

Mosses

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## III. MODERN SPECIES CONCEPTS: MOSSES

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Whatever a species might be, there is no question that most groups of plants and animals can readily be classified to species. Most problems actually are in the failure to observe characters correctly or to ascertain the significant characters. For centuries naturalists and systematists never questioned that all forms of life could be assigned to separate and distinct species. It is only very recently that newer and more sophisticated techniques have revealed groups of both plants and animals in which the classical concept of the species is difficult (but not impossible) to apply.

Most of the older bryologists thought they knew what species are. They described species and erected systems of classification in mosses and liverworts in the firm belief that there were just so many kinds and that they had only to be described, classified, and, in effect, pigeonholed. It was from this kind of taxonomic base that the early exploratory and descriptive phases of moss taxonomy in North America were launched, and it was the prevailing atmosphere in which most of the earlier works on mosses were written.

Principally because of the scarcity of workers, progress in moss taxonomy is years behind that in vascular plants. The field is still in the exploratory, floristic stage of development, and many of the commonest species are very poorly understood taxonomically, floristically, and ecologically. It was not until relatively recently, when Grout's "Moss Flora of North America" (1928-1940) was published, that keys and descriptions of mosses from the northern boundary of Mexico to the Arctic were available. Grout's treatment and Conrad's (1960) extremely useful but woefully incomplete book and a few state and regional manuals provide the only guides to the mosses of this vast region. It is not surprising, therefore, that bryologists have been few or that taxonomic investigations in the Musci have lagged far behind interest, for example, in the phytogeography and ecology of the group. Vast areas of the tropics, particularly South America, Africa, the South Pacific islands, Australasia, and large parts of eastern Asia are still poorly collected. But even in the British Isles and in many other parts of Europe where collectors have been active for two centuries, new species are still being described. Only a beginning has been made toward monographic work in North America. Relatively few genera have been revised, even by traditional methods. Family limits in many groups are vaguely drawn and the systematic positions of countless genera are still uncertain.

Moss taxonomists have been slow to use the methods of other disciplines and the "New Systematics," or the more fashionably labelled "biosystematics," is still on the bryophytic launching platform. Our knowledge and understanding of what is generally called classical or herbarium taxonomy of mosses is still too slight to make ef-

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fective applications and interpretations of the recently increased flow of physiological, developmental, cytological, and genetic data concerning mosses. This is certainly hollow justice when it is considered that it was a liverwort, *Sphaerocarpos*, that provided Allen (1917) the favorable material for the discovery of sex chromosomes in plants and for demonstrating for the first time experimentally the actual 1:1 segregation during meiosis of X and Y chromosomes from a single sporocyte. It was in mosses that the first experimental production of polyploids was accomplished by the Marchals (1907-1911). It was with mosses that Wettstein and his collaborators (1923-1924) performed the many brilliant experiments on apospory, hybridization, and genetics. Wettstein helped to pioneer genetic methods in the early 1920's using techniques that have since become commonplace bio-systematic procedures for study of the flowering plants. Yet Wettstein's data have yet to be used effectively in evaluating specific and generic concepts in the two families of mosses that furnished the material with which he worked; namely, the Funariaceae and the Bryaceae. The only serious attempts to correlate chromosome numbers and behavior with the taxonomy of sizeable groups of mosses are those of Lowry (1948), who investigated the chromosomes of the genus *Mnium*, Bryan's (1956a, b) significant contributions relating chromosome numbers and behavior to the systematic position of certain inoperculate mosses, and the cytologic investigations of Bryan and Anderson (1957) in the Ephemeraceae. It is more than a coincidence that these investigations concerned groups of plants in which there was already a solid taxonomic base, for example, by Andrews' (1940) careful and painstaking monograph of *Mnium* in this country and Kabeirsch's (1936) comparable, although less competent, treatment for Asia.

