying the osmotic concentration of the tissue fluids of epiphytes concludes that these plants show a decidedly lower concentration than those from the terrestrial vegetation. Harper (9) analyzed chemically the ash of the fronds of Polypodium polypodioides and suggests that this fern probably obtains some of the inorganic material from the bark of the tree which it inhabits as well as from the dust of the air. Wherry (31) applying the acidity indicator tests to the "soils" on which certain epiphytic ferns were growing found that Polypodium vulgare frequently grows on calcareous soil while P. polypodioides is practically an acid plant." Johnson (13) suggests that the main difference between the "half-parasite", the mistletoe, and the epiphytic P. vulgare is that ( p.241) " the mistletoe exacts its quota of salt (and of water also) from within the living host, before they have been used by the

host itself, while the air plant gets its salts from the surface of the tree after they have served the function within it." As to its origin in the United States, he suggests that it entered North America from Eurasia by way of Alaska and then spread southward and eastward. Van Oye (22) concludes from his experiments and observations on some epiphytic algae, lichens and mosses in Java that the lichens are favored by low humidity and intense sunlight. This is in accord with Plitt's (23) work on the distribution of lichens in Jamaica. Van Oye also found that mosses develop only in the sahed, while the alga <u>Trentepohlia</u> sp. seems to favor strong light.

## IV. MEASUREMENT AND COMPARISON OF ENVIRONMENTAL CONDITIONS.

### A. Climatic Conditions

A review of the botanical literature shows that the early students of epiphytes studied them primarily to determine the means by which these plants reach the ~~the~~ trees which bear them. This led to the study of dissemination of various seeds. Later the investigation of the nutrition of the epiphytes and of the structure of the roots of the epiphytes in search of a possible mycorhizal association was begun. Certain investigators studied the true tropical epiphytes, while others were studying the "false" epiphytes that occurred in Europe. The results showed that the true air plants have special peculiarities of structure which enable them to live and to grow without any connection with the soil. The "false" epiphytes, on the contrary, have no such adaptations and few reach maturity on their supporting tree. Only those reach maturity, of course, which after a time succeed in making connection with the earth through the tissues of its support. Finally, the physiological and ecological phases of the problem have attracted the attention of recent workers who have attempted to determine the osmotic concentration of the sap of epiphytes and the conditions under which the air plant grows best. It seems that the prevailing

idea among the students of the epiphytes has been that light and humidity are the main conditions that influence the distribution of these plants. However, no experimental evidence has so far been given in support of this view.

It is the aim of this paper to present the results that were obtained from a series of experiments carried on from July 1921 to July 1922 chiefly on Quercus stellata which was thickly inhabited at certain heights and on certain exposures by the epiphytic Polypodium polypodioides. The oak was located in an open pasture with no buildings or other trees within a radius of three hundred feet or more. The epiphytic flora and the location of this particular tree were described in detail above (station #6 ). This oak was particularly desirable for the study of the influence of the climatic conditions on the distribution of the epiphytic polypody, for its isolated position exposed it on all sides to the unmodified natural climatic conditions.

Prior to the work on the oak, preliminary experiments were also made on a specimen of Juniperus virginiana which was inhabited by the fern. On this tree the polypody favored no definite exposure. The location of the juniper and its epiphytic flora are

discussed in detail in the section dealing with station #4.The experiments were carried on this tree from July 4th to July 8th,1921 at a height of 12.2meters;from July 8th to July 14th, 1921,at 7.6 meters;and from July 14th to July 22nd,1921, at 1.2 meters from the ground.At each of these altitudes the instruments were placed on the south, northeast and northwest sides.

It is practically impossible at the present time to measure some climatic conditions with absolute prcision.However, methods adapted to experimentation in the field were employed which enabled the writer to obtain data of sufficient accuracy for our purpose to make the results significant.To measure the intensity of the light the writer employed the Wynne Photographic Exposure Meter which was read at each station on the tree.The readings were compared with those obtained in the open.When the instrument was exposed in the open field at noon for five successive days in July under the same conditions,it took about 1.5 seconds to change the paper to the standard color.It was then decided to use 1.5 as the standard or maximum light intensity.All the other readings were obtained by placing the instrument against the tree and recording the time it took the light to change the color of the photographic paper.These readings were computed as percentages of the intensity of the light in the open.

The relative humidity of the air was measured by means of the sling psychrometer, which was used not by whirling it, as is commonly done, but by taking the instrument out of its case and hanging it on a nail against the tree trunk where it was fanned by as uniform a swing of the arm as possible. This method made it possible to obtain the percentage of relative humidity close to the trunk or branch on which the ferns live. The percentage of relative humidity was calculated from the psychrometric tables.

The evaporating power of the air in the immediate vicinity of the stem was measured by means of ~~the~~ Livingston standardized spherical porous-cup atmometers which were set up with the non-rain absorbing mountings as described by Livingston and Thone (17). The atmometers were set up in pairs at each exposure at different heights and were read once each twenty four hours. After each reading the spheres were brushed and washed with 95% alcohol to remove any possible spores or dust. The evaporation was measured volumetrically in cubic centimeters.

On <u>Quercus stellata</u> the temperature of the bark was also measured in addition to the other factors. This was done by boring a hole in the bark large enough to hold the bulb of a thermometer. Between readings

the holes thus made on three exposures at the different heights were plugged with tightly fitting corks in order to prevent the accumulation of dust, or animal, or vegetable matter which might induce decay. On the

Fig.12
Main trunk of Q.stellata showing position of instruments at 1.2 and 3 meters above ground.

oak readings were obtained at heights 1.2 meters,3 meters, 9.1.meters, and 13.7 meters.At each altitude observations were made on the south,northeast, and northwest sides. With the exception of evaporation readings,which were taken only every twenty four hours, the readings of all the other factors were made at nine and eleven o'clock in the morning and two and four in the afternoon.

Records of the climatic conditions prevailing at A & M College during the period of experimentation were obtained from the United States Weather Bureau and are presented in Table I. It is evident from the data that the prevailing winds during the time of experimentation were from the south, consequently their drying effect was not very great.

## Results

A study of the epiphytic flora of Juniperus virginiana in the shady woods and of Quercus stellata in the open, revealed the fact that on both trees the uppermost part of the trunk bore only lichens and no green epiphytes. The main difference between the epiphytic floras of the two trees was noticeable at 1.2 meters from the ground where on the juniper at that height the fern was found abundantly and was not restricted to any particular exposure, while on the oak the fern was wanting altogether at that height. Only on the upper third of the trunk of the juniper was the polypody wanting, below that the fern was found abundantly on the stem. On the oak, on the contrary, the fern did not occur either at the base of the tree or at the uppermost part of the crown where the main axis was lost in the branches. At the other elevations, it occurred only on the northeast, north, and northwest exposures.

Table 1 Climatological Data for A & M College, Mississippi. Elevation 424 ft.

| Average hourly velocity of wind | Direction of prevailing winds | Total precipitation | Clear days | Partly Cloudy days | Cloudy days | Mean temperature | Month |
|---|---|---|---|---|---|---|---|
| 4.8 | South | 3.5 | 18 | 10 | 3 | 83.8 | July, 1921 |
| 4.6 | South | 2.55 | 15 | 14 | 1 | 82.2 | August |
| 3.5 | South | 2.99 | 19 | 8 | 3 | 83.0 | September |
| 4.8 | North | 1.22 | 23 | 7 | 1 | 63 | October |
| 4.7 | South | 1.80 | 14 | 14 | 2 | 59.6 | November |
| 5.6 | North | 3.49 | 13 | 12 | 6 | 52.2 | December |
| 7.1 | North | 5.53 | 8 | 7 | 16 | 45.7 | January 1922 |
| 6.9 | North | 6.87 | 9 | 7 | 12 | 52.3 | February |
| 7.4 | South | 10.66 | 14 | 10 | 7 | 55.4 | March |
| 6.8 | South | 5.68 | 13 | 8 | 9 | 66.2 | April |
| 5.1 | South | 3.96 | 14 | 9 | 8 | 71.9 | May |
| 4.0 | South | 3.01 | 18 | 9 | 3 | 79.2 | June |
| 4.6 | South | 1.32 | 20 | 8 | 3 | 86.0 | July |
| Total averages for the year July 1921 to July 1922. | | | | | | | |
| 5.04 | | 4.04 | 15.5 | 9 | 5 | 67.65 | |

The results obtained by measuring the climatic conditions at each altitude on both trees may shed some light on the cause of the restricted distribution of P.polypodioides at the different heights of the tree and on the different exposures of the same height. The total average evaporation per day at 12.2 meters above ground on the juniper was 37.06 cubic centimeters, on the south side, 46.79 cubic centimeters on the northeast exposure, and 37.06 cubic centimeters on the northwest side of the tree. At 7.6 meters the evaporation per day was much lower being only 14.47 cubic centimeters on the south side, 15.46 on the northeast side, and 14.83 cubic centimeters on the northwest side. At 1.2 meters from the ground, however, the average daily evaporation was a trifle lower, being only 12.64 cubic centimeters on the south side, 13.17 on the northeast side, and 14.13 cubic centimeters on the northwest side. The light intensity at each of the selected elevations on the juniper was practically the same and there was hardly any indication of its possible influence on the distribution of the epiphyte. Unquestionably, the intensity of the light exerts an influence on the evaporating power of the air and in that way only does it affect the distribution of the epiphyte.

