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Cover illustration

*Geum Peckii* Pursh

This rare species is a Northeastern endemic, known from the White Mountains of New Hampshire and from three sites in Nova Scotia.

Original artwork by Lisa Bandazian

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## FOREWORD TO THE SYMPOSIUM "RARE AND ENDANGERED PLANT SPECIES IN NEW ENGLAND"

This series of papers was presented at the Symposium on Rare and Endangered Plant Species in New England, May 4–5, 1979, at the Harvard University Science Center, on the occasion of the 755th meeting of the New England Botanical Club. This number of Rhodora and the Symposium reflect some of the Club's new activities on the flora of New England. The accounts of endangered plant species for each of the six New England States represent a preliminary phase of the work of a committee chaired by William D. Countryman. The ultimate goal of this group is a synthesis of the state reports into a comprehensive treatment of the endangered species of the whole region.

The accomplishments of individuals concerned with the Symposium merit recognition in addition to those whose papers are included here. Garrett Crow, Chairman of the Symposium, and Irene Storks, Co-Chairman, have coordinated events from the initial program through the review of papers for this publication. William Countryman, Katharine Field, Leslie Mehrhoff, Larry Morse, Norton Nickerson, and Richard Primack also served on the Symposium Committee and Christopher Campbell, Club Program Chairman, also actively worked with this group. The logistics and general operations for the May meetings were arranged by David Barrington, assisted by David Webb and Thomas Wendt.

Several other programs currently sponsored by the Club also focus on the New England flora. The Herbarium of some 250,000 specimens is being changed from the generic and species order of the 8th edition of Gray's Manual to an alphabetical sequence. New collections are being accessioned from floristically little known areas, especially in Maine and Vermont. Some early collections of rare plants such as *Potentilla Robbinsiana* that extend the ranges of the species have been added to the NEBC collections and enhance the value of the herbarium. A committee on Plant Distributions is engaged in computer documentation of herbarium records for preparation of distribution maps. The goal of this committee is to produce a series of distribution maps similar to those done for the Atlas of the British Flora. Programs are also being developed between the Club and other regional organizations for the acquisition of distribution records based on a current census of species.

The emphasis on rare and endangered species brings into focus larger problems concerning our knowledge of the general flora of New England. Several papers in the Symposium relating to analyses of rare species or populations signal the need for similar work to be done on wide ranging or aggressive plants. The New England flora is certainly one of the best known in the country but much is still to be learned about the relations of the species. The Club can serve as a vital resource in the development and documentation of new data on the species and the flora.

The Symposium was made possible by support from the United States Fish and Wildlife Service, and the participation of Richard Dyer, Botanist, of the Endangered Species Office also indicates their concern for the work. It was my special pleasure to accept the 1979 Achievment Award from the United States Fish and Wildlife Service, in behalf of the Club, for its dedicated efforts to protect the rare and endangered flora of New England.

ALICE F. TRYON, PRESIDENT
NEW ENGLAND BOTANICAL CLUB

# RARE SPECIES OF PLANTS

## WILLIAM H. DRURY

### WHAT IS RARITY?

Rarity implies both a relative quantity and a quality, that is, both biological and human aspects. In general people ascribe higher value to a rare item, and most people expect that a rare species will have qualities of elegance. The Whooping Crane (*Grus americana*), and Quetzal (*Pharomachrus mocino*), Cheetah (*Acinonyx jubatus*), and Sable Antelope (*Hippotragus niger*) fulfill this expectation. Some species project a feeling of the dramatic and thus assume an aspect of importance. Eagles, such as Golden Eagle (*Aquila chrysaetos*) and Bald eagle (*Haliaeetus leucocephalus*) do this. One occasionally comes on a few Cardinal Flowers (*Lobelia cardinalis*) blazing in a shaft of sunlight against deeply shaded woods. Species which occur in distant places, Polar Bears (*Thalarctos maritimus*) and Big Brown Bears (*Ursus arctos ssp. middendorffi*), seem more likely to be considered rare and thus preferable than are ones with which people are familiar. Consider the traditional use in rock gardens of Alpine wildflowers from Switzerland rather than those from the mountains of New England.

Yet, the Cape Sable Seaside Sparrow (*Ammospiza* [*maritima*] *mirabilis*), an undistinguished "little brown bird" of questionable species qualifications, is accorded rarity status and "an Endangered Species" status. So, in the Gulf of Maine a small and relatively isolated population of Atlantic Puffins (*Fratercula arctica*) and so in Britain, a small and relatively isolated population of Leach's Petrel (*Oceanodroma leucorhoa*) are considered rare even though these two are among the most abundant species of birds in the world. It could well be a source of puzzlement to the botanists who know the plants in the fullness of their abundance across the tundra and coniferous forests of North America to know that each stand of Labrador Tea (*Ledum* [*decumbens*] *groenlandicum*) is catalogued in Massachusetts, and a careful search is made in Maine for stands of Jack Pine (*Pinus Banksiana*), of Shrubby Cinquefoil (*Potentilla fruticosa*), and of Baked-apple Berry (*Rubus Chamaemorus*).

Thus, the human standards by which the status of rarity is conferred are complex and to some degree contradictory.

## Is Rarity Failure?

There is an old idea that rare species are failing species; that a rare species lacks the ability to displace other species, to increase its population, or to expand its range.

Some species have strong attachments to traditional range and are reluctant to colonize new or even former range once it has been abandoned. Such a species group is that of the Bighorn Sheep (*Ovis canadensis* and *O. dalli*) which, although widespread at present, is like the domestic sheep, resistant to occupying unfamiliar range (Geist, 1967, 1971) and are, as it were, preadapted to rarity. Many seabirds are similarly conservative (Lack, 1967).

Oddly, there are geographic regions where "conservative" species cluster: Newfoundland in northeast North America and the lands surrounding the Bering Sea in the northwest. In these centers of high species diversity, species of limited geographic ranges are apparently able to displace the widespread "successful" species. So they do quite well on their own sites even in the face of intense competition.

The idea that rare species are failing perhaps results from observations that many rare species occur in isolated patches in mountains, bogs, sand dunes, or islands. This idea is strengthened by traditional projections by students of climate that Arctic-Alpine plants once had continuous distribution around the borders of the ice sheets and have subsequently retreated to bogs and mountain tops. The idea is also reinforced by classical geological doctrines that beaches, mountain tops, and bogs are temporary features, doomed to disappear. Some botanists seeking to explain patterns of species diversity noted that conservative species were found in areas believed to have been islands in a sea of ice during the ice advances (Fernald, 1924, 1925; Hultén, 1937).

There is also an old idea that species run a cycle from youthful aggressiveness to mature vigor and declining powers in old age. Willis' (1922) "Age and Area" hypothesis suggested that a species begins with a small population and expands with age. Fernald's (1925, 1929, 1931) suggestion of "senescent" species in the Gaspé-Newfoundland region caught the imagination of his peers when his previous "common-sense" explanations received little notice. Ricklefs and Cox (1972) used the concept of a species cycle in their description of a sequence of bird species of West Indies islands. They suggested that a species, following colonization, rapidly spread into diversified habitat. Then as subsequent species arrived, the older colonists became progressively more restricted in distribution and specialized in habitat, because the older residents, unable to match the competitive abilities of later colonists, had their wider habitats preempted. This description fits attractively with theories which use rates of colonization and extinction to explain the number of species on islands (MacArthur & Wilson, 1963, 1967). Lack (1973), criticizing what he considered to be the too general application of the colonization/extinction model, suggested the opposite for some observed cases in hummingbirds in the West Indies. He suggested that later arrivals were unable to become established because their niche was already occupied. Numerous instances of this can be found among plants (Polunin, 1960).

## Definition of Rarity

If rarity is measured in terms of numerical relation to other sympatric species, it appears that most species of plants and animals are rare. Of a regional list of a hundred species, we can expect a dozen to be common and widespread, and usually the rest will occur in smaller numbers. In general, the larger the area sampled as one community type the larger the list of species found in small numbers, while the roster of common or "important" species does not increase.

Abundance generally is considered to be made up of three aspects: frequency, consistency, and density. All three affect our recognition of rarity or commonness. Frequency is defined: "If sample plots are distributed throughout an area. . .and the number of plots in which each species occurs is recorded. . .frquency expresses the percentage of sample plots in which a given species occurs." Consistency reflects regularity of occurrence in samples, and density reflects number of individuals per unit of area (Phillips, 1959). The spectrum of frequency appears to be continuous down to some extreme cases of very rare species (Raunkaier, 1918, 1934). Gleason (1920, 1929) and Preston (1948, 1962) showed that the distribution of commonness and rareness follows an exponential or "log-normal" curve.

If we consider only the number of individuals, a "Poisson distribution" of commonness and rarity appears. A few species such as Sugar Maple (*Acer saccharum*), or White Spruce (*Picea glauca*), or Haircap Moss (*Polytrichum commune*) occupy one limit of the distribution. They are conspicuously abundant and widespread "primary or dominant species." At the other end of the curve, a few species are conspicuously rare and endangered. In between, the large number of "secondary" inconspicuous and infrequent species occupies the bulk of the "normal" curve. Many papers were published on this general subject during the 1960s, largely in response to stimulation of MacArthur's work (1957, 1960). These studies were not really directed at the questions considered here. It seems prudent to start with a definition that does not imply quality or success until we know what these words mean and what they imply.

An operational definition of a rare species might include the characteristics that it either occurs in widely separated, small sub-populations so that interbreeding among sub-populations is seriously reduced or eliminated, or is restricted to a single population. One would expect that there are several "kinds" of rare species as well as several kinds of historical sequences, several selective mechanisms, or several habitat characteristics by which they are produced.

## Types of Rarity

Mayr (1963) suggested three main types of geographic distributions of rare species, acknowledging that there is a spectrum of intermediate types. First, the range of some species is restricted to a very few localities, and they are considered rare even though they are found in large numbers at each locality: for example, Mountain Avens (*Geum Peckii*), which grows in the alpine zone of the Presidential Range of New Hampshire, or Abbott's Booby (*Sula abbotti*) of the Indian Ocean. Such a distribution of the breeding population does not necessarily guarantee recognition of rarity for a highly mobile species. Alaska Fur Seals (*Callorhinus ursinus*), breeding on the Probilof and Commander Islands, and Greater Shearwaters (*Puffinus gravis*), breeding on three islands in the South Atlantic, are not considered rare. The reason is, I presume, that both spread widely over the oceans in the non-breeding season and are seen commonly on their wintering grounds.

Secondly, some species are found in very small numbers widely dispersed in each community where they grow, but they occur in many suitable areas over their geographic range. Many orchids, gentians and saxifrages, as well as Peregrine Falcons (*Falco peregrinus*) have this sort of widely dispersed distribution. These make satisfactory quarry for those who are interested in finding rare species.

Thirdly, some species occur as a very few individuals or small groups at widely scattered localities over a large geographic area of what appears to be suitable habitat: for example, the alder, *Alnus maritima,* or Bachman's Warbler (*Vermivora bachmanii*) in the southeastern United States. A number of ferns and raptors have this kind of distribution.

**1.** *The range of some species is restricted to isolated localities yet they occur in large numbers at each locality.* Many island sites are large enough and remain reasonably homogeneous and consistent over time to supply uniform suitable and dependable sites. An important aspect of success on such places is "sticking with a good thing" once one has it. The widespread development of loyalty to a breeding site (*Ortstreue*) among migratory birds in general and seabirds (Lack, 1967) in particular suggests that return to a locality at which parents were successful can be used to "predict" breeding success. Put in other terms: if one was successful at one site, one does better to repeat the effort at that site rather than risking an attempt at a new site.

Once a population is successful on an "island" the possibility arises that dispersal will be "too expensive", because too large a percentage of dispersing individuals perish. Thus Lindroth (1957, 1963) showed that beetle populations on islands tend to have a large proportion of wingless forms. Flightless rails on oceanic islands provide conspicuous illustration. Carlquist (1971) showed that a similar suppression of dispersal mechanisms has occurred among Beggar's Ticks (*Bidens*) on the islands of the Hawaiian chain. The hazards of this commitment to the *status quo* is illustrated by the demise of the flightless Great Auk (*Alca impennis*) while its flying close relative survived, the Razorbill (*Alca torda*).

Recent studies of isolated populations of plants and animals on mountainous or oceanic islands indicate that there are rapid and often extensive changes in species composition. The size and geographical structure of an island has an important influence on the number of species in the fauna and flora as well as on the degree of specialization and the survival of species on it (Wallace, 1869; Simpson, 1952, 1953; MacArthur & Wilson, 1963, 1967; Mayr, 1965).

There are many instances of exotic plants and animals running wild and excluding endemic species in island floras and faunas. Another disadvantage for a localized population is that a predator may turn its attention to the small population and cause catastrophic damage: for example, the fate of Stellar's Sea Cow (*Hydrodomalis gigas*), and Fur Seals (*Callorhinus* and *Arctocephalus*) or introduction of dogs, cats, goats, swine, cattle or rats onto oceanic islands.

Understanding the change from a "competitive" colonizing species to a "conservative" relict is at the heart of understanding rare species, and island biotas seem to lend themselves to the study.

**2.** *Some species are found in very small numbers widely dispersed in each community where they grow; they occur in many suitable areas over their geographic range.* At present, there appear to be no explanations adequate for the characteristics of this type of rare species. One doubts intuitively, for example, that a set of narrow niches exists widely spaced geographically and yet available for a particular suitably adapted species to occupy them.

The explanation may simply depend on combinations of chance factors. The occasional coincidence of several different, yet additive environmental factors may allow for the germination of seedlings of these "rare" species. It may be useful to see these coincidences in the same way that at sea many waves running at independent frequencies combine either to damp each other out or to reinforce each other into a giant wave. So in the case of some fish (*e.g.*, Herring, *Clupea harengus*), a coincidence of several favorable circumstances result in a successful spawning and survival of larvae (Hardy, 1959) which may affect the year-class composition of the population for many years (Hjort, 1914).

Among the advantages (or results) of a widely dispersed population is the fact that the population will probably be too dispersed to supply a favorable resource for pathogens, parasites, or predators. Any species which depends upon a rare species as a resource will have difficulty in finding its next prey (Janzen 1970, 1971, 1972).

Among the disadvantages of species having a dispersed distribution would be the possibility that if a new predator or parasite appears that consumes several different prey species without preference (that is, only in proportion to the numbers of each species present), the less frequent species will suffer disproportionate pressure. The Brown-headed Cowbird (*Molothrus ater*), whose large populations are maintained by parasitism on many species of songbirds, has been a major depressing factor on the population of rare and localized Kirtland's Warblers (*Dendroica kirtlandi*) ever since the 1890s. At that time, extension of range made the cowbird numerous in the warbler's range (Mayfield, 1960). The expansion of range of the cowbird is not the direct cause, but the factor that allows us to follow the progress of this natural "experiment."

3. *Some species occur as a few individuals at scattered localities, or are restricted to a small geographic area or a single population.* In the extreme case such species are rare and endangered. One presumes that these species are the products of coincidence of a number of factors to which the population responded by accommodation. In the course of time the circumstances and habitat to which the population has been adjusted have changed. Thus on the Green and White Mountains of New Hampshire, Vermont, and Maine the habitat available to *Geum Peckii* or *Potentilla Robbinsiana* may have been more extensive during cold periods in the past or smaller during warmer periods.

The first and third categories of distribution are most vulnerable to events which may reduce their numbers or distributions to "Rare and Endangered" status. One presumes that plants such as *Franklinia, Gingko,* and *Metasequoia*, were reduced to a few stations before being found by humans, taken into cultivation, and thus being given a "new lease on life." They are now believed to be extinct in the wild. Similarly, capricious changes in the behavior of humans — expressed as dispersed recreation in the New England Mountains, have endangered the survival of Dwarf Mountain Cinquefoil (*Potentilla Robbinsiana*) at its relict site on Mount Washington. Another example of capricious human behavior (taking of plumes) also endangered the survival of Short-tailed Albatrosses (*Diomedea albatrus*) which once nested in good numbers on islets off Japan.

## Is Rarity Correlated With Impoverishment?

During the decades 1930s through 1950s discussions of rarity were replete with references to genetic depletion to explain lack of aggressiveness. Aggressiveness implied wide ranges, large numbers, and conspicuousness. Following the work of Turesson (1925) and Clausen, Keck and Heisey (1940), reference to biotype depauperization was used to explain how "a species population" could lose the ability to occupy a variety of habitats. Although authors disagree on the mechanisms involved, in general they agree that there was a reduction in genetic materials and hence adaptive potential in rare species.

Reflecting the then current ideas that rare species are either too young or too old, Stebbins (1942) distinguished two main types of rare plants: one type was once more common, widespread, and richer in biotypes (occupied more varied habitat); the other was never common, but diverged from a small group of individuals of a widespread ancestral species.

Three possible mechanisms leading to genetic depletion have been suggested: the founder principle, local selection, and inbreeding. Although the mechanisms are real, it is important for the purposes of this argument to realize that the studies which led to their clarification began with preoccupation with failure without establishing whether rare species are, indeed, less "successful." The Solbrigs (1979, Chapter 9) give a helpful précis of these ideas.

**1.** *The Founder Principle.* The founder principle is that a small emigrant population contains restricted genetic diversity. This hypothesis has replaced Wright's earlier one (1931, 1938, 1940), which was that depletion results from random genetic processes in small isolated populations. Wright called this genetic drift.

The founder principle is not appropriate as an explanation of the early stages of the sequence proposed by Ricklefs & Cox (1972), because the new colonists have the potential of aggressiveness and the old ones are the conservatives. In many other cases populations that have been reduced to a very few individuals have retained the diversity necessary to explode. The European ibex (*Capra ibex*) was reduced by hunting to one herd in the Italian Alps; the European starling (*Sturnus vulgaris*) was released as a small flock into Central Park in New York City. Both have shown great population vigor in increasing their populations and expanding their range, as have the many other species of plants and animals introduced to new continents and islands, most notably New Zealand (Elton, 1958). Native wild flowers of restricted alpine ranges in northwestern Canada, such as *Hedysarum alpinum*, became weeds along the Alcan Highway when it was first opened.

**2.** *Local Selection.* Some authors have suggested that genetic depletion is the result of a shift toward uniformity (homozygosity) in a constant environment. As an illustration, Krukenberg (1951), studied a number of species found on serpentine rocks, where high magnesium content suppressed species characteristic of ordinary soils. The serpentine species grew well on non-serpentine soils when freed of competition. This suggests that variability in the genotype exists but is not expressed in the phenotype for a number of reasons, including masking by developmental processes or selection pressures leading to high mortality in the young stages. To the degree that genetic or phenotypic variability is restricted to the features which are suitable to the specific site, a small population on a homogeneous site can perhaps out-compete species whose local specializations are diluted by the production of less fit genotypes and phenotypes as a result of segregation of variable characteristics. Consequently, for such small populations variability is "good" only if we assume that the habitat will soon change. (O. Solbrig, pers. comm.).

If we postulate that the non-serpentine elements may be eliminated by their inability to tolerate high magnesium concentrations, this frees the serpentine species to become more homogeneously adapted to serpentine. For example, if a homozygote should arise which is superior or equal in fitness to the heterozygote in a constant environment, fixation of the allele would result. The homozygous population has the advantage in a predictable environment because each locus is self-sufficient and individuals can produce more viable young at low cost in mortality of ill-adapted gene combinations. The high cost is being less competitive in a variable environment. The heterogeneous population may be less fit in any one environment, but is able to live in a variety of environments by virtue of the diversity of its genotype. If there is a restriction in genetic resources, the mechanism of local selection to a specific adaptive background may be the most effective.

3. *Inbreeding.* Most field biologists now recognize that inbreeding has widespread importance while "random gene exchange" in a population is largely a theoretical abstraction.

Gene flow seems to refer to the movement of individuals from one population into another. Camin & Ehrlich's (1958) report on water-snakes (*Natrix sipedon*) on the islands in Lake Erie showed that despite strong selection toward non-banded forms, steady gene flow by banded immigrants onto the islands from the mainland prevented the completion of the selection process. In some cases inbreeding and reduction in inherited variation is apparently of selective advantage.

In many plants even the extreme conditions of inbreeding, autogamy and asexual reproduction may be favored. In some species, inbreeding might be forced upon the population by events in the habitat such as scarcity of insect pollinators at the time of blooming as in the case of *Leavenworthia uniflora, L. exiqua,* and *L. torulosa* (Rollins, 1963; Solbrig, 1972).

Once specialization for homogeneous habitat has started, the probability increases that isolated populations will lose gene exchange with their neighboring islands, and hence local selection pressures have an increased effect. Species on one or many islands should retain variability as long as they exist in many intercommunicating sub-populations; yet when the island's size is small or the habitat is uniform so that the whole island's population is one freely interbreeding unit, then homogeneity and specialization are favored. The major hazard may be that the area of the "island" and the number of islands among which a low level of exchange occurs become too low for the population to accommodate accidental events.

**4.** *Masked Variability.* One might ask whether in many cases there has been a depletion of the genetic resources at all. Until recently, many authors speculated on how genetic or biotype depauperization might be achieved, rather than measuring the degree to which variability exists. Recent studies of allozymes emphasize how much unexpressed potential variability exists. The term "allozyme" is used to designate different forms of an enzyme which are coded by different alleles at the same gene locus. The variation in form of the enzymes is examined electrophoretically. Extensive masked genetic variability has been found in fruit flies (*Drosophila*) (Ayala, et al., 1972a, b), in House Mice (*Mus domestica*) (Selander & Yang, 1969; Selander et al., 1969), and Horseshoe Crabs (*Limulus polyphemus*) (Selander, et al., 1970). Potential variability is not unexpected in such widespread and "successful" groups as the House Mouse or fruit flies, or in a species like the Horshoe Crab which has outlasted so many others. Furthermore, Ayala et al. (1973) found large hidden potential of gene variability in isolated populations of the giant clam (*Tridacna maxima*) in the Marshall Islands, a species which they categorized as "an ecological analog of some unsuccessful evolutionary lineages."

It seems safe to conclude from this brief review that little direct evidence is available to support the idea that rare species hold any less genetic variability than common species.

Mayr has made three points which apply. First the characteristics of each individual or population are adaptive or not, according to their match with the specific habitat where the individual is found (Mayr, 1954). Secondly, genetic fitness cannot be separated from ecology because natural selection is an ecological process (Mayr, 1963). Thirdly, he distinguished two categories of rare species, one highly localized and the other highly specialized (Mayr, 1963). Thus he identified genetic and ecological mechanisms as operating in concert. This is a widespread attitude at present.

One should expect the genetic structure of a population to reflect the ecological (including minerological, physiographical, and geographical) problems to which the population is adjusted. One should consider the interplay of several historical events combined with suitable genetic adjustment by the population to be the forces which have produced those species which we acknowledge to be rare and endangered: i.e., have small populations on restricted habitats. Those extreme cases in which a species population is narrowly restricted to a few outcrops of limestone, gypsum or serpentine may be explained in terms of intense local selection on individuals on the specific habitat they occupy.

Stebbins (this symposium) argues that rarity is a result of close, highly specific, genetic adaptation to a demanding and restrictive habitat. Yet I known of no evidence that even these species have lessened genetic diversity. All this argues for the overwhelming influence of accidents and is the opposite of the classical concept that each rare species is a member of a coadapted complex which has special suitability in its natural community. This latter attitude has strongly influenced thinking about conservation in general and rare species in particular.

## IF RARITY IS NOT FAILURE, WHAT IS SUCCESS?

Are size and numbers the best measure of biological success? Were the Mesozoic dinosaurs more successful than the Horseshoe Crab or the *Osmunda* ferns, which have apparently survived since the middle Paleozoic?

In the present section I will give several illustrations of cases in which outside forces are responsible for the establishment of patterns of abundance. They suggest that a traditional assessment of success in terms of dominance and abundance may not be very helpful. They also suggest that a great variety of explanations may apply to the many "types" of distribution of species, rare and common, and that those explanations based simply on genetics or on competition may not be helpful.

In simplest terms distribution and abundance of an organism on the local scale depend 1) upon other organisms whose activities decrease the numbers of the species, 2) upon other organisms whose presence increases the numbers of the species, or 3) upon physical habitat. I will briefly illustrate the interactions with other organisms and then dwell at some length upon plant interactions with the physical habitat because of the peculiar relevance of these to the distribution and abundance of plants.

### Predators and Parasites

Paine (1966) and Harper (1969) have pointed out the importance of herbivores in determining plant diversity. Grazers may remove dominant species which otherwise exclude inconspicuous forms and thereby increase diversity, as in the case of starfish (Paine, 1966) or sea urchins (Paine & Vadas, 1969). They may also suppress several species by their preferences as happened with sheep in the Welsh hills or in areas where the elimination of rabbits was followed temporarily by an unwonted species richesse (Harper, 1969).

Harper (1977) said the liability of pure experimental stands to pests and diseases which have been considered nuisances may be the critical clue to the real factors regulating populations in nature. He used two vivid illustrations.

Prickly pear (*Opuntia stricta*) was introduced into Australia as a decorative plant, but it "escaped" from cultivation and became a noxious weed in large areas of native vegetation and sheep range. Introduction of a moth (*Cactoblastis cactorum*) which devours the cactus was followed by a population boom in the moth, then a rapid reduction in the population of Prickly pear and moth to a condition in which the moth population is kept small when long distances between clumps of Prickly pear increase the odds against a moth finding another cactus. The cactus population is controlled by increase in the moth population when moths can find more cacti. Without knowing this history it is unlikely that one would predict that a single insect would be that important or "fine-tuned."

Similarly, the introduced Klamath Weed (*Hypericum perforatum*) became an abundant and noxious weed on the range lands of the northwest U.S. and California. Introduction of the beetle (*Chrysolina quadrigemina*) led to a dramatic decrease in the population of Klamath Weed which now persists in shady places.

> "It is believed that in the absence of previous knowledge of this programme, and unless he made specific studies, an entomologist or ecologist viewing the current picture would conclude that what we know to be the key insect species, *Chrysolina quadrigemina,* is not a significant influent of the stand of vegetation and that the few plants of Klamath weed seen here and there are not primarily limited by this insect. He might also erroneously conclude that this plant is a shade-loving species, since the beetle checks it much less effectively under shade, hence more survive there." (Huffaker, 1964, *in* Harper, 1977.)

Janzen, in a number of articles, 1969, 1970, 1971, 1972) has shown that among tropical American leguminous trees, the numbers and distribution are strongly influenced by the probability of insect predators finding "the next" seed or pod, i.e., by the same sort of behavior patterns that result in a "stand-off" between *Opuntia* and *Cactoblastus.* This occurrence as isolated individuals, not as stands of single species, may explain why tropical trees depend upon insect pollination instead of wind pollination. Insect pollination gives greater long-range precision for pollination. (Janzen, 1967, 1968.)

These tropical trees (or natural selection) face a dilemma because they need both to attract some insects to act as pollinators and to avoid other insects which act as predators. The tropical trees will become overdispersed if the distance which allows them to avoid predation on their fruits makes it difficult for their pollinators to find them. Compensating mechanisms are, of course, producing masses of flowers, giving off strong odor, and surreptitious setting of fruits. As such, the adaptations illustrate the nice compromises which one suspects are characteristic of many of the actions of natural selection.

## Biological Habitat

The size and distribution of populations are also regulated by the factors which govern the size and distribution of the species habitat. Only a small portion of these factors are directly dependent on natural selection. For example, the numbers of Great Tits (*Parus* *major*) per hundred acres of mixed pine and hardwoods habitat depends in part upon the territory size of the Great Tits (Kluyver & Tinbergen, 1953; Krebs, 1971), and upon interactions with other titmice (*P. caeruleus, P. ater, P. palustris*) and Tree Sparrows (*Passer montanus*) (Krebs, 1971). These effects can be modified by changes in the behavior of Great Tits. The important factors governing the numbers of titmice, however, are the characteristics and geographic distribution of the mixed deciduous-coniferous forest (*Pinus sylvestris, Quercus robur, Fagus sylvatica, Betula alba, Acer platanoides*). The characteristics and distribution of the mixed pine-hardwoods forest are clearly not influenced by natural selection acting on titmice.

1. *Success and Succession.* The vegetation we see today is made up of changing combinations which reflect the particular responses of different species to gradients in habitat conditions (Whittaker, 1967), to the geographic distribution of its habitat, to its neighbors, and to events or accidents of the past which determine the geography of habitat and neighbors.

This leads to one of the most intractable of all the doctrines involved in the study of ecology. If one assumes, as many biologists have, that topography and vegetation "develop" toward stable conditions (mature landscapes and climax vegetation), one is drawn to the conclusion that it is a failing tactic for a species to "choose" ridgetops, marshes or beaches, i.e., habitats which are "immature" parts of the landscape. The vegetation of such places is called successional.

A number of ill-defined ideas have been associated with these "immature," or "successional" or "stressed" sites. In simplest terms, one can say they usually support fewer species and vegetation of lower stature than do other local sites which have deeper soils and more consistent water supply (Woodwell, 1970). Examination of this relation leads to the subject of "favorableness" (Terborgh, 1973) and to the characterizations that some theoreticians give to an optimal community: production, height, biomass, species-diversity, stability, soil depth, nutrient cycling, homeostasis, and populations characterized by "feedback control" (Odum, 1969; Margalef, 1968; Bormann et al, 1974). Successional sites usually experience wide extremes of temperature, and of water supply. They usually have soils low in nutrients and organic material.

May it not be that species on these sites must have "wide ecological tolerances" because the temperature, water supply and organic materials vary widely? If each species present occupies a "lot of ecological space" it will compete with other species over a wide range of "habitat parameters." If a new species appears, it is difficult for the newcomers and the established ones to adjust to coexistence by narrowing their requirements. Thus those species which persist exclude a number of others, and the "niche space" available for "species packing" is small. In areas where environmental characteristics vary less, each species can specialize without becoming vulnerable to the events which exceed the individuals' tolerances.

However, in simpler terms, it is as if some species are selected primarily by physical factors of their habitat (Wallacian selection) while others are selected primarily by biological factors reflecting competition from their neighbors (Darwinian selection). Two extreme types of "adaptive strategy" have been suggested: (1) to become a good competitor at the cost of being able to grow in "extreme" habitats; (2) to evolve the physiological apparatus needed to use the resources of an "extreme" habitat at the cost of being able to compete in biologically "favorable" habitats, i.e., the conditions vary less. Success in the first strategy might tend, if most of the regions' habitats are "favorable," to make the species widespread and abundant, while success in the other will tend to give the species a discontinuous distribution or, in the extreme case, widely separated populations.

There is an old biological adage (perhaps a supersition) that a limited amount of energy is available to an individual in the course of its life. Individuals use this energy in different ways, but only a certain amount of variability can be expressed in an interbreeding population. So the population must choose among alternative ways of life. Colonizing ability and growth rate tend to be inversely correlated with size at maturity and with longevity. Species can grow fast and reach sexual maturity at an early age, produce many young per brood, but if they do so, the individuals will be short-lived. The members of a species may put energy into growth and size before reaching sexual maturity, produce few young in which a large amount of effort is invested, and live a long time. Many papers have been written on this topic. Those by Cole (1954), MacArthur and Wilson (1967), Gadgil and Bossert (1970), and Gadgil and Solbrig (1972) present the main ideas. The symbols "r" and "K," although [or because] tainted with association with group selection, have entered the jargon of ecology to represent these extreme "strategies." Of course, Redwoods (*Sequoia* and *Sequoiadendron*) and Douglas Fir (*Pseudotsuga Douglasii*) seeding in on mineral soil, growing fast in full sun (i.e., being early successional), and yet living to be ancient and huge trees are the "exceptions which 'prove' this rule."

**2.** *Physiographic processes as primary factors in vegetation.* If, as is consistent with current geomorphological ideas, one assumes that bedrock outcrops, sandy beaches, river bars, mountain tops or coves have been and will remain elements of the landscape indefinitely, then adaptation to any particular site along the spectrum of favorableness holds as good promise for survival as does adaptation to any other type of habitat. It is indeed the geographical distribution of habitat which has a maximum effect on distribution and abundance.

A number of botanists have pointed out the relation of plant distributions to forms of landscape (Kerner, 1863; Polunin, 1934 35; Raup, 1951; Sigafoos, 1952; Drury, 1956; Hack & Goodlett, 1960). Sigafoos (1952) considered frost action to be the major force determining patterns of vegetation in tundra, even on a microtopographic scale. Hack and Goodlett (1960) showed how the geology of the Little River region determined the major features of vegetation in a temperate forest region. Goodlett (1954) and Stout (1952) showed how microtopographic features and characteristics of the mineral soil determine the distribution of some trees in a deciduous forest.

This does not mean that there are not many important interactions among plants by which some species form an important part of other species' habitat. It does mean that the habitats of most plants are determined primarily by conditions and forces of the habitat beyond the control of the vegetaion itself (as is the case with titmice and other woodland birds). These conclusions are to be contrasted with the conclusions of those who relate the structure and distribution of vegetation to forces contained within the vegetation; e.g. development of soil profile and resolution of interspecific competition.

One can recognize consistent parts of all landscapes: convex hilltops, outcrops of bedrock, concave valley sides and depositional slopes grading into the bottoms of the valley and floodplain. Along the coasts one recognizes salt marshes and sand dunes. Each of the landscape units tends to have a characteristic community of plants, although in some areas one landscape unit may have several recognizable associations of plants and in other areas one association occupies several landscape units. It may be that a coincidence of numbers of species of plants with the number of units of topography in temperate regions is responsible for the existence there of many botanists who are convinced of the integrity of plant associations. In arctic regions (where the number of species of plants is too few) and in tropical regions (where the number of species is too many) students of vegetation have characteristically been less sanguine about the consistency of units of vegetation.

Vegetation which occupies valley bottoms will tend to have a continuous distribution. Vegetation which occupies sand dunes, sheltered coves at stream headwaters, or hilltops tends to occur in discontinuous clumps.

In classical ecological theory the floras of mountain tops were considered both relicts of formerly widespread floras (Pleistocene) and occupants of habitats destined to be destroyed by erosion, the process of peneplanation. Hence the relict species were readily considered doomed to extinction. It is perhaps poetic justice that other species persist on "islands" at the opposite end of the habitat spectrum, the shaded, well-watered coves with deep soils under isolated patches or islands of "post climax" vegetation. These coves are actually as much islands as are the knobs of the mountains and they often harbor rare species.

If species follow a river, the distribution and "tactics" of dispersal should be different from those of a species which lives on ridges. The measures of successful dispersal are as different as the meaures of stature are different between the hardwood trees of the deciduous forests and the spring wildflowers which grow on the floors of the deciduous forests in larger numbers than the trees.

Plants which grow in ranks usually use the wind to disperse their pollen. To use the wind, the plants must also occupy the "canopy," hence the technique is associated with "dominants." The use of the wind suggests that outbreeding may be either of special importance or simply a coincidence, because these plants often differ markedly in their dispersal mechanisms. Their dispersal mechanisms are suited to where the plants "want" to get to.

First, trees such as Oaks (*Quercus*), Beech (*Fagus*), or Chestnut

(*Castanea*) which grow along water courses have a "continuous" geographic distribution and their seeds are dispersed at short range. They drop or may be carried short distances by animals. The difference in purpose also results in a difference in "tactics" with regard to supply of nutrient for the seedling. Trees which have continuous distribution may emphasize a subsidy for the young plant to maintain it while it becomes established.

Secondly, some trees face the problem of dispersing their seed between islands. Aspens (*Populus tremuloides*) live on sand plains, ridges or on the coarse material collected at the end of solifluction lobes. They have seeds carried by the wind. The seeds need to be light, and if the seed lands on disturbed soil it is not likely to be suppressed. It can start to photosynthesize at once.

Some authors have argued that highly effective dispersal mechanisms are adaptations by which species of fugitive habitats reach another habitat before their successional stage is replaced. Put another way, these dispersal mechanisms are adaptations of last resort by which a species is able to escape extinction. In contrast it may be that these characteristics which we now associate with "r" are really adaptations by which species occupying islands of habitat may get to the next island. The seedlings germinate in little pockets of moisture, in drifting sand or between rocks and grow rapidly in the full sun. The effectiveness of dispersal is illustrated by the appearance of Aspens on treeless Seal Island, Penobscot Bay, Maine, in 1979, sprouting after a fire set by lobstermen in 1978. Seal Island is seven miles from the small forested islands of Matinicus and Ragged and nine to ten from Isle au Haut and Vinalhaven.

Thirdly, using Burdock (*Arctium*), Beggar-ticks (*Bidens*), Forget-me-not (*Myosotis*), or the awns on many grasses as illustrations, if the seed sticks to the fur of animals, one presumes the plant can grow well along animal trails, or where they rest.

The evidence that some animals and plants reduce their adaptations for dispersal when the distances between suitable sites (on islands) exceed a certain amount, argues that the dispersal mechanisms are effective at present and only in part reflective of events of the past.

Adaptations suitable to river banks, ridge tops, or sand plains have "preadapted" plants of "stressed" sites to occupy other sites which have been deforested. Under these circumstances such species can expand their range, as have some wildflowers in occupying the road verges along new highways in the north (e.g., *Hedysarum alpinum, Epilobium angustifolium,* or *Linaria canadense*), and thus shift into a habitat where they suddenly become a pest. In this way it may be "easy" for a usually rare plant species to become abundant. For example, Mayflower (*Epigaea repens*), which was listed by the New England Wildflower Preservation Society as a rare plant not to be picked, becomes an abundant weed after a fire in the oak-pine woods of southern New England.