Are the problems of speciation in mosses any different from those in flowering plants? Basically both groups are similar, but there is the problem of the two well developed generations which often seem to evolve quite independently and there is strong evidence that the rate of evolution is much slower in mosses. Also, in mosses we are in the awkward position of having a system of classification based primarily upon sporophytic characters — mainly the peristome — yet specific characters are generally, although by no means always, gametophytic. Evolution in the gametophyte has not always paralleled that in the sporophyte: we have the paradox in some groups of a highly developed peristome and a reduced gametophyte, while other groups (sometimes even in the same family) have a reduced peristome and a highly developed gametophyte.

The relatively few narrowly endemic bryophytes and the wide disjunction of many closely related or identical species led Herzog (1926) to postulate a slow rate of speciation as compared to that in other plants because of the relatively few morphological characters by which variation can be expressed. But the metaphysical view that the lower organisms evolve at a slower rate simply because there are

few characters that can change is not so satisfactory as it is intriguing. Other factors are involved, however, such as the fact that a large number of bryophytes regularly reproduce asexually and therefore have become widely distributed as unvarying clones.

For morphological reasons, it is generally believed that bryophytes are indeed ancient in origin. Steere (1946) aptly put it, "Nearly everyone who works with mosses and hepatics develops a feeling of the great age of these plants, perhaps because of the distant relationship between so many groups." The relationships between the Musci and Hepaticae are so remote that little more than a general similarity of life cycle holds them together in the same division. The structural and developmental differences between the Sphagnobrya, Andreaebrya, and Eubrya are more apparent to bryologists than the gross structural resemblances and the marked differences between the families of the Eubrya are surprising in such a small group of clearly related plants.

One of the problems that moss taxonomists have to face is how to treat the broad species-complexes shared by more than one continent and where the morphological differences between plants of one continent and another are so slight that species become essentially geographical. As everyone knows there are spectacular differences in dispersal mechanisms between seed plants and bryophytes. One might expect plants producing small, air-borne spores to be distributed throughout the world wherever conditions are favorable for their growth. It was once even assumed that the distributions of mosses and other cryptogams did not follow the floristic patterns of higher plants. Studies of actual distributions of pteridophytes (Christ, 1910), hepatics (Domin 1923, Fulford 1951), mosses (Herzog 1926, Imscher 1929, Sharp 1939, Steere 1947), and lichens (Du Rietz 1929, Ahti 1961), however, have clearly demonstrated that spore-bearing plants follow much the same patterns of distribution as seed-bearing plants and are apparently governed by the same rules of dispersal. In the words of Du Rietz (1940): "Long range dispersal apparently does not play the great role previously postulated in these groups and the phytogeographic conclusions drawn from phanerogamic distribution can to a great extent be tested, verified, and supplemented by a study of cryptogamic distribution." And Cain (1944) agrees that "phytogeographic conclusions concerning the flowering plants can be extended to cryptogams and are supported by cryptogams."

Many species of mosses (and hepatics) are very widely disjunct although by no means cosmopolitan or weedy in distribution. As an example, many species of mosses are disjunct in eastern North America, the highlands of Mexico and Guatemala, and parts of Europe or Asia or both. This pattern of distribution is paralleled by generic disjuncts among the higher plants. Except by sheer force of numbers, such wide distribution of identical species of bryophytes would be without significance unless it is understood that bryophytes are very ancient and evolve much more slowly than flowering plants. The

latter is perhaps the best explanation we have for the relatively high incidence of disjunction in mosses.