On Quercus stellata, where over eleven hundred readings were recorded, the evidence supports the

Table II Average Dai levations on Quercus stellata

Elevation Exposure E bstratum Temperature

FOLD OUT

IDES

a B

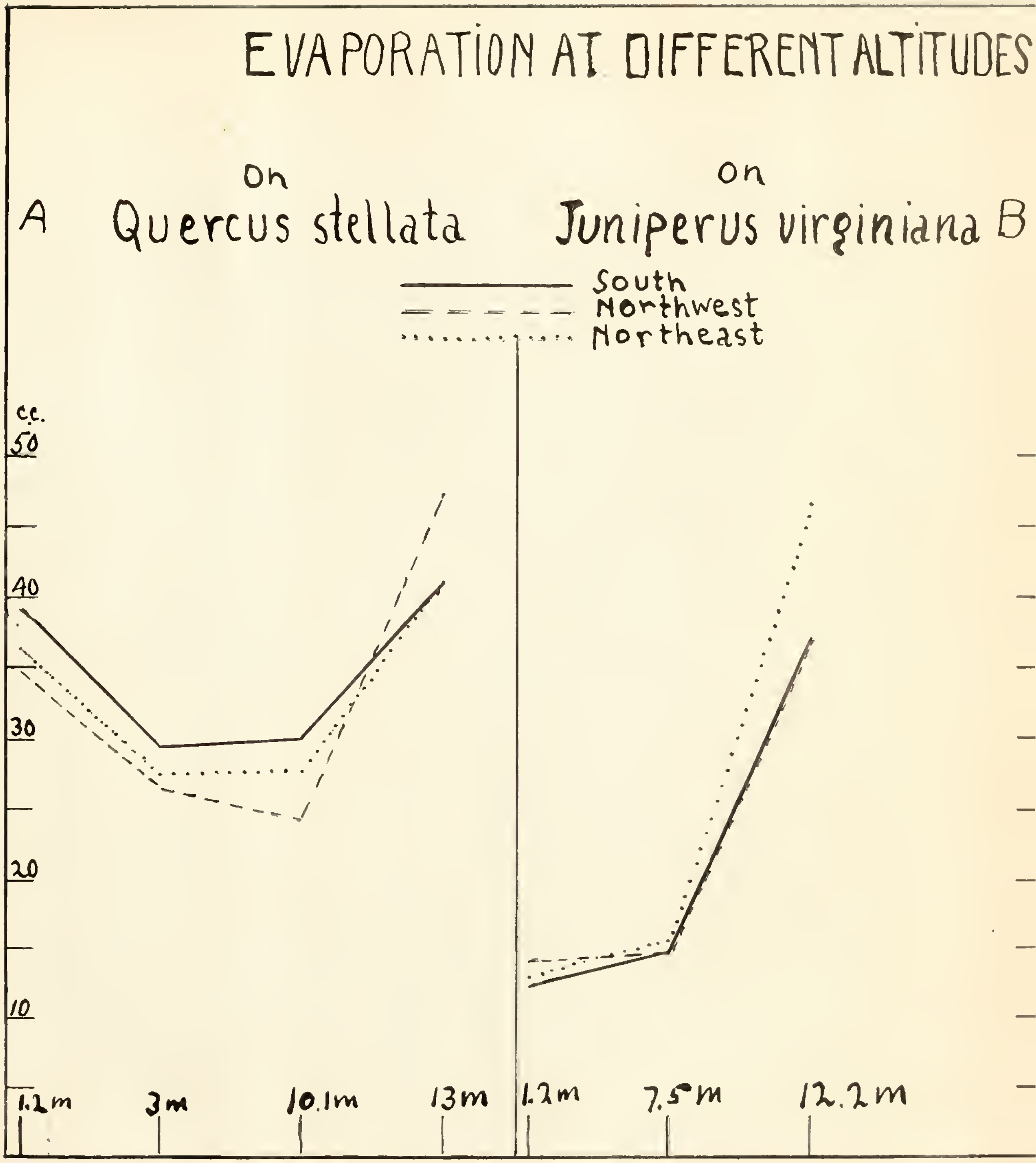
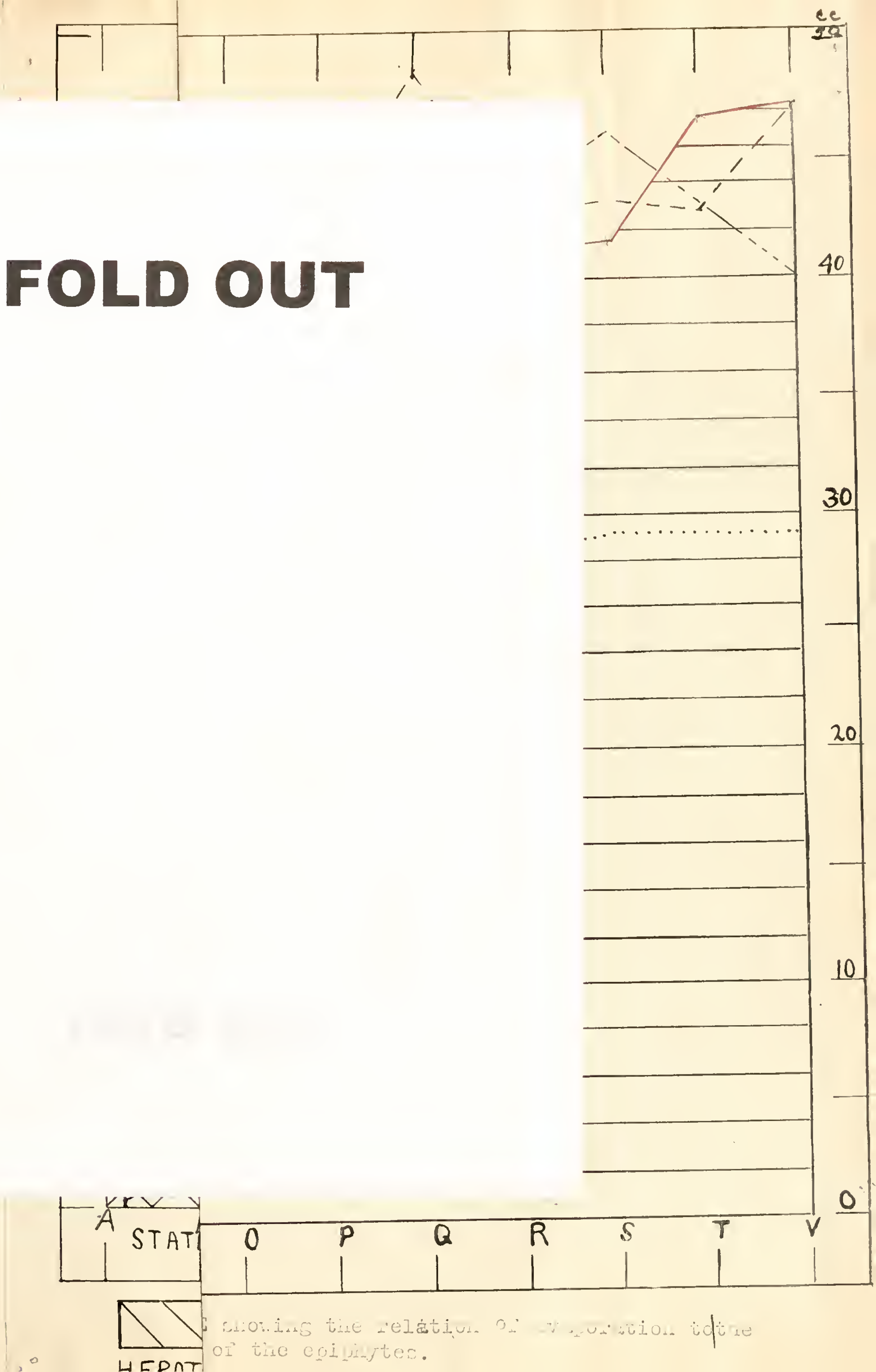



Fig. 13
A. Total average evaporation at four different heights on *Quercus stellata* on three different sides of the trunk.

B. Total average evaporation at three different heights on *Juniperus virginiana* on three different sides of the trunk.

**FOLD OUT**




showing the relation of evaporation to the
of the epiphytes.

Table III General Averages of Evaporation, Light, Humidity, Air Temperature and Substratum Temperature on *Juniperus virginiana* and *Quercus stellata* arranged according to the rate of evaporation.

| Station | Location | Evaporation in c.c. in 24 hrs. | Humidity % | Light Intensity % | Air Temp. | Sub. Temp. | Epiphytes |
|---|---|---|---|---|---|---|---|
| A | 1.2 meters from ground south side *J. virginiana* | 12.64 | 62.94 | | 24.00 C | | 1. *Frullania virginica* 2. *Entodon cladorrhizans* 3. *Clasmotodon parvulus* 4. *Leucodon julaceus* 5. *Polypodium polypodioides* |
| B | Same as A Northeast side | 13.17 | 63.31 | | 24.00 C | | Same as for station A. |
| C | Same as station A Northwest side | 14.13 | 62.10 | | 23.9 C | | Same as for Station A |
| D | 7.6 meters above ground south side *J. virginiana* | 14.47 | | 2.6 | | | 1. *Frullania virginica* 2. *Entodon cladorrhizans* 3. *Clasmotodon parvulus* 4. *Leucodon julaceus* 5. *Orthotrichum ohiense* 6. *Polypodium polypodioides* |
| E | Same as D Northwest side | 14.83 | | 2.8 | | | Same as for station D |
| F. | Same as D Northeast side | 15.46 | | 5.2 | | | Same as for station D |