The major patterns of plant distribution are determined by rainfall and temperatures, then by physiographic forces acting on a time scale far exceeding the life spans of the longest lived trees. These control regional abundance by defining the total area of habitat. In the case that we define success as survival of genes through geological time, it may be a preferable strategy to occupy beaches or ridges where mineral soil is exposed because geological processes guarantee their perennial presence. It should then be "prudent" to avoid the temptation of growth to size and dominance, hence dependence on high levels of nutrients and high moisture supply in the soil, because relatively minor geological events can change a "mesophytic" site to an "early successional" one.

## WHAT CHARACTERISTICS ALLOW SPECIES TO SURVIVE?

During the past decades people who have worked with insects and birds have contributed extensively to knowledge of populations, their regulation, and hence to theory of pest control and doctrine of conservation. To a large degree problems of pest control have been addressed by entomologists and problems of conservation have been the concern of ornithologists. During these years it was difficult to get many zoologists (or botanists) to consider seriously that plants are alive and subject to natural selection.

Birds and insects are active and mobile. They have a fixed life span through which they "rush"; if they have not reproduced successfully in that short life span they have no "fitness." The press of this commitment has dominated a lot of thinking about dangers to populations. Among these hazards was the "random walk", the idea that population fluctuations might get larger and larger until the population went extinct. During the years of debate between proponents of "density dependent" and "density independent" regulation, it was widely argued that unless a species had characteristics by which its populations were regulated, it would face inevitable, rapid extinction.

## Advantages of Discrete Subpopulations

Andrewartha and Birch (1954) suggested that movements among population centers are active elements in population biology, without arguing specifically that such movements make "the random walk" irrelevant. MacArthur and Wilson (1963) used similar ideas as the foundation for their "theory of island biogeography", again without emphasizing the implications as to the regulation of populations. Nisbet and I (1972) argued for what we called the Daphnia model — that the chief defenses a widely distributed population has against extinction is the movement of individuals between population centers. Such movements ensure the re-establishment of local centers because it is highly improbable that any single catastrophe will affect more than a part of the species range at any one time.

Movements among, and differences in survival and reproductive success in preferred and non-preferred habitats have been found to be important parts of the population biology of successful, widespread and outbreeding species, such as Herring Gulls (*Larus argentatus*) (Drury & Nisbet, 1972) and Great Tits (*Parus major*) (Kluyver, 1951). A mobile population of individuals excluded from breeding in preferred habitats exists in both these species and in many songbirds (Hensley & Cope, 1951; Stewart & Aldrich, 1951). In many animal species there is a small percentage of persistent "wanderers." Many animals are subject to periodic eruptions as a result of "uncontrolled" growth in several sub-populations. Such eruptions disperse the population and, even though accompanied by massive mortality, may allow some individuals to survive and become established in unoccupied habitat. This was apparently the case with the colonization by Evening Grosbeaks (*Hesperiphona vespertina*) of eastern North America in the late 1930s.

An illustration of ecological advantage in a population's being divided into sub-populations is given in the history of the Laughing Gull (*Larus atricilla*) in New England since 1875. Between 1875 and 1900 there were fewer than 50 Laughing Gulls in Massachusetts (MacKay, 1893) and about 35 Laughing Gulls in Maine (Norton, 1924). In Massachusetts, Laughing Gulls all settled on one large island, Muskeget, where by 1940 there were about 20,000 pairs (Noble & Wurm, 1943). Meanwhile the Maine population had been disturbed by man and sheep and had moved about between seven islands; it grew to about 250 pairs by 1940 (Palmer, 1949). After 1940, the Laughing Gull population of both states decreased. In Massachusetts, where all the birds occupied one island and its surrounding waters, the population had fallen to about 250 pairs in 1972, but the Maine population, still divided into five colonies each with somewhat different surrounding waters, remained at 250 pairs, i.e., equal to, instead of one percent of, the Massachusetts population. The population increased again in Massachusetts during the 1970s when the birds moved to a new gullery on Monomoy Point, Cape Cod. Similarly, the Heath Hen (*Tympanuchus cupido*) got into trouble after being isolated in a single population in a single habitat on Martha's Vineyard, Massachusetts (Gross, 1928).

The effects of population exchange between habitat centers are significant in management policy for rare species, and will be discussed below.

**Adaptive Advantages of Plants**

Plants and many animals apparently differ in the degree to which problems of rarity and isolation of sub-populations become serious. Most plant species (other then community dominants) probably exist in more or less isolated stations with little gene flow between them. Even many insect-pollinated species have only 10 20% cross-pollination and are mainly self-compatible. This allows a local population to build up its numbers in the habitat to which it is adjusted (the strategy of inbreeding or asexual reproduction), but yet continue to produce a low percentage of more highly diverse young to "seek" another habitat or to adjust to changes in the local one (the strategy of outbreeding or sexual reproduction). An additional pool of masked variability among plants may be provided by polyploidy.

Many invertebrate species resemble plants in having resistant resting stages, and some invertebrates have the adaptation of being able to alternate between sexual or asexual reproduction (and having the potential of self-fertilization among hermaphroditic molluscs). Another element of this adaptive complex of sessile animals and plants is to develop adaptations to ensure wide dispersal of diaspores, e.g. by ocean currents in marine invertebrates, or by the wind in spore bearing land plants.

Harper made the important point that among many plants, reference to asexual reproduction is not helpful because production of "ramets" is a way of producing more of the same individual — not producing a new genetic individual. Harper (1977) defines a "ramet" as an additional morphological expression of an existing genetic combination and a "genet" as a genetically determined new individual. The problem of separating an additional individual from modified branches of an existing individual may be serious in quantitative studies of plant populations, but the ability of plants and many invertebrate animals to "choose" between these systems of spread is of great importance as "strategy." Many ideas in the following discussion were stimulated or brought into focus by reading Harper's splendid book.

**1.** Once a seedling is established, its growth implies that its genetic combination is suitable for the site. It is therefore evident that the individual should duplicate that gene combination rather than risking waste of genes by producing different and statistically less likely-to-be-suitable combinations. Many species of plants have extensive systems of branching stems, rhizomes, sprouting roots, runners, tillers, etc. by which the individual builds up "its numbers" to occupy a space to which it is suitably adapted. According to this strategy "genets" are new combinations of genes which are dispersed "seeking" other suitable habitats. The dispersed individuals risk astronomically high rates of mortality in the "hope" of finding a new site where (it is reasonable to assume) a slightly different gene combination is likely to be suitable. Trembling Aspens, Beech (*Fagus grandifolia*), and American Chestnut (*Castanea dentata*) are examples of forest trees which form clones. The underground stems and sprouting roots of sedges and grasses which form the sedge mats of bogs or the turf of meadows illustrate the importance of this ramet system. Corals have a similar system of budding "branches."

Some branching stems grow underground and while they proliferate and grow forward, they are dying behind. Thus for an individual of Cinnamon Fern (*Osmunda cinnamomea*) growth and branching may lead to essential immortality as well as to production of a large number of virtually exact copies. For some plants and some animals successful establishment of a single individual will have tremendous implications, in contrast to the situation among most animals, especially birds.

**2.** In general plants and animals are fundamentally different in their opportunity to "extemporize" on the development of an individual and its parts. Plant parts have great latitude of development. Single lower branches of open-grown trees may be larger than entire other individuals while the lower branches of trees grown together may be short, suppressed, and soon die. A tree may have a straight bole up to the level of the canopy and there open out into a "bush," or that bushy growth form may start at the ground. Trees growing in exposed places, on ridge tops, edges of fields, or after fires may have some branches whose individual histories are as different from the rest of the same "tree" as are different clumps of *Osmunda*. Observations of the forms of trees (Horn, 1971) and review of the processes of plant embryology and morphogenesis (Torrey, 1967; Steeves & Sussex, 1972) suggest a great deal of independence for the several meristems and different elements of a plant body. While a plant continues the tremendous potential for differentiation in its initials, an animal is generally committed to rigid form at the unfolding of the early cell divisions of the embryo. It may be fair to say that an individual tree shows less unity of integration than many ecologists have credited to whole plant communities.

**3.** One of the special aspects of plant biology is the observation of "delayed maturity": many plants seem to be unhurried about their production of offspring. This contrasts with a model prepared by Cole (1954) which has affected a lot of thought about animal populations and reproduction. That model, in part, shows that an organism which reproduced in its first year, produces two offspring and dies, will be represented by as many offspring as an individual which waits until its second year and produces one young every year forever. In many cases plants do not seem bound by this compulsion to reproduce. For example, a dune grass (*Ammophila arenaria breviligulata*) will grow and produce ramets for many years, then suddenly burst into flower when its roots are exposed by a blow-out. At the same time a tree being overwhelmed by the movements of the dune will produce a heavy crop of flowers and seeds. If a plant occupies a site, it is of little benefit to it to produce seeds which germinate under itself and are shaded and suppressed each year. But once the individual is exposed to conditions that indicate its imminent demise, it is stimulated to produce an abundance of offspring. It is as if the benefits of reproduction by genets are not consistently worth even the minor costs as long as an established individual occupies the site with some sort of "de facto" immortality by ramets.

In other cases there are plants which grow for a number of years and flower, then die. If the flowers are picked off, the plant returns to vegetative growth, continuing to live. This pattern of behavior is incomprehensible to an ornithologist, most of whose theory is based upon preoccupation with a rush to sex and to inevitable early death.

**4.** Plants, like some invertebrate animals, produce elements which can persist in the soil for years, the "seed bank," of Harper and White (1974), until they receive clues that conditions have become favorable. Thus, a set of genes can "wait" for suitable conditions as well as be carried to places where the set may become established.

An additional characteristic by which plants differ from active vertebrates is in their ability to exist suppressed (sapling under the canopy or an herbaceous plant in the midst of grass turf) until release. Without thinking, we suggest that once started, life of an individual proceeds through stages of a small embryo, growing-youth, producing maturity, and declining powers of old age. Russians (e.g., Uranov et al, 1970; Uranov & Smirnova, 1969) have suggested that plants have life states which can be "recycled." A plant which has been suppressed for many years and has exhibited the characteristics of "senility," may be released and quickly take on the vigorous growth and activity of a seedling. A parallel can be formed in the lives of individual branches or other ramets. These reflect very different systems of embryology than we normally conceive of, having learned primarily animal embryology.

**5.** Structural diversity is characteristic of plants and is a "mechanism" by which plants make phenotypic adjustment to the place where they find themselves, because they are unable to move. This structural diversity may make difficult the recognition of species in many plants. In contrast, many active animals tend, because of the constraints of their activity, to be uniform structurally. An extreme case is found among some plants of the north, such as Grey Willow (*Salix glauca*). This plant varies in leaf form from small, spatulate, acute tipped forms in mountain stream beds in Alaska to large orbicular leaves in eastern Canada (Figure 1). One presumes that this variability parallels and reflects a physiological variability adjusted to features of the habitat in which the species grows in its North American range. It also occurs across Siberia and northern Europe.

Earlier, I suggested that an important reason for there being few

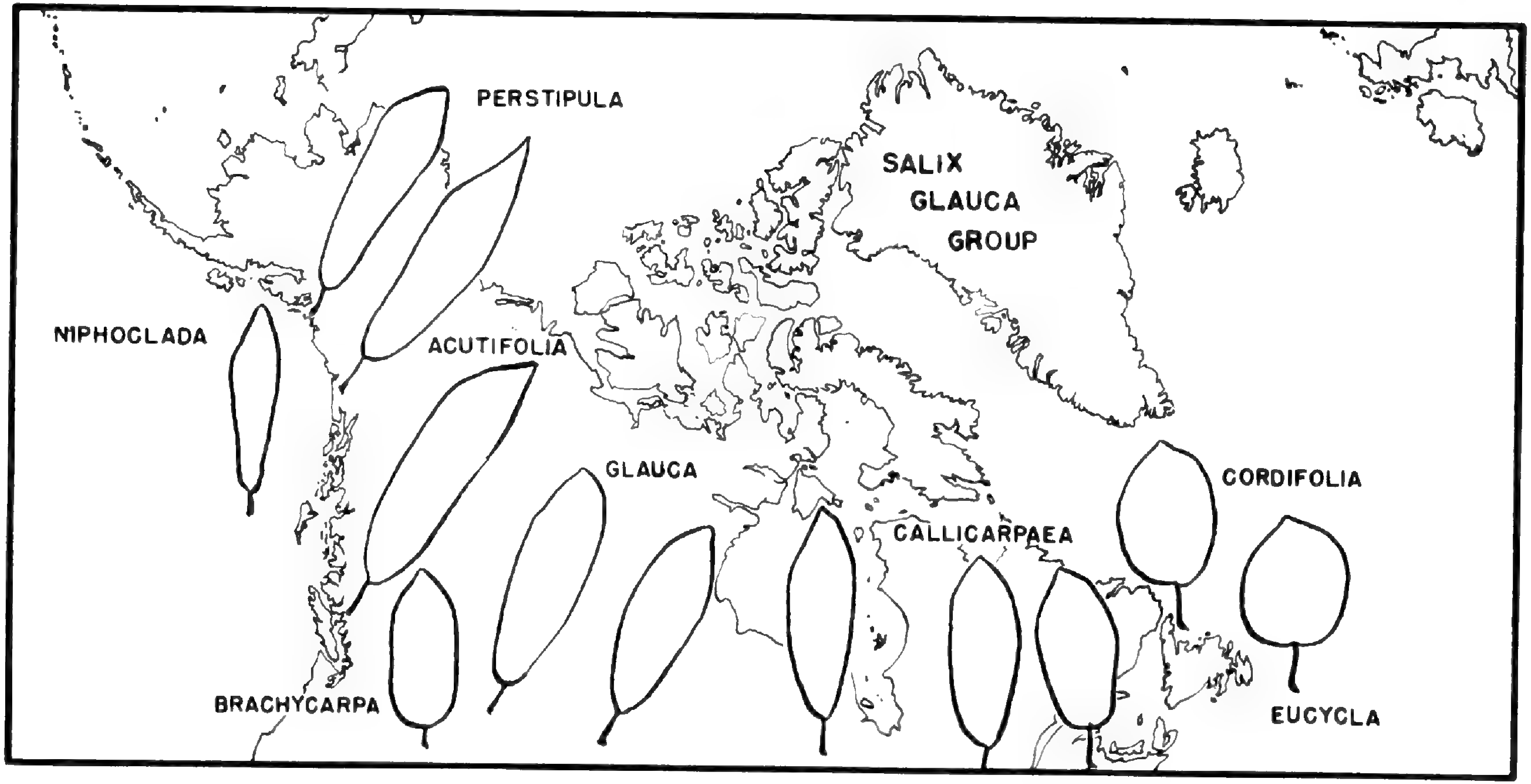

Figure 1.

**Distribution of leaf shapes of Gray Willow across North America**

The extreme variation in shapes of leaves suggests that the species contains a wide range of ecotypes. Trembling Aspen occupies similarly diverse habitats without evident morphological variation. One wonders either how the genetic structure of the species retains this wide variability or why other species do not express as much variability in form as does Gray Willow.

species in habitats whose environmental parameters vary widely (soil moisture, temperature) and whose landscapes are uniform, is that in order to survive species must have wide ecològical amplitudes. Large ďifferences in rainfall, temperature, soils, and other habitat features are found across North America and Siberia in the range of *Salix glauca*. One should not be surprised to find similarly large variability in the structural expressions of species having "wide ecological amplitude."

But this challenge of the environment presents a dilemma to the long term adaptive mechanisms of the species. To what degree can a "species" go on accreting additional variation without straining the equilibria which are suggested to exist in "adaptive gene complexes" (Mayr, 1963)? *Salix glauca* may be an extreme in the ability to tolerate variability. What is the case in those species groups (e.g., *Astragalus*, or many grasses, *Calamagrostis*) in which the "strategy" seems to be to divide up into many small populations which seem to have partial reproductive isolation? Their reproductive isolation is often based more on geography than on biological barriers to interbreeding. Again it is suggestive that the greater ability of plants to tolerate structural differences may allow production of many individuals which appear to be or are indeed "hybrids", most of which are "weeded" out by continuous natural selection.

In many cases, the numbers of these forms do not increase because counter selection can keep up with and prevent extensive "introgression." Work on Drosophila (Thoday & Boam, 1959) suggested that even among animals extreme variants within a single interbreeding population may assort preferentially so as to retain the extreme forms. Among plants the not infrequent coexistence of recognizable "varieties" within one species in one geographic region (dependent on habitat differences) suggests the everday importance of selection of individual gene combinations by their habitat.

In other cases hybridization is associated with polyploidy, and hybridization together with high levels of polyploidy seem to lead to apomixis (the production of seeds without fertilization) (C. Greene, pers. comm.). Apomixis provides an extreme case of adaptation to inbreeding and may be a "solution" that plants have "found" for the problem of controlling variability. Apomixis can be seen as a mechanism which provides for better setting of seed especially in cases in which high levels of polyploidy present problems to proper pairing of chromosomes at meiosis. At the same time the high levels of polyploidy provide masked variability and partial meiosis can supply opportunities for recombination of genes.

Apomict species present an especially awkward problem to biological systematists because it is not clear where species lines should be drawn either by morphological or behavioral characteristics. They seem to provide a case in which the now classical biological species concept is not helpful.

One wonders to what degree some problems in drawing species lines represent real difficulties reflecting the "tactics" of plant species, in response to special habitat interactions. The lines drawn, of course, also reflect the personalities and experiences of the botanists who have worked on them (splitters or lumpers). The clarification of such difficulties may be important when required in establishing the validity of species groups which have been suggested for critical or other special legal status. For example, a species of *Calamagrostis* has been suggested for inclusion in the critical areas study in Maine. Louie-Marie (1944) made the following suggestive comment about it:

> "*Calamagrostis Fernaldii* Louis-Marie
>
> The plant is certainly baffling. Following Kearney's identification, Fernald puts this collection in *C. perplexa,* but always admitting it as not identical. Scribner has assimilated it with *C. Porteri,* undoubtedly as a "pis aller," and before the publication of *C. nemoralis* Kearney. About this plant Wiegand and Eames took a very different position. In their Flora of the Cayuga Lake Basin, they wrote, under *C. perplexa*: "an inspection of that plant shows it to be not the same, and more like an offshoot of *C. Pickeringii.* The Danby plant is related to *C. Porteri.*" In general habit the Piscataquis County plant looks like *C. Pickeringii,* var. *debilis,* but inside its spikelets there is the abundance of hairs that characterizes *C. perplexa.* Nevertheless, it cannot be united to the Danby type, which has "scattered culms" and "two tufts of hairs at the base of the leaf"; it is caespitose and has no tufts of hairs at the summit of its sheaths".

Though a subject with a long history and one of debate between Darwin and Wallace, geneticists have perhaps prudently avoided facing the problem: "when and why (the selective advantage, not the mechanisms) do two populations 'become' two biological species?" Are chance events occurring in geographically isolated populations sufficient conditions as well as necessary conditions?

## WHAT SHOULD BE DONE?

Actions to be considered in a program of rehabilitation of a species should include assessment of biological and human values: the human values being those values perceived by people, and the action being applied within the biological contexts of each species. Each critical species needs to be understood as itself.

Species which are closely adapted to a narrow habitat which has a patchy distribution as if on islands are of course especially vulnerable. Thus, the problems of dispersal and conservatism that have traditionally been associated with island faunas and floras deserve special consideration. A number of published articles exist on this general topic, because theorists interested in the mathematical theory of "Island Biogeography" have developed the theme. According to theory, and contradictory to traditional conservation practice, even a patch of wilderness climax ecosystem will suffer attrition of species. Species with a rapid turnover of the population or species which require large ranges are especially prone to this attrition. On the other hand some species seem to do very well on small islands. Rare species of plants found by Rand and Redfield (1894) more than eighty-five years ago on Mount Desert Island have recently been found at the same stations.

Because most species of concern already have been reduced and to some degree isolated, their habitat can be assumed to be coveted by other (especially human) uses. This raises one of the most pressing human problems: "At what level is the species important?" One can predict that in the future decisions resolving competing demands will not be justified in absolutes, although the rhetoric of the proponents may seem to demand it.

Plants have some special attributes which need consideration; for example, "old growth" forest has a special importance that senile animals lack. Many humans value a shabby growth of old-field pine, although foresters and lumbermen are impatient with them. Many dedicated conservationists enjoy rolling vistas of meadows and prefer them to the "wall to wall" trees which often result if we "let nature take her course." While much of the charm of animals is seeing them undisturbed against a suitable landscape, the topographic element is in many cases not critical for the animal species. In contrast, as I have said, I believe that plants have a geomorphic basis for their distributions and suggest therefore that actions to be taken must consider a geomorphic context for plants. Thus, one needs to consider size of areas and sorts of landscape, as well as connection among areas to be preserved.

Some species have special human appeal. Thus, we can say that some species are peculiarly useful as tools to be used in operating within existing social institutions to create or restore circumstances that will be pleasing to us. Our work as activists is directed toward goals which combine a sense of responsibility toward the organisms around us and the conditions which make humans feel some contentment. I will discuss this further in Section 5.

## Steps to be Taken

The arguments in this paper suggest a number of courses of action in the interests of any given rare and endangered species.

**1.** Most important of all is to guarantee that several adequately large areas of suitable habitat exist. The size of the area and the patterns will depend on the peculiarities of the species.

**2.** It seems prudent, as the first step in rehabilitating a relict population, to take active steps to encourage it to break up into a number of more or less independent sub-populations. This, of course, is exactly contrary to traditional protectionist policy.

The existence in most populations of a low rate of outbreeding between independently maintained sub-populations emphasizes the importance of local populations of a wide-ranging species now isolated by changes in habitat. The bald eagle (*Haliaeetus leucocephalus*) is broken up into several population sections, most conspicuously those on the Alaska coast, the Great lakes, Maine Maritimes, and Florida. Each of these sub-populations (whether recognized by taxonomy or not) should be regarded as a population of major importance in the survival of the species. Interchange among populations should be encouraged.

**3.** It is unlikely that all young produced by any species naturally in the wild are necessary to maintain the local population. In fact, Kluyver's (1966) study of Great Tits in a closed population on the Island of Vlieland showed that adult mortality was reduced by artificially decreasing the number of young. Furthermore, although the details of behavior differ from species to species, it seems clear that many young are excluded from breeding by social interactions with established territory holders (e.g., Kluyver & Tinbergen, 1953; Watson, 1967; Krebs, 1971; Carrick, 1972). This is of course obvious for seeds which fall under their parent plants. Therefore in taking action on behalf of a relict population it seems reasonable first to measure the recruitment necessary to maintain adult breeding population size and use any reproductive surplus to establish new colonists in vacant traditional habitat. In fact, it seems probable that releasing young on former habitat now empty could improve the chances of survival of the young to the degree that their survival in the traditional habitat is compromised by competition from their parents and other established adults (Kluyver, 1966).

**4.** The evidence just reviewed referring to the genetic and geographical structure of wild populations suggests that problems of restricted genetic variability resulting from taking small samples from the wild into captivity will not necessarily be serious. Present understanding indicates that the danger of the founder principle (genetic homogeneity resulting from beginning with a small number) or inbreeding will not inescapably be disastrous and that many dangers can be overcome. The samples taken from wild inbred populations may already be homozygous (e.g., *Leavenworthia*, Solbrig, 1972), or they may not be (*Avena*, Jain & Marshall, 1967; *Tridacna*, Ayala *et al.*, 1973). What happens to them in a breeding program is what matters and enough is known of population genetics now to develop a promising strategy for successful breeding.

**5.** The traditional purpose of a breeding program is to release a large number of potential recruits to the wild population. An additional major purpose should be to increase variability in the population and allow natural selection to select suitable phenotypes from among those individuals released.

Any breeding program should follow a strategy tailored to the peculiar characteristic of each species involved, plant or animal. One major danger would be to continue inbreeding in captivity over any significantly long time. Inbreeding is usually encouraged consciously or unconsciously in a breeding program and may further reduce variability.

Another danger is the effects of unconscious selection for characteristics suitable for cultivation or captivity. In the real world natural selection acts against certain sets of characteristics and for other sets. In captivity selection by the breeder almost undoubtedly does the same (i.e., for "handsome birds" or "tame" ones, or simply those that will survive and breed in the greenhouse or cage). Conscious or unconscious selection by breeders seems a reasonable explanation of the declining fertility and vigor in populations of Ne-ne Geese (*Branta sandvicensis*) and Aleutian Canada Geese (*Branta canadensis leucopareia*) kept in captivity.

These arguments suggest that variability should be deliberately promoted in breeding stock. It is generally agreed that the promotion of variability is the function of sexuality and this variability, *inter alia*, increases the probability that some percentage of offspring will become established on habitat away from the breeding site. The cost is a high mortality rate (often over 90%) in nearly all wild populations studied. The desired variability can be promoted by ensuring constant turnover in the breeding stock, by introducing new breeders continuously from the wild, and by releasing as many offspring after as few generations of captive breeding as possible.

**6.** Conservationists have been quick to criticize lack of success in a program of captive-breeding and release. One often hears about the very high mortality of game-farm pheasants. Granted that such birds had no chance to learn how to survive on their own, it is important to have reliable measurements of mortality and compare these to data on a per-egg-laid basis for a wild population. Even in a successful, increasing species such as a Herring Gull (*Larus argentatus*), mortality rate is extremely high. For example, a pair of mature gulls can expect to live 10–12 years and produce 30–36 eggs. Even if all but three of these die before reaching reproductive age, the population is increasing. Mortality among seedlings of a Sugar Maple (*Acer saccharum*) or larvae of a Salmon (*Salmo*) is almost incomprehensible.

Because of the high mortality that must be expected, large numbers of young should be continuously produced and released over many years in a reseeding trial. No young at all may survive for several years then suddenly a successful year-class appears. Because of the variability that will be needed for the first stages of population rehabilitation, especially large numbers should be produced. This is also especially important in dealing with conservative species, those which avoid colonizing unoccupied areas. Each species, however, is likely to have its own peculiarities. Present evidence indicates that releases of wild-caught turkey poults have succeeded where releases of captive-raised ones have failed for years in New England.

It should be easier to reestablish plants as compared to animals, because of the greater ease of growing plants under cultivation and the greater control over individuals in transplanting to suitable habitat. Seed is available from wild plants and one does not have the impression that all the seed is needed to maintain the wild population. Lavish numbers of offpsring can be raised and transplants repeated until some individuals become established. There seems to be less intuitive concern at expending young ones we have raised, and it should be easier to overcome the idea that if transplants fail the effort has been poorly conceived. We may still have to overcome the traditional attitude that humans should not intrude on the ways of nature, but those interested in plants seem to have more practical or less emotional attitudes than do animal lovers. After all, they weed their gardens.

If one has the faith that biological problems can be solved by the application of imagination, effort, and resources, one must believe that the breeding can be done. The risks may be high, but cross-breeding and releases have more promise of success than does the alternative. The practice of jealously guarding those young that are produced "naturally" may be as damaging a tactic as can be used, reminiscent of the biblical character who jealously hoarded his single talent.

## PARADIGMS, POLICIES AND POLITICS

Clearly the experience of students and the philosophies or models to which they were "imprinted" affect the conclusions drawn and generalizations made as much as does the biology of the organisms studied. These influences need to be sorted out in the search toward understanding the biology of rare species and proposing steps to be taken to ensure their survival. Natural Selection is a sweeping generalization and one of the most powerful intellectual tools developed by any philosophy. But once one acknowledges that natural selection acts on individuals, each in unique situations, one is faced with a redundancy of detail that challenges generalization. As each individual plant or animal must solve its own problems in its specific habitat, so those people who assume responsibility for preservation of landscapes, habitats, and species must address situations that include a wealth of details, for which few generalizations are helpful.

In this section I will review some philosophical attitudes and present arguments familiar to many ecologists. This may seem gratuitous and roundabout to those by whom it is already acknowledged. But because this paper will be read by conservationists whose commitment is emotional, not scientific, and because most of the rhetoric of contemporary environmentalists includes arguments which I believe are false, I will repeat the argument.

During the last three decades we have witnessed chronic confrontation between proponents of industry and of environmentalism. It is usually believed that this confrontation is one between fundamentally different assumptions, but I suggest that the two are using the same "paradigm". The two major forces, both the ecological imperative (which has as its ideal the wilderness climax) and the market place imperative (which has its ideal in free operation of supply and demand) believe in what I believe would constitute a miracle. The miracle would be that the sum of individually selfish acts would create a system which is beneficial to all. The basic selfishness of human nature is well-known. Its "naturalness" was a foundation of 18th century thought. Selfishness of actions and motivations are also the basis of Darwinian natural selection. . . . Whence, we should ask, comes the delusion that individuals were supplied according to their needs in the "state of nature" or that the market place cares for the needs of the poor?

The paradigms are deterministic, and the people who use them are oblivious to their implications. I think that individuals' "needs" and "the poor" are irrelevant to these models. In the deterministic model it is assumed that conflicting forces interact within the system until an equilibrium is reached. The equilibrium is then maintained by a balance of forces. Balance plays a central role in the arguments both of the environmentalist and of the market economist. If our world were indeed to attain equilibrium, it would be a dull place.

The ecological imperative is based on early 20th century ecological models which used the "theory" of succession to argue that with passage of time communities achieve a particular, preferred configuration of species, and are characterized by a variety of "good things": maximum productivity, diversity, efficiency, large biomass, nutrient cycling, stability, "information content," etc. These are the climaxes. Disturbance of a climax was damage, which, it was believed, set into motion forces which led to "recovery." In the same model it was believed that reduction or excess of populations initiated compensatory mechanism and led to reestablishment of equilibria. It has been asserted that before the advent of western man natural populations were saturated and stable at the carrying capacity of the environment.

Repeatedly, these days, one hears conservationists using the dogma that each species fills a function in a holistically organized community whose sum creates a circumstance which guarantees the needs of all component parts. If one pulls at one part, one affects all other parts. If we do not know what the function of a part is, we should not tamper for fear that we may do irreparable damage.

I will not go into my contrary arguments here because they are published elsewhere (Drury and Nisbet, 1971, 1972, 1973). My arguments are based on observations of lack of stability of numbers, lack of coupling among subsystems, redundancy of systems, and opportunistic use of several systems by many elements of what we might like to call one ecosystem. Experience indicates that one can seldom prepare a model which will allow a *a priori* predictions of the effects of manipulation of parts of a natural system. What effects will be caused by removal of a conspicuous species such as American Chestnut (*Castanea dentata*) from the Appalachian forests or of Herring Gulls from the New England shore in the late 19th and early 20th centuries?

During the last twenty years of renewed study of natural selection, most students have come to doubt (as did Darwin) that natural selection can select one species for the benefit of another species. Harper (1977) has cogently put it:

> "A theory of natural selection that is based on the fitness of individuals leaves little room for the evolution of populations or species toward some optimum, such as better use of environmental resources, higher productivity per acre of land, more stable ecosystems, or even for the view that plants in some way become more efficient than their ancestors. Instead, both the study of evolutionary processes and of the natural behaviour of populations suggest that the principles of "beggar my neighbor" and "I'm all right Jack" dominate all and every aspect of evolution. . . Natural selection is about individuals and it would be surprising if the behaviour that favoured one individual against another was also the behaviour that maximized the performance of the population as a whole".

Harper's comments express the doubts about the achievement of compromise when resources are limited. In the same way that many conservationists plead: "let nature take her course;" so the free market proponents say: "let the market act." The patchwork of what industrial spokesmen patronizingly call "government intervention" speaks of the reservations that our society feels about a competetive market system's actually working for "the public good," when different elements of society have different goals. The exploits of John D. Rockefeller, Andrew Carnegie, *et al.* should convince doubters.

Another expression of the expectation that natural systems lead to a utopia is found in the ideal that native people have developed "proper" conservation ethics. If all animals are in balance, then true natives are in balance. We close our eyes to the forces of starvation, brutality and disease which kept "native" populations low whenever they pressed on their resources. Let us consider the people of the north. We should expect their ethics to be suitable to their environment and to their strategies as predators.

In recent history the Eskimos were a people dominated by the capriciousness of their environment. Whole villages starved when the weather changed in unexpected ways so that they could not travel or when the game went "elsewhere." The people could not travel far enough into the tundra or out onto the ice to have access to all the habitat used by their game. Dominant groups occupied the more reliable sites. Subdominant groups were forced to look for new resources. One still hears stories of misery suffered among groups that had to travel off to new regions. The people developed a fatalistic philosophy of killing as much game as they could when the game was present and hoping to freeze and store it so that they did not starve before they got the next break from the capricious spirits. Older Eskimos will say that theirs is a hungry country and that anyone who practices conservation or sportsmanship will likely starve. Conservation of limited resources and prudence in cropping of game is irrelevant to people living on an island when 50,000 walrus drift past on the icepans in spring.

The Eskimos of the northwestern Bering Sea now kill walrus for the ivory. They carve the ivory and sell the carvings to tourists. They shoot walrus with high-powered rifles from aluminum boats with 50 h.p. outboard motors, yet the walrus hunt is still the major way a man can establish his identity. Now they eat some meat from a few of the first walrus shot and cut off the heads of the rest for the tusks. Headless carcasses of walrus littered the sandy beaches of the Seward Peninsula in 1975; we counted over 450 in the course of censusing for gulls. In the last few years the people have learned that carcasses rotting on the beaches make bad public relations; they slit the bellies so the carcasses will not rot, bloat and float. The idea that they should make maximal use of any resource which they can seize is not a new idea which comes from association with the white man. A conservation ethic is simply foreign to them.

Although some native people did have a sophisticated and sympathetic land ethic, by no means all did. To suggest returning society's attitudes to those before "development" will be a form of "cop out" to avoid addressing the puzzling problems which we face.

Turning to our own economics, the market works, like natural selection, to satisfy selfish interests and to exploit, not to protect, resources. When a species becomes rarer, as have Polar Bears, the price rises and stimulates previously uneconomic search for more of that species until it (the supply) runs out. Pressures to meet short term goals inhibit or prevent attainment of long term optimization when the improvement requires a system to pass through temporarily nonadaptive conditions. The collapse of efficient public transportation in the face of selfish convenience of automobiles and the manipulation by big auto businesses illustrates the actions of the market in terms of the long range "public good".

Proponents of progress vociferously objected to the use of noise pollution and stratospheric contamination controlling the development of the Supersonic Transport; but now that economics (the aircraft are not paying for themselves) threatens to eliminate this symbol of technology, those voices are silent. Why does the profit motive still have the status of the golden calf? I suspect that many people see it as a mechanism that will divest society of the responsibility of making awkward decisions.

Our legislative/legal systems supply rules for another arena where selfish interests compete. No one of the special interests will yield its interests to the general good. For example, the discussions which led to the banning of pesticides were dominated by the power of special interests. Legislators required chemicals be available to all of the public or to none. because that is what the special interest groups demanded. The idea of restricted use in case of serious need was repugnant to those who did not trust the decision-makers. Each group insisted on defining "real need" themselves. So individuals in politics tend to manipulate legislative acts in their own interests, and it is the function of the courts to interpret those acts.

The courts play out their adversary proceedings according to an esoteric set of rules which are interpreted by the specially initiated. Lawyers admit that ours is a patched-up system, but apologize that it is all we have. The adversary system will "beggar my neighbor," as Harper says. If we espouse the adversary procedure, if we send our most eloquent and adamant proponent to the controversy, why are we surprised and annoyed when the opposition is also adamant and eloquent, — we say "intransigent"?

These pressures act on conservationists as well. The press of economic necessity pushes most conservation organizations to local concerns, because volunteers prefer to work in their own direct interests. Over time, some organizations have grown at the expense of others, primarily those have grown which are in effect insurance agencies for the environmental amenities of affluent suburbanites. The conservation organizations seem to respond first to politics as "fundamentalist institutions" — they brook little questioning of philosophical justification. Among conservation organizations as in the White House, scientific evidence is usually discarded if the science challenges political or economic "realities."

A student of natural selection sees no contradiction in observing people and other animals or plants; their motivations are selfish. Our rules were patched on as our society outgrew the villages where everyone knew each other, knew everyone's past behavior and could bring social pressure on antisocial individuals to conform to norms of the group (Trivers, 1971). Maybe our most serious problem results from the opportunities offered by anonymity.

A current flowing counter to selfishness has existed during the centuries. I think it makes humans special and gives us hope. It is a sense of responsibility. It can find biological roots in the actions of leaders who undertook some degree of "reciprocal altruism" (Trivers, 1971) for the larger group. This worked because the group gave loyalty and gratitude in return for care. In small in-breeding groups a sense of responsibility among the leaders on the one hand and of loyalty among the followers on the other increased "fitness." This responsibility may have stretched beyond the extended family group when it was advantageous for several groups to join in hunting parties for big game of the Pleistocene. The story of human progress since then can, with some justification, be presented as an expansion of the group to whom we apply sense of responsibility, and I am sure that this idea is not new to me.

A major step in the neolithic revolution is domestication of stock and cultivation of plants. This tremendous step requires assumption of responsibility for organisms which come to depend upon us and are not members of our own gene pool. There is good reason to believe that it was forced upon our distant ancestors when the mighty hunters of the late ice-age had exterminated the Pleistocene megafauna.

The Darwinian revolution challenged the easy confidence which people had had in the belief that humans are a special creation and in that ultimate arrogance "created in God's image." The social revolution which I see in the environmental movement gropes toward "internalizing" the implications of evolution in social thought. Now, if we are descended from apes, the question of who is my brother and who is my neighbor becomes even more awkward. If we feel free to pull up a wildflower which we call a weed in our garden, do we feel guilty to kill a Herring Gull which will drive Arctic Terns and Laughing Gulls from their nesting grounds? Do apes have special value? Do mammals? Do animals over plants? Does the philosophy of non-violence apply to mosquitoes?