The problem of paired or vicarious species in mosses is somewhat vexing but perhaps not so much so as in higher plants. In nearly all instances in mosses, long-continued geographical isolation of species has produced few if any changes, and the modern tendency is to reunite proposed entities that can be separated only geographically. This is especially true of the vicarious elements of the North American and East Asian floras. A few notable examples are *Brothera leana*, *Macrocoma hymenostomum*, *Homaliadelphus sharpii*, *Schwetschkeopsis denticulata*, *Entodon macropus*, *Herpetineuron toccocae*, *Hyophila tortula*, *Thuidium minutulum*, and *Trematodon longicollis*. Iwatsuki (1958), in a recent comparison of the southern Appalachian moss flora with that of Japan, found that 55% of the species known from the southern Appalachians also occur in Japan. This figure does not include certain closely related vicariads, some of which may eventually be synonymized. For example *Bruchia sullivantii*, *Mnium carolinianum*, *Schlotheimia rugifolia*, *Climacium americanum*, *Leucodon brachypus*, *L. julaceus*, *Thuidium scitum*, *Thuidium allenii*, *Diphyscium cumberlandianum*, *Pogonatum pensilvanicum*, and *Pleuropus leskeoides* are listed by Iwatsuki as differing from Japanese species in very minor ways, often only in the sexual condition. Thus a substantial number of the so-called endemic species of the southern Appalachians are identical with mosses elsewhere, especially in the tropics and in eastern Asia, and thus must be considered in the disjunctive category. Names like "*sullivantii*," "*carolinianum*," "*americanum*," and "*allenii*," may have to be traded for "*maximoviczii*," "*japonicum*," "*matsumurae*," and "*bandaiensis*."

A huge number of moss species are shared by Europe and North America, and in spite of the startled looks on the faces of European bryologists who come over and view their species in the field here, the similarities are inescapable. I see nothing to be gained by dredging up subspecific categories to apply to groups of plants that can be distinguished only by geography and intuitiveness.

Our scant knowledge of fossil bryophytes supports the theory that the group has evolved slowly. From the older Tertiary, the Mesozoic and the Palaeozoic, less than 30 bryophytes, mostly liverworts, have been described. Less than a half-dozen fossil mosses have been assigned names. The few Mesozoic and Cenozoic bryophytes that have been studied, however, show, like the fossil liverworts, a close resemblance to modern plants. Steere (1946) found that most Mesozoic and Cenozoic bryophytes from North America belong to genera and perhaps even to species still existing here. The few fossil hepatics from the Mesozoic and the Cenozoic are fragmentary, but on the basis of thallus structure and rhizoids it can be concluded that plants of very similar vegetative organization to the modern *Jungermanniales* have existed since early times. The fossil liverworts found in the upper Carboniferous deposits of England are so similar in structure and

appearance to modern species that their discoverer, Walton (1925), could scarcely believe that they had come from Paleozoic shales. Walton (1928) also described fragments of mosses from the Paleozoic that closely resemble modern genera of the Polytrichaceae.

Most Quaternary or Pleistocene fossil mosses could doubtless be identified with modern species if they were not so fragmentary and poorly preserved. Modern species of *Dicranum*, *Calliergon*, *Drepanocladus*, *Scorpidium* and *Camptothecium* are abundant in Pleistocene deposits. All, unfortunately, are species of bogs and fens. It is most regrettable that at least some of the numerous disjunct species of the uplands did not fossilize.

So close is the resemblance between modern and Pleistocene mosses that Robinson (1959) has used Pleistocene material of *Calliergon subsarmentosum* to establish its distinctness from a closely allied species, *C. sarmentosum*. Even after detailed studies he could find no morphological differences between modern and Pleistocene specimens of *C. subsarmentosum*.

It would seem then that without much question, bryophytes and flowering plants evolve at different rates and any evaluation of the ranges of species of mosses must take this into account. Specific disjunctions among the bryophytes may be just as significant as generic disjunctions among higher plants.

It is interesting to speculate on possible factors involved in the speciation in bryophytes. Not many clues are available. The following are possibilities:

The occurrence of certain bryophytes in a restricted area are removed from the normal range of distribution, such as widespread tropical and subtropical bryophytes also found in a few isolated sites in the southern Appalachian Mountains, may be highly significant. Because they occupy microenvironmental niches and are thus subject to rather uniform microclimatic influences, bryophytes can presumably resist macroclimatic changes much better than larger plants and their presence in parts of an ancient land mass far removed from their present normal range may indicate that they have occupied the same isolated niches for a very long period, undisturbed by the great climatic and physiographic influences which have completely altered the life of the phanerogams.