Table III Continued

| Station | Location | Evaporation | Humidity | Air Temp. | Subst. Temp. | Light | Epiphytes |
|---|---|---|---|---|---|---|---|
| G. | 9.1 meters from ground Northwest side *Q. stellata* | 24.66 | 59.20 | 24.4 C | 22 C | 6.92 | 1. *Frullania virginica* 2. *Leucodon julaceus* 3. *Polypodium polypodioides* |
| H. | 3 meters from ground northwest *Q. stellata* | 26.41 | 58.05 | 25.4 C | 24.1 C | 12.4 | 1. *Leucodon julaceus* 2. *Polypodium polypodioides* |
| I. | 3 meters from ground northeast *Q. stellata* | 27.49 | 59.32 | 25.4 C | 24.6 C | 12.1 | 1. *Leptogium tremeloides* 2. *Parmelia centrata* 3. *Clasmatodon parvulus rupestris* 4. *Leucodon julaceus* 5. *Polypodium polypodioides* |
| J. | 9.1 meters from ground northeast *Q. stellata* | 27.88 | 59.65 | 25 C | 22.7 C | 6.6 | 1. *Clasmatodon parvulus rupestris* 2. *Leucodon julaceus* 3. *Polypodium polypodioides* |
| K. | 3 meters from ground South side *Q. stellata* | 29.75 | 58.96 | 25.7 C | 24.8 C | 12.9 | 1. *Parmelia centrata* 2. *Xanthoria lychnea* 3. *Leucodon julaceus* |

| Station | Location | Evaporation | Humidity | Air Temp. | Subst. Temp. | Light | Epiphytes |
|---|---|---|---|---|---|---|---|
| L. | 9.1 meters from ground south side Q.stellata | 30.01 | 58.95 | 25.1 C | 24 C | 11.42 | 1. Parmelia centrata 2. Leucodon julaceus |
| M. | 1.2 meters from ground northwest side Q.stellata | 33.96 | 58.11 | 25.4 C | 20 C | 14.33 | 1. Leptogium tremeloides 2. Parmelia centrata 3. Leucodon julaceus |
| N. | Same as M Northeast side | 35.28 | 59.60 | 25.43 C | 21 C | 17.65 | 1. Leptogium tremeloides 2. Leucodon julaceus |
| O. | 12.2 meters from ground south side J.virginiana | 37.06 | | | | 4.9 | 1. Ramalina calicaris 2. Parmelia centrata |
| P. | Same as O Northwest side | 37.06 | | | | 5.4 | 1. Parmelia centrata 2. Ramalina calicaris |
| Q. | 1.2 meters from ground south side Q.stellata | 38.52 | 58.05 | 25.7 C | 21.1 C | 17.9 | 1. No epiphytes |
| R. | 13.7 meters from ground northeast Q.stellata | 41.28 | 57.1 | 29.03 | | 5.3 | 1. Parmelia centrata 2. Pertusaria wulfenii |
| S | Same as R south side | 41.52 | 58.43 | 39.76 | | 6.8 | Same as for station R |
| T. | 12.2 m. Northeast J.virginiana | 46.79 | | | | 5.8 | 1. Parmelia centrata 2. R.calicaris |
| V. | 13.7 meters northwest Q.stellata | 47.28 | 58.11 | 25.43 | | 14.3 | 1. P.centrata 2. Epra chlorina 3. P.wulfenii |

view that the evaporation , or to be more exact, the evaporating power of the air is probably the most important factor in the distribution of the epiphyte. The total averages for evaporation both on the juniper and on the oak are shown in the graph (Fig. 13) and the daily averages of evaporation, light intensity, air temperature, substratum temperature, and the relative humidity of the air for each height and exposure on the trunk of the tree, with the corresponding epiphytic flora, are tabulated in Table II. These readings are given for each period during which records were obtained. In Table III are given the total averages for all the periods for each individual station on both the juniper and the oak which are arranged in the order of the rate of evaporation, beginning with the station that has the least evaporation rate and ending with that showing the maximum rate. The corresponding epiphytic flora for each station and the total averages of the other factors are also presented in the table so that it is possible to see at a glance the relation of the occurrence of the epiphyte to the climatic conditions. It appears from the tabulated results that where the evaporation rate is low, the epiphytic fern is present and where the evaporation is high the polypody is wanting. When these readings are presented graphically the fact becomes even more obvious, as is shown by the graph (Fig. 14), that the epiphytic flora

of the tree has a definite regional distribution in both vertical and radial directions and this vertical and radial distribution is infuenced primarily by the evaporating power of the air.Thus, where the evaporation rate is the lowest the epiphytic flora consists of hepatics (Frullania virginica),of various mosses, and of Polypodium polypodioides.As the evaporation rate increases the hepatic begins to disappear leaving only the mosses and the fern;with the further increase of the evaporation the fern disappears and lichens come in.In regions on the tree where the evaporation is still greater, the mosses disappear leaving the lichens as the sole epiphytes.Evidently the evaporating power of the air plays a very important part in the distribution of the epiphytes on a tree.When each of the other conditions is presented graphically in the same manner as the evaporation;that is , starting with the lowest and gradually going up to the maximum,then,when the corresponding epiphytic flora for each station is given, there appears to be no definite relation between the distribution of any of the epiphytes and that of the maximum effect of any one of the other factors.A study of the graph of the light intensity (Fig.15) suggests that the hepatic occurs where the light is the weakest,the mosses and the fern seem to endure light of more or less moderate intensity,while the

lichens occur in weak light as well as in strong light. Apparently the light factor is not the most important one, though it undoubtedly exerts some influence on the evaporating power of the air and in that way affects the distribution of the epiphytes indirectly. The curve of the air temperature

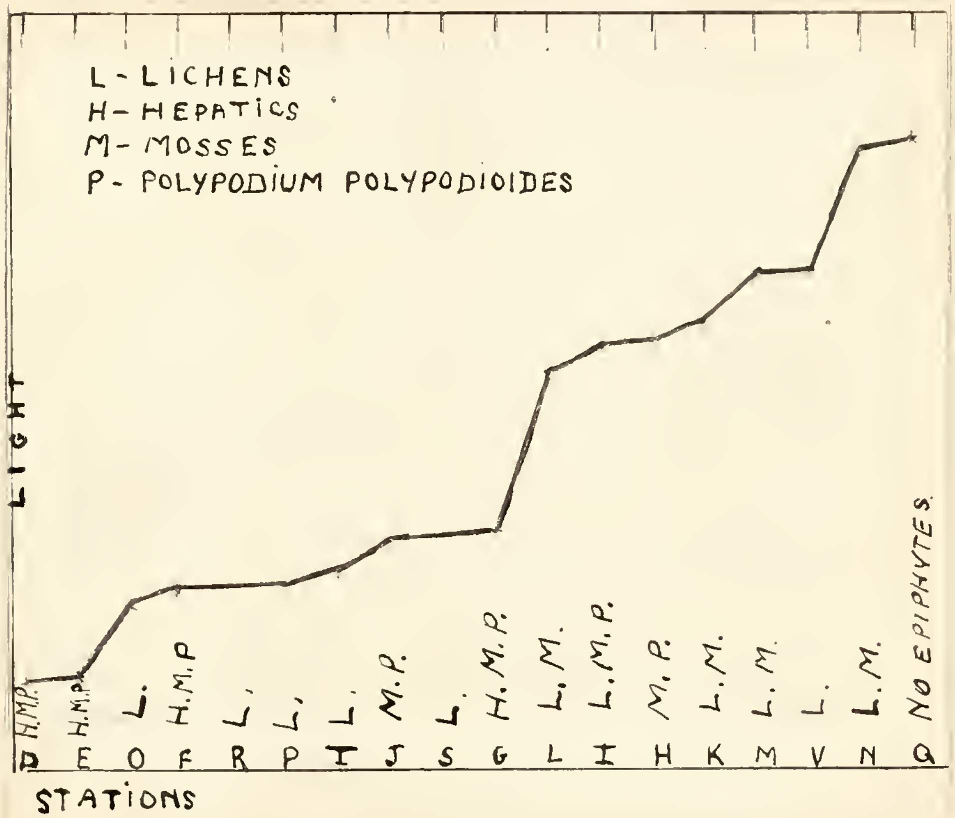



Fig.15 Graph showing the influence of LIGHT on the distribution of the epiphytes.

(Fig.16) corresponds somewhat with the arrangement of the epiphytes into regions, as was found in the evaporation curve, but this correspondence is not as definite as in the case of the evaporation curve. In the case of the air temperature it is also evident that its influence on the occurrence of the epiphyte

is an indirect one.Its direct effect is really on the evaporating power of the air rather than on the distribution of the plants on the tree.The arrangement of the epiphytes according to the relative humidity of tha air (Fig.17) also suggests an indirect effect on the regional distribution of the epiphytes on the tree. Here, it appears, that where the humidity is the greatest the hepatics occur;where it is the lowest the lichens prevail.Apparently,the effect of the relative humidity of the air on the occurrence of the mosses and the polypody is not a very marked one since both of these plants are found where the humidity is low as well as where it is relatively high.However, neither the air temperature nor the relative humidity of the air present any marked variation on the different stations on the tree.The curve of each is practically a straight line while the light and the evaporation curves are distinctly ascending curves indicating that the intensity of these was quite marked at each station on the tree. The substratum temperature curve (Fig.18) does not seem to show any definite relation to the occurrence of the epiphytes on the tree.

It is safe to conclude from the results obtained that neither the light,the realtive humidity of the air,the temperature of the air,nor the temperature of the substratum exert any direct influence on the

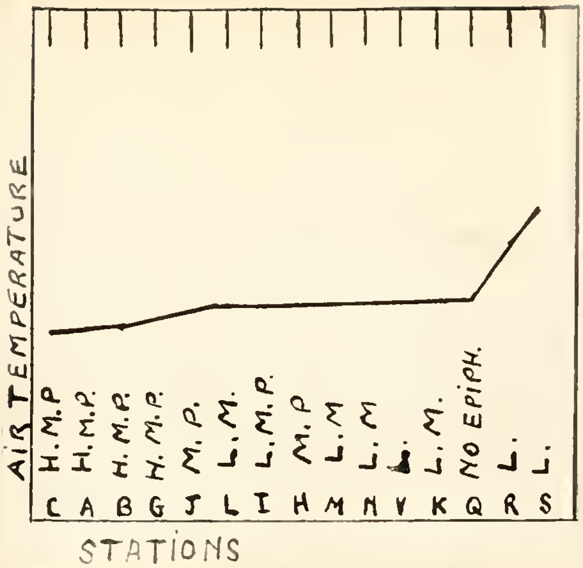



Fig. 16 Graph showing the relation of the temperature of the air to the distribution of the epiphytes.