We are committed to a debate among scientists, among conservationists, and among members of the public as to what we think is right for humans in their interactions with their habitat. Some would have natives kept as relicts of traditional ways of life. Similarly, some consider their responsibilities done when they have established wilderness where the affluent can enjoy their safaris or canoe trips. Are not those who are satisfied at setting aside sanctuaries in suburbia saying: "I'm all right Jack"?

We are now faced with a circumstance characteristic of many species of animals and plants: i.e., moving from one unsatisfactory and vulnerable adaptive peak (discredited theoretical base on contemporary ecological theory) to a defensible adaptive peak (valid theoretical justification) across a nonadaptive "valley" in which the ecological theory is considered invalid but the equally invalid market place and legal/legislative systems remain in force. We are disillusioned with our social institutions which act in the legal arena, the market place, or the legislatures. Yet those institutions are the stage upon which we must act and the ecological imperative is at present acceptable to important elements of society, including the courts and legislatures, although it may make an enlightened ecologist squirm.

This imperative may be essential to the many thoughtful people who are using whatever social institutions are available — political, legal, economic, endangered species act, restraining orders — to ensure that values which are not yet codified are not buried in the rush of economic expediency. we should wish them God's speed and should stiffen their resolve with scientifically valid support whenever we can.

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The material presented uses ideas from many directions, which, I believe, converge on the topic of the biology of rare species. My intent has been to present a set of insights which combine to form a picture of the lives of plants and animals in their world. These insights make up a way of thinking and serve the same function in the synthesis as do the spots of color by which an impressionist painter portrayed the atmosphere of a landscape. As such this work does not conform to expectations of the usual scientific paper in which a carefully delineated problem is identified and directly applicable evidence presented in a closely argued form.

Not surprisingly, the work upon which these ideas are based has had support from unusual sources. Most was through contracts to solve biological problems with pressing political implications. I would like to thank Dr. John Seubert, Animal Depredations Control Research, U.S. Fish and Wildlife Service for support for work on seagulls on the coast of New England; and Dr. David Norton, Arctic Project Office, Outer Continental Shelf Environmental Assessment Program of the National Oceanic and Atmospheric Administration for support for work on seabirds in the northern

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## SUMMARY

Our perception of a species as rare implies a low frequency and a high intrinsic value. It has usually been assumed that a rare species is not successful and that it suffers from reduction of genetic variability or depauperization of habitat. These assumptions probably stem from deterministic models of community and species development. Contemporary studies of genetic polymorphism suggest that some small populations and some inbreeding populations retain heterozygosity. When one considers the density of species it appears that most species occur at low densities. A minority are numerous and another minority are endangered. At this stage it does not seem to help our understanding to assign a degree of success or failure to any species except in a specific context.

An operational definition of a rare species might include that its numbers are divided into subpopulations so that interbreeding is restricted or, in extreme cases, the species is reduced to a single population.

Plants have advantages for survival in small populations in that they can survive for long periods in vegetative form and do not seem driven to reproduce within a fixed life span. Plant reproduction seems to tolerate both more inbreeding and more hybridization than has been credited to active animals upon whose biology much ecological and conservation theory is based. Morphological plasticity, which is one important adaptation of plants, results in many cases in difficulty in identifying species boundaries, and in the extreme case the concept of an endangered species may need clarification.

Because each subpopulation will tend to have somewhat different genetic composition, one would expect that the number of subpopulations are more important for the persistence of a species than the total population size. Because isolation of an inbreeding population may encourage specialization and "conservatism," it may be that the first steps in rehabilitating an endangered species population is to break it up into largely, but not completely, independent populations. This policy is directly contradictory to the classical view of protectionists.

Plants have advantages for rehabilitation. Among them are the facts that many can readily be divided into clones, and that few botanists suffer humanistic pangs felt by animal lovers in removing competing species from the habitat or in expending large numbers of young in an attempt to establish a new station.

We are at an awkward transition in which the goals of the environmental movement are laudable but the justifications are often not valid scientifically because the models are deterministic and natural systems are not. Similarly deterministic models are the essence of the intellectual framework of our economic and legal institutions. It seems that these contemporary social institutions require outside intervention. Otherwise they provide opportunities for prostitution of human values to money and convenience or for a cop-out for those who do not want to address the conflicts between selfish interests and the long-term values. It was "irrational" political intervention in the *laissez-faire* policies of the 19th Century that protected landscape and endangered species, and there is little to convince us that anything else is the case today. Activists use whatever tools are available — endangered species act, restraining orders — and we should wish them God's speed even though many of the biological ideas they use make an enlightened ecologist squirm.

## LITERATURE CITED

Andrewartha, H. G., & L. G. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.

Ayala, F. J., D. Hedgecock, G. S. Zumwalt, & J. W. Valentine. 1973. Genetic variation in *Tridacna maxima*, an ecological analog of some unsuccessful evolutionary lineages. Evolution **27:** 177–191.

Ayala, F. J., J. R. Powell, M. L. Tracey, C. A. Mourao, & S. Perez-Salas. 1972a. Enzyme variability in the *Drosophila willistoni* group. IV. Genic variation in Natural populations of *Drosophila willistoni*. Genetics **70:** 113–139.

Ayala, F. J., J. R. Powell, & M. L. Tracey. 1972b. Enzyme variability in the *Drosophila willistoni* group. V. Genic variation in natural populations of *Drosophila equinoxialis*. Genet. Res. **20:** 19–42.

Bormann, F. H., G. E. Likens, T. G. Siccama, R. S. Pierce, & J. S. Eaton. 1974. The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. Ecol. Monogr. **44:** 255–277.

Camin, J. H., & P. R. Ehrlich. 1958. Natural selection in Watersnakes (*Natrix sipedon* L.) on islands in Lake Erie. Evolution **12:** 504–511.

Carlquist, S. 1971. Hawaii, a natural history. Natural History Press, New York City.

CARRICK, R. 1972. Population ecology of the Australian Black-backed Magpie, Royal Penguin, and Silver Gull. Pp. 41 99. *In:* Population Ecology of Migratory Birds: A Symposium, U. S. Dept. Int. Wildl. Res. Rept. **2.** 278pp.

CLAUSEN, J., D. D. KECK, & W. HIESEY. 1940. Experimental studies on the nature of species. 1. Effects of varied environments on western North American plants. Carnegie Inst. Wash. Publ. **520.**

COLE, L. C. 1954. The population consequences of life history phenomena. Quarterly Rev. Biol. **29:** 103-133.

DRURY, W. H. 1956. Bog flats and physiographic processes in the upper Kuskokwim River Region, Alaska. Contr. Gray Herb. No. **178.** 130 pp.

______., & I. C. T. NISBET. 1971. Inter-relations betwen developmental models in geomorphology, plant ecology, and animal ecology. General Systems **16:** 57-68.

______. 1972. The importance of movements in the biology of Herring Gulls in New England. Pp. 173-212 *In:* Population Ecology of Migratory Birds: A Symposium, U. S. Dept. Int. Wildl. Res. Rept. **2,** 278 pp.

______. 1973. Succession. J. Arnold Arb. **54**(3): 331-368.

ELTON, C. S. 1958. The ecology of invasions. Methuen, London.

FERNALD, M. L. 1924. Isolation and endemism in northeastern America. Amer. J. Bot. **11:** 558 572.

______. 1925. Persistence of plants in unglaciated areas of boreal America. Mem. Amer. Acad. Arts & Sci. **15:** 238 342.

______. 1929. Some relationships of the flora of the Northern Hemisphere. Proc. Int. Cong. Plant Sciences **2:** 1487 1507.

______. 1931. Specific segregations and identities in some floras of eastern North America and the Old World. Rhodora **33:** 25 63.

GADGIL, M., & W. BOSSERT. 1970. Life historical consequences of natural selection. Amer. Naturalist **104:** 1 24.

GADGIL, M. D., & O. T. SOLBRIG. 1972. The concept of r- and K- selection: evidence from wildflowers and some theoretical considerations. Amer. Naturalist **106:** 14 31.

GEIST, V. 1967. A consequence of togetherness. Nat. Hist. **76:** 24 31.

______. 1971. Mountain Sheep. University of Chicago Press, Chicago.

GLEASON, H. A. 1920. Some applications of the quadrat method. Bull. Torrey Bot. Club **47:** 21 33.

______. 1929. The significance of Raunkiaer's law of frequency. Ecology **10:** 406 408.

GOODLETT, J. C. 1954. Vegetation adjacent to the border of the Wisconsin drift in Potter County, Pennsylvania. Harvard Forest Bull. **25.** 93 pp.

GROSS, A. O. 1928. The Heath Hen. Boston Soc. Nat. Hist. **6:** 491 588.

HACK, J. T., & J. C. GOODLETT. 1960. Geomorphology and forest ecology of a mountain region in the central Appalachians. U. S. Geol. Surv. Prof. Pap. **347,** 64 pp.

HARDY, A. 1959. The open sea: its natural history. II Fish & Fisheries. Collins, London. 342 pp.

HARPER, J. L. 1969. The role of predation in vegetational diversity. Pp. 48 62 *In:* Diversity and Stability in Ecological Systems. Brookhaven Symp. in Biology **22.**

———. 1977. Population Biology of Plants. Academic Press. 892 pp.

———., & J. White. 1974. The demography of plants. Ann. Rev. Ecol. Syst. **5:** 419-463.

Hensley, M. M. & J. B. Cope. 1951. Further data on the removal and repopulation of the breeding birds in a spruce-fir forest community. Auk **68:** 483-493.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. Proc. Verbaux **20:** 1-228.

Horn, H. S. 1971. The adaptive geometry of trees. Princeton Univ. Press. 144 pp.

Huffaker, C. B. 1964. Fundamentals of biological weed control. Pp. 74-117 *In:* P. DeBach & E. I. Schlinger (Eds.), Biological Control of Insect Pests and Weeds. Chapman & Hall, London.

Hultén, E. 1937. Outline of the History of Arctic and Boreal Biota During the Quaternary Period. Bokförlags Aktiebolaget Thule, Stockholm.

Jain, S. K., & D. R. Marshall. 1967. Population studies in predominantly self-pollinating species. X. Variation in natural populations of *Avena fatua* and *A. barbata*. Amer. Naturalist **101:** 19-33.

Janzen, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution **21:** 620-637.

———. 1968. Host plants as islands in evolutionary and contemporary time. Amer. Naturalist **102:** 592-594.

———. 1969. Seedeaters versus seed size, number, toxicity and dispersal. Evolution **23:** 1-27.

———. 1970. Herbivores and the number of tree species in tropical forests. Amer. Naturalist **104:** 501-528.

———. 1971. *Cassia grandis* L. beans and their escape from predators: a study in tropical predator satiation. Ecology **52:** 964-979.

———. 1972. Escape in space of *Sterculia petala* seeds from the bug *Dysdercus fasciatus* in a Costa Rican deciduous forest. Ecology **53:** 350-361.

Kerner, A. von Marilaun. 1863. Das Pflanzenleben des Danauländes. The Plantlife of the Danube Basin. Translated by H. S. Conard. The background of plant ecology. State College Press, Ames, Iowa.

Kluyver, H. N. 1951. The population ecology of the great tit, *Parus m. major* L. Ardea **39:** 1-135.

———. 1966. Regulation of a bird population. Ostrich **38:** (Suppl. 6) 389-396.

———., & L. Tinbergen. 1953. Territory and the regulation of density in titmice. Archs. Neeerl. Zool. **10:** 265-289.

Krebs, J. R. 1971. Territory and breeding density in the great tit, *Parus major* L. Ecology **52:** 2-22.

Krukenberg, A. R., 1951. Intraspecific variability in the response of certain native plant species to serpentine soil. Amer. J. Bot. **38:** 408-419.

Lack, D. 1967. Interrelationships in breeding adaptations as shown by marine birds. Pp. 3-42 *In:* D. W. Snow (Ed.) Proceedings of the XIV International Ornithological Congress. Alden Press.

———. 1973. The number of species of hummingbirds in the West Indies. Evolution **27:** 326-337.

Lindroth, C. H. 1957. The faunal connections between Europe and North America. Almquist & Wiksell, Stockholm.

______. 1963. The faunal history of Newfoundland, illustrated by carabid beetles. Estomologiska Sallskapet, Opuscula Entomologica Suppl. **23:** 1-96.

Louis-Marie. 1944. The Ancylatheran *Calamagrostis* of eastern North America. Rhodora **46:** 290-291.

MacArthur, R. H. 1957. On the relative abundance of bird species. Proc. Nat. Acad. Sci. **43:** 293-295.

______. 1960. On the relative abundance of species. Amer. Naturalist **94:** 24-36.

______. & E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution **17:** 373-387.

______. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N. J.

MacKay, G. H. 1893. Observations on the breeding habits of *Larus atricilla* in Massachusetts. Auk **10:** 333-336.

Margalef, R. 1968. Perspectives in ecological theory. Univ. Chicago Press, Chicago. 111 pp.

Mayfield, H. 1960. The Kirtland's Warbler. Cranbrook Institute of Science, Mich.

Mayr, E. 1954. Change of genetic environment and evolution Pp. 157-180 *In:* J. Huxley, A. C. Hardy, & E. B. Ford (Eds.), Evolution as a Process. Allen & Unwin, London.

______. 1963. Animal species and evolution. Harvard University Press, Cambridge, Mass.

______. 1965. Avifauna: turnover on islands. Science **150:** 1587-1588.

Noble, G. K., & M. Wurm. 1943. The social behaviour of the Laughing Gull. Ann. N. Y. Acad. Sci. **45:** 179-200.

Norton, A. H. 1924. Notes on birds of the Knox County region. Maine Naturalist **4:** 35-39.

Odum, E. P. 1969. The strategy of ecosystem development. Science **164:** 262-270.

Paine, R. T. 1966. Food-web complexity and species diversity. Amer. Naturalist **100:** 65-75.

______., & R. L. Vadas. 1969. The effects of grazing by sea urchins *Strongylocentrotus* spp., on benthic algal populations. Limnol. & Oceanogr. **14:** 710-719.

Palmer, R. S. 1949. Maine Birds. Bull. Mus. Comp. Zool. Harv. **102.** 656 pp.

Phillips, E. A. 1959. Methods of vegetation study. Holt, Rinehart, & Winston, Inc. 107 pp.

Polunin, N. 1934-1935. The vegetation of Akpatok Island. J. Ecol. **22:** 337-395; **23:** 161-209.

______. 1960. Introduction to plant geography and some related sciences. McGraw-Hill, N. Y.

Preston, F. W. 1948. The commonness and rarity of species. Ecology **29:** 254-283.

______. 1962. The canonical distribution of commonness and rarity, Part I. Ecology **43:** 185-215.

______.1962. The canonical distribution of commonness and rarity, Part I. Ecology **43:** 185-215.

RAND, E. L., & J. H. REDFIELD. 1894. Flora of Mount Desert Island, Maine: a preliminary catalogue of the plants growing on Mount Desert and the adjacent islands. John Wilson & Sons, Cambridge. 286 pp.

RAUNKIAER, C. 1918. Récherches statistiques sur les formations végétales. Biol. Meddel. Kongel. Danske Videnske Selsk. **1:** 1–80.

———. 1934. The life forms of plants and statistical plant geography. Clarendon Press, Oxford.

RAUP, H. M. 1951. Vegetation and Cryoplanation. Ohio J. Sci. **51**(3): 105–116.

RICKLEFS, R. E., & G. W. COX. 1972. Taxon cycles in the West Indian avifauna. Amer. Naturalist **106:** 195–219.

ROLLINS, R. C. 1963. The evolution and systematics of *Leavenworthia* (Cruciferae). Contr. Gray Herb. **192:** 1–98.

SELANDER, R. K., W. G. HUNT, & S. Y. YANG. 1969. Protein polymorphism and genic heterozygosity in two European subspecies of the house mouse. Evolution **23:** 379–390.

SELANDER, R. K., & S. Y. YANG. 1969. Protein polymorphism and genic heterozygosity in a wild population of the house mouse (*Mus musculus*). Genetics **63:** 653–667.

———, ———, R. C. LEWONTIN, & W. E. JOHNSON. 1970. Genic variation in the horshoe crab (*Limulus polyphemus*), a phylogenetic "relic". Evolution **24:** 402–414.

SIGAFOOS, R. S. 1952. Frost action as a primary physical factor in tundra plant communities. Ecology **33**(4): 480–487.

SIMPSON, G. G. 1952. Probabilities of dispersal in geologic time. Bull. Amer. Mus. Nat. Hist. **99:** 163–176.

———. 1953. The major features of evolution. Columbia University Press, N.Y.

SOLBRIG, O. T. 1972. Breeding system and genetic variation in *Leavenworthia*. Evolution **26:** 155–160.

———, & D. J. SOLBRIG. 1979. Introduction to population biology. Addison-Wesley Publ. Co. 468 pp.

STEBBINS, G. L. 1942. The genetic approach to problems of rare and endemic species. Madroño **6:** 241–272.

STEEVES, T. A., & I. M. SUSSEX. 1972. Patterns in plant development. Prentice Hall. 302 pp.

STEWART, R. E., & J. W. ALDRICH. 1951. Removal and repopulation of breeding birds in a spruce-fir forest community. Auk **68:** 471–482.

STOUT, B. B. 1952. Species distribution and soils in the Harvard Forest. Bull. Harvard Forest No. **24.**

TERBORGH, J. 1973. On the notion of favorableness in plant ecology. Amer. Naturalist **107:** 481–499.

THODAY, J. M., & T. B. BOAM. 1959. Effects of disruptive selection: III. Polymorphism and divergence without isolation. Heredity **13:** 205–218.

TORREY, J. G. 1967. Development in flowering plants. MacMillan. 184 pp.

TRIVERS, R. L. 1971. The evolution of reciprocal altruism. Quart. Rev. Biol. **46:** 35–37.

TURESSON, G. 1925. The plant species in relation to the habitat and climate. Hereditas **6:** 147–236.

Uranov, A. A., & O. V. Smirnova. 1969. Classification and basic features of the development of perennial plant populations. Bull. Moscow Soc. Natur. **74:** 119–134 (in Russian)

Uranov, A. A., V. M. Grigorieva, V. N. Egorova, I. M. Ermakova, & A. R. Matveev. 1970. The variability and dynamics of age spectra in some meadow plants. Pp. 194–214 *In:* Theoretical Problems of Phytocenology and Biogenocenology (to the 90th birthday of V. N. Sukachev). Nauk Moscow (in Russian).

Wallace, A. R. 1869. The Malay Archipelago, 2 Vols. Macmillan, London.

Watson, A. 1967. Territory and population regulation in the Red Grouse. Nature **215:** 1274–1275.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biol. Rev. **42:** 207–264.

Willis, J. C. 1922. Age and area: a study in geographical distribution and origin of species, Cambridge, England.

Woodwell, G. M. 1970. Effects of pollution on the structure and physiology of ecosystems. Science **168:** 429–433.

Wright, S. 1931. Evolution in Mendelian populations. Genetics **16:** 97–159.

______. 1938. The distribution of gene frequencies under irreversible mutation. Proc. Nat. Acad. Sci. **24:** 253–259.

______. 1940. The statistical consequences of Mendelian heredity in relation to speciation. Pp. 161–183 *In:* J. Huxley (Ed.) The New Systematics. Clarendon Press, Oxford.

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# RARE PLANT MANAGEMENT — AFTER PRESERVATION WHAT?

SUSAN POWER BRATTON AND PETER S. WHITE

Conservation of rare species is often thought of primarily as a battle to protect the lands on which they occur. After snatching a bog from highway builders, halting a power company dam, or wrestling a tract of virgin timber from a logging company, everyone pats himself on the back for a job well done. Bringing critical habitat under some type of legal protection is, of course, the first step in insuring the survival of rare species (Meijer, 1973; Drury, 1974; Smithsonian Institution, 1975; Nature Conservancy, 1975; Smith, 1976). The job of preservation and ecologically sound population management does not stop, however, after the purchase papers are signed and a property is transferred to a conservation group or a government agency to administer for "all eternity." Human activities may still threaten species, and disturbances and ecological changes continue, even in protected areas.

Some of these changes may be related to preserve size and geographical relations (Hooper, 1971; Willis, 1974; Terborgh, 1974; Diamond, 1975), others to environmental change, natural disturbance, or community processes such as succession (Stone, 1965; Watt, 1971; Westhoff, 1971; Owen, 1972; Wright, 1974; Dolan et al., 1978; White, in press). No preserve is totally free of human influence (Owen, 1972; Miller & Botkin, 1974). People are attracted to preserves, in part due to their scarcity in the developed landscape. There is currently a worldwide trend for visitor pressure to increase, e.g., in Europe (Brotherton, 1975; Dory, 1977; Slater & Agnew, 1977), Australia (Boden & Ovington, 1973), Japan (Simmons, 1973), and the United States.

Giving a natural area legal protection does not guarantee the perpetuation of the species present nor does it solve many of the philosophical issues involved in endangered species management. The purpose of this paper is to discuss some of the major issues involved in decision making for rare plant management in a reserve setting. Most of the examples of botanical management and the associated problems will be taken from Great Smoky Mountains National Park (GRSM).

## WHY PRESERVATION?

The Great Smoky Mountains National Park has relatively high species diversity for an eastern forest area. About 1500 vascular species (including exotics) have been recorded from its 209,000 hectares (Hoffman, 1962). Twenty-one vascular species have been proposed for national status as endangered or threatened (Smithsonian Institution, 1975) and one fungus has also been proposed for national status as endangered (Peterson, 1974). One hundred species found in GRSM are considered endangered or threatened in North Carolina (Cooper et al, 1977) and 79 are considered endangered or threatened in Tennessee (Committee for Tennessee Rare Plants, 1978) with 29 species appearing on both state lists (herafter referred to as the state lists). The park flora includes Appalachian endemics, species with disjunct distributions, species at the edge of their range and species with very narrow habitat preferences.

Looking at the history of GRSM, however, one realizes that the inclusion of some of the rarer species was at least partially coincidental and many of the populations were not located until long after the boundaries of the area had been determined. Although "the unexampled variety of trees, shrubs and plants . . ." was a primary reason for choosing the Smokies location for a park (Campbell, 1960, p. 29), the protection of the tracts of virgin timber and the preservation of the rugged mountain scenery were probably the most important goals of early park advocates.

Parks and reserves are established for a variety of reasons, or become multiple purpose as their use increases.
Typical motives for protecting land include:

1) Preserving scenery
2) Preserving unusual ecosystems
3) Preserving representative ecosystems
4) Preserving pristine ecosystems
5) Preserving rare species
6) Preserving geologic formations
7) Preserving historic or archeological sites
8) Providing for recreational use
9) Providing for educational use
10) Providing for research use

Although other managerial objectives are not necessarily in conflict with rare plant management, they frequently overshadow it.

Also, the initial thrust of a management program is usually determined by the qualities of a reserve area which are conceptualized as most important. If the presence of a population of a rare plant species is not as "important" as some other element, it may not be considered when policies are established.

Even preserves which are established for primarily botanical reasons will probably be visited by a wide variety of people. One might expect:

1) Biologists, plant or animal collectors, (whether informal or research oriented)
2) Other scientists such as geologists, archeologists
3) Field trips of university, school, or nature groups
4) Recreation or wilderness seekers
5) Gardeners, fishermen, and hunters, with or without permission

and, if the area is heavily developed for visitors,

6) Sightseers and organized tour groups.

Any of these users may impact an area and all of them influence its management, whether directly or through political action. In addition, outside groups not directly using a preserve may also have political influence (e.g., hunting clubs which view GRSM as an important reservoir of wild boar for lands adjacent to the park which are open to hunting). The location of a preserve near large centers of population means that visitor pressure may be high. GRSM, for instance, experiences over nine million visitor days annually (records in GRSM files).

## THE GREATEST THREAT

Man is still present in a preserve system and exerts his influence both directly and indirectly. Despite legal protection, the greatest threat to rare plant populations in most preserve settings is anthropogenic interference. The reserve is a microcosm which is still potentially subject to disturbances which endanger plant species elsewhere. In the case of GRSM, one mandate for the park was "to preserve and protect the native flora and fauna" but another was "to provide for the enjoyment" of the American people (U.S. Department of the Interior, National Park Service, 1970). Providing for public use usually means developments such as roads, trails, campgrounds, and museums, all of which have direct impacts on the native flora.

Initial land acquisition for GRSM began in 1927 and status as a national park was finalized in 1940. Despite over forty years as a preserve and much scientific research, a major lesson from the history of the park is that there is still a need to focus management goals, set policy, and carry out basic research. Below we will discuss problems experienced in the last 50 years at GRSM. For purposes of discussion we have divided human impacts into direct (discussed first) and indirect.

## Direct Impacts

When the GRSM was first established very little attention was paid to the potential effects of development. Early advocates of the park promised to have a road built between Tennessee and North Carolina and thus gained the backing of the local citizenry. The Newfound Gap road was eventually struck across the main ridge, through virgin forest and a high elevation "beech gap". At that time, Environmental Impact Statements were unheard of, and no surveys of natural resources were required prior to construction. It is now known that the road disturbed the type locality of a rare snail and probably removed several populations of rare plants as well. Was the Newfound Gap road a mistake, or was it a logical trade made in the preservation and use of an extremely important natural area?

The promise of some kind of development or access to the public is a continuing issue in most national parks and in many state or other agency properties. Groups fighting to protect various areas frequently propose nature centers, trail systems, scenic roads, and other recreational developments, either because they believe they are necessary or because they will attract public support. The GRSM, over 40 years after its official dedication, is still having difficulties with development as a threat to native species. Despite a wilderness proposal for the park, road construction is a continuing issue with strong lobbies, both for and against, in several communities near the park.

Throughout the history of the park quite a number of roads have been proposed both by various interest groups and government planning teams. Until recently, no botanical survey was completed before a proposal was made and routes were chosen for scenic, engineering, or economic reasons. A typical conflict concerns an agreement made on acquiring an additional 20,000 ha from the Tennessee Valley Authority in 1944. A TVA reservoir had flooded a county road; the park agreed to build a road along the shore of the

Fontana reservoir on its newly acquired TVA land. Since 1944, two alternative road routes to the one along Fontana have been suggested, one supposedly better for traffic flow and tourist use and the other supposedly causing less environmental damage. After 25 years, the matter is still unsettled. There have been numerous public hearings and much conflict between different interest groups.

Although the original route has never been ecologically surveyed, the other two proposed are now known to present threats to rare plants (Baron & Mathews, 1977). Ironically, the route best accepted by groups interested in protection of wildnerness probably presents the greater danger to unique botanical resources. Within 100 m of the most likely right of way is the type locality and one of the two known populations of *Gleocantharellus purpurascens,* a fungus which has been proposed for national status as endangered (Peterson, 1974). This route also traverses several wild flower areas and unlogged white oak stands (Baron & Mathews, 1977).

Most politicians probably prefer mushrooms with beef and gravy, and may not be very pleased when a small purple fungus with no common name thwarts a possible settlement of an old squabble over a road likely to be economically advantageous to local business. The fungus, however, has as yet no special legal status. The park, at the time the issue first arose, did not have any detailed policy on maintaining population levels of individual plant species. It may seem silly to have to continue to protect the native flora from development once it is inside a national park, but the multi-purpose use of the park, lack of information, and shifting managerial directions have all led to conflicts over where developments should be placed.

Smaller preserves and wilderness areas may never be damaged by heavy construction, but less intensive development than road building can also cause difficulties in all types of areas. For instance, the presence of a lodge and a backcountry shelter, accompanied by high day use, has probably impacted a number of rare species on Mt. LeConte in GRSM. Of particular concern are *Calamagrostis cainii,* which is endemic to the park, and a population of *Geum radiatum,* which is nominated as nationally endangered (Nichols, 1977; Bratton & Whittaker, 1977). A recent survey of human impacts in eight heavily used backcountry campsites in GRSM found that four of the sites had plants on the state lists growing in or near them, including *Glyceria nubigena* (also of national concern), *Cacalia rugelia, Stachys clingmanii, Streptopus roseus, Clintonia borealis* and *Chrysoplenium americanum* (Linda Stromberg & Susan Bratton, unpublished data).

In some cases, human use, without any development, affects plant populations. In GRSM, visitors poach plants along roadsides and nature trails, taking those with showy flowers, such as *Lilium* spp. Commercial diggers illegally impact *Panax quinquefolium*, and possible other species having medicinal value. The use of *Panax quinquefolium* by the local population has a long tradition — both medicinally and as a source of cash in an economically depressed region. The taking of ramps (*Allium tricoccum*) leaves and roots is also a traditional part of regional culture and, unlike collection of *Panax* and ornamentals, is currently permitted in GRSM. The use of these plants underscores the kinds of pressures a park manager must be aware of in the local commmunities. Current NPS policy allows the taking of fruits such as mushrooms, blueberries, and acorns for personal (non-commercial) use and allows the gathering of dead wood and down wood for burning in campsites within the park.

In some preserves, sensitive areas such as dunes, bogs or alpine meadows may become so heavily used that trails or boardwalks are required. Technical climbers are able to disturb rock outcrops unavailable to the casual tourist. Even use by researchers and school groups stresses sites, and some rare plant populations are easily over-collected or trampled. Visitor loads in established areas tend to increase through time, and a preserve manager may find both developed facilities and undeveloped areas are becoming overused and deteriorating. The question recurs and recurs — how much human use and under what circumstances?

Recreation and public access, even for educational purposes, are in direct conflict in most parks with preservation of systems whose value and rarity stem from their being relatively man-free (Stone, 1965; Boden & Ovington, 1973; Simmons, 1973; Brotherton, 1975). This conflict is often explicitly decreed in the founding legislation of many parks (*e.g.* GRSM).

## Indirect Impact

Unfortunately, not all human threats are due to direct impact and cannot be controlled by limiting the numbers of people in a preserve. Some impacts, in fact, are rather subtle and may not be immediately thought of as human in origin. Foremost among these "indirect impacts" in GRSM is the introduction of exotic species. The demise of the *Abies fraseri* by the exotic balsam wooly aphid, for instance, was not anticipated by the people instrumental in securing the virgin spruce-fir forests of the Smokies for the park, and began just after the disastrous chestnut blight had eliminated American chestnut as a dominant tree in the park.

One of the primary threats to rare species in GRSM at present is the European wild boar (*Sus scrofa*). Originally introduced into North Carolina in 1912 as a game animal, the species probably entered the park in the late 1940's. Park records indicate the species was not recognized as present until 1951. The hog population was probably well entrenched when control officially started in 1959 (Bratton, 1975, 1977).

Not only was the hog invasion unexpected, and action delayed until damage was noticeable in highly visible areas such as the grassy balds, but no serious attempts were made to determine the impact of the wild boar on the native flora until the 1970's. Wild boar are thought to eat a number of species on the state lists, including *Stachys clingmanii, Lilium canadense* and *Lilium philadelphicum*. Other species may be eaten or disturbed by rooting activity, including *Disporum maculatum, Streptopus roseus* and *Phacelia purshii* (Bratton, 1977; Bratton, 1979). Hogs severely disturbed high elevation wild flower areas, grassy balds, and low elevation successional areas near old homesites (Bratton, 1974, 1975; Howe & Bratton, 1976). The National Park Service has, as a policy, controlled exotic species, but the effect of hogs on rare plant species was not investigated until approximately twenty-five years after the hogs entered the park.

Besides the introduction of exotic species, a variety of other human impacts are likely to originate outside of a preserve and a manager may have no control over their source. Air pollution is a widespread concern, including the direct effects of agents such as ozone, sulfur, and heavy metals, and possibility of climatic effects, such as a general warming (Johnson & Bratton, 1978). In GRSM, as in some areas of New England, there is evidence that lead deposition is greater at high elevations (Wiersma et al., 1978; Schlesinger et al., 1974), and therefore more likely to affect rarer species.

Unfortunately, very little is known about the tolerances of rare plant species for pollutants. High ozone levels, for instance, are presently damaging and sometimes killing white pine (*Pinus stro-*

*bus*) along the Blue Ridge Parkway (John Skelly, Virginia Polytechnic Institute, pers. comm.). The effects of these ozone levels on *Lilium grayii* are, by contrast, totally unknown. Pesticide traces have been found even in remote GRSM watersheds. Their source is presumably agricultural dust transported by atmospheric circulation. GRSM is downwind from both midwestern agricultural centers and local farmland.

An equally insidious, but often more dramatic, anthropogenic impact is a change in ecosystem structure due to interference with the hydrologic regime or geologic substrate originating either inside or outside the preserve. Canal building and drainage outside the Everglades National Park is modifying the hydrology of 500,000 ha; dredging near Gulf Islands National Seashore is influencing patterns of sand deposition. Rather than just losing a species or two to this activity, Petit Bois Island itself may become extinct (Shabica et al., 1978). A small preserve, such as a marsh or bog which does not control its own watershed, is especially vulnerable to this sort of disturbance.

Accidental or purposeful manipulation of populations of native animal species may in turn affect plant populations, especially through overgrazing. In the case of large predators, migratory species, or game animals, the preserve manager, again, may not have complete control over the agent of disturbance. These animals are not restricted by legislated reserve boundaries. Throughout the eastern United States, the white-tailed deer is liable to become a problem species, and rodents like rabbit and beaver may also "overpopulate" an area.

In GRSM, overbrowse by deer is affecting the major limestone area in the park, Cades Cove. The extirpation of the wolf and near extirpation of the mountain lion may be related to an increase in the deer population, but the primary factor appears to be the maintenance of part of Cades Cove under an agricultural regime (Bratton et al., in prep.). In areas like the Alleghenies or Adirondacks, logging, which provides browse, and the states' attempts to maintain a "huntable" deer herd, may result in heavy browsing in adjacent preserves, such as Hearts Content, Pennsylvania, which may themselves be protected from logging.

Ironically, the conflict in GRSM is between resources within the park: Cades Cove not only contains sinkholes, swamps and limestone outcrops which support rare plants and unusual communities, but also contains dozens of historic buildings and archeological sites. The whole valley below the 2000 foot contour is now included in the National Register of Historic Places as an historic district, and is managed to retain the vistas provided by the open fields. Deer and other wildlife flourish with an abundance of both food, such as hay, and cover. Even though historical management is not intended to influence the surrounding natural area or to disturb the non-cultivated portion of the historic district, a number of rare plant species on the state lists could be affected by the deer and by manipulation of drainage. *Agrostis borealis, Campanula aparanoides,* and *Carex trisperma,* occur or have occurred in the Cove. It is only within the past two years that the impacts of agricultural management on native species have been investigated, and that area has been surveyed for rare species. The situation in Cades Cove is not only a case of weighing the value of certain resources, historic versus botanical, but also a case where the management of one area affects the adjoining systems. The large deer herd around Cades Cove creates browse pressure in surrounding natural areas, up to 1 km away from the Cove itself (Bratton, in press). Human preferences are important here, as is the all too frequently held idea that an historic area does not require natural management and vice versa.

As many elements in a community are interdependent, removal of animal or plant species can be as undesirable as over population. In GRSM, beaver were extirpated before the turn of the century (Lindzey & Lindzey, 1970). Marsh and pond plants are now uncommon in the Park, and the reintroduction of beaver could possibly result in more wet habitat in the form of beaver meadows. Although beaver were previously present, managerial action has been postponed until the consequences of encouraging the species (which may be reinvading on its own from animals stocked in western North Carolina) can be determined. Possible problems include: flooding of roads, invasion of properties near the park, overpopulation and damage to big tree stands. No one knows, of course, if any plant species originally disappeared with the beaver.

In summary, then, human impacts may still damage or destroy plant populations in a preserve, and some of these impacts may be unexpected. Some changes may be initiated years after a preserve is established and may have their source far outside of the preserve itself.

## NATURAL MANAGEMENT

Preserves can never be totally free of human influence, whether direct or indirect (Owen, 1972). In addition preserves experience dynamics initiated by natural factors and have special problems associated with their size and proximity to other natural landscapes. The first step after legal protection is inventory and monitoring (Dawkins, 1971; Miller & Botkin, 1974; Johnson & Bratton, 1978). A strictly hands-off preservationist attitude is, in most cases, no longer possible; active management, if only to regulate visitation, will usually be necessary (Stone, 1965; Owen, 1972). This introduces a paradox: management policies, designed to preserve resources, also impact natural systems, change the environment of a species, its population structure, and genetic constitution (Berry, 1971). We turn next to a discussion of management goals, problems, and dilemmas.

One of the first questions which the manager has to answer is at what "genetic level" should we manage — species, subspecies, variety, deme, hybrid, or local population? The national and most state lists of endangered or threatened vascular plants emphasize species but include rare subspecies, varieties, and even some persistent hybrids (Mathews, 1977). Forms and "chance" hybrids are usually not considered.

Preserves may also have unique populations. *Geum radiatum* is not only nationally endangered, but the population on Mt. LeConte in GRSM has a number of minor morphological differences from populations further to the north, and is now probably completely disjunct as a reproductive unit (Robert Farmer, Tennessee Valley Authority, pers. comm.). How important is it to maintain the integrity of such a population?

A related question concerns the geographical significance of rare species. Many of the plants on the state lists are abundant in GRSM. Their rarity stems from the fact that they are found within North Carolina and Tennessee only within GRSM or the adjacent counties. On the other hand, some of the rarest plants in the park are abundant in other parts of the two states, and hence are not listed (e.g., limestone plants found commonly westward in Tennessee and low elevation plants found generally away from the mountains). Should we manage for protection of species whose significance and endangerment are of local import only? Where should the line be drawn?