Reproduction in mosses differs dramatically from flowering plants. The sexual process is clumsy, requires water and a rather precise seasonal timing. Even the successful production of sporophytes does not by any means assure that reproduction will be accomplished. The spores must be disseminated and they must not only fall in a favorable micro environment but must also overcome vagaries of wind, washing, and other disturbing factors. A protonematal stage must be undergone and sufficiently favorable conditions must prevail to allow bud formation before the leafy gametophytes can be re-established. The extent to which these so-called annual mosses overwinter through protonemata or buds is not known. The Ephemeraceae prob-

ably produce protonematal structures that persist in the soil from year to year. Annual mosses — such as *Funaria*, *Physcomitrium*, *Ditrichum*, *Weissia* — unquestionably reproduce from spores, but the possibility should not be ruled out that they also reproduce by leaves or stems which persist from one season to the next. It is my contention that reproduction in perennial mosses (and perhaps in many annuals) is almost entirely other than by spores. Many bryophytes produce gemmae or propagula and a great many if not all mosses can reproduce vegetatively from leaf and stem fragments. It is not easy to visualize mosses which grow on steep rock faces going through a complete life cycle, or for that matter those inhabiting tree trunks and other such habitats. Keever (1957), in working with *Grimmia*, a moss restricted to rocks, was unable to germinate spores on rock surfaces although they germinate on agar. She found that it was not difficult, however, to initiate colonies of *Grimmia* on bare granitic surfaces from leaf fragments. She even found that leaf and stem fragments from herbarium specimens up to 10 years old would still produce protonematal filaments and buds.

Abandonment of sexuality may, therefore, be an important factor in the slow evolution in the mosses. Obviously evolutionary potentialities of a species depend upon how great a variety of gene combinations the species is capable of producing; the larger the area of the field of gene combinations available, the greater is the chance that a "new adaptive peak," as Dobzhansky (1951) calls it, may be discovered. But asexuality in most bryophytes, although not all, is facultative and not obligate. Furthermore, many mosses are monoicous and of these the synoicous species, with antheridia and archegonia in the same cluster, would undergo practically obligate self-fertilization. This would similarly rob the species of evolutionary plasticity.

The low incidence of crossability in bryophytes is borne out by the fact that very few natural hybrids are ever seen or described. Considerably less than 50 natural hybrids have been noted in the literature and unquestionably a good number of these suspected hybrids are not hybrids at all. More than half the putative hybrids are in the two families, *Funariaceae* and *Bryaceae*. Nearly all of the so-called hybrids involve annual species that inhabit soil in old fields, cultivated soil, or waste places. It may be that these places are among the few habitats for which closely related species compete and consequently where closely related species are apt to be found growing side by side. Such conditions would be required for producing natural hybrids. Genera in which natural hybrids have been described include *Weissia*, *Dicranella*, *Ditrichum*, *Pleuridium*, *Physcomitrella*, *Physcomitrium*, *Funaria*, *Tetraplodon*, and *Bryum*.

Rocks provide another habitat for which closely related species often compete, notably in the genera *Grimmia*, *Rhacomitrium*, and *Orthotrichum*. It is not surprising therefore that hybrids have been reported in all three of these genera. However, in a genus as variable

as *Grimmia*, and one in which the discontinuities are not always obvious, little reliability should be placed on suspected hybrids.

It is also perhaps significant that all the reported hybrids involve acrocarpous mosses. Not a single suspected hybrid has been reported for a pleurocarpous moss. This is surprising because pleurocarpous mosses, like the hepatics, exhibit great stability of chromosome numbers. Probably more than two-thirds the pleurocarpous mosses have a basic chromosome number of 11. One thinks of genera like *Anomodon*, for example, in which *A. rostratus* and *A. attenuatus* frequently grow intermixed at the base of tree trunks and *A. attenuatus* often competes with *A. minor* and even *A. rugelii*. All four species have the same chromosome number, including a small m-chromosome, a pair of heterochromosomes, and appear to have the same chromosome morphology (Anderson, unpublished). All the requisites for hybridization and introgression are here yet these four species are among the most distinctive mosses and intergradation and overlapping of characters essentially do not exist.

Evaluation of species in mosses should take into account the fact that there has been a substantial retrogression of functional sexuality. Gemmell (1950), for example, reports that more than 10% of the species in the moss flora of the British Isles never produce capsules. Of those known to produce capsules, a substantial number produces them only rarely. The number of species that regularly fruits comprises probably less than 30% of the total.