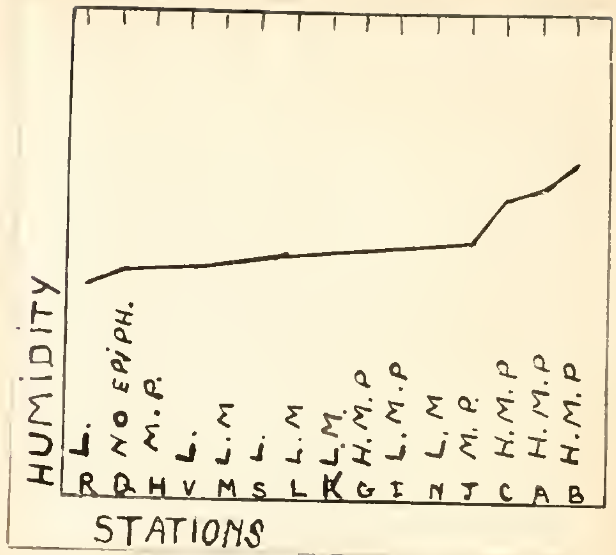



Fig. 17 Graph showing the influence of the relative humidity of the air on the distribution of epiphytes.

L-Lichens
H.-Hepatics
M-Mosses
P. Polypodium polypodioides

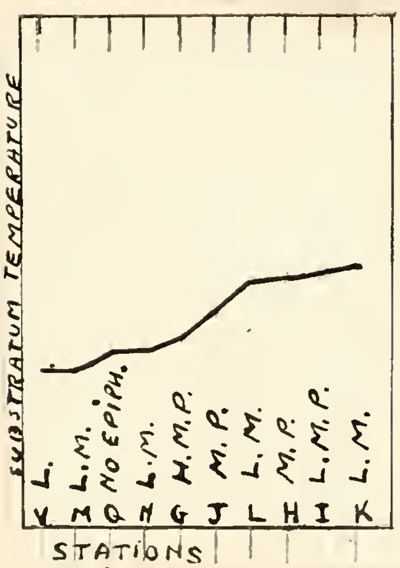



Fig. 18 Graph showing the influence of [illegible] on the distribution of the epiphytes.

L-Lichens H-Hepatics M-Mosses
P-P. polypodioides

occurrence and distribution of P.polypodioides nor on the epiphytes associated with it. It is the sum total effect of the first three conditions on the evaporating power of the air in the immediate vicinity of each station on the tree which is responsible for the definite epiphytic flora on the given station.

## B. CHEMICAL ANALYSES

Having determined the influence of the climatic conditions on the distribution of Polypodium polypodioides the writer was confronted with the problem of the source of water supply and of mineral nutrients needed by the epiphyte in its development and growth. In order to determine whether the epiphyte derives the necessary material from the substratum which it inhabits or from the dust of the air, chemical analyses were made of the "humus" gathered from the bark of the tree on which the epiphyte was growing. An analysis was also made of the epiphyte itself. To determine how much of a contribution to the chemical composition of the "humus" the bark itself made, the bark of the trees that bore epiphytes was analyzed and likewise the bark of those trees that did not bear them. In connection with this work, the writer wishes to express his thanks to Dr. W. F. Hand, State Chemist of Mississippi and his assistant Mr. H. Solomon for

TABLE IV CHEMICAL ANALYSIS

| Material | Sample | Moisture % | Ash % | Si % | N % | K % | Phosphoric Acid % | Remarks |
|---|---|---|---|---|---|---|---|---|
| Carya alba | Humus | 3.4 | | 35.2 | 0.48 | | | small clump at ground |
| Carya glabra | " | 4.35 | | 32.5 | 0.67 | | | " " |
| Carya ovata | " | 8.30 | | 20.2 | 0.70 | | | " " |
| Crataegus sp. | " | 13.30 | | 4.2 | 1.52 | | | 20mm clump on stem |
| Diospyros virginiana | " | 7.83 | | 23.7 | 0.76 | | | small clumps at ground |
| Juniperus virginiana | Ash of humus | | | | | 0.38 | 3.34 | |
| " | Bark | 25.40 | | | 0.51 | | | |
| " | Humus | 13.30 | | | 1.65 | 0.05 | 0.45 | large clump on stem |
| Pinus taeda | Bark | 10.85 | 1.7*<br>1.9# | | 0.21*<br>0.24# | 0.10*<br>0.11# | 0.15*<br>0.17# | No epiphytes |
| " " | Ash of bark | | | | | 5.89 | 8.84 | |
| Polypodium polypodioides | Ash of plant | | | | | 8.85 | 5.10 | Epiphyte on Q.stellata |
| " | " | | | | | 8.76 | 4.89 | Epiphyte on J.vitginiana |
| | Plant | 9.33 | *7.46<br>8.23# | | *1.38<br>1.52# | *0.66<br>0.73# | *0.38<br>0.42# | Epiphyte on Q.stellata |
| Quercus falcata | Humus | 11.0 | | 12.2 | 1.07 | | | 30mm clump at ground |
| Q.stellata | Humus | 10.5 | *15.6<br>17.5# | | *1.7<br>0.2# | *0.08<br>0.09# | *0.27<br>0.30# | Huge clump on trunk |
| " " | Bark | 8.85 | 12.7*<br>13.94# | | 0.51*<br>0.56# | 0.05*<br>0.05# | 0.11*<br>0.12# | |
| | Ash of bark | | | | | 0.39 | 0.87 | |
| | Ash of humus | | | | | 0.51 | 1.73 | |
| Ulmus americana | Humus | 2.35 | | 37.0 | | 0.23 | | small clump at ground |
| | " | 10.35 | | 12.3 | | 1.25 | | Large clump on trunk |

(*) Calculated on original basis
(#) " " dry "

making the chemical analyses. The results of these analyses are presented in Table IV.

A study of the data reveals the fact that where nitrogen was abundant, the clumps of the epiphytic fern were fairly large. That the nitrogen was not obtained from the dust of the air is evident from the fact that samples which showed a high percentage of silicon, generally showed a low percentage of nitrogen; where the silicon content was low the nitrogen content of the sample was high. Regarding the silicon content as an index of the amount of dust accumulated in the crevices of the bark (since silicon is abundant in the dust of the region), it appears that the main source of nitrogen was not the dust of the air but the accumulated decaying organic matter which composed the bulk of the humus and which originated on the bark through the masses of epiphytic bryophytes and animal matter associated with them. The luxuriant growth of the fern on the substratum rich in nitrogen indicates that the nitrogen content of the substratum has a marked effect on the development and growth of the polypody. This is particularly evident in the case of <u>Crataegus</u> which, in spite of possessing a smooth bark and being only slightly over eight centimeters in diameter, was able to support a good sized clump of the polypody, doubtless due to the high nitrogen content of the humus on which it thrived.

Although the ash of the epiphyte,as a rule, shows a high percentage of potash, the "humus" generally shows a low potash content,which seems to indicate that most of the potash obtained by the plant comes from the dust of the air.This is probably true also for the phosphoric acid,for very small amounts of this substance were found in the "humus",while the ash of the epiphyte showed a much higher percentage of the acid.It is possible that the high phosphoric acid content in the ash of the epiphyte is due to metabolic processes.It is evident from the chemical study that the fertility of the substratum is of as much importance to development and growth of the fern as are the low rate of evaporation and an abundance of moisture for the beginning of the epiphyte on the tree.It is indeed remarkable that the nitrogen of the hūmus on the bark of the tree is frequently as high and at times even higher than the nitrogen content of the most fertile soils,for very few soils have as much as 1.6% nitrogen. It is no wonder,then,that the polypody thrives so well on such trees as <u>Quercus stellata</u>, <u>Juniperus virginiana</u>, or <u>Ulmus americana</u> and develops on these trees an extensive root system and an abundance of leaves.

Acidity and Alkalinity Tests of the Substratum.

Chemical determinations in the field,by means of the La Motte set of indicators,of the acidity of the bark of trees on which the epiphytes occurred and also of the

bark of those trees which bore no epiphytes, showed no marked difference in the acid content. In fact, the acidity of the bark or of the "humus" on the bark appeared to vary with the moisture content ~~the~~ of the air as well as with the time of the day. It was found that the acidity was slightly higher early in the morning than it was at noon, and during a rain or immediately after, the bark or the "humus" also showed a slightly higher acidity than in dry weather. It was found further that the bark of those trees which never bore any epiphytes contained an acidity of the same concentration as the bark of those that bore an abundance of the epiphytic fern and mosses. The tests also revealed that the fern occurs not only on slightly acid "soil" but is frequently found also on slightly alkaline "soil". It is true, however, that on the bark of the pine which exhibited an acidity of 4.5 ($P_H$ values) the fern never occurred. There, it is believed, the real cause of the absence of the epiphytes was not the high acid content of the bark, but the physical character of the pine bark (Pinus taeda and P. echinata). It thus appears from a study of the chemical reactions that acidity or alkalinity of the substratum does not influence the occurrence and distribution of Polypodium polypodioides.

## C. EFFECT OF PHYSICAL CHARACTER OF THE BARK ON THE DISTRIBUTION OF P.POLYPODIOIDES

Observations in the field indicated that the fern occurred abundantly on trees the bark of which possessed crevices.It was particularly abundant on bark which was deeply furrowed and which was sufficiently soft to allow the young roots of the fern to penetrate into the interlaminar spaces.On such bark the polypody was found developing a copious root system in the interlaminar spaces,where the young root hairs were always found to be turgid and functioning regardless of the weather conditions. A flaky bark such as that of the juniper

Fig.19
The underside of a mass of P.polypodioides showing the massive root system in the interlaminar spaces.

also appears to be suitable for this epiphyte. The thickness of the bark, is, apparently, also important since in thick bark the young roots can make their way into the spaces between the layers fartherst away from the surface and be protected from excessive evaporation. The polypody has never been found on trees with smooth bark nor on those the bark of which breaks or peels off frequently, as in the case of the pine or sycamore.