In cases where populations have been severely depleted, the temptation is always present to transplant individuals from other areas. Under what circumstances should this be done? An example from the GRSM is the case of the eastern mountain lion. Lion sightings are becoming increasingly frequent in the Smokies and Blue Ridge (Bratton, 1978). Although it is thought that this might be a recovery of the eastern mountain lion population, western mountain lions are known to have escaped in the east, and the status of the present population is not known (Culbertson, 1977). Would the introduction of lions from stock outside the Appalachians be appropriate? How important is the "purity" of the gene pool (e.g., native eastern versus western mountain lions) versus the ecological role of the species — in this case a top carnivore? The GRSM is currently discussing the possibility of reintroducing extirpated animals such as river otter.

Most endangered species lists ignore hybrids and odd forms or varieties, yet these may be the basic building blocks in the process of evolution. Should these be given special protection in a reserve? An example from GRSM is the hybrid swarm of azaleas on Gregory Bald. A mixture of at least three species, the variety of flower color is unknown from any other locality. Since the population is not a species, it is not on any endangered list. It is, however, a completely unique resource. As will be mentioned later, the grassy balds were previously disturbed, and may require artificial management to maintain them —— should this very aesthetically appealing population of hybrids be protected by the park?

The problem of "genetic level" is related to the more general problem of management for "species" or some other genetic unit, versus managment for evolutionary or ecological "processes" (Drury, 1974; Dolan et al, 1978). This brings us from the static view of species as a biological entity at a fixed point in time to the concept of genetic change which includes evolution and extinction of various varieties, the appearance and disappearance of mutants and hybrids, and ultimately the process of speciation itself. The time scale for "natural" evolutionary change is rather long compared to that for "man-caused" changes in species genetics and distribution, but both may operate simultaneously.

Perhaps the most difficult process to accept or manage, is that of "natural extinction". Preserves are in many ways islands, and through time some gain and loss of species is to be expected

(Hooper, 1971; Willis, 1974; Terborgh, 1974; Diamond, 1975). Unfortunately, very little is known about rates of extinction for rare plant species or about the role of minor species in the communities in which they occur.

In GRSM a number of species on the state lists have been collected from one or two localities and a number of other native species have been collected at a single site. Some of these populations could be easily extingiushed by a fire, landslide or by competition with other native species. *Prunus virginiana* is known from one cove, for instance, and *Woodwardia virginiana* is found only in a poorly drained sinkhole. Some species may be relicts of glacial times and their habitats may now be "naturally" disappearing. A specimen of *Linnaea borealis* was collected in "the mountains of Sevier County," Tennessee in 1891. This collection was probably made in GRSM but *L. borealis* has not been seen since. Is this a case of recent natural extinction — related to climatic shifts? Should a manager in a preserve like GRSM accept a reduction in such relict populations?

Similarly, successional habitats are critical for some species and either a long-term trend which is slowly modifying a successional process or a temporary lack of a particular disturbed community, such as intensively burned areas, may help to eliminate a species from a preserve. The question of the disappearance of some communities, such as bogs in glacial deposits, is problematic —— the habitat may be undergoing cyclical changes rather than directional succession (Drury & Nisbet, 1973). Either may naturally modify species composition.

The GRSM has limestone areas where a number of sinkholes are slowly filling with sediment. These sites are of varying sizes and depths, and several have their own distinctive communities, or are the only known site for a rare plant species. Although sinkhole formation is an ongoing geologic process, the collapse of a new area would not necessarily provide habitat like that of other existing sites. Succession in one area could eliminate a species, at least within the park.

Successional habitats could also be substitutes for late glacial alpine or wet environments, thus changes in climate and in the successional management of a preserve could be synergistic, encouraging either extinction or population expansion of a rare species. Very little is known about the biology of relict or disjunct species, and some may have already "outlived" their habitat, whereas others may be able to perpetuate themselves indefinitely under the appropriate conditions.

In the face of apparent long-term climatic, geologic, or successional changes, should a manager try to maintain species or communities that are naturally disappearing or changing in geographic distribution? Should a manager try to reestablish a species eliminated by a natural catastrophic event? Should a manger try to provide habitat for a species whose range is swiftly decreasing? Should a manager maintain disturbance-dependent species by artificially interrupting succession (Green, 1972; Owen, 1972; Smith, 1976)?

Related to the question of natural loss of successional communities is the present role of natural disturbances in a preserve. Some catastrophic events, such as landslides, may be difficult to prevent; therefore managerial options concerning them are few. Others, such as fire, flooding, and herbivore utilization may be at least partially controlled by a preserve manager. The attempt to control or suppress natural disturbances has often led to detrimental and unforeseen changes, including enhanced damage by subsequent natural disturbance (Brown, 1961; Mutch, 1970; Schroeder et al., 1976; Johnson et al., 1976).

In GRSM, fires were much more frequent in pre-park days than at present (Mark Harmon, unpublished data; Lindsay & Bratton, in press), and may have influenced the distribution of a number of rare species including *Carex misera* and *Gillenia stipulata* (Bratton, 1978). The present park policy is to suppress all fires including those caused by lightning. The manager must now ask not only what is the natural fire regime for the park, but also what is the most manageable fire regime for the park?

In developing a "natural" fire management program the first temptation is to declare lightning-caused fires "good and acceptable" and man-caused fires "bad and unacceptable". The second temptation is to suggest controlled burning to select for fire-dependent species or to improve habitat for rare plants and wildlife. The matter of "naturalness" or "historic authenticity" is not at all clear in GRSM, however. The settlers burned extensively (Lindsay & Bratton, in press) and an earlier timber cruise (1936) of the park indicates that many of the stands sampled had been burned at least once during the previous 20 to 30 years (Frank Miller, data in GRSM archives). To complicate matters, the Indians certainly burned when clearing for agriculture and may have burned when hunting. Escaped campfires were also likely. The lower elevations then have probably been subject to some man-caused fire for several thousand years, more than enough time to influence community structure and select for pyric elements in the flora. A "lightning fire only" policy is not necessarily the equivalent of any conditions that have existed in post glacial times, and controlled burning could, under many circumstances, also be a new variant in terms of evolutionary pressure. Would a burning regime that had no historic precedent be appropriate for maintaining a rare plant population? Controlled burning is often aimed at reducing the likelihood of a conflagration rather than allowing for fires with a variety of intensities. Therefore the burning policy which is usually safest in terms of property damage and personal injury may not be helpful for maintaining some rare plant populations unless it is applied under special conditions.

In many instances, the decisions presently being made about disturbance management are based on preconceptions of naturalness or idealized views of wilderness. The population ecology and genetics of the rarer disturbance-dependent species is often not well understood. In the case of a plant like *Glyceria nubigena* which now grows on grassy balds and burn scars from logging fires, around parking areas and highly disturbed campsites, as well as in blowdowns and small canopy openings, the manager needs to know where the species was found originally and what conditions maintained the populations in the past.

Disturbance management is problematic even if the disturbance is recent or clearly anthropogenic. The grassy balds of GRSM were once cleared and intensively grazed by livestock (Lindsay and Bratton, 1979). Since coming under the protection of the park, woody plant invasion has slowly reduced the grass sward and thus the open successional habitat. Natural phenomena do not appear to be creating new grassy balds in the Park and the communities could well be relicts of earlier agricultural practices (Lindsay & Bratton, 1979). Although the bald flora was maintained and influenced by settler activities, botanists have collected several rare species including *Glyceria nubigena, Prenanthes roanensis, Carex misera,* and *Polygonum cilinode* on the balds or at their edges (Lindsay & Bratton, 1979; Bratton 1979). The hybrid azaleas of Gregory Bald could predate the sheep and cattle grazing or their presence could be related to disturbances caused by agriculture. The grassy bald, like some of the grasslands and heathlands of Great Britain (Duffey et al., 1974), might be termed an "historic plant community", a grouping created at some point in time by a complex of factors no longer present. Does the presence of rare plant species warrant the continued anthropogenic disturbance of the areas, or should natural succession be permitted to proceed? Should unusual or rare "historic" plant communities be maintained inside a reserve or natural area? People have long been important in the state of European vegetation; many preserves there are managed to maintain communities that are anthropogenic in origin (Wells, 1969; Haber, 1973).

Populations of some rare disturbance-dependent species can potentially be increased by creating bands of successional vegetation around developments like parking areas, by raising plants in a greenhouse and transplanting them, or by modifying mowing, burning, or clearing schedules. Is it desirable to increase a population by artificial means or to move it to an "unnatural habitat"? What effect will human interference with ecological and evolutionary processes have on a species? Will we influence its evolution (Berry, 1971)?

The same types of questions follow if managing for aesthetics is a major goal. Is clearing a grassy bald to allow for better vistas of surrounding mountains a practice encouraging a weedy flora? Is clearing the oak saplings away from the hybrid azaleas on Gregory Bald creating an azalea garden?

## SHOULD A PRESERVE BE AN ARK?

Ofttimes, like Noah, we try to load a selection of everything into a safe place and float above the flood of mankind's mistakes. The ark philosophy has started and helped protect many preserves but it can present some difficult managerial decisions.

One dilemma concerns the transplantation or reintroduction of endangered species from other locales (Wayre, 1969; Rawes & Welch, 1972; Drury, 1974; Thompson, 1974, 1976). This has rarely been approached in botanical management, but suppose a bog plant were threatened with extinction because its habitat was being drained; would it be better to move it to a protected bog elsewhere or to a botanical garden? An animal example, which illustrates the complexities of this issue, is a recent informal suggestion that a pair of red wolves be placed on Horn Island in Gulf Islands National Seashore. No one may ever be certain if red wolves were on Horn in the past, so the introduction could be "unnatural". On the other hand, relatively undisturbed and protected coastal habitat is hard to find today. Further, Horn Island has two exotic species, nutria and feral hogs, that have impacted the island's flora and need to be controlled. What is more important, getting the wolves out of the Takoma Zoo, or keeping the island fauna to its historically certain elements?

A second dilemma concerns managing for maximum possible species diversity. This would be an easy issue if succession weren't such an important element in most reserves. In GRSM, the changes occurring in former agricultural areas may well eliminate species from the park. Since the park is bordered by farms, housing developments, and logged forests, most new elements in the flora are likely to be adventitious species, invading along the roads. Is the total species count in the park of any importance? Is it worth preserving some examples of historic communities to maximize the number of habitats represented in the park?

Sometimes new species (usually Eurasian exotics) once added are difficult to control or exclude. Even a species which disturbs the native elements of the biota may have its fan club, and public pressure can favor exotics such as wild horses or wild boar. Introduced species may be "ecological equivalents" of species extirpated in the late Pleistocene. Should the manager accept such species and let "nature seek a new balance"? If complete eradication isn't possible, should partial control be initiated (which makes the manager an integral part of the ecosystem)?

## THROUGH A GLASS DARKLY

The flora of North America has been profoundly influenced by two major phenomena in the last few thousand years: the coming and going of the glaciers and the arrival of man. The key to managing rare species in a preserve setting is not just understanding ecological and evolutionary processes, but also understanding our role in them.

Administrative policy may, like a great glacier slowly advancing and receding, change through time and the magnitude of its impacts may vary (Dory, 1977). Managerial systems evolve, strengthen, and decay as a function of public interest, financial support, public pressure on the resource, fashions in our perception of the natural world, chance variations in staffing, and the increment of changes in the ecosystems themselves. The best example of this type of managerial history is the continual change in attitude toward the policy on the role of fire in our national parks and forests. A typical trend might be from uncontrolled fires on slash, to complete fire suppression, to controlled burning, to some allowance for natural fire, and then possibly even a return to controlled burning. In each case, cost-benefit, manpower, the physical resources of the agency, scientific information, and public opinion will all have been considered, at least informally.

The structuring of policy on rare and endangered plants is likely to go through similar processes, and it is well to remember that there may be no greater threat to an endangered species than an unsympathetic bureaucrat or politician. The very fact that so little is known about the biology of most rare plants indicates that the opinions of the scientific community are likely to change through time, and that some mangerial experiments may be conducted on an inadequate data base or with insufficient understanding of ecological processes, and are therefore likely to fail. The need in a preserve like GRSM is to establish management which is strong enough and directed enough to offer the individual species and the associated ecosystems and ecosystem processes the best protection possible and yet is flexible enough to evolve with an increased knowledge of the biology of the systems.

On the other hand, we need to realize that the academic tendency towards infinite data collection is a severe burden to management, and that administrators will frequently use "lack of information" as an excuse to do nothing, when a positive management alternative already exists. The ultimate managerial program for rare plants must have policy safeguards that prevent the program from slowing down, being dissolved, or becoming too much a function of public pressure, administrative convenience, or mere managerial opinion (Dory, 1977). Research and management action need to be balanced and coordinated with each other.

Sometimes managers have the feeling that non-interference with the ecosystem is the best and most "natural" policy. Frequently, this is true (Stone, 1965; Owen 1972), but the hand of man is everywhere today — there are traces of pesticides in even the most inaccessible streams in GRSM. There is no way to lock up a preserve absolutely to keep man out. We should, at the very least, be monitoring our own effects (Dawkins, 1971; Miller & Botkin, 1974; Johnson & Bratton, 1978), and if something needs to be done to protect a rare plant in a preserve, there is no reason not to take action, even if it is only deciding what we need to know. Foremost among research needs are population biology of rare plants (Jeffrey, 1971; Dring & Frost, 1971; Namkoong & Roberds, 1974; Massey & Whitson, 1977), and ecology of natural disturbances and community dynamics (Watt, 1971; Wright, 1974; Franz & Bazzaz, 1977; Dolan et al., 1978; White, 1979).

## ESTABLISHING A DIRECTION

In the concluding section of this paper, we would like to establish a direction, show how rare plant management might be instituted in a preserve, and suggest tentative answers (relative to GRSM) to some of the questions we have proposed. Each preserve has its own problems, of course, and each has its own mandates and reasons for being, but the basic procedures for developing managerial programs are often rather similar.

The following, using GRSM as an example, is a typical sequence for establishing a program:

*Step One:* **Establishing a basic policy.** Even before a data base is accumulated, certain policy decisions have to be made. In GRSM original policy was "to protect the native flora and fauna", thus excluding exotic plantings, etc. A new preserve might establish a policy that no developments be constructed before a resource inventory of a set standard was completed, or that virgin forest areas be excluded from all types of controllable anthropogenic disturbance. Policy on acquiring a data base, and on establishing managerial flow charts and decision making structures is usually an immediate problem. Most preserves should have as an initial policy, complete protection of rare plant species and the construction of an inventory of their populations and locations. It is important to establish some policy on rare species as soon as possible.

*Step Two:* **Inventory and basic data collection.** In GRSM, the first inventory effort, conducted largely in the 1930's, consisted of developing species lists, accumulating vouchers, conducting a timber cruise and drawing a vegetation map. After this initial effort, the interest in "inventory" declined and the records were not consistently updated. The present approach in GRSM is aimed more at monitoring than at simple listing of species occurrences, and is also intended to allow for and encourage continual updating.

The vascular species list for the park has been computerized and each species has its own six letter code. Additional information such as phenology, height class, and status in the park is being added for each species and may eventually be included for varieties. The two main herbarium collections for the park, one in GRSM, and one at the University of Tennessee, Knoxville, are presently being computerized also. The computer records include collector, date, forest type, Universal Transmercador coordinates, etc. The information can be sorted by species, county, watershed, collector, and so forth. This permits quick construction of floristic lists for specific areas of the park, and can also be used to answer a multitude of questions about the quality of the data base, i.e., which areas tend to be under-collected (Peter White, unpublished instructions and data).

An attempt has also been made to keep computerized field records, for sightings where no collection was made. This is obviously a critical data management problem, especially in the case of endangered species where collection may be undesirable. Eventually this information should interface with the herbarium records.

The GRSM, as part of the International Biosphere Reserve Program, is establishing permanently marked plots, in all major vegetation types and in a variety of geographic locations throughout the park. A number of plots (usually 1 ha, 20 × 50m) have been placed in unique habitats or near rare or endangered plant populations. Species on the state lists have also been recorded in plots established for a variety of other monitoring purposes, including quantifying campsite, deer, and wild boar disturbance. This year the program should be continued to include permanent herb plots in specialized areas for careful census of very limited populations. These herb plots should be exactly relocatable, whereas those in a 1 ha plot are laid out in a regular pattern but are not placed relative to rare species or exactly marked. Data collection will include type and intensity of natural and unnatural disturbances.

*Step Three:* **Prioritization of research and management issues.** After basic data is accumulated the manager can begin to sort through potential management problems. Not only should rare plant management, in general, be given a priority (usually a high one), but the status of the individual species should be evaluated. The position of the species on a national or state list may not reflect the condition of populations in the preserve. In GRSM, *Cacalia rugellii* has an extensive and probably stable population but is of high concern on both state lists. A number of plants such as *Lilium* spp., are not only rarer, but are being disturbed by wild boar or other agents.

Some species and situations may need close attention, others very little. In GRSM, most rare species can still be found where they were originally discovered, and few radical changes can be expected in most populations over short periods of time. The exceptions to this should be at the head of the research/management lists.

There is presently a preliminary report for GRSM which lists rare species, their known status and possible threats (Bratton, 1979). This is being thoroughly revised and all species on the park vascular species list which are on the national or state endangered lists are being field checked. Eventually all the species (and areas where such species are concentrated) will have individual files containing the information suggested in Henifin et al (1979).

The resources manager can then not only organize species according to the anticipated management program but can locate sites on master quad maps and integrate rare plant information into other managerial decisions.

*Step Four:* **Answering critical questions and converting to active management.** Management then has to turn towards collecting more data on top priority problems and implementing actions where necessary. Frequently, the effects of management actions themselves will have to be monitored.

In GRSM, for instance, resources management is trying to eliminate wild boar from certain high elevation deciduous forests where damage is extreme. Management has also been proposed for the visitor-trampled areas on the top of Mt. LeConte and for some of the poorly drained limestone areas in Cades Cove. Some of these sites should eventually have individual management plans and continual checks on the success of the program.

*Step Five:* **Detailed policy decisions on all philosophical questions and on rare plant problems that are integral parts of other managerial issues.** Eventually, rare plant management has to interface with other managerial issues such as fire management.

The following is an abbreviated example of a possible set of policies on rare, threatened or endangered plants in a park or preserve in a temperate deciduous forest. We have included this list, partially to show that, although we enjoy philosophizing, we also believe it is necessary to make decisions and to act on them. The list is not intended to be an absolute statement of the best policies but is included as an example of how one could make a series of coordinated decisions for an area such as GRSM.

**I.** Any plant considered of concern on a national or state level will be considered for special status in the preserve.

**II.** Ubiquitous species, those frequently found in a major vegetation type in the preserve, may be excluded from the list if vegetation samples indicate low levels of disturbance (i.e., trail construction) are not a threat to the population.

**III.** The preserve will manage to protect unique gene pools of regional or local significance which may include protection at the subspecies, variety, form, hybrid, or local population level. Hybrids or other genetically unique populations will be given high priority for protection if they are endemic to the preserve or of very limited distribution elsewhere. In practice, it is recognized that "unique gene pools" and "local significance" are subjective and relative terms; hence, botanical research and informed judgment are required in this process.

**IV.** *First priority* on the preserve list will be given to species with very limited populations which are also endemic to the preserve and to species which are nationally endangered.

*Second priority* will be given to nationally threatened species, those in the highest category on the state list(s) (endangered) and to regional endemics with limited populations.

*Third priority* will be given to species considered threatened by the state(s), and species with disjunct distributions which have limited populations in the preserve, and variants or hybrids limited to the preserve.

*Fourth priority* will be given to all other native species known from ten sites or fewer, and to varieties or hybrids limited to the preserve.

**V.** Management priority will be adjusted according to the status of the plant in the preserve.

*First managerial priority* will be given to any plant in the first category above which is in immediate danger of extinction.

*Second management priority* will be given to any plant in the first three categories which is in immediate danger of extirpation from the preserve.

*Third management priority* will be given (in order of the above categories) to plants whose populations are being reduced by anthropogenic disturbance.

*Fourth management priority* will be given to all other species.

**VI.** Populations eliminated by natural catastrophic events will only be artificially reestablished if the removal of the population in question is detrimental to the species' chances for survival in toto (not just in the preserve) or if the preserve population is considered significantly different (genetically) from those outside the preserve, and the population can be replaced by native stock.

**VII.** Any population of a rare species removed by an anthropogenic disturbance may be artificially reestablished, but natural propagation is to be favored where possible.

**VIII.** No attempt will be made to maintain populations of rare exotic species or of species common in the adjoining states, but rare in the preserve due to lack of habitat (i.e., certain roadside weeds and successional species).

**IX.** An attempt will be made to protect unique natural habitats.

**X.** Artificial mixing of preserve populations with gene pools from outside the preserve will only be practiced where there is no viable alternative for maintaining the population of a native species. Removal of material from the preserve, artificial propagation, and return to the preserve is to be preferred where introduction is necessary.

**XI.** Species thought not to be native to the preserve will not be introduced, even if they are native to surrounding state(s) and/or are endangered in their original habitat.

**XII.** Severe natural disturbances should be allowed to occur whenever and wherever other considerations such as visitor safety or possible damage to property outside the preserve do not inhibit them.

**XIII.** Artificial disturbances, particularly natural factor imitators like controlled burning, may be used on sites where rare plant populations are disturbance-dependent, but the natural disturbance regime cannot operate due to cultural restrictions.

**XIV.** All rare plant populations will be monitored. This effort may be limited by available manpower, but the most desirable scheme would include annual population estimates for species thought to be in flux, and longer term (once every five years) checks for species with larger and/or stable populations.

**XV.** Scientific collection of rare species will be limited to those having permits specifically for those species and conducting work which will further our knowledge of their biology without damaging the populations in the preserve.

**XVI.** Individual species and areas of concern will each have a management plan. Each plan should include:
A. Geographic location and description of the area
B. Reason for protection status or management action
C. Present status of species or site (including threats)
D. Managerial needs and alternatives

## CONCLUSION

The mere establishment of legal boundaries does not protect plants in preserves from human impacts. Active policy formation and management are usually necessary and should be instituted as early in the history of the preserve as possible. In order to manage rare plant populations, decisions concerning philosophical issues have to be made. Important areas for future research and discussion include allowable disturbance levels and population reduction for rare species, relationships between process oriented and species oriented management, impacts of management on the population genetics of species, and accurate methods of monitoring rare plant populations.

## LITERATURE CITED

BARON, J., & R. C. MATHEWS, JR. 1977. Environmental analysis of the proposed Foothills Parkway. Manage. Rep. No. **19,** U.S. Dept. of the Interior, National Park Service, Southeast Regional Office. Vol. I, 100 pp.

BERRY, R. J. 1971. Conservation aspects of the genetical constitutions of populations. *In:* E. Duffey & A. S. Watt, eds., The scientific management of animal and plant communities in conservation, pp 177 206. Blackwell Scientific Publications, Oxford.

BODEN, R. W., & J. D. OVINGTON. 1973. Recreation use patterns and their implications for management of conservation areas. Biol. Conserv. **5:** 265 270.

BRATTON, S. P. 1974. The effect of the European wild boar (*Sus scrofa*) on the high elevation vernal flora in Great Smoky Mountains National Park. Bull. Torrey Bot. Club. **101:** 198 206.

———. 1975. The effect of the European wild boar, (*Sus scrofa*) on gray beech forest in the Great Smoky Mountains. Ecology **55:** 1356 1366.

———. 1977. The effect of the European wild boar on the flora of the Great Smoky Mountains National Park. *In:* G. W. Wood, ed. Research and management of wild hog populations; pp 47 52. Belle W. Baruch Forest Science Institute of Clemson Univ., Georgetown, SC.

———. 1978. Is the panther making a comeback? Natl. Parks and Conserv. Mag. **July:** 10 13.

———. 1979. Preliminary status of rare plants in Great Smoky Mountains National Park. Manage. Rep. No. **25,** U.S. Dep. of Interior National Park Service, Southeast Regional Office, Atlanta, GA.

———. In press. The impact of white-tailed deer on the vegetation of Cades Cove. *In:* Proc. Conf. Assoc. Southeastern Fish and Wildlife Resource Agencies 1979.

———. R. C. Mathews, Jr., & P. S. White. In prep. The impacts of an agricultural area within a natural area: Cades Cove: a case history.

———. & P. Whittaker. 1977. Great Smoky Mountains National Park: Disturbance and visitation on Mount LeConte. Rep. for the Superintendent, Great Smoky Mountains National Park. U.S. Dep. of Interior, National Park Service, Uplands Field Research Laboratory. 59+10 pp.

Brotherton, D. I. 1975. The development and management of country parks in England and Wales. Biol. Conserv. **7:** 171 154.

Brown, W. L. 1961. Mass insect control programs: four case histories. Psyche **68:** 75 111.

Campbell, Carlos C. 1960. Birth of a national park in the Great Smoky Mountains. The University of Tennessee Press, Knoxville. 155 pp.

Committee for Tennessee Rare Plants. 1978. The rare vascular plants of Tennessee. J. Tenn. Acad. Sci. **53:** 128 133.

Cooper, J. E., S. S. Robinson & J. B. Funderburg, eds. 1977. endangered and threatened plants and animals of North Carolina. North Carolina State Museum of Nat. Hist., Raleigh. 444 pp.

Culbertson, N. 1977. Status and history of the mountain lion in the Great Smoky Mountains National Park. Manage. Rep. No. **15,** U. S. Dep. of Interior, National Park Service, Southeast Regional Office, Atlanta, GA. 70 pp.

Dawkins, H. C. 1971. Techniques for long-term diagnosis and prediction in forest communities. *In:* E. Duffey & A. S. Watts, eds. the scientific management of animal and plant communities in conservation, pp. 33 44. Blackwell Scientific Publications. Oxford.

Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biol. Conserv. **7:** 129 146.

Dolan, R., B. P. Hayden, & G. Soncie. 1978. Environmental dynamics and resource management in the U.S. National Parks. Environ. Manage. **2:** 249 258.

Dory, M. A. G. 1977. Covadonga National Parks, Asturias, Spain. Its history, conservation interest and management problems. Biol. Conserv. **11:** 79 85.

Dring, M. J., & L. C. Frost. 1971. Studies of *Ranunculus ophioglossifolius* in relation to its conservation at the Badgeworth Nature Reserve, Gloucestershire, England. Biol. Conserv. **4:** 48 56.

Drury, W. H. 1974. Rare species. Biol. Conserv. **6:** 162 169.

———, & I. C. T. Nisbet. 1973. Succession. J. Arnold Arb. **54:** 331 368.

Duffey, E., M. G. Morris, J. Sheail, Lena K. Ward, D. A. Wells, & T. C. W. Wells 1976. Grassland ecology and wildlife management. Chapman Hall, London. 281 pp.

Franz, E. H., & F. A. Bazzaz. 1977. Simulation of vegetation response to modified hydrologic regimes: a probabilistic model based on niche differentiation in a floodplain forest. Ecology **58:** 176-183.

Green, B. H. 1972. The relevance of serial eutrophication and plant competition to the management of successional communities. Biol. Conserv. **4:** 378 384.

Haber, W. 1973. Conservation and landscape management in Germany, past, present, and future. Biol. Conserv. **5:** 258 264.

Henefin, M. S., L. E. Morse, J. L. Reveal, B. MacBryde, & I. I. Lawyer. 1979. Guidelines for the preparation of status reports on rare and endangered plant species. *In:* L. E. Morse & M. S. Henefin, eds. Geographical data organization for rare plant conservation. New York Botanical Garden, Bronx, NY.

Hoffman, H. L. 1962. Checklist of vascular plants of the Great Smoky Mountains. Castanea **29:** 1-45.

Hooper, M. D. 1971. The size and surroundings of nature reserves. *In:* E. Duffey & A. S. Watt, eds. The scientific management of animal and plant communities in conservation, pp. 555 561. Blackwell Scientific Publications, Oxford.

Howe, T., & S. P. Bratton. 1976. Winter rooting activity of the European wild boar in Great Smoky Mountains National Park. Castanea **41:** 256 264.

Jeffrey, D. W. 1971. The experimental alteration of a *Kobresia*-sward in Upper Teesdale. *In:* E. Duffey & A. S. Watt, eds. The scientific management of animal and plant communities in conservation, pp. 79-89. Blackwell Scientific Publications, Oxford.

Johnson, W. C., & S. P. Bratton. 1978. Biological monitoring in UNESCO Biosphere Reserves with special reference to the Great Smoky Mountains National Park. Biol. Conserv. **13:** 105 115.

———, R. L. Burgess, & W. R. Kaemmerer. 1976. Forest overstory vegetation and environment on the Missouri River floodplain in North Dakota. Ecol. Monogr. **46:** 59 84.

Lindsay, M. M., & S. P. Bratton. In press . The vegetation of grassy balds and other high elevation disturbed areas in the Great Smoky Mountains National Park. Bull. Torrey Bot. Club.

Lindsay, M. M., & S. P. Bratton. 1979. Grassy balds of the Great Smoky Mountains; their history and flora in relation to potential management. Environ. Manage. **3:** 417 430.

Linzey, A. V., & P. W. Linzey. 1970. Mammals of Great Smoky Mountains National Park. The University of Tennessee Press, Knoxville. 114 pp.

Massey, J. R., & P. D. Whitson. 1977. Species biology: definition, direction, data, and decisions. *In:* Proc. Conf. on Endangered Plants in the Southeast, pp. 89 94. U.S. Dep. of Agriculture, Forest Service General Tech. Rep. **SE-11**. Asheville, NC.

Mathews, J. F. 1977. Definition and classification of endangered and threatened plant species (I). *In:* Proc. Conf. on Endangered Plants in the Southeast, pp. 2-5. U.S. Dep. of Agriculture, Forest Service General Tech. Rep. **SE-11.** Asheville, N.C.

Meijer, W. 1973. Endangered plant life. Biol. Conserv. **5:** 163-167.

Miller, R. S., & D. B. Botkin. 1974. Endangered species: models and predictions. Am. Sci. **62:** 173-181.

Mutch, R. W. 1970. Wildland fires and ecosystems — a hypothesis. Ecology **51:** 1046-1051.

Namkoong, G., & J. H. Roberds. 1974. Extinction probabilities and the changing age structure of redwood forests. Am. Natur. **108:** 355-368.

Nature Conservancy. 1975. The preservation of natural diversity; a survey and recommendations. Final rep. for U. S. Dep. of Interior, Contract No. CXOCA-5-040. 212 pp.

Nichols, R. 1977. The ecological effects of LeConte Lodge in the Great Smoky Mountains National Park. Rep. for the Superintendent, Great Smoky Mountains National Park, U.S. Dep. of Interior, National Park Service, Uplands Field Research Laboratory, Gatlinburgh, TN. 45+[52] pp.

Owen, J. S. 1972. Some thoughts on management in national parks. Biol. Conserv. **4:** 241-246.

Petersen, R. 1974. Petition to Office of Endangered Species, U.S. Fish and Wildlife Service, to place the fungus *Gloeocantharellus purpurascens* (Hesler) Singer on the list of endangered species. Mimeo in files, Great Smoky Mountains National Park. 10 pp. +maps.

Rawes, M., & D. Welch. 1972. Trials to recreate floristically-rich vegetation by plant introduction in the northern Pennines, England. Biol. Conserv. **4:** 135-140.

Schlesinger, W. H., W. A. Reiners, & P. S. Knopman. 1974. Heavy metal concentrations and deposition in bulk precipitation in montane ecosystems of New Hampshire, U.S.A. Environ. Pollut. **6:** 39-47.

Schroeder, P. M., R. Dolar, & B. P., Hayden. 1976. Vegetation changes associated with barrier-dune construction on the Outer Banks of North Carolina. Environ. Manage. **1:** 105-114.

Shabica, S. V., P. P. Brannon, & R. Herrmann. 1978. The extirpation of an island: The dilemma of Petit Bois Island, Gulf Islands National Seashore, Mississippi. *In:* Proc. of the Symp. on Technical, Environmental, Socio-economic and Regulatory Aspects of Coastal Zone Management, San Francisco, CA.

Simmons, I. G. 1973. The protection of ecosystems and landscapes in Hokkaido, Japan. Biol. Conserv. **11:** 21-27.

Slater, F. M., & A. D. Q. Agnew. 1977. Observations on a peat bog's ability to withstand increasing public pressure. Biol. Conserv. **11:** 21-27.

Smith, R. L. 1976. Ecological genesis of endangered species: the philosophy of preservation. Am. Rev. Ecol. Syst. **7:** 33-35.

Smithsonian Institution. 1975. Report on endangered and threatened plant species of the United States, submitted to the 94th Congress, 1st session, Ser. No. **94-A.**, U.S. Government Printing Office, Washington, DC. 200 pp.

Stone, E. C. 1965. Preserving vegetation in parks and wilderness. Science **150:** 1261-1267.

TERBORGH, J. 1974. Preservation of natural diversity. The problem of extinction prone species. Biol. Sci. **24:** 715 722.

THOMPSON, P. A. 1974. The use of seed-banks for conservation of populations of species and ecotypes. Biol. Conserv. **6:** 15 19.

———. 1976. Factors involved in the selection of plant resources for conservation as seed in gene banks. Biol. Conserv. **10:** 159 167.

U.S. DEP. OF INTERIOR, NATIONAL PARK SERVICE. 1970. Compilation of the administrative policies for the national parks and national monuments of scientific significance (Natural Area Category). U.S. Government Printing Office, Washington, DC.

WATT, A. S. 1971. Factors controlling the floristic composition of some plant communities in Brackland. *In:* E. Duffey and A. S. Watt, eds. The scientific management of animal and plant communities in conservation, pp. 137 152. Blackwell Scientific Publications, Oxford.

WAYRE, P. 1969. The role of zoos in breeding threatened species of mammals and birds in captivity. Biol. Conserv. **2:** 47 49.

WELLS, T. C. E. 1969. Botanical aspects of conservation management of chalk grasslands. Biol. Conserv. **2:** 36 44.

WESTHOFF, V. 1971. The dynamic structure of plant communities in relation to the objectives of conservation. *In:* E. Duffey and A. S. Watt, eds. The scientific management of animal and plant communities in conservation, pp. 3 14. Blackwell Scientific Publications, Oxford.

WHITE, P. S. 1979 Pattern, process, and natural disturbance in vegetation. Bot. Rev. **45**: 229 299

WIERSMA, G. B., K. W. BROWN, & A. B. CROCKETT. 1978. Development of a pollutant monitoring system for Biosphere Reserves and results of the Great Smoky Mountains pilot study. *In:* 4th Joint Conf. on Sensing of Environmental Pollutants, pp. 451 455. Am. Chem. Soc.

WILLIS, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecol. Monogr. **44:** 153 169.

WRIGHT, H. E., JR. 1974. Landscape development, forest fires, and wilderness management. Science **186:** 487 495.

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# RARITY OF PLANT SPECIES:
# A SYNTHETIC VIEWPOINT

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Botanists and evolutionists have long been fascinated by species that have narrowly restricted or localized patterns of distribution. Every field botanist can recall the thrill of excitement that comes with the discovery of a new, previously unrecognized species, or of a well known species far outside of its normal range of distribution. In modern times, the preservation of these rarities has become a major concern. This is because they often provide the evolutionist with particularly good opportunities for learning about evolution, in addition to the esthetic pleasure that their very existence provides to countless nature lovers. Learning about them, and about the reasons why they are restricted serves a double function. Such learning is both an avenue toward greater scientific knowledge and a means of increasing the desirability of their preservation.

For more than a century, botanists have theorized and argued about the reasons why some species of plants are rare or local, but no theory has proved altogether satisfactory. This is because the factors involved are numerous and complex. In this article, I shall review some of the theories that have been proposed, and attempt a synthesis to explain the examples known to me.

## HISTORICAL THEORIES

Two well known theories are both based primarily upon knowledge or inferences about the past history of floras. One of these, proposed by J. C. Willis (1922), maintains that most rare species are youngsters that have not had time to spread. The opposite theory, that many rare species are "senescent" and are becoming extinct because of old age, has been promoted by many botanists. In his criticism of Willis, M. L. Fernald (1926, p. 242) stated: "The world not being static, life has followed an almost inextricable series of factors. . .with the result that no single factor, especially *age*, can be isolated as all-controlling" (italics by Fernald).

Well documented examples are now available to show that rare and localized species can be either young, ancient, or of an intermediate age. Three hybrid polyploid (amphiploid or allopolyploid) species are known to have arisen less than a century ago: the Town-send marsh grass, *Spartina townsendii*, (Marchant, 1966); and two species of goatsbeard, *Tragopogon mirus* and *T. miscellus* (Ownbey, 1950). Several localized species, that are either sympatric with or exist close to their nearest relatives, can be inferred on the basis of genetic and distributional evidence to be no more than a few hundred or at most a thousand years old. Among them are *Stephanomeria malheurensis* (Gottlieb, 1973), and *Clarkia lingulata* in the Sierra Nevada of California (Lewis & Roberts, 1956; Gottlieb, 1974).

Several examples of rare or localized species are well known to be ancient and relictual. One of the most renowned of them is the California Big Tree (*Sequoiadendron giganteum*). Well documented evidence shows that its tertiary counterpart was widespread in western North America (Raven & Axelrod, 1977). Fossil evidence also supports the ancient, relictual nature of other modern tree species, such as *Torreya taxifolia* in the southeastern United States, *Metasequoia glyptostroboides* in central China, and *Ginkgo biloba*, a species that is extinct as a wild tree, being known only in cultivation.

One can easily find, in addition, examples of rare species that are neither ancient nor recent. The Monterey Pine (*Pinus radiata*), now confined to three restricted localities along the coast of California, plus Cedros Island off the coast of Baja California, was much more widespread during the Pliocene and Pleistocene epochs (Axelrod, 1967), and so must be regarded as relictual. Nevertheless, it belongs to one of the most advanced sections of the pine genus (Mirev, 1967), and so is not an ancient species compared to other pines. Rare species that on the basis of distributional evidence must be regarded as neither ancient nor very recent include most of those that are being discussed in the present symposium, such as *Geum peckii*, *Potentilla robbinsiana*, and *Pedicularis furbishiae*. Distributional and systematic evidence with respect to most of the rare species known to me causes me to place them in this category. Consequently there appears to be little correlation, either positive or negative, between rarity or localized distributional patterns of species and their chronological age.