In the flowering plants we think of a species in terms of a group (or groups perhaps) of populations which are actually, or at least potentially, able to exchange genes so that in the collective sense the species has a genotype. With the emphasis on asexual reproduction, as the case seems to be in mosses, we begin to get a species make-up that corresponds somewhat, but not entirely to that of some asexual genera of higher plants, such as *Crataegus*, *Hieracium*, and *Rubus*. The result is the establishment of pure lines or clones consisting of individuals which, barring mutation, are similar in genotype to each other and to their ancestors. Such lines would not exchange genes and, assuming that successful mutations would occur from time to time, would eventually lead to a large number of lines or populations differing in small ways.

It should be remembered, however, that in a sterile moss a mutant would automatically be perpetuated as a result of the purely vegetative method of reproduction. The persistence of the variant would then depend solely on the ability of the mutant to survive the competition of the parent form and other plants. Natural selection would operate very rapidly for in the haploid state all genes are functionally dominant. There would be no chance of recombination in sterile mosses since there is no sexual reproduction. This dramatically abrupt operation of natural selection would quickly eliminate deleterious genes or, if the mutation conferred any biological advantage the mutant haploid plant, would be very successful because its



action would not be masked by the parent allele. On the other hand, if the mutation resulted in a notable deficiency of function, which on the analogy of other plants seems most likely, it would be very rapidly eliminated from the population.

If the mutation should take place in an antheridial or archegonial branch, however, and if sexual reproduction should occur, a heterozygous capsule might arise. But homozygosity would be obtained in the next generation if the spores should become established and the same abrupt operation of natural selection would be in effect.

One thinks immediately of almost countless species complexes in mosses in which the species is composed of an almost infinite number of biotypes differing from each other in minor but often distinctive ways, frequently by a single character, but the biotypes often merging imperceptibly. In some species the biotypes are characterized by different combinations of characters so that the number of biotypes is equal to the number of possible combinations of the basic characters involved. If specific or subspecific names are applied to the biotypes, a chaotic taxonomic situation results. *Rhacomitrium heterostichum* is an excellent example of this kind of complex. Here five characters — shape of upper leaf cells, presence of short lateral branches, unistratose or bistratose upper lamina, presence of a hair point, and smooth versus papillose leaf cells (a geographically restricted character) — can be found in nearly all the expected combinations. Because particular combinations are apt to be fairly uniform throughout a single population, there has been a strong temptation to name them. (The mechanical ease with which the combinations can be determined is probably also a factor.) As one would expect, an impressive list of names associated with the *R. heterostichum* complex has accumulated.

Another example of this kind of complex is offered by *Fissidens bryoides* — around which the closely related species *F. viridulus*, *F. pusillus*, *F. minutulus*, *F. exiguus*, *F. andersoni*, *F. texanus*, *F. repandus*, and *F. tamarindifolius* — have been described. Moreover most of these “species” are currently recognized in manuals. In connection with preparation of a manual of mosses of eastern North America, Howard Crum and I recently studied this complex (unpublished). The sexual condition — upon which some workers have placed great reliance in differentiating species, including Nyholm’s (1954) recent Fennoscandian treatment — we found to vary greatly. It is possible to demonstrate, sometimes in the same collections, apparently dioicous plants as well as autoicous and synoicous ones. At its best development, *F. bryoides* has small, rather convex and therefore relatively obscure leaf cells whereas *F. viridulus* usually has larger, flatter, and more pellucid ones. There is no constancy in these or any of the other forms supposedly differing from them. The relative lengths of the leaf border and the development of the apiculus are equally worthless in sorting out named categories because of a complete series of intergrades from *F. bryoides* (typically with a