A study of the water absorbing power and water losing power of the bark of different trees seems to indicate that only those barks which absorb and hold water fast serve as satisfactory substrata for these epiphytes. The bark of the pine is not suitable for the development and growth of the epiphyte, for water is absorbed rapidly and is lost just as rapidly so that the bark becomes very dry shortly after it has been wetted. Nor does a bark which is horny or stony in character, as that of the red oak or of the hickory make a desirable substratum, for such barks have a very low imbibing power. These conclusions were reached after samples of bark of different trees were soaked in water for twenty four hours and then dried for twenty four hours, their weight being determined before soaking, after soaking and after drying. The writer realizes of course, that this method is not absolutely precise,

for it is quite possible that in some barks the water might never have reached into the interior of the sample,while in others the water undoubtedly penetrated far into the interior.But it was impossible to secure definite blocks of bark which could be measured in three dimensions and their swelling or shrinking areas determined,for that reason the gravimetric method was used which although not very accurate presents, nevertheless,an explanation sufficiently plausible and which seems to coincide with the explanation derived from the field observations.

## D.DISCUSSION

From the study of the distribution of the epiphytic polypody,it may be stated that the fern begins its life on the tree in either of two ways. It may start from spores blown into the crevices of the bark or on a mass of mosses on the tree trunk. These spores if they find sufficient moisture germinate and develop prothallia which later produce young sporophytes.Such stages of development of the fern were found abundantly on the trunks of Juniperus virginiana both in the autumn and in the spring. The other mode of origin is that from the vegetative fragments of the sporophyte which are washed down from higher branches to the lower ones by heavy rains.

This apparently happens on Quercus stellata where small clumps of the epiphyte were found in the crotch of a lower branch immediately below a huge mass of the fern two meters above. A search for young sporophytes or prothallia proved unsuccessful.

It was found further that Quercus stellata, Ulmus americana and Juniperus virginiana serve as the best supports for the epiphyte, for on these the polypody was found in abundance. On the oak the epiphyte invariably inhabits the oldest branches and the main trunk on the north, northeast, and northwest sides. On the elm it is found often inhabiting the trunk from the very ground to the oldest branches. On the juniper the epiphyte generally occurs in small clumps all along the stem. It may be added, that on the latter tree the fern was never found in the fruiting stage, which seems to indicate that the bark of this tree is favorable for the start of the epiphyte but that long before the fern matures the bark together with the polypody is shed. This was found true in many cases, for a number of clumps of the fern were found lying on the ground apparently recently detached from the tree.

This definite distribution of the epiphytes in relation to climatic conditions and to

their supporting plant has interested botanists for a long time.The early workers, in fact, attributed the occurrence of epiphytes in some places and their absence in others chiefly to differences in light and atmospheric humidity.To quote Schimper p.90 (25), "Licht, feuchte Luft,reichliche Thaubildung,häufige Regengüsse stellen die wessentlichen Bedingungen eines üppigen epiphytischen Pflanzenlebens dar."It was Byer (2),however, who suggested that "only such plants can live as epiphtes....which can stand the hot sun and the drying winds." In other words,he suspected that the water supply and water loss is the most important problem of the epiphyte. His suggestion indicates that only those plants can exist as epiphytes which are capable of resisting excessive evaporation.

That the evaporating power of the air is actually an important factor in the occurrence and distribution of the epiphytes is evident in the case of P.polypodioides The graphical representation of the results obtained (Fig.14) as tabulated in Table III shows clearly that it is the evaporating curve alone which bears a definite relation with the distribution of the epiphytes. Thus, where the evaporating power of the air is low the hepatics, the mosses and the polypody occur;where the evaporation rate becomes high, the hepatics begin to disappear, while the mosses and the fern still persist; as the rate of evaporation increases the fern disappears

but the lichens begin to appear. With the further rise of evaporation, the mosses also disappear leaving only the lichens to occupy the areas of highest evaporation.

The definite distribution of epiphytes on the tree corresponds somewhat to the results obtained by Shreve (26) in the Blue mountains of Jamaica. He says p. 189; "The trees of the upper slopes have the same epiphytic flora that would be found in the upper two-thirds of the trees of the ravines. The trees of the ridges and peaks have only those that are characteristic of the uppermost third and the midheight species are restricted in these habitats to the side of prostrate trunks or fallen logs." Thus, the vertical and radial distribution of epiphytes on an individual tree appears to be comparable to a certain degree to the similar distribution of epiphytes in the mountains. Not only is the vertical distribution of the epiphytes on an individual tree well marked but even at the same height different sides of the tree will bear different types of epiphytes, as is shown in the case of Q. stellata where, for instance, at ten meters above ground the south side of the trunk bears only mosses, while the northeast and the northwest sides bear huge clumps of the polypody entangled in mosses. It was found, however, that at different sides at the same height and at different heights of the same tree the evaporating power of the air is

not at all the same, which undoubtedly accounts for the variation in the distribution of the epiphytes. The vertical distribution of the epiphytes on one tree may thus be compared with the vertical distribution of the vegetation on a mountain.The mosses and the polypody correspond to the mesophytic vegetation of the middle region of the mountain, while the lichens of the dry regions of the tree are comparable with the xerophytic vegetation of the summit of the mountain where the drying winds prevail.The hygrophyllous vegetation which can not endure high evaporation,if such is present,would be found at the base and would correspond then to the hepatics in regions on the tree where the evaporation is the lowest.

Not only do climatic conditions affect the distribution of the fern but even the chemical and physical characters of the bark exert a marked influence on the occurrence and development of the epiphytes.It appears that a substratum rich in nitrogen causes a vigorous growth of the epiphyte;the other elements seem to be supplied in sufficient amounts by the dust of the air.Furthermore,the bark itself in order to make a desirable substratum for the epiphyte must be sufficiently soft to allow the penetration of the young roots of the fern.When that is done , the absorbing roots remain practically imbedded within the bark,while those which earlier functioned for absorption are later found in

in the outer layers of the bark and have retained only the function of anchoring roots which hold the fern in place and also aid in the accumulation of humus.The question arises whether this fern is to be regarded as a true epiphyte when such conditions are established. In answering this question one may suggest a classification of epiphytes based upon that of Went though somewhat modified.

Epiphytes may be classified into Eu-epiphytes, Hemi-epiphytes and Pseudo-epiphytes. As euepiphytes, or true epiphytes, we may regard those plants only which no longer derive their minearl elements or water from the substratum to which they are attached.These epiphytes have undergone some modification of their organs so that they can obtain these substances from the air.The attachment to the substratum is usually accomplished by modified roots which function solely for anchoring To this group belong many bromeliads and orchids. Hemiepiphytes,or facultative epiphytes, are those plants which although having lost connection with the earth still derive water and other nutrient substances from the substratum to which they are attached by more or less modified soil roots which are imbedded in the substratum.These epiphytes may occasionally occur on the ground also, though their most usual habit is one

on trees and dry rocks.Exaples of this type are Polypodium polypodioides and P.vulgare and many other tropical ferns and orchids. Pseudoepiphytes, or false epiphytes,are those forms which are ordinarily terrestrial plants but by some agency or "accident" they are brought to the tree and succeed in growing there for some time.These plants possess no special adaptations and practically never reach maturity on their supporting plant.Such epiphytes have no definite regional distribution and are found in all parts of the earth.As soon as condtions for development and growth become distictly different from those on the ground,they wither away and die.

PHYSIOLOGICAL STUDIES

While studying the effect of the climatic conditions on the distribution of the polypody, the writer observed carefully the peculiar curling of the leaves of this fern. This characteristic behavior of the leaves of _Polypodium polypodioides_ in dry weather seems at first sight to serve as a special adaptation against dessication.

Fig.20
The polypody in wet weather with leaves expanded

Fig.21
The polypody in dry weather with leaves curled up.

The curling on drying begins, as a rule, by the rolling inward of the pinnae from the ends with the upper surface inward. As the entire leaf is folding, each individual pinna also folds with its upper surface inward so that there is really a double folding in each pinna, one main rolling in endwise of each pinna towards the rachis and the other a

curling upward and inward of the margins of each pinna towards its midrib.The folding of the individual pinnae is soon followed by the curling of each leaf and while this takes place the rachis begins to twist and to curl.Thus, in all cases, the curling of the leaf causes the upper epidermis to be hidden from the outside,while the lower epidermis,which is covered with numerous scales,remains exposed.This characteristic curling which conceals the upper surface and leaves only the lower surface exposed, suggests at once that this is an adaptation of the leaf to xerophytic conditions.It might be assumed from such a behavior of the leaf that its upper epidermis loses water more readily than its lower one,and by being rolled in when the air is dry the leaf avoids the danger of excessive transpiration from the upper surface.The scales which cover the lower surface of the leaf might well be assumed to function as an aid in lessening the evaporation from the lower epidermis. To determine definitely whether these assumptions are correct and to learn which side of the leaf really loses the greater amount of water under given conditions,experiments were carried on in the laboratory both on living and dead leaves of the epiphytic fern.Abundant material for these experiments was obtained from Mississippi through the kindness of Professor J.M.Beal and a large clump of the living fern was sent from Athens,Ga. by Professor J.M.Reade to both of who the writer here expresses his sincere thanks.