## GENETICAL THEORIES

Most systematic botanists and plant geographers, having long since discarded purely historical theories, have replaced them with theories that emphasize the genetic diversity or homogeneity of their populations. Depletion or depauperization of the gene pool is often invoked. Such theories were stimulated during the 1930's and 1940's largely by the theories of Sewall Wright (1931), who pointed out that in populations of greatly reduced size, chance fluctuations in gene frequency ("genetic drift") would often lead to fixation of alleles and so to depletion of the gene pool. I theorized along these lines at that time (Stebbins, 1942) but had no good evidence to support my hypothesis. How good are such theories at the present time?

Several rare, endemic species are known to possess very little genetic variability, indicating a much depleted gene pool. A good example is the annual composite, *Stephanomeria malheurensis,* confined to a single locality in eastern Oregon (Gottlieb, 1973). Nevertheless, depleted gene pools are by no means confined to localized endemics. they exist also in widespread species that are largely self-fertilizing (Chapman, 1967). The opposite situation, rare species having relatively rich stores of genetic variability, is also well known. The California Big Tree, *Sequoiadendron giganteum,* has been cultivated in Great Britain for little more than a century, and the majority of trees found there probably were grown from seed collected in the wild. Nevertheless, horticulturists have recognized about twenty-five morphologically recognizable variants among the cultivated specimens that they have grown. This most famous of rare and endemic species appears to contain in its restricted populations nearly or quite as much variability as many common and widespread species. Another example is a rare and localized species of western buckwheat, *Eriogonum apricum,* found in the foothills of California's Sierra Nevada. Although the populations of this species contain hundreds of thousands of individuals, they are confined to a small area of highly sterile soil that is about ten miles long and one to two miles wide. Within each population, differences in leaf form and branching pattern are obvious to the careful observer. In addition, a careful study of morphological variation in neighboring populations has shown that differences between them are great enough so that two different subspecies can be recognized, each of which occupies its own restricted area, the two areas being about five to six miles from each other (Myatt, 1968).

The example of *Eriogonum apricum* needs further investigation, particularly if it turns out to be favorable material for estimating biochemical variability with respect to isozymes. The common, widespread species, *Eriogonum nudum* occurs sympatrically with *E. apricum*, but on less sterile soils and in company with widespread foothill species. I am willing to predict that a series of populations of *E. nudum* taken from an area equal in extent to that of *E. apricum* will contain no more genetic variability than that present in the totality of populations of *E. apricum*. The widespread distribution of *E. nudum*, in my opinion, is most probably due to the existence of a large number of genetically different populations that are adapted to a wide spectrum of different habitats and climatic zones.

There appears to be no recognizable correlation, either positive or negative, between the amount of genetic variation within populations of plant species and the rarity or commonness of the species as a whole. Other causes for the rarity of species must be sought.

Other theories to explain the occurrence of rare species place great emphasis on ecological fctors. Some botanists living in the eastern United States have suggested that rare species are usually pioneers in temporary habitats. Their rarity is then ascribed to the localized occurrence of such habitats and to the possibility that new species can originate in conjunction with the appearance of new and ecologically different pioneer habitats. This hypothesis explains very well the occurrence of several of the endemics discussed in the present symposium. *Geum peckii, Potentilla robbinsiana, Pedicularis furbishiae,* the New england species of *Astragalus*, as well as the rock plants that inhabit the calcareous cliffs of northern Vermont; all are confined to pioneer habitats. The same is true of the remarkable series of rare species that inhabit the Appalachian shale barrens, the pond margins of Cape Cod, the pine barrens of New Jersey and the major river estuaries along the Atlantic Coast. There are, however, some exceptions, even in the flora of eastern North America. *Shortia galacifolia*, a remarkable endemic of the southern Appalachians, grows under the canopy of climax or subclimax forests. *Prenanthes crepidinea*, one of the rarest species found in the Mississippi Valley, is also an inhabitant of climax forests.

The western United States contains a large number of rare and localized species that, far from being confined to pioneer habitats, form a sort of super climax. The best known of these is *Sequoiadendron giganteum*, but other woody species, such as the Monterey Pine (*Pinus radiata*), Torrey Pine (*Pinus torreyana*), Santa Lucia fir (*Abies bracteata*), and weeping spruce (*Picea breweriana*) are likewise climax or superclimax species. Another feature of the western flora is the large number of pioneer species that are relatively common and widespread. Nearly all of the species belonging to such large and highly diverse genera as *Astragalus, Eriogonum, Cryptantha,* and *Penstemon* are pioneers. Many examples exist in the western flora of rare species and their common relatives, both of which are equally well adapted to colonizing pioneer habitats. The predominance of pioneers among the rare species found in mesic areas of relatively low relief, like eastern North America, is due to the comparative rarity of such habitats. In semi-arid regions of the west, where climax forests are often rare and local, species adapted to mesic climax habitats may likewise include a fairly high proportion of rare and endemic taxa.

In discussing the rare and localized species found in California, I have elsewhere (Stebbins, 1976) elaborated on the presence of many of these species on "ecological islands." These "islands" are defined as small areas in which some environmental factor or combination of factors is so different from conditions that prevail in the surrounding areas that with respect to their ability to become established in neighboring areas, the species growing on these "islands" are as isolated as if they were growing on an island in the ocean. Most commonly, the conditions that produce an ecological island are soils of an unusual type. In California, small patches or larger areas of soil derived from ultrabasic or mafic metamorphic rocks, frequently serpentine, form the largest number of ecological islands. Other unusual soils are derived from Tertiary volcanic deposits, such as mud-flow breccia, pumice from recently extinct volcanoes, the sterile soil of raised beaches, and a few localized limestone cliffs in regions that contain predominantly acidic rocks.

While ecological explanations account for most occurrences of rare and localized species, they are no more satisfactory as complete explanations than are any others that rely upon a single factor. For example, they cannot account for the fact that in some instances groups of related species, all of which grow in ecological islands, include some that are narrowly endemic, and others that are widespread. For instance, species of the genus *Streptanthus* or jewel flower (Cruciferae) are among the best known endemics of serpentine barrens in central California. Nevertheless, on these same barrens grow annual species of *Streptanthus* belonging to the same species groups, but relatively widespread. They may consist of similar populations on several different serpentine areas (*Streptanthus* *breweri, S. polygaloides*), or include populations both on and off of the serpentine areas (*S. glandulosus*, Kruckeberg, 1957). Obviously, no strictly ecological theory can explain the differences between these kinds of distributional patterns. Other factors, either different genetical makeup, different past histories, or both must be invoked to explain these differences.

Clearly, the only theories that will provide complete explanations of rarity and endemism of species must be of a synthetic nature. They must take into account ecological factors, genetic structure of populations and past history of the evolutionary lines concerned, and balance these factors among each other in a complementary fashion. A framework for such theories can be a well recognized principle of evolution. This is that rates and directions of evolution may vary greatly, even among related evolutionary lines. The particular rate and direction that will be characteristic of any line will depend upon particular population-environment interactions, mediated by natural selection. I should like to propose a theory based upon this principle, which I am calling the gene pool-niche interaction theory.

According to this theory, the primary cause of localized or endemic distribution patterns is adaptation to a combination of ecological factors that are themselves localized. Factors of soil texture or chemical composition are the most common but by no means the only ones. As pointed out long ago by John Muir, the California Big Tree grows only in parts of the Sierra Nevada that escaped the glacial ice, and are underlain by deep, heavily weathered soils. Nevertheless, *Sequoiadendron* occurs in only a small proportion of these areas. In some instances, temperature and moisture can be recognized as controlling factors, but they do not explain patterns by themselves. For instance, two species of closed cone pines, *Pinus muricata* and *P. radiata*, both occur along the coast of California and are concentrated in areas where summer fog is prevalent, and the mountains do not rise abruptly from the seacoast. The greater tolerance of a cool, rainy winter climate on the part of *P. muricata* as compared to *P. radiata* is evident from its abundance to the north of San Francisco, where *P. radiata* is absent. Nevertheless, *P. muricata* occurs also in south central California, south of the southernmost mainland groves of *P. radiata*, and in a milder, drier climate. This anomaly is probably explained by the genetic structure and past history of the two species. Evidence from artificial hybridization suggests that *Pinus muricata* as recognized in the floras actually consists of two species, the more southerly of which occurs south of the mainland localities for *Pinus radiata* (Critchfield, 1967). The more southern or typical *P. muricata,* moreover, appears to be closely related to and apparently descended at least partly from a series of populations once described as *P. remorata,* which were apparently adapted to a relatively mild climate (Axelrod, 1967).

Next to climatic and edaphic factors, those inherent in the gene pool of the population are of critical importance. They include the total amount of variability, the amount of variability that can be released at any one time, and the amount of variation that can be generated with respect to those particular characteristics that affect most strongly the establishment of new populations. Prominent among the latter are seed production, the distance to which seeds can be dispersed, as well as seed size and other characters that aid in the establishment of seedlings.

A good example of the effect of the nature of seed dispersal mechanisms upon rare or endemic vs. widespread distribution of species is the contrast between the distribution of species of juniper (*Juniperus*) and cypress (*Cupressus*) in the western United States. These related genera form trees or large shrubs having very similar vegetative characteristics. They are both wind pollinated and form seeds approximately similar in size. Both genera include species adapted to arid habitats, and others that are more mesic. The most conspicuous difference between them is that the seeds of *Cupressus* are borne in hard, woody cones, from which they drop to the ground when ripe, while those of *Juniperus* are borne in berries that are eaten by birds, which excrete them at considerable distances from the parental tree. It is no accident, therefore, that species of *Juniperus* are all widespread, some of them extremely so, while *Cupressus* contains a higher proportion of localized species than any other woody genus of North America.

One way in which an impression can be gained of the ways in which these factors interact is to visualize the niche as a depression that is partly filled by a liquid, the gene pool. Ecological islands such as serpentine barrens surrounded by large areas of acidic soils would then be deep, narrow depressions. If the "pool" should occupy such a depression, its store of variability would be represented by the depth of the liquid. Since even a relatively deep "pool" would have a surface far below the rim of the depression (i.e. even the most extreme variants that a rich gene pool could generate would fall far short of adaptation to the surrounding area), the size of the gene pool would in this case affect relatively little the ability of the species to colonize new areas and expand its range. Ecological islands based upon more subtle environmental factors, such as those that apparently affect the distribution of species like the giant Sequoia and the Monterey Pine, can be visualized as relatively shallow depressions. In these examples, a species having a restricted gene pool can be likened to a thin film of liquid at the bottom of the depression, from which few or no droplets can rise and spread to neighbouring depressions. Species having larger gene pools fill the depression more completely, so that their restriction does not depend upon a simple kind of population-environment interaction that keeps them in place. Their restriction is due either to low vagility, usually conditioned by seeds having poor dispersability or difficulty of establishment, to a great distance that separates one favorable niche or depression from another, or to a combination of these and other factors.

Like every other problem of evolution, that of the nature and occurrence of rare species is not a simple one that can be solved by applying indiscriminately one or a few general principles. Each example of such species has its unique features, and must be considered with respect to three major parameters: the intricate mosaic of the environment in which it grows; the complex genetic structure of its populations, including the amount and nature of genetic variability, as well as the way in which it becomes revealed and exposed to natural selection; and finally the past history of the populations, that may provide a clue to understanding why a particular genetic structure and environment-population interaction exists. The problem of the evolution and persistence of rare and endemic species is merely one facet of the much larger problem of biological evolution in general. The synthetic method is the only rational approach to all evolutionary problems.

The very fact that problems posed by the occurrence of rare and endemic species are isolated facets of evolutionary problems in general confers on such species a particular importance. As already recognized half a century ago by Fernald (1926), a full understanding of their nature and origin can give us particular insight into rates and directions of evolution. To the dedicated naturalist, the thrill of discovering or rediscovering these priceless rarities can be matched by the succession of pleasures and satisfactions that accompany unravelling, step by step, the mysteries of their origin. Whenever one of them becomes extinct, future generations of naturalists are deprived of one more chance to experience these thrills and pleasures while adding to mankind's knowledge about the world in which we live.

## LITERATURE CITED

AXELROD, D. I. 1967. Evolution of the California closed cone pine forest. *In:* R. N. Philbrick, ed., Proc. Symp. Biol. Calif. Islands. Santa Barbara Bot. Gard., Santa Barbara, Calif.: 93 149.

CHAPMAN, S. R. 1967. Patterns of genetic variability associated with a highly inbreeding species. Proc. Montana Acad. Sci. **27:** 26 32.

CRICHFIELD, W. B. 1967. Crossability and relationships of California closed cone pines. Silvae Geneticae **16:** 89 97.

FERNALD, M. L. 1925. The persistence of plants in unglaciated areas of Boreal America. Mem. Amer. Acad. Sci. **15:** 239 342.

———. 1926. The antiquity and dispersal of vascular plants. Quart. Rev. Biol. **1:** 212 245.

GOTTLIEB, L. D. 1973. Genetic differentiation, sympatric speciation and the origin of a diploid species of *Stephanomeria.* Amer. J. Bot. **60:** 545 553.

———. 1974. Genetic confirmation of the origin of *Clarkia lingulata.* Evolution **28:** 244 250.

KRUKEBERG, A. R. 1957. Variation in fertility of hybrids between isolated populations of the serpentine species *Streptanthus glandulosus* Hook. Evolution **11:** 185 211.

LEWIS, H., & M. R. ROBERTS, 1956. Origin of *Clarkia lingulata.* Evolution **10:** 126 138.

MARCHANT, C. J. 1966. The cytology of *Spartina* and the origin of *S.* × *townsendii. In:* C. D. DARLINGTON & K. R. LEWIS, eds. Chromosomes Today, Vol. 1, Oliver and Boyd, Edinburgh and London: 71 72.

MIROV, N. T. 1967. The Genus *Pinus.* Ronald Press. New York.

MYATT, R. G. 1968. The ecology of *Eriogonum apricum* Howell. Thesis, M. Sc. University of California, Davis.

OWNBEY, M. 1950. Natural hybridization and amphiploidy in the genus *Tragopogon.* Amer. J. Bot. **37:** 487 499.

RAVEN, P. H., & D. I. AXELROD, 1977. Origin and relationships of the California Flora. Univ. Calif. Publ. Bot. **72:** 1 134.

STEBBINS, G. L. 1942. The genetic approach to problems of rare and endemic species. Madroño 6: 240–258.

———. 1976. Ecological islands and vernal pools of California. *In:* S. Jain, ed., Vernal Pools, their Ecology and Conservation. Inst. Ecol. Univ. Calif. Davis no. 9: 1–4.

WILLIS, J. C. 1922. Age and Area. Cambridge Univ. Press. Cambridge, England.

WRIGHT, S. 1931. Evolution in Mendelian populations. Genetics 16: 97–159.

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# PHENOTYPIC VARIATION OF RARE AND WIDESPREAD SPECIES OF *PLANTAGO*

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The notion that populations of restricted species are genetically depleted is based on population models which show rapid gene fixation because of genetic drift and selection in small populations (Rothstein, 1973; Babbel & Selander, 1974). If this is true, populations of rare species should show less phenotypic variability in the field than populations of widespread, closely related species due to lower amounts of genetic variation. With the exception of the genus *Becium*, in which leaf dimensions of a widespread species were shown to be more variable than those of a restricted species (Wild & Heyting, 1966), this assumption has not been tested for plants. In order to test further this assumption, I examined the phenotypic variability of reproductive characters within populations of *Plantago* (Plantaginaceae) species, commonly known as plantains, in relation to the distributions of the species. In addition, herbarium specimens were examined for these species to gain a rough measure of the total phenotypic variability found throughout the ranges of the species. Would widespread species show more phenotypic variability than restricted species?

The genus *Plantago* is well suited for such a comparison of geographical distribution and phenotypic variability; species of *Plantago* vary from endemic species with highly restricted distributions and specialized habitat requirements to cosmopolitan species that occupy a wide variety of habitats. However, species of *Plantago* share the same floral characters associated with wind-pollination (Primack, 1978a) and the same fruit type, a circumscissile capsule.

## MATERIALS AND METHODS

### Data from herbarium material

Reproductive characters were determined for *Plantago* species using herbarium specimens. The range, habitat, and longevity for each species are presented in Table 1. Species and individuals within populations show variation in four reproductive characters which have been used taxonomically and which collectively determine the total weight of seeds produced per plant, the seed yield (Primack, 1978b). In this study, species are contrasted for their variation in these four characters. The following characters were measured: inflorescence number per plant (Infl.), capsule number per inflorescence (based on the inflorescence which is median in size) (Caps.), seed number per capsule based on a sample of at least three capsules (Seed no.), and the weight per seed based on a sample of at least ten mature seeds (Seed weight). An individual was ordinarily a single rosette on a shortened stem, though occasionally there was more than one rosette per stem. The herbarium specimens were picked at random from those available, and included specimens from throughout the distribution of the species. A detailed description of the way in which the herbarium specimens were evaluated is given elsewhere (Primack, 1976, 1978b, 1979). This sampling procedure considers only the overall variation of a species, not distinguishing between genetic and environmental components contributing to this variation and the underlying population structure of the species. Taxonomy follows Pilger (1937).

Mature seeds could not be obtained from every specimen. Consequently, the variation in weight per seed is not reported for every species. Many herbarium specimens contain some capsules which have already shed their seeds. However, this study did not involve actually counting each seed per plant, but rather involved measuring the four reproductive characters for each plant.

### Data from field collections

Individual plants were collected randomly from populations of sixteen species of *Plantago* found in North America (see Primack, 1978b, for localities), and examined for the four reproductive characters. Seven species were perennials and nine were annuals. In four species (*P. eriopoda, P. tweedyi, P. cordata,* and *P. heterophylla*), the seeds were not mature at the time of sampling.

### Statistical analysis

Coefficients of variation were calculated for each reproductive character in order to determine which species were the most variable. Species are grouped into five distribution classes according to available information on the extent of their geographical range (Table 1). Further investigation might show that particular species should be re-assigned to an adjacent distribution class. However, this classification system does separate out the most restricted and the most widely distributed species for comparison.

Both parametric and non-parametric correlation matrices were calculated for the coefficients of variation in order to determine: 1) if species which are variable for one character are likely to be variable for another character, and 2) if species which are particularly variable for a character based on herbarium specimens are also likely to be variable for that character based on population samples.

## RESULTS

### Relationship of range to the amount of phenotypic variation

Species show a wide variety of coefficients of variation using herbarium specimens, with some species being relatively invariable, while others are quite variable (Table 1). There is no obvious pattern of increasing variation with increasing distribution. If anything, species with restricted ranges seem to have more variation for seed number per capsule than species with larger ranges.

Similarly, species show a wide variety of coefficients of variation using population samples (Table 1). There is again no obvious pattern of increasing variation with increased distribution for three of the characters. There is a trend toward greater variation in capsule number per inflorescence in species with increased range. However, this observation must be treated cautiously because of the large variability of values within each distribution class.

In summary, the amount of phenotypic variation found within single populations and within the total species is not related to the range of the species.

### Correlation analysis

The results of the parametric and non-parametric tests gave similar values and the same levels of significance. Consequently, only parametric tests are presented.

There is no correlation among species for their coefficients of variation using herbarium specimens (Table 2), except that species which are more variable for inflorescence number per plant are

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Table 1. Coefficients of variation (CV = (standard deviation mean) × 100) for *Plantago* reproductive characters, based on population samples and herbarium samples. Species are arranged in classes of increasing range. Sample sizes (N) are the same for all characters within a species and sampling method except where listed separately in parentheses. Habitat and life span for each species given by Primack (1978b). Data from Primack (1978b).

| Species | Distribution |
|---|---|
| Restricted distribution; specialized habitat requirments: | |
| *P. cordata* | E. North America |
| *P. macrocarpa* | W. coast of N. America |
| *P. tweedyi* | W. North America |
| *P. eriopoda* | North America |
| *P. sparsiflora* | S. E. United States |
| *mean* | |
| Somewhat restricted distribution: | |
| *P. bigelovii* | W. North America |
| *P. pusilla* | Central United States |
| *P. elongata* | W. North America |
| *mean* | |
| Occurring on part of a continent: | |
| *P. wrightiana* | S. United States |
| *P. hookeriana* | S. North America |
| *P. rhodosperma* | S. North America |
| *P. helleri* | S. Central United States |
| *P. heterophylla* | S. E. United States |
| *mean* | |
| Widespread within much of a continent: | |
| *P. aristata* | E. North America |
| *P. bellardi* | Mediterranean |
| *P. virginica* | North America |
| *P. rugelii* | E. North America |
| *P. amplexicaulis* | Mediterranean |
| *mean* | |
| Widespread; occurring in a variety of habitats or on two or more continenents | |
| *P. patagonica* | Americas |
| *P. linearis* | Tropical Americas |
| *P. psyllium* | Cosmopolitan |
| *P. ovata* | Mediterranean, S. Asia |
| *P. major* | Cosmopolitan |
| *P. hirtella* | Americas |
| *P. depressa* | E. & Central Asia |
| *P. lanceolata* | Cosmopolitan |
| *P. maritima* | Northern Hemisphere |
| *P. coronopus* | Cosmopolitan |
| *mean* | |

| Herbarium Samples | | | | | Population Samples | | | | |
|---|---|---|---|---|---|---|---|---|---|
| N | Infl. | Caps | Seed No. | Seed Weight | N | Infl. | Caps. | Seed No. | Seed Weight |
| 20 | 40 | 44 | 28(19) | | 15 | 47 | 29 | 12 | |
| 20 | 43 | 48 | 27 | | | | | | |
| 20 | 46 | 54 | 17 | | 18 | 43 | 46 | 29 | |
| 20 | 53 | 30 | 26 | 30(13) | 19 | 50 | 51 | | |
| 14 | 66 | 33 | 20 | | 19 | 29 | 20 | 19 | 22 |
| | 50 | 42 | 24 | 30 | | 42 | 36 | 20 | 22 |
| | | | | | | | | | |
| 12 | 57 | 61 | 38 | | | | | | |
| 20 | 85 | 40 | 14 | | | | | | |
| 19 | 93 | 56 | 13 | | | | | | |
| | 78 | 52 | 21 | | | | | | |
| | | | | | | | | | |
| 20 | 97 | 35 | 0 | | 20 | 59 | 46 | 0 | 11 |
| 15 | 72 | 79 | 0 | | 19 | 44 | 29 | 9 | 16 |
| 20 | 62 | 58 | 0 | | 20 | 75 | 31 | 3(19) | 15(16) |
| 20 | 123 | 46 | 0 | | 20 | 64 | 56 | 3 | 23 |
| 20 | 92 | 47 | 23 | 26(11) | 20 | 73 | 50 | 36(15) | |
| | 89 | 53 | 5 | 26 | | 63 | 42 | 10 | 16 |
| | | | | | | | | | |
| 19 | 78 | 42 | 0 | 28(12) | 18 | 35 | 50 | 13 | 23(17) |
| 20 | 112 | 58 | 0 | | | | | | |
| 19 | 80 | 57 | 12 | | 20 | 44 | 26 | 3 | 9 |
| 18 | 99 | 58 | 31 | 32(16) | 20 | 43 | 47 | 15 | 20 |
| 17 | 106 | 72 | 9 | | | | | | |
| | 95 | 57 | 10 | 30 | | 41 | 41 | 10 | 17 |
| | | | | | | | | | |
| 20 | 81 | 51 | 0 | | 20 | 0 | 78 | 0 | 13(13) |
| 20 | 86 | 55 | 0 | | | | | | |
| 20 | 123 | 45 | 0 | | 20 | 90 | 36 | 9 | 20 |
| 20 | 111 | 48 | 0 | | | | | | |
| 19 | 43 | 74 | 34 | 30(16) | 20 | 41 | 47 | 24 | 22 |
| 20 | 53 | 55 | 13 | | | | | | |
| 14 | 58 | 48 | 7 | | | | | | |
| 20 | 58 | 84 | 26 | | | | | | |
| 20 | 78 | 48 | 19 | 40(11) | 20 | 87 | 41 | 24 | 23 |
| 20 | 85 | 83 | 28 | 29(10) | | | | | |
| | 78 | 59 | 13 | 33 | | 54 | 50 | 14 | 20 |

significantly less variable for seed number per capsule. Generally, the fact that individuals of a species show a high degree of variation for one reproductive character does not mean that the species will be more or less variable for the other characters.

There is no overall correlation among species for the coefficients of variation using population samples, except that there was a significant positive correlation among species for the coefficients of variation for weight per seed and seed number per capsule (Table 2).

Correlation analysis was also used to determine if the species showing the most variation for a character using herbarium specimens are also the most variable using population samples. There was no significant correlation between the two sampling methods for inflorescence number per plant ($r = +0.36$, $n = 16$) and capsule number per inflorescence ($r = -0.09$, $n = 16$), but there was a significant correlation for seed number per capsule ($r = +0.68$, $n = 15$, $p < 0.01$). Not enough species were available to compare the variation of weight per seed using the two methods.

Considering that fifteen correlation coefficients are being reported, one significant correlation coefficient would be expected by chance. Since only three correlation coefficients out of fifteen are statistically significant and only two positively so, there appears to be at best a weak relationship between the amount of variation for pairs of characters and for the same character using the two methods.

## DISCUSSION

Populations of restricted species may have more genetic variability than has previously been suspected. Restricted seed dispersal, nearest neighbor pollinations, and local adaptations to the environment may all contribute to a genetically heterogenous population (Levin, 1977; Keeler, 1978). In this case, genetic differences might occur between sub-populations within the population. However, genetic variability may still not allow a population to persist if the environmental changes are beyond the physiological tolerances of the species (Meagher, Antonovics, & Primack, 1978).

The phenotypic variation found within a population is caused by both genetic differences among plants and differences in the immediate environment in which the plants are growing. This study has shown that populations of rare *Plantago* species do not contain less phenotypic variation than populations of common species. If one

Table 2. Correlation coefficients among species using coefficients of variation for inflorescence number per plant (I), capsule number per inflorescence (C), seed number per capsule (S), and weight per seed (W). Sample sizes are given in parenthesis.

For herbarium samples:

| | C | S | W |
|---|---|---|---|
| I | -0.07<br>(28) | -0.55*<br>(28) | -0.01<br>(7) |
| C | — | 0.20<br>(28) | -0.06<br>(7) |
| S | — | | 0.06<br>(7) |

For population samples:

| | C | S | W |
|---|---|---|---|
| I | -0.31<br>(16) | 0.18<br>(15) | 0.21<br>(12) |
| C | — | -0.06<br>(15) | 0.03<br>(12) |
| S | — | | 0.72*<br>(12) |

* $P < 0.01$

assumes that populations of rare species have less genetic variation than populations of common species, then these populations of rare *Plantago* species must have increased environmental variation in order to still have the same overall amounts of phenotypic variation as the common species. This does not seem likely. The equivalent phenotypic variability found in rare and common species probably indicates that populations of these *Plantago* species have similar amounts of genetic variation. If this is true, plant species may be rare more for historical and ecological reasons than for genetic reasons. Further studies comparing the amounts of variation in common and rare species should consider that the amount of variation that a species shows for one character gives no indication as to how much variation that species will show for other characters. Consequently, the results may be strongly affected by the choice of characters.

Rare species are often assumed to be prone to extinction since little genetic variation is available to respond to changes in the environment (see Drury, 1974), for a discussion of this point). However, the botanical evidence to confirm these assumptions is limited. This is surprising since plant species are well suited for answering genetic questions. Individuals of closely related rare and widespread species can be grown from seed under different sets of standard greenhouse conditions and directly measured for their amounts of genetic variability for morphological characters, as suggested by Stebbins (1942). Specific experimental designs for examining and testing differences between species in their amounts of genetic variability have been developed by Lewontin (1966) and Marshall and Jain (1968). In one study where this procedure has been used, the widespread species, *Stephanomeria exigua* ssp. *coronaria* (Compositae), showed more morphological variability than the restricted and recently derived species, *S. "Malheurensis"* (Gottlieb, 1973).

Another promising technique for comparing the genetic variability of rare and common species is electrophoresis to examine enzyme polymorphisms. In comparative studies, this technique has shown that populations of restricted species have less genetic variation than populations of widespread species in the genera *Stephanomeria* (Gottlieb, 1977) and *Lupinus* (Babbel & Selander, 1974). However, enzyme studies must be evaluated cautiously, because only a small part of the genome is being sampled and the technique may not be sensitive enough to separate out similar bands (Johnson, 1977). For example, enzyme studies failed to show differences between populations of *Typha* (Mashburn, Sharitz, & Smith, 1978) and sub-populations of *Veronica* (Keeler, 1978), where greenhouse studies of morphological and physiological characters had shown these units to be different genetically. Consequently, greenhouse studies may still be the most effective way to compare the genetic variability of rare and common species.

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## LITERATURE CITED

BABBEL, G. R., & R. K. SELANDER. 1974. Genetic variability in edaphically restricted and widespread plant species. Evolution **28:** 619–630.

DRURY, W. H. 1974. Rare species. Biol. Conserv. **6:** 162–169.

GOTTLIEB, L. D. 1973. Genetic differentiation, sympatric speciation and the origin of a diploid species of *Stephanomeria*. Amer. J. Bot. **60:** 545–553.

———. 1977. Phenotypic variation in *Stephanomeria exigua* spp. *coronaria* (Compositae) and its recent derivative species "Malheurensis." Amer. J. Bot. **64:** 873–880.

JOHNSON, G. B. 1977. Assessing electrophoretic similarity: the problem of hidden heterogeneity. Ann. Rev. Ecol. Syst. **8:** 309–328.

KEELER, K. H. 1978. Intra-population differentiation in annual plants: II. Electrophoretic variation in *Veronica peregrina*. Evolution **32:** 638–645.

LEVIN, D. A. 1977. The organization of genetic variability in *Phlox drummondii*. Evolution **31:** 477–494.

LEWONTIN, R. C. 1966. On the measurement of relative variability. Syst. Zool. **15:** 141–142.

MARSHALL, D. R., & S. K. JAIN. 1968. Phenotypic plasticity of *Avena fatua* and *Avena barbata*. Amer. Naturalist **102:** 457–467.

MASHBURN, S. J., R. R. SHARITZ, & M. H. SMITH. 1978. Genetic variation among Typha populations of the Southeastern United States. Evolution **32:** 681–685.

MEAGHER, T. R., J. ANTONOVICS, & R. B. PRIMACK. 1978. Experimental ecological genetics in *Plantago*. III. Genetic variation and demography in relation to survival of *Plantago cordata*, a rare species. Biol. Conserv. **14:** 243–257.

PILGER, R. 1937. Plantaginaceae. *In:* A. Engler & L. Diels, eds., *Das Pflanzenreich* Vol. **IV**, 269, (Heft 102). Engelmann, Leipzig.

PRIMACK, R. B. 1976. The evolutionary basis of population dynamics in the genus *Plantago*. Ph.D. thesis, Duke University, Durham.

———. 1978a. Evolutionary aspects of wind pollination in the genus *Plantago* (Plantaginaceae). New Phytol. **81:** 449–458.

———. 1978b. Regulation of seed yield in *Plantago*. J. Ecol. **66:** 835–847.

———. 1979. Reproductive efforts in annual and perennial species of *Plantago* (Plantaginaceae). Amer. Naturalist **114:** 51–62.

ROTHSTEIN, S. I. 1973. The niche-variation model — is it valid? Amer. Naturalist **107:** 598–620.

STEBBINS, G. L. 1942. The genetic approach to problems of rare and endemic species. Madroño **6:** 241–258.

WILD, H., & A. HEYTING. 1966. An analysis of variation of leaf dimensions in *Becium homblei* (De Wild.) Duvign. & Plancke and *Becium obovatum* (E. Mey.) N. E. Br. Botaniska Notisera **119:** 349–357.

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# SPECIES BIOLOGY, THE KEY TO PLANT PRESERVATION

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The enactment of the Endangered Species Act has resulted in the initiation of a number of programs and activities to increase our understanding of rare and endangered species and to promote their preservation. We see, in response to the Act, three types of information being generated: (1) general information mostly associated with list preparation and evaluation; (2) population, habitat, and threat inventories, and species status reports, mostly involved in legal listing and delisting activities; and (3) specialty area oriented studies such as population ecology, reproductive biology, and germination ecology. All such information and studies are of value, but they often give a narrow and disjointed view of a species and its populations.

An overview of our approach to collecting information on endangered species is presented in Table 1. We feel that the four-unit program is a logical progression of activities which result in intermediate products that may be used as the various steps or units are completed. Unit I involves the retrieval of information from herbaria, libraries, and individuals. Completion of this unit requires that we summarize the state of our knowledge on a particular species. Unit II is essentially a population inventory which permits us to up-date, refine, and elaborate on the general information. These field data not only indicate what we have to work with, but allow us to establish priorities for protection, management, and study. The establishment of permanent field plots or sample areas for monitoring purposes should be an integral part of the population inventory. Unit III (Species Biology) requires that we assess at a particular level the biological status of a species at a point in time and recognize important environmental factors. Unit IV involves experimental studies of factors. This unit should be completed when factor identification and analysis seem warranted for species preservation through drastic habitat manipulation.

## SPECIES BIOLOGY

Species biology, the third unit of our program, is one of the major topics of this symposium on Rare and Endangered Plants in New

Table 1. **Overview of Species Information Program**

- Unit I
  - Species General Information
    - Species Taxonomic Status
    - Species Phenology
    - Species Legal Status
    - Historical Distribution
    - Habitat Preference
    - Habitat Development Status

- Unit II
  - Species Population, Habitat, and Threat Inventory Status Information
    - Locality Reconnaissance
    - Authentication of Species
    - Precise Population Location
    - Land Inventory
    - Population Inventory
    - Habitat Inventory
    - Threat Inventory
    - Author Inventory

- Unit III
  - Species Biology Status Information
    - Reproduction Status
    - Dispersion Status
    - Establishment Status
    - Maintenance Status

- Unit IV
  - Environmental Factor Status Information
    - Influence on Reproduction Status
    - Influence on Dispersion Status
    - Influence on Establishment Status
    - Influence on Maintenance Status

England. The brief discussion that follows emphasizes the concepts, principles and values of species biology.

We define species biology as the study of individuals, populations, and population systems of a species utilizing the products, processes, and habitat relationships of each major life cycle phase within a particular time reference. The use of a life cycle model promotes a broad and systematic view of a species and its basic biology, yet is specific in detail and provides an excellent organization for the formulation of basic questions, design of studies, and evaluation of results. The use of a life cycle processes and products approach to life cycle success or failure places emphasis on the basic biology of species and is based on demographic composition of the component populations. This system promotes the detection of many different relationships between life cycle phase processes and products, and the habitat of a species on an interpopulational basis. It also provides a current and sound basis for comparisons between species.

The following concepts or principles have guided the development of our program:

1. Preservation is persistence of populations or species through time with or without habitat manipulation or management.
2. Long-term preservation will often depend on an adequate understanding of the biology and the interrelationships of a species to its habitat.
3. Biological investigation of rare or endangered species should include studies of all life cycle phases on a population by population basis.
4. Life cycle success or failure as assessed by plant products and processes not only indicates how a population or species is faring at a point in time, but may be used to identify significant or limiting environmental factors and relationships.
5. Specific factor manipulation or management may often be required for species preservation.
6. Detailed species biology studies of selected species may be used to make comparisons and generalizations which will allow us to focus more rapidly our research, management strategies, and efforts on other similar species and habitat types.

To implement the Species Biology unit, we have generated a matrix of high priority questions (Table 2). Using this hierarchical matrix of questions, detailed information systems for each major life cycle phase have been developed to assist in the acquisition of information (Whitson & Massey, 1979). A summary of these information categories is presented in Table 3.

## VALUES OF SPECIES BIOLOGY

Although many individuals may object to a systematized approach to the study of rare or endangered species, we feel that in the interest of time and resources, such an approach is desirable.

Table 2. **Question Matrix**
(after Whitson & Massey, 1979)

| **Reproduction** | **Dispersion** | **Establishment** | **Maintenance** |
|---|---|---|---|
| Is reproduction occurring? | Are propagules present? | Are new individuals present? | Is there a range of classes? |
| What types of reproduction are occurring? | What types of viable propagules are present? | What are the origins of the new individuals? | What are the origins of the classes? |
| What breeding systems are operative? | What dispersal systems are operative? | What establishment processes are operative? | What are the %'s of each class in the population? |
| What pollination systems are operative? | What are the dispersal units and or agents? | What are the spatial of establishment processes? | What are the spatial relations of the classes? |
| What is the reproductive capacity or status of the population? | What is the dispersal effectiveness of the population? | What is the establishment effectiveness based on origin? | What is the survivorship of each class progressing to the next class? |

The major values of the Species Biology Unit are discussed below.

1. *Organization of information and information acquisition.* This unit promotes cooperation between investigators and comparability of information from studies, thereby reducing duplication of effort and saving time and resources.

2. *Identification and comparison of operative products and processes, successes and failures, and potential limiting factors of each life cycle phase.* Species biology encourages a holistic view of the species and its habitats. Population to population comparisons result in improve species status reports, an appreciation of unique habitats, a better understanding of interrelationships of population composition and other habitat factors, and a sound basis for population monitoring.