strong border often appearing confluent with a strong apiculus) to *F. viridulus* (usually with the border ending a few cells below the apex) to *F. minutulus* (generally with the border slightly shorter and with an acute, or sometimes bluntly apiculate apex) to the very similar *F. pusillus* (with the cells at the tip of the border rather short and obliquely arranged) and finally to *F. exiguus* (with the border ending near the apex of the vaginant laminae, but frequently extending well above them in some leaves). *F. repandus* Wils., a common species throughout the American tropics, seems scarcely separable from *F. bryoides* in a narrow sense, especially since their only difference is a dioicous inflorescence in *F. repandus*. This can be demonstrated, however, in the typical form of *F. bryoides* here and abroad as well as in other members of the complex. Specimens of *F. sublimbatus* from our range, at least, also belong to this concept. Here again is a complex series of biotypes, each recurring with sufficient frequency to tempt the systematist to maintain some taxonomic designation for the more recognizable ones. After considerable study of this complex, Crum and I concluded that the variants cannot be distinguished by purely taxonomic means, not at least the traditional ones at our disposal. But the problem is an extremely interesting one and should be approached ecologically, cytologically, genetically, and biometrically.

From a practical standpoint, I earnestly believe (and Crum and I are adopting this view in our projected manual), that our ignorance of the mechanisms involved in these species complexes forces us into a conservative position and that considerable "lumping" is in order. There are too many species of mosses that cannot be satisfactorily separated and that cause one to wonder — after hours of tedious dissection and observation, comparisons with descriptions, illustrations, and specimens and correspondence with colleagues — just exactly what one does have after the identification is made.

Mosses are not without genera in which it is difficult to find appropriate discontinuities. One almost immediately thinks of the genera *Bryum*, *Barbula*, *Drepanocladus*, or the whole Amblystegiaceae where even generic discontinuities are difficult to find and where even family lines are not too clearly drawn. In many of these genera we have problems that partially parallel the apomictic species of higher plants. Many vascular plant taxonomists feel that a special taxonomy must be reserved for apomicts and perhaps this is what eventually the bryologist will decide.

The study of chromosome numbers and behavior has recently proved valuable as a tool in bryophyte taxonomy as it has long been in the taxonomy of flowering plants. In general, although the chromosomes of mosses may have some features of interest to the cytologist, the taxonomic interest they provide is similar in kind and extent to that derived from chromosome studies of flowering plants.

In bryophytes, as in higher plants, there are some genera or larger groups in which all, or nearly all, the species have the same chromo-

some number. The basic number of 7 extends throughout the Polytrichaceae, with tetraploid numbers known for several species. In *Sphagnum* all species (but three or four tetraploids) have  $n = 19$  (with 2-6 m-chromosomes in addition) (Bryan 1955).

Numerous species are known in which there are both polyploid and aneuploid races which cannot be distinguished morphologically from the regular diploids (Anderson & Crum 1958). But the opinion of most bryologists parallels that of most flowering plant taxonomists; they do not readily accept "species" not recognizable by the normal procedures of taxonomy.

Numerous genera are known in which there are diploid and tetraploid species pairs which differ sufficiently to be acceptable as distinct species. For example, *Fissidens cristatus* has the number  $n = 12$  while *F. adiantoides*, a close relative, has the number  $n = 24$  (Anderson & Bryan 1956). *Polytrichum formosum* has  $n = 7$  while *P. gracile* has  $n = 14$  (Holmen 1958). Also, as in flowering plants there are doubtful polyploid pairs, as in the genus *Mnium*. *Mnium punctatum* has the number  $n = 7$  while *M. pseudopunctatum* (Lowry 1948), differing practically only in sexual condition, has  $n = 14$ . *Mnium orthorhynchum* and *M. marginatum* are closely related with 6 and 12 chromosomes respectively. *Mnium affine* and *M. medium* have 6 and 12 chromosomes respectively and are doubtfully distinct. So, as in flowering plants, while some polyploids are striking enough to be recognized, described, and named, others differ from the diploids only slightly or not at all and have not been recognized. The lack of a correlation between the chromosome multiplication and the external traits has been especially emphasized by Wettstein (1940). For example, cell size in some species is positively correlated with the chromosome number over the whole range of variations studied, from the haploids to octoploid and higher. In others a maximum cell size is reached, and a further chromosome multiplication produces no new increase, or may even result in a reduction of the new cell size and a subsequent dwarfism of the plants.