## Methods of Experimentation

Three experiments were performed on detached leaves of P. polypodioides. In the first experiment four groups of four leaves each were placed in a desiccator containing a uniform layer of calcium chloride. In the first group each leaf received a thin layer of petrolatum on both the upper and lower epidermis thus sealing up both surfaces completely. The leaves of the second group received a layer of the petrolatum on the upper surface only, leaving the lower one open; those of the third group were sealed only on the lower side, leaving the upper side untouched; but the leaves of the fourth group were left in the natural condition so that transpiration could take place normally from both the upper and lower surfaces. In each case only the leaf blade was used, in order to avoid any complications arising from an uneven sealing of the cylindrical petiole. After the sealing of each leaf, it was weighed and then dried in the desiccator for twenty four hours and weighed again at the end of that time. The weighing was repeated daily for one week. At the end of the experiment the recorded weights of each group were averaged and the percentage of water lost from each surface was calculated from the results obtained. Having thus determined the rate of water loss from each surface of the leaves, these same leaves were then suspended from wires in a moist chamber so that each leaf was a centimeter or so above the water level but not actually in contact

with the water. This was done in order to determine the water absorbing power of each surface of the leaf. As previously done, the leaves were weighed daily for one week. At the end of this test the average percent of gain for each group was then calculated.

In the second experiment the method was somewhat modified. Instead of using calcium chloride as the drying agent, sulphuric acid was used since by means of this acid it was possible to establish different degrees of drying. Forty cubic centimeters of concentrated sulphuric acid (100%) constituted the drying agent in the first mason jar which was sealed tightly by a paraffined cork. From the inner side of the cork eight leaf blades were suspended from hooks fastened in the cork. Of the eight leaves, two were vaselined on both sides, two on the upper side only, two on the lower side only, and two remained uncoated for control. In no case were the leaves allowed to be close to the acid; they were generally about six centimeters above the acid. The leaves in the second jar were similarly arranged but this contained forty cubic centimeters of diluted sulphuric acid in the proportion of one part of water to three parts of acid (75%). A third jar contained a like quantity of half water and half acid (50%); a fourth contained one part of acid to three parts of water (25%); a fifth one part of acid to nine parts of water (10%); and a sixth jar contained only distilled water (00%). Thus, each

jar contained a series of leaves some with the upper surface free; some with lower surface uncoated; some with both upper and lower surfaces clear and some with both surfaces sealed by the vaseline. It may be mentioned here that white vaseline was used in preference to cocoa butter since the latter tends to harden, crumbles and drops off when the leaf begins to curl thus introducing an error when the leaves are weighed. All leaves of each series being in the same jar were exposed to precisely the same drying conditions. The very same experiment was also made with leaves which had been previously killed by being subjected to chloroform vapor for three hours, after which time they became brown and began to curl. Thus, both living and dead leaves were subjected to precicely the same drying conditions. Each leaf from every desiccator was weighed once in twenty four hours for one week.

The third experiment was designed to determine any internal structrual changes in the leaf under either dry (curled) condition or the moist (expanded) condition. Small pieces from curled and expanded leaves were cut from plants grown in the open. These were immediately dropped into absolute alchohol and kept there for thirty six hours frequently changing the alcohol to insure complete dehydration. The material was thus fixed before any internal changes could take place. Later the ordinary method was used in imbedding and sectioning this fixed material. For fixing the sections on the slide no water was used, nor was there any water or dilute alcohol used in the staining

of the preparations,this being done in absolute alcohol entirely.Throughout this proceedure the leaves retained their original shapes as cut in the field and the sections cut from them showed the difference between the internal structure of the curled leaf and that of the expanded one.

## Results

The results of the first experiment show that normal unsealed leaves lost on an average 68.13% of their weight during the first twenty four hours;during the second day the loss amounted to 8.75% of their weight;while for the rest of the week these leaves lost no more in weight.The total average loss from the uncoated leaves for the entire week amounted to 76.88% of their original weight.The one externally evident result of this enormous loss was the curling of the leaf.The leaves of which the lower surfaces were sealed showed an average loss during the first day of 11.16%, on the second 5.12%,on the third day 8.72%,on the fourth 0.32% and on the fifth 1.07%.No more loss in weight took place during the rest of the week.Those leaves of which the upper surfaces were sealed lost during the first day an average of 42.30%,during the second 3.67% and during the third day 7.4%.No further loss was observed for the rest of the week.The leaves with both surfaces sealed lost the least,the first day's loss being 6.04%,during the second day the loss was 1.33% and on the fourth day a loss of 4.82% was observed.These leaves showed no further loss for rest of the week.Theoretically these leaves should

lose no water at all but since a complete sealing of the leaf is practically impossible, it may be assumed that the recorded loss took place from the unsealed edges of the leaf. At any rate, the result of prime interest here is that the leaves lost the most water when both surfaces were open. From the lower surface alone the leaves lost 53.18% during the entire week; while from the upper surface alone the leaf lost only a total of 26.39% during the whole week. It is evident from these results that the leaves of this fern lose water almost twice as rapidly from their lower surface than from the upper one. This appears rather a puzzling result for it is actually this side that is exposed when the leaf curls up in dry weather, while the side losing the least water is concealed and subject to very little desiccation.

The results obtained from the second experiment are indicated in Tables V and VI. A study of the data reveals the fact that when the leaves were subjected to artificial drying in the sulphuric acid desiccator they behaved essentially as they did in the calcium chloride desiccator. In other words, although the leaves were dried by two different methods, the results were the same; in both cases the greatest amount of water was lost from the lower surface of the leaf. This is true not only for living leaves, but likewise for leaves which had been killed by chloroform. It is safe to conclude from these results that the lower surface although covered with scales and apparently resistent to drought is really the surface which

Table V Living leaves in sulphuric acid desiccator tested for their capacity to lose water

| Series (*) | Surface sealed | Percent loss in weight during 1st day | 2nd | 3d | 4th | 5th | 6th | 7th | Total percent loss |
|---|---|---|---|---|---|---|---|---|---|
| | None | 57.4 | -- | -- | -- | -- | -- | -- | 57.4 |
| I | Upper | 36.2 | 2.0 | 4.0 | -- | -- | -- | -- | 42.2 |
| 100% | Lower | 20.5 | 10.0 | 6.6 | -- | -- | -- | -- | 37.1 |
| Acid | Both | 6.0 | 1.1 | -- | -- | -- | -- | -- | 7.1 |
| | None | 45.2 | 9.8 | -- | -- | -- | -- | -- | 55.0 |
| II | Upper | 36.6 | 4.7 | 2.3 | -- | -- | -- | -- | 43.6 |
| 75% | Lower | 11.5 | 3.3 | 6.9 | -- | -- | -- | -- | 21.7 |
| Acid | Both | 7.3 | --- | --- | -- | -- | -- | -- | 7.3 |
| | None | 55.5 | 9.5 | -- | -- | -- | -- | -- | 65.0 |
| III | Upper | 54.4 | -- | -- | -- | -- | -- | -- | 54.4 |
| 50% | Lower | 21.3 | -- | -- | -- | -- | -- | -- | 21.3 |
| Acid | Both | 6.2 | 2.3 | -- | -- | -- | -- | -- | 8.5 |
| | None | 50.9 | -- | -- | -- | -- | -- | -- | 50.9 |
| IV | Upper | 27.6 | 5.3 | 7.3 | -- | -- | -- | -- | 40.2 |
| 25% | Lower | 10.1 | --- | 2.5 | -- | -- | -- | -- | 12.6 |
| Acid | Both | 7.2 | -- | -- | -- | -- | -- | -- | 7.2 |

Table VI Leaves killed by chloroform and placed in sulphuric acid desiccator to test their capacity to lose water

| Series (*) | Surface sealed | Percent loss in weight during 1st day | 2nd | 3d | 4th | 5th | 6th | 7th | Total percent loss |
|---|---|---|---|---|---|---|---|---|---|
| I | None | 52.9 | 3.3 | -- | -- | -- | -- | -- | 56.2 |
| 100% | Upper | 35.3 | -- | -- | -- | -- | -- | -- | 35.3 |
| Acid | Lower | 17.5 | 8.2 | -- | -- | -- | -- | -- | 25.7 |
| | Both | 11.4 | 8.4 | -- | -- | -- | -- | -- | 19.8 |
| II | None | 44.5 | -- | -- | -- | -- | -- | -- | 44.5 |
| 75% | Upper | 41.1 | -- | -- | -- | -- | -- | -- | 41.1 |
| Acid | Lower | 26.2 | -- | -- | -- | -- | -- | -- | 26.2 |
| | Both | 11.1 | --- | -- | -- | -- | -- | -- | 11.1 |
| III | None | 40.5 | -- | -- | -- | -- | -- | -- | 40.5 |
| 50% | Upper | 32.5 | -- | -- | -- | -- | -- | -- | 32.5 |
| Acid | Lower | 18.9 | -- | -- | -- | -- | -- | -- | 18.9 |
| | Both | 9.3 | -- | -- | -- | -- | -- | -- | 9.3 |

(*) In the series containing 25% acid the killed leaves showed no decrease in weight. In the desiccator containing 10% acid or pure water neither the living nor the killed leaves showed any decrease in weight.

loses water most rapidly.It is needless to say that when an appreciable amount of water is lost, a folding or a curling of the leaf results.In both living and dead leaves those of which neither surface was sealed, curled up completely when subjected to dry conditions;those of which only the lower side was sealed curled not quite as markedly as in the former case; the leaves of which the upper side only was sealed became only partially folded;while those with both surfaces sealed remained completely expanded throughout the experiment.The condition of the living leaves remained unchanged in the jar containing 10% acid and in the one contanining distilled water indicating that there was no loss of water from the leaves .The killed leaves,however, failed to show any loss in weight even in the jar containing 25% acid.Furthermore, these soon became infected by a fungus in the jars contaings 25% and 10% acid as well as in the one containing pure water.