3. *Evaluation and synthesis of results to verify or formulate insights and relationships about the biology, habitat factors and their interrelationship.* Species biology studies should assist us not only in establishing priorities of limiting factors to be investigated in detail, but also in making generalizations about species clusters, population and habitat site types, plant habitat types, and reproductive strategies, which could save time and resources.

4. *Application of biological and habitat information to species preservation.* Species biology studies should give us insight into management techniques such as grazing, burning, weed control, etc., as well as an indication of the effects of land use, forms of protection, and succession patterns on specific populations and species.

## SUMMARY

It is our belief that long term species preservation will require deliberate actions, not simple protection through land acquisition. These protection-management actions should be based on sound biological information on species and their habitats.

Preliminary results from several studies using this approach indicate that a preponderance of rare species are successional, that the predominant means of population persistence is by asexual reproduction, that safe sites for sexual propagules are rare, and that conditions for germination and other establishment processes often differ markedly from maintenance conditions. When one considers

Table 3. **Summary of the Species Biology Information Unit**

| **Reproduction** | **Establishment** |
|---|---|
| Reproductive System Types | New Individual Origin |
| Sexual | Sexual |
| Asexual | Asexual |
| Breeding System Types | Pre-Establishment Processes |
| Selfing | Kind by origin |
| Outcrossing | Distribution |
| Pollination System Types | Establishment Processes |
| Pollination types | Origin census states |
| Vectors | |
| Reproductive Capacity | Establishment Distribution |
| Census by origin | Origin census states |
| Population census | Population census states |
| Reproductive Effectiveness | Establishment Effectiveness |
| Actual | Population percentages |
| Potential | Origin percentages |
| **Dispersion** | **Maintenance** |
| Diaspore System Type | Population Classes |
| Diaspore origin | Specific |
| Diaspore type | Relative |
| Dispersal System Type | Class Origins |
| Release mechanism | Sexual |
| Transport-vector | Asexual |
| Dispersal Status | Population Composition & Distribution |
| Dispersal unit type | Sociability of individuals |
| Dispersal census | Distribution census |
| Dispersal Effectiveness | Maintenance Effectiveness |
| Actual | Class survivorship |
| Expected | Vitality vigor of individuals |

these findings it becomes quite clear, in view of changing land use and rapid habitat destruction, that Species Biology is indeed the key to plant preservation.

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## LITERATURE CITED

WHITSON, P. D. & J. R. MASSEY 1979. Information Systems for use in Studying the Biological Status of Threatened and Endangered Plant Populations. *In:* Morse, J. L. & M. S. Henifin (eds.). Geographical Data Organization for Rare Plant Conservation. New York Botanical Garden, Bronx, New York.

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# POPULATION ECOLOGY OF THE FURBISH LOUSEWORT, *PEDICULARIS FURBISHIAE* S. WATS.

LAZARUS WALTER MACIOR

The Furbish Lousewort is a rare and endangered plant species with a total of about 700 native individuals endemic to the St. John River Valley in Maine-New Brunswick. It was discovered by Kate Furbish in 1880 at Van Buren, Aroostook Co., Maine and described by Sereno Watson (1882) of Harvard University, where Furbish's original herbarium specimens of the species are deposited. A study by Macior (1978) indicated that *Pedicularis furbishiae* prefers calcareous, well-drained, sandy loam of north-facing, relatively stable but eventually transient, river terrace habitats shaded in part by a boreal coniferous forest. It is usually associated with Downy Alder (*Alnus crispa* (Ait.) Pursh), but mature plants of *Pedicularis furbishiae* were not observed to be root parasites as are some other species of *Pedicularis*. It reproduces by seed following pollination by bumblebee workers (*Bombus vagans* Sm.), which forage mostly for nectar but occasionally for pollen polylectically. Present reproductive rates of the plant in the field approximate replacement levels with some potential for population increase. Thus, the expansion of present populations appears immediately limited by availability of suitable habitat.

In view of the fact that *Pedicularis canadensis* and *P. lanceolata* of eastern temperate North America are root parasites (Piehl, 1963 & 1965) and since little is known about seedling development in the genus, the present study was designed to investigate seed germination, seedling development, and possible parasitic relationships in *Pedicularis furbishiae*.

## MATERIALS AND METHODS

Seeds of *Pedicularis furbishiae* were collected from populations at Allagash, Aroostook Co., Maine in the fall of 1977. One portion of seeds ("fall-sown") was surface sterilized for 10 minutes in 100 ml of a 10% commercial Clorox solution to which one or two drops of a liquid detergent were added. The seeds were rinsed several times with sterile water and incubated under sterile conditions on moist filter paper in 100mm × 20mm Petri dishes. The seeds were started on February 13–14, 1978. Cultures were maintained at room temperature under constant illumination. Since only 11 seeds germinated by March 23, the ungerminated seeds were transferred to sterile, moist sand in deep 100mm culture dishes.

A second portion of seed was given a cold treatment by exposure to four 10-day periods at 3° C alternating with four 10-day periods at 18° C, and was sown on March 23 on moist, sterile filter paper as with the fall-sown seed. Only 10 seeds germinated by Mar 31, at which time the remaining seeds were surface sterilized for 1 hr in a 1% Clorox solution, rinsed several times in sterile water, soaked for 24 hr in a 2,000 ppm solution of gibberellic acid ($A_3$), rinsed several times in sterile water and sown on moist, sterile filter paper in Petri dishes.

A third portion of seed was frozen from April 8 until May 23 and treated in the same manner as the cold-treated seeds.

Within 5 days the cold-treated seeds and the frozen seeds germinated abundantly. The fall-sown seed also began rapid germination on June 14. Seedlings were planted in a commercial "Terralite" potting mixture and grown in a controlled environment chamber under a 15 hr day at 400 ft candles and temperatures of 21° C during the day and 18° C at night.

In order to establish sterile cultures of *Pedicularis furbishiae* seedlings, small portions of fall-sown, cold-treated, and frozen seed treated as above were sown individually on sterile nutrient agar (Baslerova & Dvorakova, 1962) containing ammonium nitrate (0.2g), monobasic potassium phosphate (0.1g), magnesium sulfate (0.1g), calcium chloride (0.1g), ferric chloride (0.005g), dextrose (5.0g), and agar (10.0g) in 1 liter of distilled water.

The generally poor growth of *Pedicularis furbishiae* seedlings encountered under all experimental cultural conditions prompted a brief investigation of possible mineral nutrient deficiency. Potted seedlings were regularly nourished with a total of one liter of the following solutions: 0.1g/1 KCl (5 seedlings); 0.005g/1 $FeCl_3$ (6 seedlings); 0.2g/1 $NH_4NO_3$ (4 seedlings); 0.2 $NH_4NO_3$+0.1g $KH_2PO_4$+ 0.1g $MgSO_4$+0.1g $CaCl_2$+0.005g $FeCl_3$/liter (8 seedlings).

The possibility of obligate root parasitism in early stages of development of *Pedicularis* seedlings was investigated by sowing seeds of Crimson Clover (*Trifolium incarnatum* L.) with potted seedlings of *Pedicularis furbishiae* beginning on June 23. At this time all the experimental *Pedicularis* seedlings were small and chlorotic.

## RESULTS

The results on the germination of fall-sown, cold-treated, and frozen seeds are summarized in Table 1. Frozen and cold-treated seeds germinated at higher rates than fall-sown seeds. Since these higher rates of germination may have ben caused by treatment with gibberellic acid, however, the effects of thermal and hormonal treatment cannot be identified separately.

Seed germination in sterile cultures is shown in Table 2. Although all of the fall-sown seeds in sterile culture germinated, the small sample size may not be statistically significant for comparison with the results from the frozen and cold-treated seeds. Seedling growth was initially very rapid. The first true leaves appeared within 10 days of the protrusion of the radicle from the seed coat. In all cases subsequent seedling growth was very slow. The seedlings produced 4 to 6 small chlorotic leaves and suspended further growth. They did not, however, die immediately.

Table 1. **Seed Germination in *Pedicularis furbishiae*.**

| Treatment | Total Sown | Total Germinated | Percent Germination |
|---|---|---|---|
| Fall-sown | 1,045 | 322 | 31 |
| Frozen* | 603 | 541 | 90 |
| Cold-treated* | 636 | 561 | 88 |
| Total | 2,284 | 1,424 | 62 |

*These seeds were also treated with gibberellic acid ($A_3$) at 2,000ppm for 24 hr.

Table 2. **Seed Germination of *Pedicularis furbishiae* in Sterile Culture.**

| Treatment | Total Sown | Total Germination | Percent Germination |
|---|---|---|---|
| Fall-sown | 10 | 10 | 100 |
| Frozen* | 29 | 17 | 59 |
| Cold-treated* | 102 | 82 | 80 |
| Total | 141 | 109 | 77 |

*These seeds were also treated with gibberellic acid ($A_3$) at 2,000ppm for 24 hr.

The slow growth of potted seedlings supplied with supplemental nutrients may indicate that retarded growth was not caused by mineral deficiency. These seedlings remained small and chlorotic and eventually died.

The appearance of *Pedicularis furbishiae* seedlings grown with those of *Trifolium incarnatum* was in striking contrast to that of the controls without Crimson Clover (Fig. 1). The *Pedicularis* leaves expanded greatly, became dark green, proliferated abundantly, and were similar to those of young native plants in the field. This change occurred about 4 to 6 weeks after the *Trifolium* seedlings had become well established. Examinations of the roots of both plants clearly indicated the presence of *Pedicularis* haustoria firmly attached to the *Trifolium* roots. Morphologically and anatomically the haustoria closely resemble those of other *Pedicularis* species (Piehl, 1963 & 1965). The survival rates of *Pedicularis* seedlings with or without the *Trifolium* host are summarized in Table 3. Data were taken 20 weeks after *Trifolium* was sown with *Pedicularis*. The 53% loss of *Pedicularis* seedlings growing with *Trifolium* is in large measure due to the lack of development of haustorial attachments to the host. Eventually all the 97 seedlings that had survived without a host for 20 weeks died.

A preliminary test of wheat (*Triticum aestivum* L.) as a host for *Pedicularis furbishiae* roots gave similar results. Leaves of *Pedicularis* plants grown in association with wheat expanded and turned dark green, while those of the controls remained small and chlorotic.

In the fall of 1978 the older leaves on the surviving *Pedicularis furbishiae* seedlings began to die. Closer inspection revealed the formation of large terminal buds at the crown of each plant. Since these changes suggested the onset of dormancy, the environmental chamber temperature was lowered to a constant 15° C throughout the winter months. In the spring of 1979 the terminal buds expanded to produce short stems with pinnatifid leaves more closely resembling the cauline leaves of flowering plants than those of basal rosettes. Because of the difficulty of maintaining the annual *Trifolium* host with the perennial *Pedicularis furbishiae* seedlings, the latter eventually died.

## DISCUSSION AND CONCLUSIONS

The delay in germination of fall-sown *Pedicularis furbishiae* seeds

Fig. 1. Photograph taken on August 16, 1978 of *Pedicularis furbishiae* seedlings grown from frozen seed treated with gibberellic acid and planted June 8, 1978. Pot at left planted with *Trifolium incarnatum* June 30, 1978. Control without *trifolium* at right.ht. ×0.06.

Table 3. **Parasitic Survival of *Pedicularis furbishiae* Seedlings**

| Host | Total Sown | Total Surviving | Percent Survival |
|---|---|---|---|
| *Trifolium incarnatum* | 486 | 228 | 47 |
| None | 817 | 97 | 12 |

suggests that they may require an extended latent period coinciding with the dormancy period of plants in nature during the winter. Although the possible effect of the application of gibberellic acid to cold-treated and frozen seeds cannot be separated from the effects of low temperature *per se*, it is possible that thermal treatment hastens germination and that the application of gibberellic acid further enhances the process. That neither of these factors is absolutely necessary for germination is indicated by the substantial germination of untreated fall-sown seed.

The demonstration that *Pedicularis furbishiae* is an obligate root parasite in the seedling stage but apparently not obligately parasitic as an adult plant suggests that at early stages in development it requires some chemical component that it cannot synthesize or acquire from the physical environment directly. Since *Pedicularis* in nature grows in nitrogen-poor soil, *Trifolium* was chosen as an experimental symbiont for *Pedicularis* with the thought that nitrogen-fixing bacteria in the clover root nodules may provide a needed nitrogen supplement for seedling development. However, *Pedicularis furbishiae* did parasitize *Triticum* as effectively as *Trifoliium*, so this possibility can be eliminated. Furthermore, since neither of these cultivated host plants is native to the *Pedicularis* habitat, it is quite probable that *P. furbishiae*, like most other species known to be root-parasites (Sperlich, 1902; Maybrook, 1917; Sprague, 1962; Piehl, 1963 & 1965), is not host-specific. If this is so, it has an abundance of potential hosts in the diverse riparian plant community in which it grows.

The curious association of *Pedicularis furbishiae* in its native habitat with the perennial *Alnus crispa*, which is, in turn, obligately associated with an actinomycete on its roots, remains to be investigated. Seedlings of *Alnus* grown without the actinomycete closely resemble the small, chlorotic seedlings of *Pedicularis* without its host (Lalande, pers. comm.). Grown with the actinomycete, *Alnus* exhibits vigorous growth like that of *Pedicularis* growing with *Trifolium* or *Triticum.* The possible reciprocal or unilateral developmental relationship of seedlings of *Alnus crispa* and *Pedicularis furbishiae* in relation to root parasitism is currently under investigation.

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## LITERATURE CITED

Baslerova, M., & J. Dvorakova. 1962. Algarum, Hepaticarum Muscorumque in culturis collectio. Czech. Acad. Sci., Prague. 59p.

Macior, L. W. 1978. The pollination ecology and endemic adaptation of *Pedicularis furbishiae* S. Wats. Bull. Torrey Bot. Club **105:** 268–277.

Maybrook, A. C. 1917. On the haustoria of *Pedicularis vulgaris,* Tournef. Ann. Bot. **31:** 499–511.

Piehl, M. 1963. Mode of attachment, haustorium structure, and hosts of *Pedicularis canadensis.* Amer. J. Bot. **50:** 978–985.

————. 1965. Studies of root parasitism in *Pedicularis lanceolata.* Mich. Bot. **4:** 75–81.

Sperlich, A. 1902. Beiträge zur Kenntniss der Inhaltsstoffe in den Saugorganen der grünen Rhinanthaceen. Beih. Bot. Centralbl. **11:** 437–485.

Sprague, E. F. 1962. Parasitism in *Pedicularis.* Madroño **16:** 192–200.

Watson, S. 1882. Contributions to American botany. Proc. Amer. Acad. **17:** 375.

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# THE STATUS OF THE VERY RARE *PRUNUS GRAVESII* SMALL

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In 1897, J.K. Small described a new species of *Prunus*, naming it in honor of Dr. Charles B. Graves, a Connecticut physician and amateur botanist. Graves discovered this plum on an esker (today known as Esker Point) along the Connecticut shore of Long Island Sound in the town of Groton. Numerous herbarium specimens (Arnold Arboretum, A; University of Connecticut, CONN; Gray Herbarium, GH; and New England Botanical Club, NEBC) the earliest of which I have seen was dated 25 Sept. 1894 (A), were taken of this plant in the years immediately following its description.

*Prunus Gravesii* has received almost no attention in the intervening 82 years since its description. In spite of intensive collecting throughout coastal New England and the New York City-New Jersey area, no other stations for *P. Gravesii* have been found. The stand of *P. Gravesii* at the type locality occupies roughly 60 $m^2$. There are more than 30 large ($>$ 3 cm in diameter) healthy stems reaching a maximum height of about 2.5 m. There are also several young stems around the edges of the stand. The growth form of the Graves Beach Plum looks much like the vegetatively propagated colonies of its closest relative, *P. maritima* Marsh., the Beach Plum. The latter forms colonies by producing shoots from underground runners (roots). Excavations of parts of the *P. Gravesii* stand showed organic connection between the upright stems.

The logical conclusion from this is that *Prunus Gravesii* is indeed very rare; indeed it is represented by a single, relatively large, multi-stemmed individual. According to a note on a herbarium specimen collected by Graves in 1899 (8 Sept., in GH), "This type locality was burned over several years ago, leaving only a few mature shrubs. There are plenty of sprouts but they do *not* flower or fruit." *Prunus Gravesii* thus apparently was, and continues to be, a single vigorous plant.

Rare objects and organisms are of interest for several reasons (Stebbins, 1942; Drury, 1974; see this symposium). In this instance, the question of the nature of origin of the species (*Prunus Gravesii*) is of particular interest, because there is presently only the single, presumably long-persisting, individual. Three questions were formulated which provided the structure upon which the work described below was based. The questions are.

Is *P. Gravesii*—

a) a distinct, but relict species?
b) an interspecific hybrid?
c) a mutant derivative of *P. maritima*?

## MATERIALS AND METHODS

**Morphology**—A total of 38 features were measured, scored, or calculated for *Prunus Gravesii* and *P. maritima.* These features were derived from 10–15 samples of the *P. Gravesii* plant (the mean values were used in statistical tests), and from 40–60 individuals of *P. maritima.* The latter were collected along the coasts of New Hampshire, Massachusetts, and Connecticut. The small stand of *P. maritima* growing adjacent to *P. Gravesii*, and greenhouse-grown seedlings of both *P. maritima* and *P. Gravesii*, were treated as distinct samples for some analyses. See Appendix A for specimen citation. Representative specimens have been deposited in GH. Other specimens are in the author's collection or CONN.

A t-test modified for comparison of a single specimen (*P. Gravesii*) with a sample population (*P. maritima*) was used to test for significant differences (see Simpson et al., 1960, for the test).

**Fertility**—Pollen viability was estimated by staining grains with aniline blue in lactophenol (Hauser & Morrison, 1964). Seed germination was tested using a method modified from the U.S.D.A. "Seeds of Woody Plants in the U.S." (1974). The fleshy exocarp and mesocarp were removed from the fruits, the endocarps dried for a few days, and then planted about 1 cm deep in flats containing a mixture of 1 part sand: 1 part peat. The seeds were stratified as follows: 14 days in sunlight in the greenhouse, and 160 days in a dark cold room (120 days was less satisfactory). Flats were then moved back to the greenhouse. Germination usually followed in 4–6 weeks.

**Crosses and pollination tests**—Hand pollinations to test self- and inter-compatibility were made on flowers which had been enclosed in paper bags (glassine envelopes or Carpenter Paper Co. "Pollen-Tectors") as unopened flower buds. Such bags were also used to enclose flowers to test for automatic self-compatibility and apomixis. Tests for the effectiveness of wind pollination were made by enclosing unopened buds in screen-mesh bags with a pore size of 1.2

mm, i.e., large enough to allow the pollen (35–40 μm diameter) to pass through, but small enough to exclude virtually all potential pollinators. Open pollination was tested simply by counting and marking a large number of unopened buds. For all the above tests, fruit set was counted in late August or early September. More ovaries began enlarging (early June) than developed into full-sized fruits.

**Chromosome analyses** Both mitotic and meiotic divisional figures proved difficult to find. The time of division especially for pollen mother cell meiosis is very critical. Cells divide for only a short period of time about 3 weeks prior (late April 1979) to flowering. Branchlets were fixed in Carnoy's or Newcomer's solutions and stained with aceto-orcein.

Staining proved very difficult for mitotic studies. The most successful technique involved fixing root tips as above, followed by staining first with Schiff's reagent (following hydrolysis in dilute HCl) and then with 1:1 aceto-orcein and 1 N HCl.

**Chromatography** Flavonoids were extracted in 80% methanol from dried leaves of the five species listed below. Two dimensional chromatograms utilizing butanol- acetic acid -water (6-1-2) and acetic acid (5%) were used for separation. The chromatograms were viewed under ultra-violet light, and the positions of spots in the presence and absence of ammonia were recorded. In addition to *Prunus Gravesii* and *P. maritima*, three other species were run for comparison. Two of these (*P. angustifolia* and *P. alleghaniensis*) are morphologically similar to *P. Gravesii* and *P. maritima*, and the third (*P. serotina*) was included as a representative of another subgenus.

## RESULTS

**Phenology**—Although Small (1897) reported that *Prunus Gravesii* preceeded *P. maritima* in some phenological features, in five seasons' observations, I have found the opposite to be true of leaf emergence and flowering. Exact flowering time depends on the season, but, in general, *P. Gravesii* begins flowering 1–2 weeks after *P. maritima*; thus *P. Gravesii* usually flowers in mid to late May. Although *P. maritima* is well past its peak in flowering (in Connecticut) by the time *P. Gravesii* begins, the two flowering periods do overlap. Furthermore, some individuals of *P. maritima* reach their maximum flowering later than the average. E. H. Eames noted such plants at Milford Point, Milford, Ct., which are "about 2 weeks later than abundant normal plants as seen here and elsewhere" (*Eames 11945*, CONN); I have noted the same phenomenon (and perhaps the same plants) at this locality.

**Morphology**—Only four of the 38 characters assayed differ significantly ($P \leq 0.05$) between *Prunus maritima* and *P. Gravesii.* These characters (style length, "seed" size-actually endocarp size, leaf length, leaf length/width ratio) are shown in Fig. I (A–D). The mean values of several other features of the two taxa differ but not significantly. Even for the 4 significantly different characters the standard deviations of *P. Gravesii* in some instances, and the ranges in all instances, overlap those of *P. maritima.* It is of interest to note that for some of the features, the values for *P. Gravesii* seedlings (PG$_S$) and *P. maritima* Esker Point (PM$_E$) are intermediate between those of *P. Gravesii* (PG) and typical *P. maritima* (PM) (e.g., leaf length), and for others, the PG$_S$ and PM$_E$ values are very similar to those of *P. maritima* (e.g., style length, leaf length/width ratio).

The scatter diagram shown in Fig. II couples one significantly different feature with two others which show differences (though not significnt differences) between the two taxa. THis figure has several notable features. First, the *P. Gravesii* points (PG) are quite distinct from the other points. This is in striking contrast to the seedlings of *P. Gravesii* (PG$_S$). The three which flowered fall within the center of distribution of typical *P. maritima*; *P. Gravesii* does not breed true for any of the characters examined. *Prunus maritima* from Esker Point (PM$_E$), as expected, also scattered throughout the PM points. Also the range of variation for *P. maritima,* which is derived from several genetically independent indidivuals, is much broader than that of *P. Gravesii.*

**Pollen fertility**—*Prunus Gravesii* exhibits a degree of pollen stainability which is on the average as high as or higher than that of *P. maritima* (Fig. III). The range of stainability for *P. Gravesii* is greater than for any other group tested, but the mean and standard deviation are reasonably close to those of the other groups tested. In fact, the few greenhouse-grown seedlings of *P. Gravesii* (PG$_S$) showed a significantly higher stainability than the seedlings of *P. maritima* (PM$_S$). The *P. maritima* growing in the vicinity of *P. Gravesii* (PM$_E$) manifested the highest stainability of any of the groups tested.

**Seed fertility**—The data in Table 1 indicate that both *Prunus Gravesii* and *P. maritima* show relatively high seed germination in

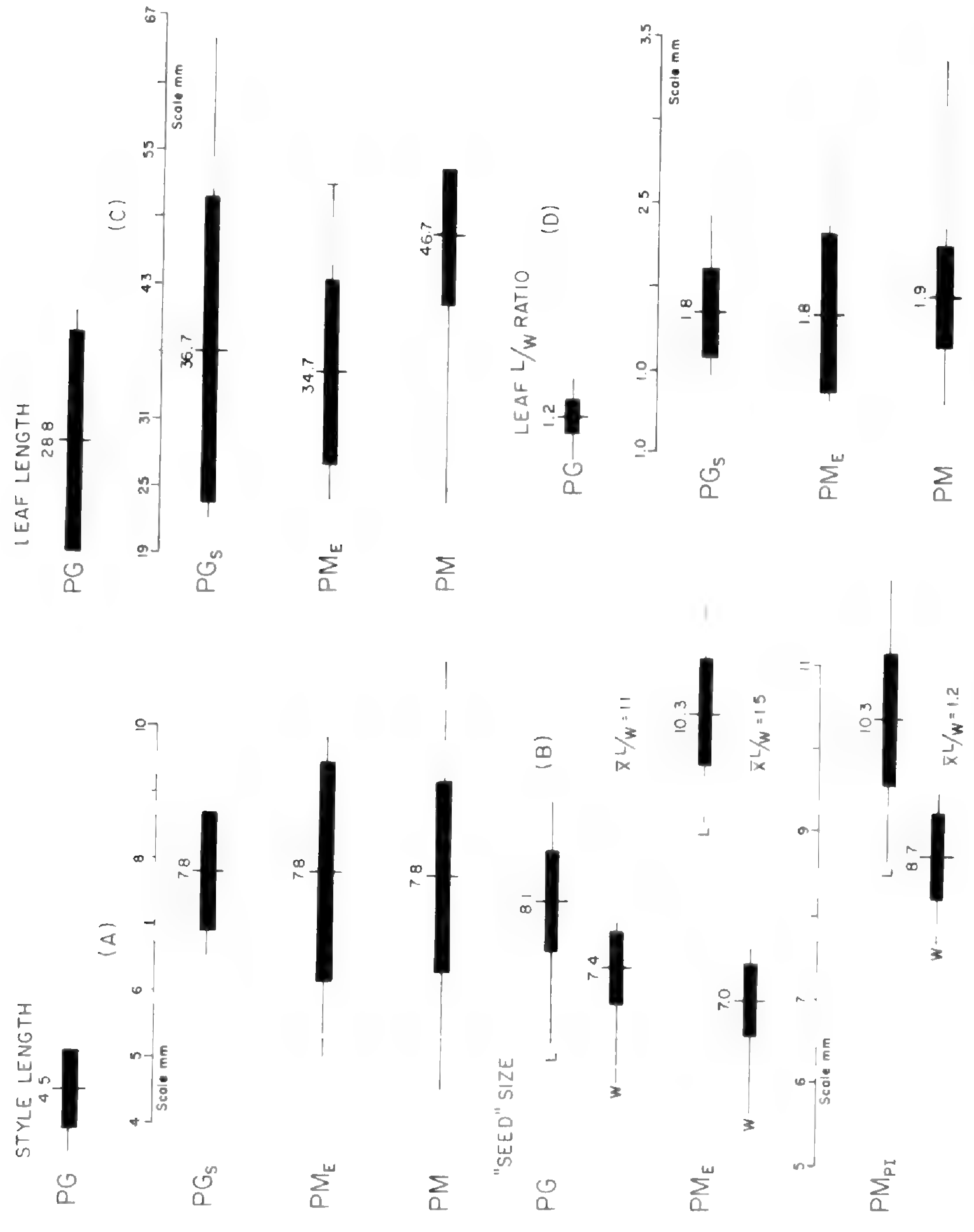

Figure I. Statistically significant morphological differences between *P. Gravesii* and *P. maritima*. PG-*P. Gravesii*, PG$_S$-greenhouse-grown seedlings of *P. Gravesii*, PM-*P. maritima*, PM$_E$ *P. maritima* from Esker Point, Ct., PM$_{PI}$-*P. maritima* from Plum Island, Mass. For all 4 features (A D), the following are given: mean (vertical line and number), range (thin horizontal line), and standard deviation (broad horizontal line).

the first year following planting. As mentioned above, the seedlings of *P. Gravesii* ($PG_S$) are morphologically similar to *P. maritima*, and not to *P. Gravesii*. Such morphology has been maintained by two- and three-year old seedlings as well.

**Breeding system and crossability**—Both *P. Gravesii* and *P. maritima* are protogynous. Frequently the styles and expanded stigmas of *P. maritima* are long-exserted from unopened buds. In some *P. maritima*, and in *P. Gravesii*, the styles are not exserted from the bud, but the stigmas appear fully expanded and receptive before the

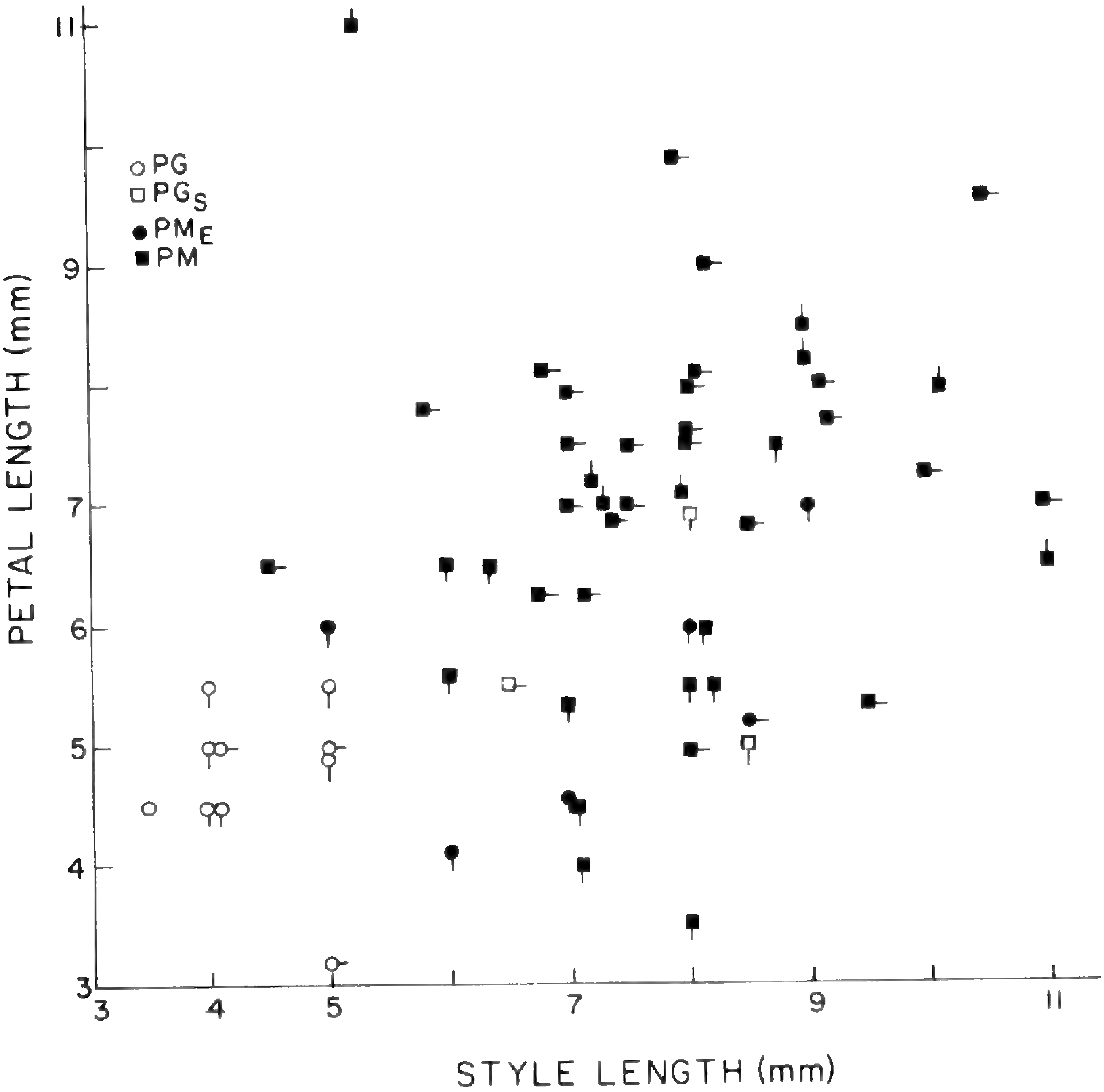

Figure II. Scatter diagram of selected floral features. The abbreviations with the symbols are the same as for Fig. 1. The whisker represents sepal length; ♀ 2.0 mm or less, O-2.1-3.0 mm, ♂ 3.1 mm or more. The PG points represent different flowers from the same plant; all other points represent different individuals.

anthers dehisce. The flowers of both *P. maritima* and *P. Gravesii* are of the "dish-bowl" type and bear nectar at the base of the hypanthium. As a result of their generalized shape, flowers are visited by, and pollination is apparently accomplished by, a range of insects including honey bees, native bumble bees, and other small bees. Ants and non-hymenopterans have also been seen in the flowers.

Efficiency of pollintion and fruit set have been tested over a period of three years. The results of these studies are given in table 2. Several features are noteworthy:

1) Fruit set per flower is very low in both *P. maritima* and *P. Gravesii;* it falls below 1% in all cases (see "controls") except where artificial hand-pollinations were involved.
2) Both *P. Gravesii* and *P. maritima* are self-incompatible. Except for the single fruit set for *P. Gravesii* (1976) which on planting did not germinate, none of more than 900 flowers that were self-pollinated by hand resulted in fruit set. Furthermore, none of the nearly 2500 additional flowers enclosed in paper bags resulted in fruit. These also represent in part a test of self-incompatibility because over 25% of the *P. maritima* flowers and over 50% of the *P. Gravesii* flowers possess styles which bend back to the anthers in such a way that at least some of them are self-pollinated.
3) The lack of fruit set by either *P. Gravesii* or *P. maritima* flowers covered by screen bags seems good evidence that neither species is anemophilous.
4) In *P. maritima,* hand pollinations between individuals ("sisters") yielded a large increase in fruit set over controls. One of the resulting seeds germinated.
5) Crosses made between PM×PG with *P. Gravesii* as the pollen parent were also successful. Although the resultant seeds were full-sized, none have yet germinated. Although no "sister" crosses could be performed with *P. Gravesii* (there is only the single individual), a single cross with a *P. maritima* pollen parent (and *P. Gravesii* as the female) was successful. However, the resulting seed did not germinate.

**Chromosome number and behavior** Counts of chromosomes in mitosis indicated that *Prunus Gravesii* is a diploid with $2n = 16$. This is the same chromosome number as reported for *P. maritima*

(Sax, 1931), and for the majority of *Prunus* species (Federov, 1969). The chromosome number was also verified in analysis of pollen mother cell meiosis. In addition, as expected based on the relatively high fertility estimates (pollen stainability), no gross abnormalities of structure or pairing were detected in meiotic cells.

**Chromatography**– The chromotograms (Fig. IV) show *P. Gravesii* to be identical with *P. maritima;* all compounds are shared, with two not found in any of the other 3 species tested. Surprisingly, *P. angustifolia* is more similar to *P. serotina* (85% of the compounds are shared) than it is to either *P. maritima - Gravesii* or to *P. alleghaniensis* (about 30% of the compounds shared). As pointed out above, the latter three species and *P. angustifolia* are morphologically similar. *Prunus alleghaniensis* has more spots in common (about 50%) with *P. angustifolia - serotina* than it does with *P. maritima - Gravesii* (about 30% shared).

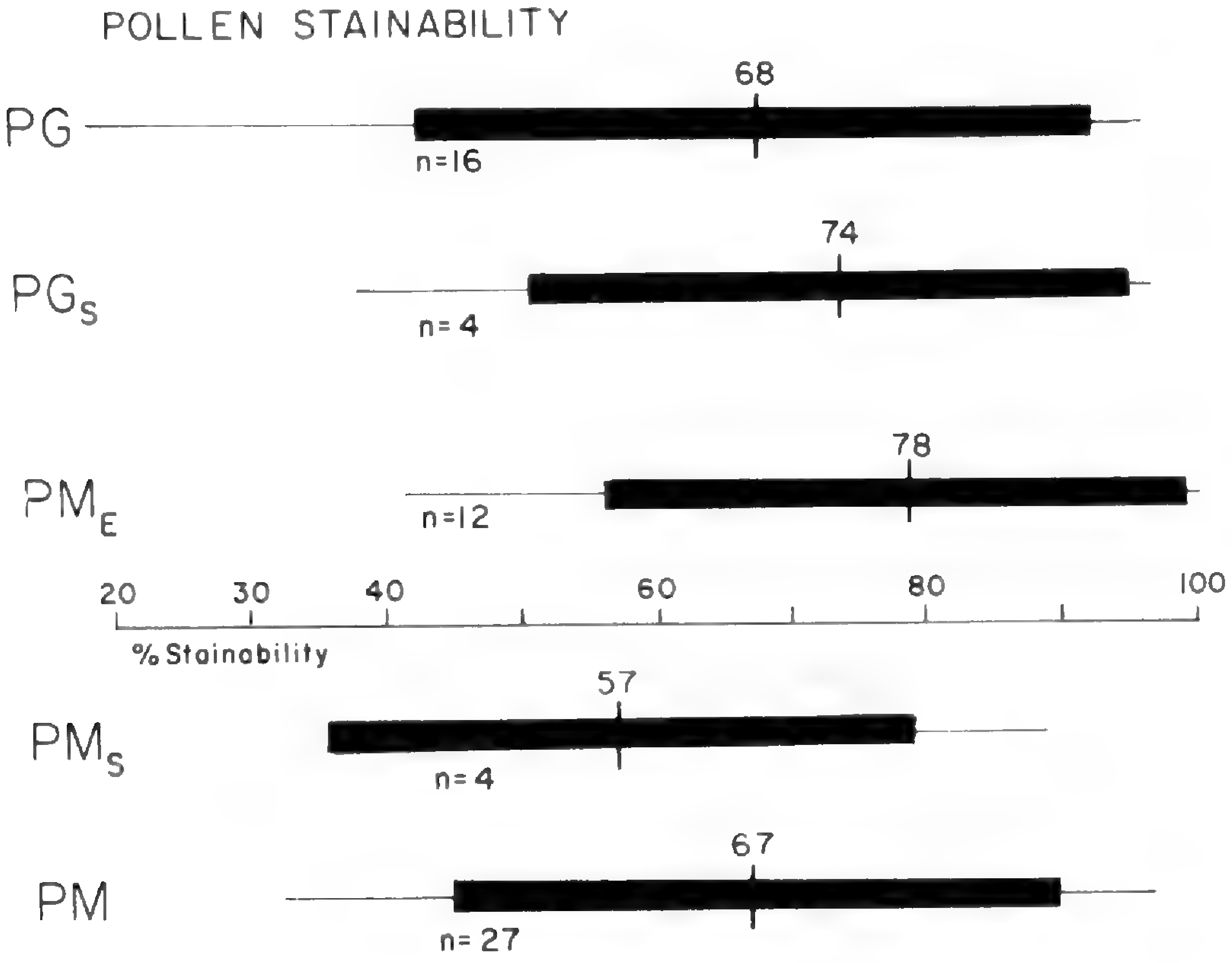

Figure III. Pollen stainability. The lines and bars represent means, ranges and standard deviations (as in Fig. I) of the percent stainability. $PM_S$-greenhouse-grown seedlings of *P. maritima*. The sample sizes are for different individuals except for PG where the sample is of different flowers from the same individual.