Wettstein's observations on *Bryum caespiticium* still have not been explained. Experimentally induced chromosome doubling in a haploid gametophyte ( $n = 10$ ) in which the sexes are separate gave rise to a diploid ( $n = 20$ ) synoicous strain with large cells, pronounced "gigas" characters, and low fertility. Among the  $F_1$  generation plants, one individual which showed a greater tendency to develop sporogones, and consequently to be fertile, than its siblings. This plant was maintained for many years. Year after year the development of the sporogones gradually improved until after eleven years normal spores were produced. These spores, surprisingly, gave rise to a viable and fertile offspring. Hand in hand with the improvement in fertility, cell size decreased. The resulting strain appeared to be a new species and was named *B. corrensii*. It is noteworthy that a related *Bryum* species, known in nature, has the same chromosome number,  $n = 20$ , and is similarly synoicous.

It is lamentable that experimental crosses in bryophytes, such as those by Wettstein, have not been continued although taxonomic applications of Wettstein's work have yet to be made and the full meaning of his experiments is still not evident. His ability to make intergeneric crosses among various species of three genera of the Funariaceae that bryologists regard to be not very closely related has potentially very important overtones although Wettstein noted varying degrees of sterility among the hybrids, a fact that might well be applied to interpretations of relationships when our knowledge of the taxonomy of the groups concerned reaches the point that we can. Wettstein's biosystematic studies are proof that experimental taxonomy to be efficiently employed must be preceded by classical studies to the extent that the problems can be recognized and properly oriented so that a sufficient base can be established to apply the experimental data effectively.

A few bryologists, notably Walther (1934) and Malta (1926), have attempted to use biometric methods in analyzing subspecies and varieties of the aggregate species *Polytrichum juniperinum* and *Zygodon viridissimus*. Statistical methods have been used effectively in England by Lodge in unpublished studies on *Drepanocladus* and by Agnew in *Sphagnum* (cited by Richards, 1959).

Culture methods ought to be as valuable in bryophyte as in the taxonomy of other plants but bryologists have been slow to adopt them. The most effective culture work has been carried out with hepatics, notably by Buch (1953), who showed that a few species previously regarded as distinct were modifications of a single taxon. Not much has been published concerning culture experiments with mosses, although many bryologists have cultured mosses in the laboratory under identical environments in the hopes of evaluating the worth of so-called varieties and species. Bopp (1954) cultured moss sporophytes on agar, a technique which may offer possibilities for evaluating the taxonomic worth of characters involving capsules and setae. Studies of morphological changes in mosses in response to environmental variations, however, have been confined mainly to bud formation and protonematal development. Transplant experiments and the growth of plants under controlled environments have scarcely begun. Forman (1962) has made a significant beginning in this direction by a careful study under controlled conditions of the precise physiological requirements of a single species, *Tetraphis pellucida*. He found that the natural geographic range of this species was predictable, coinciding very closely with its range as shown by herbarium specimens. It will be from comparable studies that the extent and nature of ecotypic species in mosses can be determined.

Thus the species problems in mosses roughly parallel those in other groups of plants. There is the same lack of discontinuities, the inevitable unexplained morphological variations, the puzzles of sub-specific categories, how to deal with vicariousness and the problems of disjunct distributions. Chromosome studies and the limited breed-

ing data provide the same kinds of taxonomic information to the bryologist as higher plant systematists have obtained from similar studies on flowering plants. As stated by Steere, Anderson and Bryan (1954), "species of mosses, and of bryophytes in general, in spite of their relatively simple morphology, present the same kind and degree of complexity as those of higher plants, and that speciation within natural populations of mosses is governed by the same patterns of cytological behavior." Much that is puzzling in the speciation in mosses may, therefore, be expected to yield to the application of more expertly directed studies of traditional morphology in combination with the disciplines of cytology, genetics, physiology, ecology, anatomy, experimental morphology, biochemistry, and biometry. Bryologists must seek to apply more vigorously every tool at their disposal to make new attacks upon the structure and make-up of species and how they arose.

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