The results of the experiments on the water losing power of the leaves,which show that the lower surface loses water about twice as rapidly as the upper,discredit at once the idea that the protection of the upper surface by curling is a very effective adaptation against excessive transpiration.The rolling inward of the upper surface does, of course,reduce the transpiring area in half,but it leaves the more active half,which contains all of the stomata, still exposed.The question, then, arises whether the lower surface might not really be especially capable of water absorption

so that when a limited amount of water is present it would at once be absorbed by this hairy surface. Dried curled leaves were placed in a moist chamber in order to determine the water absorbing power of each surface of of the leaf. When those unsealed leaves which had been kept in the desiccator and which were completely curled after drying, were later placed in the moist chamber, they gained 44.53% of their weight during the first twenty four hours and became fully expanded. During the second day the gain was 4.84%, on the third 4.58%, on the fifth 6.15% and during the sixth and seventh days the leaves showed no more gain in weight. The average total percent of gain for the whole week amounted to 60.10%. Those leaves whose upper surfaces only were sealed gained during the first day 16.29%, on the second 3.45%, on the third 7.8%, during the fourth 1.82%, during the fifth 0.63% and during the sixth and seventh days together the gain observed was only 0.62% making a total of 30.61%. At the end of the fifth day these leaves began to unfold and by the end of the sixth day they were fully expanded. The leaves whose lower surfaces were sealed showed a gain of only 1.25% during the first day, of 1.64% during the second day, of .52% during the fourth, and of 0.01% during the fifth and sixth days together thus making for the whole week a total gain of only 3.42%. This gain in weight was accompanied by no appreciable difference in the physical appearance of the leaf. Whether any part of the observed gain in these three experiments was due to the actual condensation by the leaf itself of the water vapor present

about it is an unsettled question. It is certain that no leaf actually came in contact with the liquid water which covered the floor of the chamber. It is quite possible, however, that during the night the water vapor was condensed on the surface of the leaves so that the leaves may have obtained the water entirely by the imbibition of the liquid water condensed on their surfaces, and not by condensing the water vapor that penetrated to the interior by way of the stomata. At any rate, it is noteworthy that the leaf increased in weight nearly ten times as rapidly when the lower surface was unsealed as when the upper one was left uncoated. Whether this enormous increase in weight is due to the fact that all of the stomata of the leaf are found on the under side of the leaf and none on the upper side and thus offer more absorbing surface is a question that needs further investigation.

The difference in the appearance of the leaf under wet and dry conditions suggests that there may be internal structural differences between the expanded form and the curled one. Paraffin sections were made of both curled and expanded leaves fixed in absolute alcohol. These showed a remarkable difference in the tissues of the leaf. The cells of the expanded leaf seemed to be turgid and maintained their maximum size and smooth outline. The cells of the curled leaf, on the contrary, greatly reduced in size and wrinkled in outline. The shape of a cross section of a curled leaf is shown in Fig. 22. The diagrammatic drawings in Figs. 23 and 24 show the comparative size and shape of the cells from

a cross section respectively of a curled leaf and of an expanded one. Both of these sections come from the same region of corresponding pinnae, and the same magnification is used for both.

Whether the loss and gain of water by the leaf is entirely an osmotic phenomenon or is accomplished partly or entirely only by imbibition might be answered by a measurement of the cells of the leaf in the curled condition and of those of the leaf in the expanded condition. Paraffin sections of curled leaves were mounted on slides, the paraffin dissolved off by xylol and the preparation covered with a cover slip. In this manner, while the sections were still in xylol under the cover glass, individual cells picked at random in three different regions of the upper and lower epidermis and in the palisade tissue were measured in width and length. The two dimensions of a number of cells of each region of a given tissue were then averaged and these were regarded as the dimensions of a typical cell of the curled leaf. After the measurements were obtained, the xylol was drawn out from beneath the cover slip and replaced by absolute alcohol while the sections were still under observation under the microscope. When all the alcohol was drawn out water was introduced at one edge of the cover glass and its effect on the cross section of the curled leaf noted. As soon as the water came in contact with the cell wall of the cells in the section, the cells began to swell and to expand so that at first a vertical straightening of both ends of the section took place and shortly

Table VII Increase in size of cells in a cross section of a curled leaf after wetting

| Condition of leaf | Tissue | Region in leaf | Average Width in μ | Average Length in μ | Percent increase in width | Percent increase in length |
|---|---|---|---|---|---|---|
| Curled (before wetting) | Upper epidermis | midrib | 7.5 | 14.6 | | |
| | | margin | 10.5 | 16.3 | | |
| | | intermediate | 7.8 | 15.8 | | |
| Expanded (after wetting) | Upper epidermis | midrib | 19.3 | 17.8 | 157.3 | 21.9 |
| | | margin | 18.7 | 17.5 | 78.6 | 4.5 |
| | | intermediate | 18.9 | 18.7 | 143.8 | 18.7 |
| Curled (before wetting) | Lower epidermis | midrib | 10.5 | 12.3 | | |
| | | margin | 10.7 | 12.2 | | |
| | | intermediate | 11.0 | 12.4 | | |
| Expanded (after wetting) | Lower epidermis | midrib | 18.7 | 15.2 | 82.0 | 23.6 |
| | | margin | 20.6 | 17.1 | 92.5 | 40.1 |
| | | intermediate | 22.7 | 14.8 | 106.3 | 19.4 |
| Curled (before wetting) | Palisade | midrib | 5.0 | 23.8 | | |
| | | margin | 6.2 | 22.0 | | |
| | | intermediate | 5.0 | 25.0 | | |
| Expanded (after wetting) | Palisade | midrib | 13.0 | 36.4 | 106.0 | 52.8 |
| | | margin | 12.5 | 28.7 | 101.5 | 30.5 |
| | | | 15.0 | 40.0 | 200.0 | 60.0 |

after, the midrib region expanded and in straightening forced the two ends in opposite directions resulting thus in the expanded shape of the normal leaf under moist conditions. By this means it was possible to actually measure the cells in the curled state and then again of the same leaf in the expanded state. When the sections were fully expanded, a number of cells in each of the three different tissue layers in the different regions of the leaf were again measured, precisely as in the case of the curled section. The results obtained from measuring the dimensions of the cells in both conditions are tabulated in Table VII. It is evident from the data that all the cells of the leaf do not increase in size equally when water is introduced. The cells of the upper epidermis above the midrib increase about twice as much in width as those of the epidermis on the lower side of the midrib. The increase of the cells near the margin in the upper epidermis is slightly less than in the lower epidermis; while the epidermal cells in the region between the margin and the midrib of both the upper and lower sides show a considerable increase, though the cells of the upper side increased about a third more than those of the lower side. It will be noted that the greatest increase takes place in the width of the cells of both of these tissues; the increase in length is decidedly smaller and is practically alike in both tissues. In the palisade tissue the greatest increase in length and width occurs in the region between the midrib and the margin, while the smallest increase

occurs at the margin.

If we regard the increase in size of the cells after the introduction of water as an index of their capacity to lose water during drying, it becomes evident that the cells of the upper epidermis at the leaf margin must lose least water, while those of the midrib region must lose most. The lower epidermal cells of the midrib region, however, lose less water than the upper epidermal cells of the same region. It is further evident that the greatest decrease in size, under dry conditions, in all the cells measured, is that in width. It thus appears that the curling of the leaf is caused chiefly by the unequal rate of water-loss of the cells of the different parts of the leaf.

## Physiological Significance of the Scales

The presence of the scales on the lower surface of the polypody suggests their its possible function as a protection against dessication. According to Karsten (14) the scales present on the underside of the stem of Polypodium imbricatum serve to distribute the water drops which settle on the stem. In Polypodium sinuosum, however, the scales serve for absorbing water which appears on the stem in the form of drops. Schimper (25) and Mez (18) both attribute the function of water absorption in Tillandsia to the scales. Mez regards the mechanism by which the water is absorbed by the scale as either osmotic or capillary. So far as the writer knows, the function of the scales in P. polypodioides has not been determined. Although in a number of sections of dry leaves the wing

of the scale was found pressing closely against the surface of the leaf,other sections, on the contrary,seemed to show that the scale stood up above the surface so that there was a space between the surface of the leaf and the wing of the scale.A similar behavior of the scales was also observed in sections of the expanded leaf.It is therefore difficult to ascribe any definite function to the scales. There are some indications that they aid in the absorption of water, for the thick walled cells of the wing were seen to absorb water rapidly. Whether the water aborbed by the thick cell walls of the wing were later carried over by capillarity to the living stalk cells and from there to the interior of the leaf the writer is unable to say with any degree of definiteness.It is also possible that they help to protect the plant against drought.Their primary function seems to be,however, that of holding a film of water on the under surface of the leaf long enough to allow sufficient water to be imbibed by the cell walls and in that way to help restore the leaf to the expanded form.This is particularly suggestive when one considers the short time it takes a dry and curled leaf to expand after a rain.Long before the roots within the bark are able to take up and supply to the leaves the water absorbed by the bark during a rain, the scales by holding a film of water over the entire surface of the leaf allow the surface cells to absorb water and to begin to enlarge and thus to begin the uncurling of the leaf.

Relation of Water Content of Leaf to Leaf-movement.

It appears obvious both from the physiological study of the leaf and from the study of its internal strucure that evaporation takes place more rapidly from the lower surface. The peculiar curling of the leaf which exposes this surface and conceals the upper one,and the presence of an abundance of scales on the lower surface are both concerned in producing the striking change that occurs in the tissues of the leaf under dry conditions.When the leaf is placed in the dessicator while still expanded the scales stand out somewhat so that there is a space between the wing of the scale and the surface of the leaf.When transpiration begins the lower surface containing the stomata naturally loses more water than the upper one which is devoid of stomata.A stage then is reached when the cells of the lower epidermis begin to shrink due to the loss of water.At about this time the scales begin to be drawn close to the surface due to the shrinkage of the cells of the lower epidermis.Such a shrinkage would naturally be expected to cause a curling of the leaf with the lower epidermis on the inside and the upper one on the outside.A curling of this sort would seem the logical outcome of the known facts,since the lower surface loses the greater amount of water.In reality quite the contrary occurs.It is the upper epidermis that is found inside in the curled leaf, while the lower one is always on the outside .The explanation for this unexpected curling

must be sought in the different changes in size of the cells of the two sides of the leaf as it dries.These are indicated by measurements made of the cells in curled and expanded leaves.