The colors of the compounds under ultra-violet light in the presence and absence of ammonia are given in Appendix B.

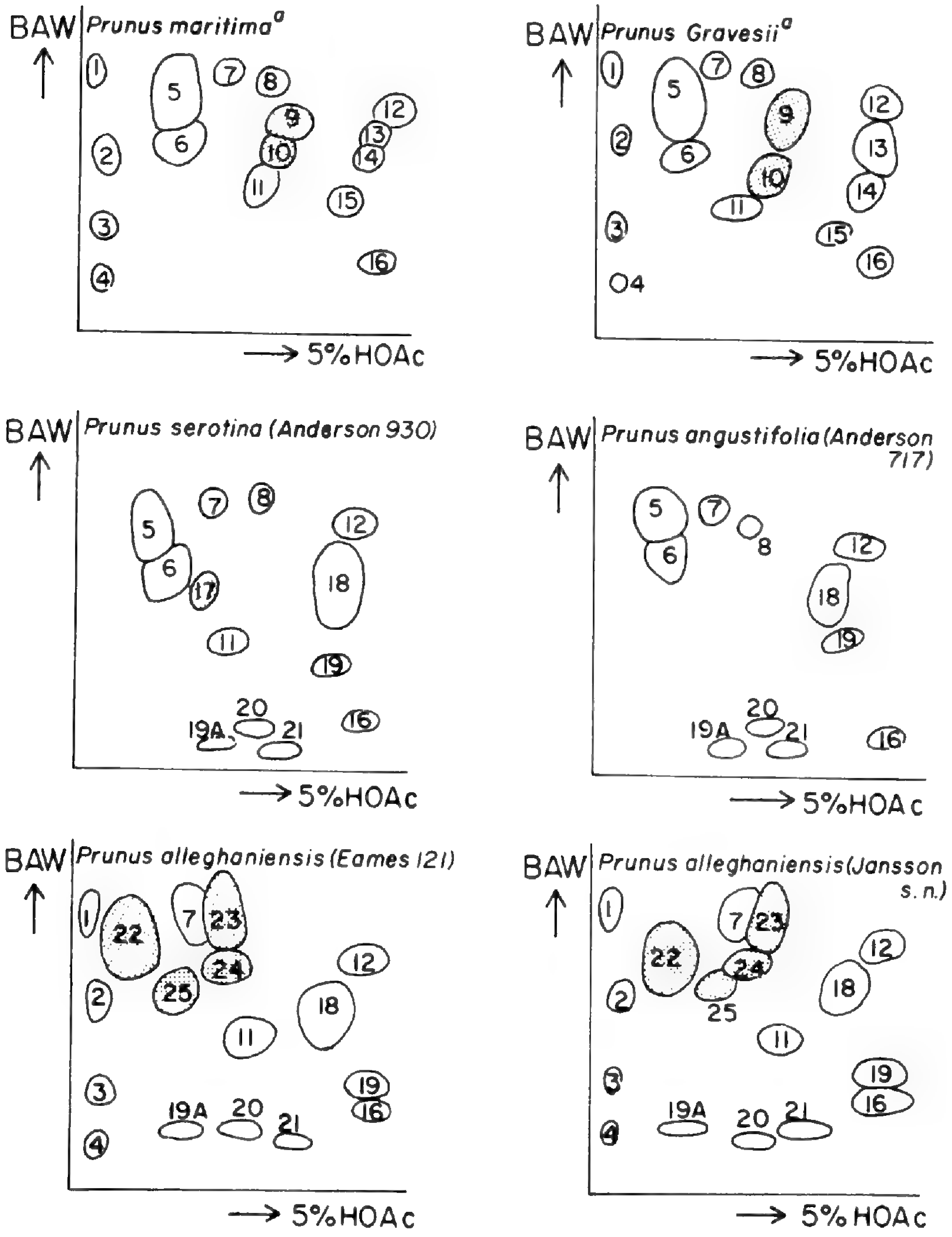

Figure IV. Chromatographs. BAW-butanol-acetic acid-water (6-1-2), HOAc-acetic acid. Spots with stippling are unique to the species (or species groups) given. a- numerous specimens were tested for each of these species.

## DISCUSSION AND CONCLUSIONS

It is perhaps most appropriate here to return to the 3 questions posed in the introduction.

a) Is *Prunus Gravesii* a distinct, but relict species?

Certainly *P. Gravesii* has a sufficient array of morphological distinctions to justify its recognition as a separate species. Some taxa in other groups are distinguished by fewer differences. Furthermore, *P. Gravesii* is both pollen and seed fertile. However, intensive collecting has never yielded any other individuals of *P. Gravesii* than the one in Connecticut, and for whatever reason (see below) *P. Gravesii* does not breed true. The *P. Gravesii* plant has been growing vigorously in the same place for more than 85 years (Graves' first known collection is 1894) without leaving any recognizable offspring. Thus, although *P. Gravesii* is morphologically distinguishable, it is represented by one individual and has not achieved any means by which to reproduce itself. Given these factors, *P. Gravesii* can hardly be recognized as a distinct species.

The next two possibilities are best considered together because the same data are appropriate for distinguishing between them.

b) Is *P. Gravesii* of hybrid origin?

c) Is *P. Gravesii* simply a mutant derivative of *P. maritima*?

*Prunus Gravesii* undeniably appears to be quite distinct from *P. maritima,* but when the distinctions between them are critically analyzed, there are few which "hold up". Small (1897) cited 6 differences (several of which were provided by Graves, since Small apparently did not see the living plant) betwen *P. Gravesii* and *P. maritima.* These differences together with comments are given below.

1.a) "maximum height of about 12 decimeters" as compared with *P. maritima,* which is up to 2.5m high—perhaps in the late 1800's, but today the plants are nearly twice that size.

b) *Prunus Gravesii* plants are lower and more delicate and the leaves and fruits mature earlier than *P. maritima.* The first part of the statement is not true of *P. Gravesii* today, and, although I am not sure about fruit maturity, 5 years of observations confirm that *P. Gravesii* leafs out, and flowers later than *P. maritima.*

2. *Prunus Gravesii* has a "small orbicular type of leaf"—this remains the best feature for distinguishing the two taxa.

3. *Prunus Gravesii* has "smaller flowers with suborbicular petals" which are "abruptly narrowed at the base". The flowers of *P. Grave-*

Table 1. Seed germination.

SEED GERMINATION

| YEAR | *P. Gravesii* | | *P. maritima* | |
|---|---|---|---|---|
| | PLANTED | GERMINATED | PLANTED | GERMINATED |
| 1978-79 | 136 | 35 | 330 | 96 |
| 1977-78 | 138 | 80 | 312 | 112 |
| 1976-77 | 47 | 19 | 925 | 508 |
| 1975-76 | 22 | 3 | 457 | 80 |
| TOTALS | 343 | 137 | 2024 | 796 |
| %GERMINATION | 39.9% | | 39.3% | |

*sii* do have a lower mean size than those of *P. maritima*, but the sizes are not significantly different, nor are the petal bases of *P. Gravesii* much different from those of *P. maritima*.

4. *Prunus Grvesii* has a "small very turgid stone". The *P. Gravesii* endocarps assayed in this study were significantly smaller than those of *P. maritima*, but did not differ in length/width ratio.

5. *Prunus Gravesii* has a "smaller, always globose, short pedicelled drupe". I did not measure exocarp size or fruiting pedicel length. However, flowering pedicels of *P. Gravesii*, although shorter on the average, are not significantly shorter than those of *P. maritima*.

6. *Prunus Gravesii* "Sprouts arising from the ground never produce flowers". I am not sure of either the validity or value of this distinction.

Thus, only 2 (possibly three if drupe length follows endocarp length) features from the above list serve to distinguish *Prunus Gravesii* from *P. maritima*. Additionally, I found 2 other characters which show statistically significant differences: leaf length (a manifestation of shape) and style length. Given that chromosome number, habit, habitat, and leaf flavonoids also are not different, the two taxa can be recognized by only the above 4 features. Furthermore, in all of these 4 features the range of *P. maritima* overlaps

Table 2. Fruit set. a. self-pollinations, b. buds enclosed in pollen-proof bags, c. buds enclosed in screen bags, d. crosses between different individuals of the same species, e. crosses between the 2 species; crosses are listed with the species used as the female parent.

| | FRUIT SET | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ⊗[a] | | BAGGED[b] | | WIND[c] | | CONTROL | | SISTERS[d] | | PMxPG[e]<br>PGxPM | |
| SPECIES | FLS | FRS | FLS | FRS | FLS | FRS | FLS | FRS | FLS | FRS | FLS | FRS |
| P M | | | | | | | | | | | | |
| 1978 | 134 | 0 | 953 | 0 | 1123 | 0 | 4737 | 16 | 27 | 2 | 72 | 3 |
| 1977 | 113 | 0 | 373 | 0 | 170 | 0 | 7439 | 81 | 1 | 0 | | |
| 1976 | 197 | 0 | 117 | 0 | 112 | 0 | 473 | 1 | | | 111 | 0 |
| TOTALS | 444 | 0 | 1443 | 0 | 1293 | 0 | 12649 | 98 | 28 | 2 | 183 | 3 |
| % | | | | | | | | 0.78% | | 7.14% | | 1.64% |
| PG | | | | | | | | | | | | |
| 1978 | 135 | 0 | 682 | 0 | 396 | 0 | 1669 | 0 | | | 78 | 0 |
| 1977 | 57 | 0 | 89 | 0 | 40 | 0 | 2574 | 24 | | | 35 | 1 |
| 1976 | 276 | 1 | 252 | 0 | | | 859 | 0 | | | 137 | 0 |
| TOTALS | 468 | 1 | 1023 | 0 | 436 | 0 | 5102 | 24 | | | 250 | 1 |
| % | | 0.21% | | | | | | 0.47% | | | | 0.4% |

by 1/3 to 2/3's that of the range of *P. Gravesii.* The only unequivocally distinctive feature of *P. Gravesii* is the shape of the leaves; no leaves of *P. maritima* are orbiculate with truncate apices. In light of these morphological data and of the relatively high seed and pollen fertility of *P. Gravesii,* it is not unreasonable to conclude that it originated by one or very few mutation(s) from *P. maritima.* The range of morphological variation of *P. maritima* clearly encompasses much of that of *P. Gravesii.* Further, as noted in the Phenology section, notable later flowering individuals of *P. maritima* (simultaneous with the peak of blooming of *P. Gravesii*) have been recorded. Thus, in total, the differences between the two taxa are such that *P. Gravesii* can be considered to have arisen by mutation from *P. maritima.*

On the other hand, many of these data would not be incongruous with the hypothesis that *Prunus Gravesii* is a hybrid. Such an origin cannot be ruled out with certainty. If *P. Gravesii* were self-compatible, or if there were two individuals, it would be possible to look at the segregation, or lack of it, in offspring for several characters and thus attain stronger evidence for or against a hybrid origin. It is theoretically possible to distinguish between the segregation ratios of: a) a backcrossing hybrid or, b) a mutant form crossing with a typical form. However, given the paucity of differences between the two taxa that one could follow, and the lack of any information on the genetic basis of characters in *P. maritima* (or *P. Gravesii*), it seems unlikely that such data even from large populations would enable one to reach a definite conclusion. However, for the following reasons, I am inclined to consider a hybrid origin to be less likely at this point:

a) *P. Gravesii* is as fertile as *P. maritima.*
b) *P. Gravesii* is chemically identical with *P. maritima.*
c) The distinctive morphological features of *P. Gravesii* are not clearly indicative of features of any other *Prunus* species in the northeast U.S. The species which have leaves that are more orbiculate (e.g., *P. mahaleb* or *P. armeniaca*) have other characteristics which do not appear in *P. Gravesii.*

The chemical data are most unequivocal. Not all interspecific hybrids are necessarily sterile, and transgressive variation might explain the development of fetures found in no other species, but, in many instances (e.g., Alston & Turner, 1963) chemical profiles have clarified the hybrid nature of plants or populations which were otherwise not detected. The fact that other related species of *Prunus* do have recognizably distinct flavonoids which are not present in *P. Gravesii,* and the fact that the latter is chemically identical with *P. maritima* make it even less likely that *P. Gravesii* originated through hybridization.

**Conclusions**—The acceptance of *Prunus Gravesii* as simply a mutant derivative of *P. maritima* allows for some interesting speculations. The self-incompatibility of *P. Gravesii* means that it must depend on *P. maritima* as a pollen source. This would explain why the morphology of *P. Gravesii* seedlings is more similar to that of *P. maritima* than it is to the female parent. The fact that *P. Gravesii* seeds germinate at a rate equal to that of *P. maritima,* and that the former has been growing for more than 80 years, suggests that offpsring should exist somewhere. Given the somewhat aberrant morphology of some of the *P. maritima* plants at Esker Point ($PM_E$), it seems reasonable to consider that they are *P. Gravesii* offspring. The mean values for several morphological features (e.g., leaf length, petal length, sepal length) of $PG_S$ and $PM_E$ are very similar and intermediate betwen those of typical *P. maritima* and *P. Gravesii.*

The entire individual of *P. Gravesii* is today, and apparently was when Graves studied it at the close of the 19th century, uniform throughout. That is, no stems of *P. maritima* type morphology grow close enough to be considered part of it. Thus, it would sem most likely that the mutation or mutations which gave rise to *P. Gravesii*: a) took place in a flower yielding the single *P. Gravesii* seed, or possibly b) some environmental extreme caused somatic mutations in a seedling of *P. maritima*. In either case, because the range of variation in *P. maritima* encompasses most of that found in *P. Gravesii* for most features, it is not necessary to postulate many mutations to yield *P. Gravesii*. If pleiotropic effects of genes are considered, perhaps several distinctive features of *P. Gravesii* (e.g., those dealing with different lengths) are attributable to a few or even a single gene.

If *P. Gravesii* can no longer be recognized as a species, should it be considered for protection? It does not fit into the usual categories for protection of endangered species; it is not a species. However, I would argue for its protection on the grounds that it is no less interesting now than prior to this work. In fact, recognition of its long persistence, and an understanding of its possible origin make it perhaps even more valuable to protect. Furthermore, *P. Gravesii* may exemplify the kind of event that occurs more commonly than expected in nature. Possibly some other rare species are likewise narrowly distributed mutant variants, or morphological, or physiological, or ecological extreme types of more well-established species. In *P. Gravesii,* and perhaps in some other rare taxa, distinctive attributes, sufficient to warrant recognition as a species are acquired, but isolating barriers have not developed in the process of speciation. In addition, a breeding system capable of perpetuating *P. Gravesii* is also lacking. The adaptive value of the distinctive morphological features of *P. Gravesii* has not been tested beyond the single individual bearing them. Thus, *P. Gravesii* is perhaps worthy of protection as a well-documented illustration of the kind of event which occurs more frequently in nature than is generally detected or recognized.

*Prunus Gravesii* will be formally recognized as a variety of *P. maritima* in a subsequent note.

## SUMMARY

*Prunus Gravesii* is among the rarest species in the northeast U.S. It has been represented by a single, long-lived individual since its

discovery. The plant from which the species was described by J.K. Small in 1897 still grows vigorously. *Prunus Gravesii* differs from its closest relative, *Prunus maritima*, by only 4 statistically significant morphological features. Both species have $2n = 16$ chromosomes, are intercompatible, and share a virtually identical array of leaf flavonoids. *Prunus Gravesii* is insect pollinated, self-incompatible, and is both pollen and seed fertile. However, seedlings of *P. Gravesii* resemble *P. maritima*. It is concluded that *P. Gravesii* is a mutant derivative of *P. maritima*, which depends on the latter as a pollen parent. *Prunus Gravesii* is best treated as a variety of *P. maritima*.

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## LITERATURE CITED

ALSTON, R. E. & B. L. TURNER. 1963. Natural hybridization among four species of *Baptisia* (Leguminosae). Amer. J. Bot. **50:**159–173.

DRURY, W. H. 1974. Rare species. Biol. Conserv. **6:**162–169.

FEDEROV, A. A. (ed.). 1969. Chromosome numbers of flowering plants. Academy of Sciences of the U.S.S.R., V.L. Komarov Botanical Institute.

HAUSER, E. J. P. & J. H. MORRISON. 1964. A cytochemical reduction of nitro blue tetrazolium as an index of pollen viability. Amer. J. Bot. **51:**748–752.

SAX, K. 1931. The origin and relationships of the Pomoideae. J. Arnold Arbor. **12:**3–22.

SIMPSON, G. G., A. ROE, & R. C. LEWONTIN. 1960. Quantitative Zoology. Harcourt, Brace & World, Inc., N.Y.

SMALL, J. K. 1897. An apparently undescribed species of *Prunus* from Connecticut. Bull. Torrey Bot. Club. **24:**44–45.

STEBBINS, G. L., JR. 1942. The genetic approach to problems of rare and endemic species. Madroño **6**:241-272.

U.S. DEPARTMENT OF AGRICULTURE, FOREST SERVICE. 1974. Seeds of woody plants in the United States. U.S. Dep. Agric., Agric. Handb. **450.**

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## APPENDIX A

The following are localities and representative collections from which population samples were taken.

*Prunus alleghaniensis*
  Connecticut
    Fairfield County: Bridgeport; *E.H. Eames 121.* (CONN).
    New London County: Cultivated, Connecticut College Arboretum, New London; *K.P. Jansson s.n.*, 9 Sept. 1933, (CONN).

*Prunus angustifolia*
  Connnecticut
    New London County: Occum; *W. Linke s.n., Anderson 717* (CONN).

*Prunus Gravesii*
  Connecticut
    New London County: Esker Point, Groton: *Anderson 526, 562, 580, 621, 719.*

*Prunus maritima*
  Connecticut
    New London County: Esker Point, Groton; *Anderson 525, 563, 564, 581, 582, 720.*
      Barn Island; *Anderson 561.*
      Bluff Point, Groton; *Anderson 527, 622.*
      Griswold Point, Old Lyme; *Anderson 525, 536, 537.*
    New Haven County: Milford Point, Milford; *Anderson 528, 529, 530, 532.*
      New Haven; *Anderson 534*
  Massachusetts
    Essex County: Parker River Wildlife Sanctuary, Plum Island; *Anderson 544-558, 586-588, 591-597.*
  New Hampshire
    Rockingham County: Seabrook Beach; *Anderson 598-611.*
  Rhode Island
    Washington County: Misquamicut; *Anderson 538, 539, 540, 620.*
      Weekapaug; *Anderson 560.*

*Prunus serotina*
  Connecticut
    New London County: Esker Point, Groton; *Anderson 930.*

## APPENDIX B

Color changes of chromatographic compounds under ultraviolet light following fuming with ammonia. 1. yellow→yellow. 2. yellow→yellow. 3. yellow→bright yellow. 4. yellow→no change. 5. dark mauve→bright yellow. 6. dark mauve→bright yellow. 7. pale blue→blue. 8 pale blue→pale mauve. 9 bright yellow→orange yellow. 10. bright yellow→orange yellow. 11. dark mauve→yellow green. 12. dark blue→bright blue. 13. bright blue→green blue. 14. green→bright green. 15. yellow→bright yellow. 16. mauve→bright mauve. 17. pale yellow→yellow. 18. pale blue→bright blue. 19. blue→blue. 19A. dark→yellow. 20. mauve→mauve. 21. dark→yellow. 22 blue-green→blue. 23. dark→yellow. 24 dark→yellow. 25. dark→yellow.

# THE LIFE HISTORY AND ECOLOGY OF *POTENTILLA ROBBINSIANA*

RAYMOND E. GRABER

Plants with restricted distributions have received increasing attention recently because of their obvious vulnerability. *Potentilla robbinsiana* Oakes (*ex* Torrey & Gray, 1840) is an extreme case in that it survives, in significant numbers, on a single site in the alpine zone of Mt. Washington. This refugium consists of a single hectare of barren landscape bisected by one of the most heavily travelled paths in North America, the Appalachian Trail.

*Potentilla robbinsiana* was discovered by James Robbins in 1829 (Pease, 1917) and described by the botanist-explorer William Oakes (Torrey & Gray, 1840).

But even before its discovery, *Potentilla robbinsiana* had felt the hand of man. Abel Crawford built his famous path (now part of the Appalachian Trail) through the center of the *P. robbinsiana* colony in the summer of 1819 (Burt, 1960). In 1840, the trail was converted to a bridle path opening the way to horseback parties. We have no knowledge of changes in the trailside *P. robbinsiana* population during the 1800's. It is likely that most travellers of that day were unaware that they were trampling the small *P. robbinsiana*.

The quest for new information on the distribution of plants, coupled with the collecting of herbarium specimens, also took a toll in the 1800's. Some 40 herbarium sheets, containing more than 100 plants, have been counted in the various herbaria in New England.

Edward Tuckerman made collections of *Potentilla robbinsiana* at two locations, both now extinct. One was made in 1839 on a "stony tract on the northeast side of the peak of Mt. Washington." This is in the vicinity of the location on which the Mt. Washington Toll Road was constructed in the summer of 1861 (Burt, 1960). Tuckerman's other collection was made at Mt. Mansfield, Vermont. No other known collection of the plant was ever again made at either of these sites.

Much later, *Potentilla robbinsiana* was found in the Franconia Range at two locations, a north station in 1897 by F. Endicott and a south station in 1915 by M. L. Fernald (Steele, 1964). The north station has not been relocated in nearly 65 years and is undoubtedly extinct. The south station was relocated by Steele in 1963; it consisted of only 3 small clumps of plants. This station has not been found since 1965 and Steele (personal communication), after searching the area in 1979, believes the plants are dead.

In 1970, Donald White discovered a colony consisting "of only a few plants" at an undisclosed location in Vermont (Countryman, 1978). These few plants in Vermont are now believed to be the only natural population of the plant apart from the Appalachian Trail colony on Mt. Washington.

Little was known of the population stability at the Appalachian Trail *Potentilla robbinsiana* colony on Mt. Washington until very recently. Steele (personal communication) has estimated that the plants are confined to about ¼ of the territory they occupied in 1934. Harris (personal communication) observed *P. robbinsiana* growing on both sides of the trail as recently as 1965. By 1972, the plant was gone from that part of the barren to the west of the trail. On the east side, the nearest plant is now 8.6 meters from the edge of the trail.

The purpose of my research was to study the life history and ecology of *Potentilla robbinsiana* and to document the population changes of the colony on Mt. Washington. I hoped to discover the causes of its decline and to suggest protective measures which would ensure its survival.

The *Potentilla robbinsiana* colony on Mt. Washington grows on a fell-field with a stony pavement, subject to frost heaving in every month of the year. The stony surface layer protects the loamy sand soil from the high winds and severe storms that would otherwise blow or wash it away. The soil is derived from fine-grained mica schist bedrock and is weakly calcareous (Löve & Löve, 1965; Fowler, 1971).

*Potentilla robbinsiana* is a very low, almost stemless plant with a dense tuft of leaves above the ground and a deep taproot beneath it. The dense rosette of compound leaves consists of toothed leaflets in threes. In the early spring, there is no sign of life, only the rosette of last year's dead leaves. The new leaves begin development in May. Occasionally, after unusually warm weather, a few flowers will bloom during the last week of May. In most years, flowering begins during the first week of June, peaks between the 10th and 20th, and is complete by the 26th of June (Figure 1). An occasional blossom

Figure 1. *Potentilla robbinsiana* flowers in mid June. The leaf rosette diameter of this plant is 2.4 cm and its age is estimated at 15 to 25 years.

can be found almost anytime until October. No plants with a leaf rosette diameter of less than 1.4 cm was ever observed to flower.

An important objective was to determine the area occupied by the *Potentilla robbinsiana* colony. I mapped the exact location of each plant growing on the perimeter of the colony (Figure 2). While the fell-field habitat was approximately 1 hectare in size, the *P. robbinsiana* occupied only 1142 m$^2$ or about 1/10th of it.

The entire 1142 m$^2$ was searched carefully and all *Potentilla robbinsiana* of flowering size (rosette diameter of 1.4 cm or larger) were counted. I found 1801 plants. Fifty-eight 1-m$^2$ quadrats were randomly distributed over the area to measure the size distribution of the population. The population consisted of 3721 established plants, 52% of which were less than 1.4 cm in diameter or non-flowering (Figure 3).

An additional component of this population was the newly germinated plants less than one year old. I found 772 newly germinated seedlings during a single growing season, yet only 328 remained at the end of the first summer. The total plant population at the end of the growing season was then 4,049.

About 50 to 75% of the mature plants flowered each year producing an average of three (3.1) flowers each. However, a single large plant was observed to produce as many as 30 flowers. Löve and Löve (1965) believe that *Potentilla robbinsiana* produces seed through apomixis. The smooth green achenes, clustered in the dried flower heads, are apparent by the end of June. The maturation of the seeds, in mid to late July, was signaled when the seed coat turned brown (Figure 4). The average fruiting plant produced 21 viable seeds (range 1–115). The total seed production of the entire colony averaged approximately 24,000 viable seeds. Seed viability was high, averaging 90.4%. The mean weight of an oven—dried viable seed was 20 $\mu$g. The seeds were dispersed by simply falling to the ground on dry, windy days. Seldom did a seed travel more than a few centimeters. In no case were new seedlings ever discovered more than 14 cm from the mother plant. For this reason, the plants tend to be clustered and very slow to become reestablished if eliminated from some part of their natural habitat. The seeds germinate, after overwintering, in June and July. It appears to me that a major portion of the seeds produced annually germinate, but do so under less than favorable conditions, and quickly die. Approximately 800

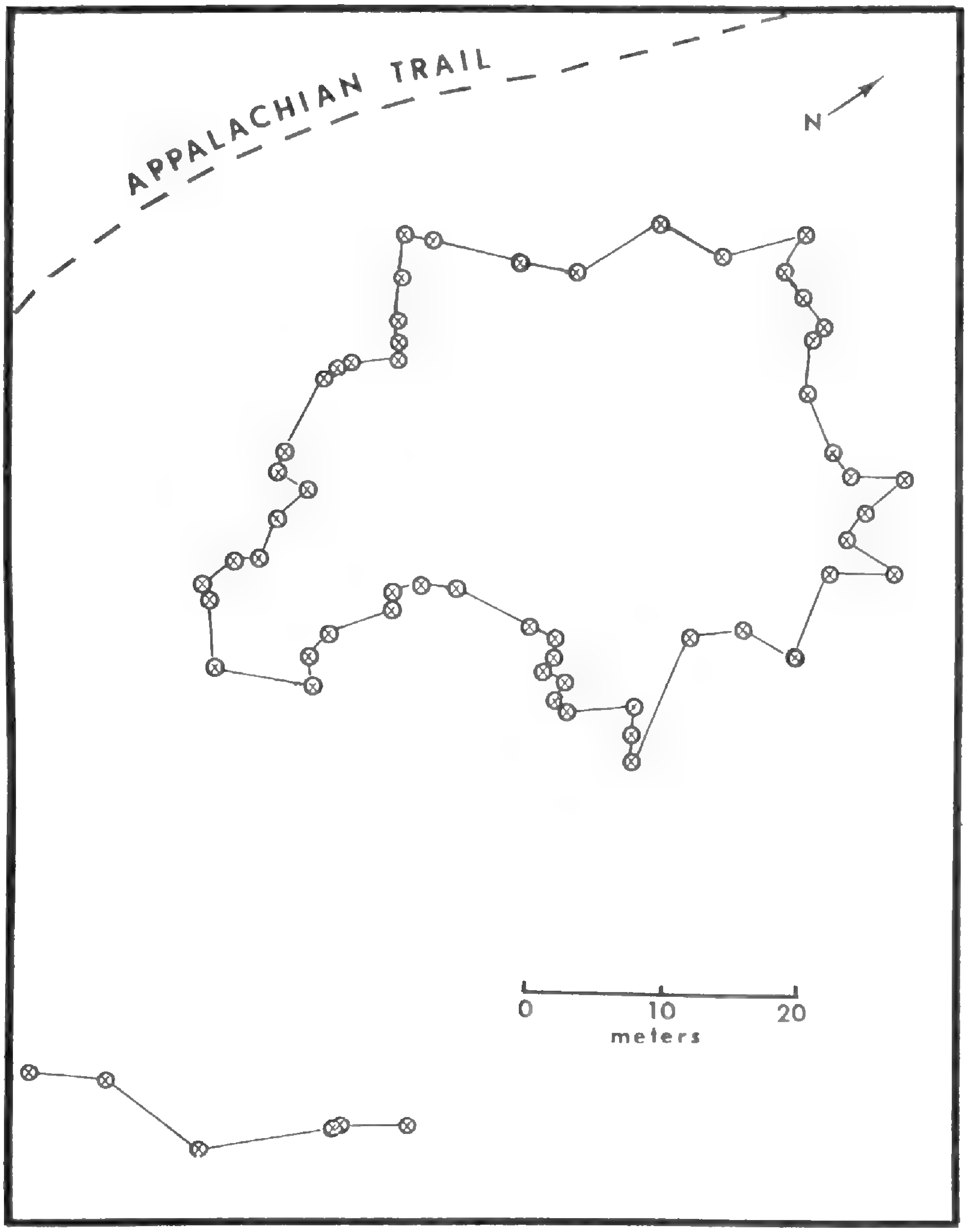

Figure 2. Peripheral plant locations of the *Potentilla robbinsiana* colony are mapped. The area enclosed is 1142 $m^2$.

new seedlings become established each summer, but only about 40% survive until October.

The harsh climate is the most important natural cause of plant mortality. Most seedling mortality occurred during hot, dry periods and is believed due to drought. During the spring and fall, frost heaving is the most common cause of plant death. No animals or insects were ever found to cause damage to seeds or seedlings. No diseases were noted. While *Potentilla robbinsiana* suffered high rates of mortality during the first years after germination, mortality declined among surviving plants and persistence for one or more decades is common. Some of the largest plants are estimated to be 40 years old.

Human activities are the major threat to the survival of *Potentilla robbinsiana*. Hiker traffic on the Appalachian Trail has increased dramatically in recent years. The nearly barren *P. robbinsiana* habitat is open and offers no natural obstacle to the hiker who wishes to step off the trail to rest, or to the group of hikers who prefer to walk abreast. A plant may be crushed in the process, but even more damaging is the shifting and dislodging of the stony pavement that occurs as hikers walk along. The abrasion and churning caused by the hiker's footsteps can eliminate the protected spaces between the individual stones, which often hold fine soil and organic particles. These minute sheltered spots are the nurseries for the newly germinated *P. robbinsiana*, and it is only here that they can become established. When the stony pavement is disturbed by hikers, the soil between the stones loosens and is soon blown or washed away. Once this precious bit of soil is lost, there is little or no chance of establishing and nurturing a seedling until the soil is replaced by natural processes. The hiker travel zone is widening and further destruction of the *P. robbinsiana* will likely occur. The only long-term solution to the problem is to greatly reduce the human traffic. A logical way to achieve this would be to relocate approximately ½-mile of the Appalachian Trail.

Regardless, we must provide this rare plant better protection than it has received in the past. The reduction of man's impact on this fragile alpine plant community is the first step in providing for its survival in an unimpaired form.

The need to establish new colonies of *Potentilla robbinsiana* to ensure its survival was recognized by Harris (1967). He moved

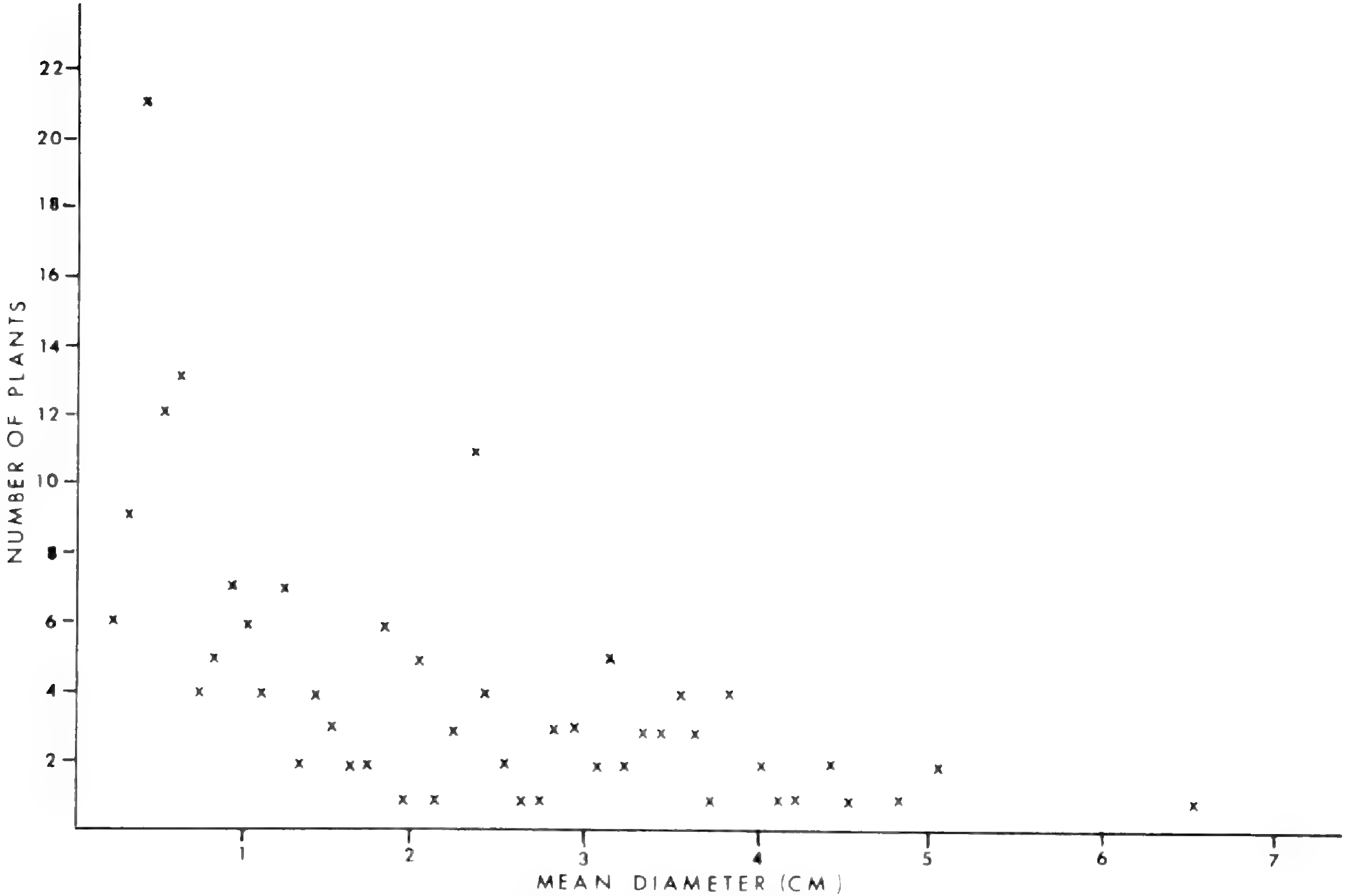

Figure 3. *Potentilla robbinsiana* rosette diameter distribution. The mean plant diameter is 1.2 cm. The plants do not flower until they are 1.4 cm or larger.

Figure 4. The mature seeds of this *Potentilla robbinsiana* are in the process of being shed. They fall to the ground near the mother plant.

plants from the Mt. Washington colony to a similar habitat about 900 m away. His transplants died for unknown reasons (A. R. Hodgdon, personal communication). I began transplantings in 1974. Seeds had been collected in July of the preceding year. Germinated seeds were planted in the greenhouse in February. The seedlings were grown in styrofoam blocks with planting cavities of two sizes: 40 and 125 cc. The blocks were filled with an artificial soil of equal parts peat, vermiculite and perlite. They were fertilized weekly with a complete nutrient solution. By mid-June, the plants were 3 to 5 cm in diameter, as large as the natural plants on Mt. Washington after a decade or more of growth. Transplanting to plots on Mt. Washington was done in late June and July. The seedlings were planted by forcing a dibble into the ground; then removing a seedling from the container complete with soil and placing the root-bound soil cone into the dibble hole. Eighteen plantings were made to provide a range of environmental conditions of varying aspect, elevation, and plant competition.

Mortality during the first summer was very low as most losses of mature plants tend to occur during the dormant season. After three years, heavy mortality had occurred on some of the planting sites. At lower elevations, where the fog was less frequent and the planting site was warm and dry, survival was nil. On the cool, foggy northwestern slopes of the upper mountain, the survival rate was very poor. Where plant competition by sedges and dwarf shrubs was significant, plant mortality rates were also high. *Potentilla robbinsiana* did best on the barren stony sites, where conditions were most similar to those of the natural colony. On these sites, transplant survival ranged from 17 to 90 percent, averaging 65 percent. Many of these transplants are now producing flowers, seeds, and seedlings.

## LITERATURE CITED

BURT, F. A. 1960. The story of Mount Washington. Dartmouth Publications, Hanover, NH.