Measurements of cells of the upper epidermis,of the palisade and lower epidermis from three different regions of the leaf seem to show that the lower epidermal region shrink least in width, while those of the same region in the upper epidermis shrink most in width.On the other hand,the shrinkage in length is practically the same in the cells of both the upper and lower epidermis near the midrib. It is further evident that the shrinkage of the palisade cells in width corresponds more to that of the cells of the upper epidermis than to those of the lower epidermis. Furthermore,the shrinkage in width of the cells of the lower epidermis in the intermediate region is much greater than in those at the same epidermis near the midrib,while at the margin the shrinkage in width is practically the same in both the upper and lower epidermis.Correlating these measurements with the loss of water and the curling of the leaf the following explanation may be offered for the characteristic curling of the leaf.While the cells of the lower epidermis are decreasing in size owing to the loss of water, their osmotic concentration is undoubtedly becoming greater than that of the mesophyll cells;this causes ,therefore a withdrawl of the water from the mesophyll cells by osmosis.

When this takes place, the cells of the lower epidermis again increase in size while those of the mesophyll tissue decrease and ultimately draw water out of the palisade cells. But the palisade cells soon begin to decrease in size and they ultimately draw water out of the cells of the upper epidermis causing them to decrease in size. As the water is continually being drawn out of the cells of the lower epidermis by evaporation, these keep on replacing the loss with water obtained by the process of osmosis from the mesophyll cells, and the latter in turn continue to replace their loss by water obtained from the palisade cells which likewise continue to absorb water from the cells of the upper epidermis. This process continues until a certain limit is reached beyond which the leaf does not give off any water. When that stage is reached the cells of the upper epidermis have shrunk the most, since there was no reservoir from which they could draw their supply of water to replace the loss. Those of the palisade tissue shrink about as much as those of the upper epidermis, while those of the lower epidermis having had a continual supply during the entire process of evaporation shrink considerably less than those of the upper tissues so that the cells of the least size appear on the upper epidermis and those of the greatest size are found in the lower epidermis. For this reason the lower epidermis is exposed during curling, while the upper one is concealed. This explanation seems plausible when we consider the increase in size of the cells during expansion (as shown in Table VII ) as an index of the shrinkage during evaporation.

Harshberger (11) who studied the curling of Rhododendron maximum in which it is the upper epidermis , instead of the lower one that becomes exposed during curling, claims that the rolling movement of the leaf is due to the gradual passage of the sap into the intercellular spaces or due "to the movement of the liquid from cell to cell by means of protoplasmic bridges so that one part of the leaf becomes highly turgescent and the other part more or less flaccid". He also believes that low temperature is responsible for the moving of the liquids toward the upper side of the petiole and of the leaf;while a higher temperature reverses the process It is believed by Harshberger that turgidity is the main factor in the mechanism of these movements.

It was found from a study of cross sections of a curled leaf that the cells showed considerable shrinkage and deformation.According to Steinbrinck (29) the loss of water from a plant tissue not only decreases the size of the cells of the tissue and deforms them but also affects the concentration of the cell sap which during the giving off of water pulls the cell membrane along with it.As the turgor becomes diminished the membrane weakens and the cohesion of the concentrated cell sap draws the cell membrane along with it to the center producing thus a decrease in volume of the tissue.This explanation seems applicable also to the decrease in volume and to deformation of the cells of the leaf in the curled state.

Concerning the physics of the curling and expanding of the leaf of this epiphytic polypody, the writer believes that the curling is not entirely an osmotic phenomenon. The loss of water from the cell walls themselves probably causes a shrinkage and a deformation of the cell wall. The so-called "resurection" of the leaves is probably largely due to imbition of water by the cell walls. Such seems clearly true from the behavior of these walls as it was observed under the microscope, in cross sections of fixed and imbedded leaves where no osmotic action could occur. These cells, many of them cut open so that turgor is impossible, expanded quickly to their normal plump form upon the introduction of water. In the living leaf, however, there is reason to believe that both osmosis and imbibition aid in the expansion of the leaf immediately after a rain. Undoubtedly, the process of expansion then begins with an imbibtion of water by the cell walls and later the osmotic action carries the water from cell to cell within the leaf thus aiding in the distribution of the water imbibed by the cell walls.

## VI. HISTOLOGICAL STUDIES

A study of the structure of the root and of the root hairs of P. polypodioides show first of all no signs of mycorrhizal association. The stucture of the root as whole seems to present the appearance of a typical fern root, though the root hairs differ somewhat from the ordinary type. Instead of being more or less uniform in thickness as root hairs generally are, these are swollen or bulbous at the base and taper off to a more or less blunt point at the tip (Figs.25.)

It will be well to describe the development and mature structure of the scales of the leaf of this epiphytic polypody since this knowledge should aid in solving the problem of their function. A sagittal section of a very young leaf of a mature plant, or of a young sporophyte, reveals the fact that each scale arises from an epidermal cell. The scale is, of course initiated very close to the growing point of the leaf. The epidermal cell from which the scale arises first divides by a transverse wall which thus forms two cells, an inner cell and outer one. The inner cell remains on the level with the epidermal cells, while the outer one buldges out and soon divides by a second transverse wall forming again an inner cell and an outer cell. The outer of these two cells continues to divide several times forming a plate of cells, while the lower cell by several successive transverse and one median longitudinal division, gives rise to the stalk of the scale. The cells of the plate grow out more rapidly towards the growing point of the leaf so that in the mature scale the

plate or wing of the scale is wider towards the tip of the pinna. The mature scale consists of a sunken funnel-shaped body the lower end of which is sunken in the tissue of the leaf and the upper plate-like flat portion resting on the surface of the epidermis. The plate-like portion consists of a peripheral, membraneous, radially ribbed, paranchymatous celled wing and a central cluster of cells. The cells of the wing are thick walled and are devoid of protoplasm as are also the cells of the central clustr except that the latter are brown in color. The cells of the funnel-shaped body, the stalk of the scale, unlike those of the plate are thin walled and contain protoplasm as is indicated by the presence of large nuclei. Several stages in the development of the scale are shown in Figs.26-31.

## SUMMARY

1. _Polypodium polypodioides_ may occur on any side of a tree and an at any height where the environmental conditions allow.
2. Of the climatic factors influencing the distribution of the polypody, the first in importance is the evaporating power of the air. High evaporation entirely prevents the growth of the fern.
3. Light also plays a part in controlling the distribution of the epiphyte. Its influence is probably not direct but

through modifying the evaporating power of the air, it exerts an indirect influence on the distribution of the fern.

4. The relative humidity of the air and the air temperature affect the distribution of the fern only as they affect the evaporating power of the air.

5. Of all the epiphytes studied the lichens can withstand the highest evaporation; the liverwort <u>Frullania virginica</u> endures the least evaporation.

6. The capacity of the bark for losing water rapidly affects the fern only in its influence on the evaporation from the roots of the fern which are imbedded in the bark.

7. The fern secures most of its necessary nitrogen from the humus accumulated in the crevices of the bark. The other mineral elements are obtained more largely from the dust of the air.

8. Where the humus of the bark shows a high nitrogen content, the fern grows luxuriantly. Where the bark is poor in nitrogen only a poor growth of the fern is developed.

9. The fern occurs equally abundantly on barks which show an acid reaction and on those which show a neutral or alkaline reaction.

10. A deeply furrowed, soft bark, which has a high water absorbing power and loses water slowly, furnishes the best substratum for the epiphytic fern.

11. The leaf under dry conditions loses the greater amount of water from its lower surface with the surprising result that a curling of the leaf occurs, which leaves the lower epidermis exposed and the upper epidermis concealed on the inside.

12. The curling of the leaf is perhaps due to the unequal loss of water from the cells of the upper and lower epidermis.

13. The curling of the living leaf is apparently the result of osmotic phenomena; the expanding is entirely due to imbibition in dead leaves and to both osmosis and imbibition in the living ones.

14. The function of the scales is probably to facilitate an equal and gradual distribution of water over throughout the lower surface of the leaf after a rain and also to absorb water, that is present on the surface of the leaf, and to pass it to the internal tissues of the leaf.

15. The scales originate from epidermal cells near the growing point of each pinna.

16. No mycorrhizal fungus was seen in the roots of this fern.

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Louis Jerome Pessin was born in Kremenchug, Russia, on May 19th, 1894. He came to the United States in November 1908. He received his early schooling in the Russian Gymnasium and completed his high school education in the city of New York. He entered the University of Georgia in 1912 and graduated with the degree of Bachelor of Science in 1916. In the fall of the same year he became Rufus J. Lackland Fellow in the Shaw School of Botany of Washington University at the Missouri Botanical Garden. There he majored for one year in Plant Physiology and Plant Pathology. In the fall of 1917 he entered the Johns Hopkins University majoring in Botany with a first subordinate in Plant Physiology and a second subordinate in Zoology. During 1918-19 he served in the Medical Detachment of the 146th Infantry in France and Belgium. He returned to the Johns Hopkins University in April 1919 and in the summer of the same year he studied the flora, especially the epiphytic flora, of the Blue Mountains in Jamaica, B.W.I. He was student-assistant in Botany at the Johns Hopkins University during 1917-18 and 1919-20. He was instructor and later Assistant Professor of Botany at the Mississippi Agricultural and Mechanical College from 1920 to 1922. He returned to the Johns Hopkins University in the fall of 1922. As a result of his studies in Jamaica he published a paper entitled "Epiphyllous plants of certain regions in Jamaica" in the Bull. Tor. Bot. Club 49:1-14, 1922.