COUNTRYMAN, W. D. 1978. Rare and endangered vascular plant species in Vermont. The New England Botanical Club in cooperation with the U.S. Fish and Wildlife Service (Region 5, Newton Corner, MA).

FOWLER, B. K. 1971. Surficial Geology of the Washington-Monroe Col. Appalachia, **68** (December): 148 163.

HARRIS, S. K. 1967. Notes on flora of Coos County, New Hampshire. Rhodora **69:** 29 34.

LÖVE, A., & D. LÖVE. 1965. Taxonomic remarks on some American Alpine Plants. Univ. Colo. Studies, Series in Biol. No. **17,** 43 p.

PEASE, A. S. 1917. Notes on the botanical explorations of the White Mountains. Appalachia **14:** 157 178.

STEELE, F. L. 1964. *Potentilla robbinsiana* in the White Mountains of New Hampshire. Rhodora **66:** 408 411.

TORREY, J., & A. GRAY. 1840. A flora of North America. Vol. **1,** Pt. 3. Wiley and Putnam, NY.

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# CONNECTICUT'S ENDANGERED SPECIES PROGRAM

LESLIE J. MEHRHOFF

Connecticut is a small state, even by New England standards, with only 5,009 square miles. It is, however, a state of remarkable natural diversity. Traveling a distance of just 60 miles inland from Long Island Sound, one experiences an elevational change from sea level to slightly more than 2,300 feet. In this distance a variety of habitats, including saltmarshes, bogs, and upland woods, can be encountered. It is apparent, however, that much of this land has been altered by industrialization and urbanization, effectively destroying actual and potential habitats for many of the state's unique species of plants and animals. With more habitat disappearing each year due to these impacts, there is increasing reason for concern about the state's rare, threatened or endangered plant species.

The citizens of Connecticut have been aware of rare plant destruction in the state for over a hundred years. According to Daniel Cady Eaton in *Ferns of the United States of America and British North American Possessions,* a law was passed in 1869 to protect the Hartford or Climbing Fern, *Lygodium palmatum* (Bernh.) Sw. (Eaton, 1879, p. 5):

> "The carefully pressed fronds are much used as an article of parlor ornament or decoration in the cities of Connecticut, and the custom is spreading to other States. The plant is gathered in August and September, and is exposed for sale in Hartford, New Haven, and New York, in great quantities, both in the fresh condition and as pressed specimens. Indeed, the gathering of it became so destructive, that in 1869 the legislature of Connecticut passed a special law for its protection. This law has since been codified in the revision of the statutes of 1875; and under title XX, chapter iv., section 22, it is made an offense, punishable by a fine not exceeding one hundred dollars, or imprisonment not more than twelve months, or both, to wilfully cut, destroy, or take away from the land of another person any 'cranberries, *creeping-fern*, crops, shrub, fruit, or vegetable production.' [Eaton's italics]
>
> This is probably the only instance in statute law where a plant has received special legal protection solely on account of its beauty."

In 1974 the State of Connecticut created a General Fund position for a Biologist whose main responsibility is to identify and evaluate the state's rare, threatened, or endangered species. After two years of literature search, herbarium study and extensive field work, the Connecticut Geological & Natural History Survey of the Natural Resources Center, Department of Environmental Protection, published the *Rare and Endangered Species of Connecticut and Their Habitats* (Dowhan & Craig, 1976), which listed 81 vertebrate taxa as well as 275 vascular plant taxa including eight of the ten species proposed in the June 16, 1976 Federal Register. At that time no specimens from Connecticut had been seen of the Ram's-head Ladyslipper, *Cypripedium arietinum* R. Br. (a single sheet has since been located at the U. S. National Herbarium) or of *Panicum aculeatum* Hitchc. & Chase (the specimens from Connecticut had been incorrectly identified).

In this document, the *Rare and Endangered Species of Connecticut and Their Habitats,* Connecticut set forth the basis for its Ecoregion Program. Simply stated, this is a multidisciplinary land classification system based upon such parameters as landforms, bedrock geology, soils, hydrology, climatology, and biology. It is a hierarchial system including three main levels of integration.

The first level is the Ecoregion. These are apolitical regions of distinctive landscapes and regional climate as expressed by vegetation patterns and composition and by the presence or absence of certain indicator species or species groups. Eleven ecoregions are described in this publication. There are also three subregions delineated in the western part of the state based upon the underlying marble bedrock.

The next level of integration is the Land System. Land Systems are distinguished by recurring patterns of landforms, soils, and vegetation chronosequences (successional stages). Since 1976, the work of the Connecticut Geological and Natural History Survey has concentrated on the North Central Lowlands Ecoregion, an area with, preliminarily, four Land Systems. Two of these are fairly distinct, the Trap Rock Ridge System and the Riverine Land System. The other two, the Till Midlands System and the Terrace and Plains System, are less distinct and need further evaluation.

The third level is the Land Type. This is an area which is characterized by fairly homogeneous combinations of soils and potential vegetation development. At this level the soils-vegetation relationships are especially pronounced. The Riverine Land Systems in the North Central Lowlands Ecoregion and the South Central Lowlands Ecoregion are presently being investigated by biologists from the Department of Environmental Protection's Natural Resources Center.

This program will be useful to land planners and managers because it will give them a sound, multidisciplinary basis for their decisions. The program should also have important applications to endangered species work. Herbarium labels frequently give names of towns for locality information and little else. By knowing the Land Type in which a species is most likely to occur, predictions can be made of places in which to search for historic as well as for previously unknown populations.

The Ecoregion Program will also be helpful in the reintroduction of rare plants to areas where they were once known. A pilot study is being considered for *Panax quinquefolius* L. (Ginseng), once known from 33 towns within Connecticut and now thought to be extant in 14 towns. Fruits will be harvested from native plants this fall and seedlings will be grown in the University of Connecticut greenhouses until they can be transplanted into the wild. By knowing the Land Type in which Ginseng is mostly likely to occur, the best localities for reintroduction to towns where it was historically known can be predicted. All work of this nature will be thoroughly documented.

In 1978 reports on Rare and Endangered Vascular Plant Species for each of the New England states were prepared by members of the New England Botanical Club's Endangered Species Committee and published by the U. S. Fish & Wildlife Service. The Connecticut report lists 282 vascular plant taxa. Sixteen were dropped from the 1976 Connecticut Geological & Natural History Survey list and 23 were added for consideration. Additional information received concerning plants will be used in the preparation of an updated state publication on rare and endangered plants. This revised document, with information for naturalists as well as professional botanists is slated for completion in 1981. Data files are also being established for all species of plants and animals with which the Endangered Species Program is concerned.

My work with the Connecticut Geological & Natural History Survey's Endangered Species Program has involved both continued field work and educational efforts. Much of the field work revolves around relocating historic populations as well as verifying new stations. Along educational lines, the Connecticut Geological & Natural History Survey has recently been awarded a small grant from the New England Wild Flower Society to put together a self contained slide and cassette program on Connecticut's rare and endangered plants and their habitats. This will be available to the people of the state through the Department of Environmental Protection's Information and Education Section. Through this program, we hope to increase public awareness about the needs of endangered plant species and programs for their protection.

With the signing of a Federal Cooperative Agreement for endangered species work between the U. S. Fish & Wildlife Service and the Connecticut Department of Environmental Protection, new impetus has been given to our Endangered Species Program. This Cooperative Agreement will be the first in the nation to include plants under the terms of the agreement. Our state program has the potential for sound endangered species management within a state which is rapidly growing in population and industry.

## LITERATURE CITED

DOWHAN, J. J., & R. J. CRAIG. 1976. Rare and Endangered Species of Connecticut and Their Habitats. Connecticut Geological & Natural History Survey, Report of Investigations **6**, Hartford.

EATON, D. C. 1879. Ferns of the United States of America and British North American Possessions, Volume **1**. Bradlee Whidden Publisher, Boston.

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# PLANT CONSERVATION CONCERNS IN RHODE ISLAND

GEORGE L. CHURCH

In 1973 an inventory of the "Natural Areas in Rhode Island" was completed under the joint sponsorship of the Rhode Island Audubon Society and the New England Natural Areas Project. 308 natural areas comprising 69,000 acres representing 9% of the total state area are designated. The Audubon Society maintains 7 wildlife refuge areas comprising over 1200 acres and owns as much again in the category of open space areas. The state of Rhode Island in addition maintains some 40 acres as state parks or state management areas.

Narragansett Bay and the associated islands, especially the islands of Rhode Island, Prudence, and Conanicut, bring the total coastline to 419 miles in length. Yet only 4000 acres of salt marsh remain unspoiled. In collaboration with other naturalists, particularly at the University of Rhode Island Coastal Resources Center, George L. Seavey has published an excellent and informative survey of 28 coastal natural areas needing formal protection and management.

Richard L. Champlin of Jamestown, R.I. is a well known naturalist whose extensive knowledge of the state flora has contributed liberally to these surveys.

In 1978 Professor Irene H. Stuckey of the University of Rhode Island published "Endangered Plants of Rhode Island" illustrated with 16 exceptionally fine color plates. Over 300 species are listed.

As a contribution to the project of the New England Botanical Club Committee on Rare and Endangered Species, George L. Church compiled in 1972 a list entitled "Species of Vascular Plants that are Rare, Scattered or Endangered in their Rhode Island Distribution". Initially based on specimens in the herbarium of the New England Botanical Club as well as those in the herbarium of Brown University, the notes as to stations and habitats were augmented by consulations with Elmer A. Palmatier, George L. Seavey, Richard L. Champlin, and the late Albert E. Lownes. The list was never published but is available from the author or William D. Countryman, the committee chairman.

In the current report by Church and Champlin on "Rare and Endangered Vascular Plant Species in Rhode Island", published by the U.S. Fish and Wildlife Service, the authors have reduced the list of 190 species in the 1972 report to 124. The co-author Champlin has for many years made careful observations of the flora of the state and has delineated the areas of particular concern described in this paper.

BEAVERTAIL POINT consists of a small, rocky coastal area on the southern tip of Conanicut Island in lower Narragansett Bay. Most of the area is under the jurisdiction of the U.S. Coast Guard, which operates here one of the oldest known lighthouses. It is a well known area for the study of marine algae, migrating monarch butterflies, and many unusual birds such as snowy owls and razor-bill auks. It is, of course, a very popular place for visitors.

In October of this year, Champlin discovered a colony of *Eupatorium leucolepis* var. *novae-angliae* of about 25 plants in a nearby boggy meadow. This variety, first described from Plymouth County, Mass. by Fernald in 1914, was also known from a single station in southern Rhode Island where it has not been seen for some years. The habitat of the new station is about 50 feet above the shore and salt sprays are frequent. Associated species include *Spiraea tomentosa, Verbena hastata, Vaccinium macrocarpon,* and *Dioscorea villosa* at about the northern limit of its range. Shrubs include both the southern *Viburnum dentatum* and the northern *Viburnum recognitum* at a meeting of the range limits of each. *Baccharis halimifolia* is known from a salt marsh in South Kingstown where Stuckey reports it to be increasing lately due to salt spread on an adjacent road in winter. Only 3 plants were found this year at Beavertail. *Lycopodium alopecuroides,* new to the state in 1977, is here at its only Rhode Island station. *Ophioglossum vulgatum* is found here and at the only other station at Wallum Lake in the northwestern part of the state. *Liparis loeselii,* which seems to have disappeared from several sites, was seen here last year by the hundreds.

The land, which is owned by the U.S. Navy, is about to be transferred to the state in order to build a public park. Plans include the construction of a parking lot and a road through this area of botanical interest which is thus very definitely threatened.

The LIME ROCK area in the town of Lincoln is the only extensive outcropping of limestone in the state. On the edge of a working lime quarry is the only known station in the state for *Pellea atropurpurea,* which, however, is a population of about 100 plants. Here, also, is the only extant station for *Parnassia glauca.* On a single boulder is the only station for a few plants of *Camptosorus rhizophyllus.* Nevertheless, this site has been observed for over 100 years! In nearby woodlands may be found a few plants of *Liparis liliflora,* represented only by very small stands at three other sites in the western part of the state. *Cornus rugosa,* observed in a small stand here last year, was noted also only in a very threatened station at Huntinghouse Brook in North Scituate. Other rarities include *Hepatica americana* at its only reasonably abundant stand as well as a few plants of *Viola pubescens.*

This unique area is becoming increasingly difficult to protect with businesses and the limestone industry encroaching on one side and housing developments on the other.

The south side of the HUNTINGHOUSE BROOK area in North Scituate includes an area of rich botanical interest but unfortunately without a clear record of ownership. Here is the only station in the state for *Acer spicatum, Adlumia fungosa,* and *Sanguinaria canadensis.* Only one other station is known for *Asclepias quadrifolia* and three others for *Liparis liliflora.* Other rarities include *Cypripedium calceolus, Habenaria hookeri, Habenaria hyperborea, Adiantum pedatum,* and *Botrychium virginianum.*

The future integrity of this natural area is very much in doubt. Lately, new houses have been constructed adjoining the wild area and traffic, including that of motorcycles, is increasingly threatening. After recent visits, Champlin thinks that the area is unfortunately beyond protection.

The CLEAR RIVER area at Burrillville in the northwestern corner of the state presents a rather northern aspect with *Acer pennsylvanicum, Taxus canadensis, Viburnum alnifolium,* and *Streptopus roseus. Dalibarda repens* was found here last year for the first time in Rhode Island. It is the only station for *Aletris farinosa* in any abundance and the only extant site for *Malaxis uniflora.*

A power line as well as a natural gas line bisect this area but fortunately as yet without harm to the rich flora.

In the nearby ROBBINS BROOK area is a dense tamarack-spruce bog with occasional *Chamaecyparis thyoides* and including a few plants of the rare *Rhododendron canadense, Menyanthes trifoliata,* and *Gaultheria hispidula.* The land is owned by the Boy

Scouts of Rhode Island, who have had plans to flood the area. At present, however, there appears to be a lack of interest in continuing with such plans.

The BOWDISH RESERVOIR floating islands, adjacent to the interstate highway in Glocester, carry such Rhode Island rarities as *Andromeda glaucophylla, Kalmia polifolia, Picea mariana,* and the only station for *Arceuthobium pusillum. Larix laricina* and *Eriophorum spissum,* originally here, have disappeared.

The water level needed to maintain these species is controlled by a dam. Although the shore is largely owned by local residents, there seems to be no clear title to ownership of the reservoir. Local residents may charge a fee to cross to the islands by boat and there is the possibility of access being denied.

The state owned DURFEE HILL management area in West Glocester contains sandstone cliffs about 150 feet in length where Champlin discovered the only station in the state for *Asplenium montanum* in 1961. It is still flourishing in rock crevices, along with the widespread *Polypodium virginianum.* The *Asplenium* is at the northeastern limit of its range. The area is not supervised and occasional vandalism has been noted.

In West Greenwich is one of five stations in the state for *Lygodium palmatum* where the site is rather remote and safe from immediate development hazards. The station of two acres, however, is all privately owned.

A pine barrens area in South Kingstown is owned by a gravel company and the integrity of the station for *Hudsonia tomentosa* in a pure stand of *Pinus rigida* could be threatened.

This past year Champlin found a small colony of *Helianthemum dumosum* along Narrow River in Saunderstown in dry soil with *Cetrarea islandica* and *Quercus velutina.* The Block Island stations reported by Fernald in 1913 and 1914 as well as the Tucker Pond station on the mainland have not been observed for some time. However, Stuckey reports 10 plants on a Block Island site in 1977.

*Isotria medeoloides,* the Small Whorled Pogonia, is one of the well known rarities on the Federal Register of endangered species and a history of field observations made on this orchid in Rhode Island over the last 30 years is of particular interest. The site in Glocester is on privately owned land, yet the owner is unknown! An adjacent woodlot has recently been cleared and a new house built upon it. In 1970, the witch-hazel brush on the land was cut away without the cutters being aware of the presence of the orchid.

The station was discovered in 1947 by the late Charles Bryan, who reported 17 plants; later in September of that year he counted 28 plants with the late John Hudson. In the course of the next five years, the colony varied from 20 to 36 individuals. Lewis Carpenter and Richard Champlin have noted declining numbers in the population over the last 20 years and only four plants remained last year.

The surrounding vegetation within a 25 foot radius includes: *Clethra alnifolia, Hammamelis virginiana, Azalea nudiflora, Fraxinus americana, Quercus rubra, Acer rubrum, Ilex verticillata, Gaylussacia frondosa,* and *Lycopodium obscurum.*

It is obviously difficult to predict the future for this population of *Isotria.* It may go into a dormant period which in some cases has been reported to be 10 20 years. The land may be cleared or natural forest succession may eliminate the stand. Then again, the orchid may survive simply by being overlooked in a not so unusual ecosystem.

At the only other station for this orchid in Rhode Island at West Greenwich, Lewis Carpenter observed 23 plants in 1957 and the number dwindled to 4 in 1973. In the past year no plants could be found.

Perhaps, then, the best protection for *Isotria medeoloides* is to allow it to follow its own strategies for survival.

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# RARE PLANT SPECIES IN MASSACHUSETTS

KATHARINE G. FIELD[1] AND JONATHAN CODDINGTON

242 vascular plant species were listed as rare in Massachusetts (Coddington & Field, 1978). There are several problems inherent in a state list of rare plants. Because the boundaries of states are political rather than natural, the plant species in a state represent diverse communities and ecosystems, some of which may be better represented elsewhere. The historical occurrences of species in states are usually established from herbarium records, some of which may be inaccurate and need evaluation by experts. The publication of a state rare plants list usually causes new information to come to light, rapidly making the list obsolete.

In Massachusetts, all of these problems obtain. Nevertheless, certain patterns of rarity can be distinguished among Massachusetts rare plant species, and these patterns are broad enough to indicate general patterns in the distribution of rare plant species in the state.

The 242 species on the Massachusetts rare plants list can be divided into groups: 1) species rare throughout their ranges; 2) range limits: species at the northern or southern limits of their ranges; 3) species with highly disjunct distributions; and 4) species with a restricted total range: endemic to Massachusetts, endemic to New England, or endemic to a small geographic area. With the exception of a few species made rare by human activity alone (e.g. *Rhododendron maximum* (Ericaceae), collected by gardeners; *Ribes americana* (Saxifragaceae), the object of a government control program because it is the alternate host of a plant disease), most of the species on the Massachusetts rare plants list fit into these categories.

## SPECIES RARE THROUGHOUT THEIR RANGES

This category is typified by the orchid *Isotria medeoloides*, which occurs from Ontario (Stewart, 1978) to North Carolina and Missouri (Fernald, 1950) but is nowhere common. The only known occurrence of this species in Massachusetts is documented by a herbarium sheet dated 1899.

*Setaria geniculata* (Gramineae), another Massachusetts species rare throughout its range, is one of the rare prairie species studied by Rabinowitz (1978). The species appears to be adapted for long-distance dispersal.

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## RANGE LIMITS

Range limit species are at the extreme edges of their distributions due to a combination of factors, such as reduced availability of suitable physical habitat and increased competition (Grant & Antonovics, 1978).

Many species on the Massachusetts rare plants list are at the northern limits of their distributions. A few of these are found in western Massachusetts. One occurs in woods (*Cimicifuga racemosa,* Ranunculaceae). The others are found in open habitats such as roadsides (e.g. *Aster prenanthoides,* Compositae) and meadows (e.g. *Carex Bushii,* Cyperaceae). A larger number of species at the northern limits of their ranges are found in eastern Massachusetts. A few of these occur in shaded habitats such as woods (e.g. *Tipularia discolor,* Orchidaceae). Most occupy open or relatively open habitats, commonly sandy or peaty pond shores (e.g. *Rhynchospora inundata,* Cyperaceae), sandy dry barrens (e.g. *Onosmodium virginianum,* Boraginaceae), and other open habitats such as tidal mud flats, lake shores, fields, and roadsides. Some species at the northern limits of their distribution are found in both eastern and western Massachusetts. For these, the most common habitat is fresh-water pond shores (e.g. *Fuirena pumila*, Cyperaceae). Note that this habitat is found both in coastal areas and in western Massachusetts on sandy plains on the site of glacial Lake Hitchcock.

A few species reach the southern limit of their ranges in Massachusetts. Five of these species occur in shaded habitats such as woods (e.g. *Polystichum Braunii,* Polypodiaceae). The others occur in habitats which are mostly open, such as bogs (e.g. *Platanthera obtusata,* Orchidaceae) and open mountain tops (e.g. *Luzula parviflora,* Juncaceae).

In eastern Massachusetts the species at the southern limits of their ranges are found in mostly open habitats such as pond shores (e.g. *Isoetes faveolata,* Isoetaceae), sea beaches (*Elymus arenarius,* Gramineae), ledges and rocky beaches (e.g. *Sagina nodosa,* Caryophyllaceae), and salt flats (e.g. *Suaeda americana,* Chenopodiaceae).

## DISJUNCTS

In Massachusetts there are many disjunct localities of species that occur mainly to the south of the state. Only a few of these are found in shaded habitats such as woods (e.g. *Carex Willdenowii,* Cyperaceae) and swamps (*Magnolia virginiana,* Magnoliaceae). Most of the others occur in open habitats such as fresh water pond shores (e.g. *Psilocarya nitens,* Cyperaceae, and *Echinodorus tenellus,* Zosteraceae), and barrens.

A few disjunct localities of species occurring mostly to the north of the state are found in Massachusetts, occurring in such habitats as woods (e.g. *Halenia deflexa,* (Gentianaceae), sea beaches (e.g. *Rumex pallidus,* Polygonaceae), and "boreal" habitats such as mountain tops (e.g. *Lycoodium Selago,* Lycopodiaceae).

Some disjunct species in Massachusetts cannot be characterized as northern or southern species. Some are widespread species infrequently distributed throughout their ranges. Others are restricted in total distribution. Several Massachusetts disjunct species occur in Nova Scotia, Cape Cod and Massachusetts offshore islands, Block Island, Rhode Island, Long Island, New York, and New Jersey, sometimes extending farther south along the coastal plain. Examples of this include *Sabatia Kennedyana* (Gentianaceae), which occurs in Nova Scotia, eastern Massachusetts and Rhode Island, southeastern North Carolina and northeastern South Carolina (Perry, 1971); and *Corema Conradii* (Empetraceae), found in northeastern Canada including Nova Scotia, sporadically south on the coast to outer Cape Cod, and in the New Jersey Pine Barrens (Fernald, 1950).

## ENDEMICS AND RESTRICTED-RANGE SPECIES

There are taxonomic questions about many of the taxa listed as Massachusetts or New England endemics and restricted species. Sometimes named as species and sometimes as varieties, these taxa may represent hybrids, geographically isolated populations, ecotypes, newly-evolved or relict species. With the exception of *Paronychia argyrocoma* var. *albi-montana* (Caryophyllaceae), all of them are associated with the coastal plain, and most occupy open habitats.

Only two plant taxa have ever been considered to be endemic to Massachusetts. One, *Juncus pervetus,* was only known from one locality on Cape Cod, where it apparently persisted for a few years. The habitat at this site has been severely altered, but even before habitat changes occurred, the plant could no longer be found. Unless it can be relocated, its status as a species will remain in question.

The other Massachusetts endemic is *Amelanchier nantucketensis* (Rosaceae), a Nantucket shrub. This was originally distinguished from other *Amelanchier* species because of its smaller size, spreading habit, and short petals (Bicknell, 1911). Later studies of the genus (Weigand, 1912; Jones, 1946) considered *A. nantucketensis* to be part of such other species as *A. oblongifolia* var. *micropetala* and *A. canadensis.* According to both Weigand (1912) and Fernald (1946, 1950), the genus *Amelanchier* frequently forms hybrids. Field observations by Coddington (1978, unpublished) suggest that whatever the origin and species status of *A. nantucketensis,* it is a recognizable entity in the field. It occurs on shores of fresh water ponds and in sandy barrens.

Three taxa on the Massachusetts rare plants list are endemic to New England: *Isoetes foveolata* (Isoetaceae), *Paronychia argyrocoma* var. *albimontana* (Caryophyllaceae), and *Eupatorium leucolepis* var. *novae-angliae* (Compositae). The genus *Isoetes* is poorly understood and poorly collected (R. J. Hickey, pers. comm.); until more work is done on it, the status of *I. foveolata,* a shallow-water aquatic found in southern New Hampshire and Massachusetts, remains questionable. *Paronychia argyrocoma* var. *albi-montana* is a highly disjunct variety of a species which otherwise occurs in Virginia, West Virginia, North Carolina, Georgia, and Tennessee (Core, 1941). Variety *albi-montana* is found at a few localities on rocky mountains in southern Maine and New Hampshire, and on a rocky island at sea level in northeastern Massachusetts. *Eupatorium leucolepis* var. *novae-angliae,* another disjunct variety, is limited to southeastern Massachusetts and Rhode Island, where it occurs in sandy soil near fresh water ponds.

Twelve species on the Massachusetts rare plants list have a restricted distribution. Two are western disjuncts (*Ludwigia polycarpa,* Onagraceae, and *Psilocarya nitens,* Cyperaceae), occurring in extremely limited areas on the eastern coastal plain and also in the midwest. Other species (e.g. two *Isoetes* species, two *Bidens* species) are poorly defined and understood taxonomically. *Sabatia Kennedyana* (Gentianaceae), a notable disjunct mentioned above, occurs in Nova Scotia, coastal Massachusetts and Rhode Island, and the Carolinas. Two species of dry sandy areas, *Helianthemum dumosum* (Cistaceae), and *Agalinis acuta* (Scrophulariaceae), occur only in eastern Massachusetts, Rhode Island, Connecticut, and Long Island. Populations of *H. dumosum* were relocated on Cape Cod and Nantucket in 1978 (J. Coddington, unpublished). Recent searches for *A. acuta* throughout its range (J. Canne, *in litt.*) and in Massachusetts (J. Coddington, K. Field, unpublished) failed to locate the species. This species is believed to be a root parasite (Musselman and Mann, 1977).

## HISTORICAL CAUSE FOR MASSACHUSETTS PLANT DISTRIBUTIONS

Some of the patterns of distributions of Massachusetts rare plant species can be explained by examining the recent glacial, geological, and vegetational history of the state. Features of late Wisconsin glaciation which are important to an understanding of plant distribution are the following:

1) During the late Wisconsin, ice covered most or all of present-day Massachusetts. The ice sheet extended to central Long Island (Sirkin, 1971), Block Island, Rhode Island (Sirkin, 1976), Martha's Vineyard (Kaye, 1964a & 1964b), off Nantucket, across southwestern and northern Georges Bank to the edge of the Nova Scotian Shelf (Pratt & Schlee, 1969; Schlee & Pratt, 1970).

2) The area around the northwestern Atlantic, especially between latitudes 42° and 60° north, experienced severe cooling during the late Wisconsin, estimated at —18° C maximum cooling at about 18,000 BP (before present) (MacIntyre et al., 1976; CLIMAP, 1976). The severity of the cooling was caused by a southward shift in the Gulf Stream during maximum glaciation (CLIMAP, 1976).

3) Sea level reached a low approximately 130m below its present level at about 16,000 BP (Milliman & Emery, 1968).

4) Lack of shoals off Nova Scotia and the dispersal of gravel at the edge of the Nova Scotian Shelf indicate that the glacier flowed directly into the sea in this area (Schlee & Pratt, 1970). However, on and to the west of Georges Bank, the ice was separated from the shoreline by a broad band of exposed continental shelf (Pratt & Schlee, 1969).

5. Fossil peat which was deposited in fresh water and salt marsh environments is now found as far out from the present-day coastline as Georges Bank and the Nantucket Shoals (Livingston, 1964; Emery et al., 1967; Field et al., 1979). This shows that a much larger coastal land area was exposed in southern New England following glaciation. Evidence from salt marsh peat on Cape Cod (Redfield &

Rubin, 1962) and in southern New Hampshire (Keene, 1971) shows that the sea has been slowly covering this exposed land for 6000 to 7000 years.

Changes in climate during and following the Wisconsin glaciation are often inferred from paleobotanical evidence. It is known that during glaciation, temperate species were displaced far to the south of their present ranges. Tundra vegetation occurred in New Jersey (Sirkin et al., 1970) and far south in the Alleghenies (Maxwell & Davis, 1972); boreal forest species occurred in Georgia and Florida (Whitehead, 1973) and in the Delmarva Pensinsula (Sirkin, et al., 1977).

Using radiocarbon-dated assemblages of fossil pollen, the sequence of vegetation immediately following glacial retreat has been reconstructed in many areas of glaciated northeastern North America (e.g. Long Island, Sirkin, 1971; Connecticut, M. Davis, 1969; Block Island, Sirkin, 1976; central Massachusetts, M. Davis, 1958; Martha's Vineyard, Ogden, 1963, Kaye, 1962, 1964a, 1964b; Maine, R. Davis et al., 1975; southeastern Canada, Livingston, 1968). The sequence differs slightly in different areas, yet the general pattern is similar throughout the Northeast.

Vegetation immediately south of the glacial edge consisted of mostly non-arboreal species such as sedges and grasses, along with birch and willow. This open vegetation was gradually replaced by boreal forest, often passing through a stage of "forest-tundra" or "park-tundra" (e.g. see Sirkin, 1976; M. Davis, 1969). As temperate species invaded from the south, the vegetation usually passed through a pine stage and a pine-oak stage.

The rate of invasion of temperate forest species following glaciation was controlled by the dispersal and colonizing ability of each species, more than by climate (Livingston, 1968; M. Davis, 1976). Rapidly colonizing species were able to move north quickly, and may have occurred farther to the north than their present-day distributions during a period of maximum warming at about 5,000 BP (M. Davis, 1976). On the other hand, the ranges of some slow-colonizing species may still be expanding to the north (M. Davis, 1976).

Pollen spectra cannot give an absolutely accurate picture of post-glacial climate and habitats, for several reasons. Attempts to correlate modern pollen with vegetation have shown that some pollen is transported great distances before deposition (R. Davis & Webb, 1975). In addition, pollen can often be identified only to family or genus. Therefore, a particular pollen assemblage will contain an average sampling of a diverse group of plant communities, but can give little information about particular habitats and communities. Habitats and communities must be inferred from other data.

What was post-glacial Massachusetts like? First of all, a broad expanse of coastal plain was exposed for a long period of time. Numerous glacial lakes existed in Massachusetts during and after ice retreat (e.g. see Brooks & Deevey, 1966). Beavers were active in New England as early as 12,000 BP (Kaye, 1962), creating their characteristic open habitats. Some of the same Massachusetts deposits that contain beaver-chewed wood also contain charred wood. Kaye (1962) reasoned that this indicates a drier climate which allowed forest fires to occur naturally. However, presence of humans on the exposed continental shelf, along with other large mammals such as moose, muskox, and mastodon, also occurred quite early (see Edwards & Emery, 1977), so it is possible that not all fires occurred naturally. It has been frequently been observed that present-day coastal areas in southern New England are much more open than inland areas; on certain isolated coastal areas such as Block Island, very few trees are found at all.

To summarize, in post-glacial Massachusetts, it is likely that because of the presence of glacial lakes, beavers, large grazing mammals and humans, large areas of open habitat occurred for thousands of years. In addition, many of the dominant temperate tree species invaded slowly, and at the extreme edge of the coast, probably did not occur at all.

Fernald (1925, 1929, 1939) explained the presence of endemics and plant species with Cordilleran affinities by hypothesizing that certain high mountains remained uncovered by ice during the Wisconsin glaciation. A pre-Pleistocene flora survived in these areas, and was later restricted to them. The suggested areas are parts of Nova Scotia, Labrador, the Gaspé Peninsula, and islands in the Gulf of St. Lawrence, as well as isolated mountain tops to the south. In addition, Fernald hypothesized that plants survived glaciation on the exposed continental shelf (Fernald, 1918, 1942, 1943).

The idea that plants persisted in nunataks during glaciation is frequently found in the literature. Most recent authors favor continental shelf refugia, however. For example, Terasmae (1973, p. 210) states that "both arctic and boreal species grew in these unglaciated coastal areas that extended from the Grand Banks (east of Newfoundland) southward to the Georges Bank region east of New York".

Geological evidence has shown that this area did exist, although it did not occur along Nova Scotia. However, with an average annual temperature anomaly of 18° C during glaciation (CLIMAP, 1976), it is unlikely that temperate species could have survived on the continental shelf. Instead, the exposed shelf probably served as a dispersal corridor after glaciation, as well as an area of open habitats where some of the coastal endemics of open habitats probably evolved. Rising sea level later restricted coastal plant species into disjunct populations.

Fernald himself and many authors since Fernald have suggested that east-west dispersal occurred along the foot of the retreating glacier across North America (Drury, 1969). The habitat immediately south of the glacier supported an arctic-alpine type flora, which later became restricted to arctic and montane habitats. This theory seems better able to explain relationships between eastern and Cordilleran floras than does the presumed survival of a pre-Pleistocene flora in nunataks.

## DISCUSSION

Four groups of Massachusetts rare plant species have been discussed and geological-historical explanations for three of these groups have been presented.

Group 1). Geological explanations do not explain species that are rare throughout their ranges.

Groups 2 and 3). Species at the southern and northern limits of their ranges, and disjuncts: Since boreal species migrated northward through New England from southern areas following glaciation, it is to be expected that some of them would still persist in patches of "boreal" habitat in New England. In Massachusetts, a large proportion of species at the southern limit of their ranges are found in Berkshire County, where cold, high areas in the mountains create boreal habitat conditions.

Southern species at the northern limit of their ranges are more common in eastern Massachusetts, where temperate coastal-plain habitat occurs. Again, species have been migrating north since glaciation. It is likely that populations of southern species became established during the period of warming that occurred 5000 years ago.

Climatic cooling and rise of sea level left disjunct populations of these species. An example of this is *Magnolia virginiana* (Magnoliaceae) in Massachusetts.

Plants from the east and west mixed in open arctic-alpine habitats along the southern border of the retreating ice-sheet. The retreat of the glacier left disjunct populations; this explains the presence of western disjuncts in the flora of Massachusetts.

Group 4). Endemics and restricted species: Following glaciation, there was a large exposed land area with a variety of open habitats such as meltwater estuaries, shores of glacial lakes and sand deposits left after these lakes dried, beaver meadows, and coastal barrens. This allowed coastal endemics to evolve or become established. In the last 6000 years, coastal areas have been shrinking because of rising sea level and coastal subsidence, and many of the factors creating open habitats are no longer present. This explains the large number of coastal endemics and species of open habitats which are now rare.

The history of Massachusetts since the last glaciation, including changing habitats and vegetation, explains the present distribution of many rare plant species. In addition, a large proportion of rare plant species exist in "rare habitats". Some, such as open habitats on the coastal plain, were more common in the past; others, such as serpentine and limestone outcrops, were always rare. In order to preserve rare plants in Massachusetts, therefore, it is necessary to preserve the specialized habitats of these species.

## REFERENCES CITED

Bicknell, E. P. 1911. The ferns and flowering plants of Nantucket. VIII. Bull. Torrey Bot. Club **38:** 447 460.

Brooks, J. L., & E. S. Deevey. 1966. New England. pp117 162 *In:* D. G. Frey (ed.) Limnology in North America. University of Wisconsin Press, Madison, Wisconsin.

CLIMAP Project Members. 1976. The surface of the ice-age earth. Science **191:** 1131 1137.

Coddington, J., & K. G. Field. Rare and Declining Vascular Plant Species in Massachusetts. U. S. Fish & Wildlife Service, Newton Corner, Massachusetts.

Core, E. 1941. The North American species of *Paronychia*. Amer. Midl. Nat. **26:** 369 397.

DAVIS, M. B. 1958. Three pollen diagrams from central Massachusetts. Amer. J. Sci. **256:** 540 570.

________. 1969. Climatic changes in southern Connecticut recorded by pollen deposited at Rogers Lake. Ecol. **50:** 409-422.

________. 1976. Pleistocene geography of temperate deciduous forests. Geosci. and Man **13:** 13 26.

DAVIS, R. B., T. E. BRADSTEET, R. STUCKENRATH, JR., & H. W. BORNS, JR. 1975. Vegetation and associated environments during the past 14,000 years near Moulton Pond, Maine. Quatern. Res. **5:** 435 465.

DAVIS, R. B., & T. WEBB, III. 1975. The contemporary distribution of pollen in eastern North America: a comparison with the vegetation. Quatern. Res. **5:** 395 434.

DRURY, W. D., 1969. Plant persistence in the Gulf of St. Lawrence. *In:* K. N. Greenidge (ed.) Essays in Plant Geography and Ecology. Nova Scotia Museum, Halifax, Nova Scotia.

EDWARDS, R. L., & K. O. EMERY. 1977. Man on the continental shelf. *In:* W. S. Newman & B. Salwen (eds.) Amerinds and their Paleoenvironments in Northeastern North America. Annals N. Y. Acad. Sci. **288:** 245 256.

EMERY, K. O., R. L. WIGLEY, A. S. BARTLETT, M. RUBIN, & E. S. BARGHOORN 1967. Freshwater peat on the continental shelf. Science **158:** 1301 1307.

FERNALD, M. L. 1918. The geographic affinities of the vascular floras of New England, the Maritime Provinces, and Newfoundland. Amer. J. Bot. **5:** 219 247.

________. 1925. The persistence of plants in unglaciated areas of Boreal America. Mem. Amer. Acad. Arts Sci. **15:** 239 342.

________. 1929. Some relationships of the floras of the Northern Hemisphere. Proc. International Congr. Plant Sci. **2:** 1487 1507.

________. 1939. The problem of conserving rare native plants. Smithsonian report for **1939:** 375 391.

________. 1942. Misinterpretation of Atlantic Coastal Plain species. Rhodora **44:** 238 246.

________. 1943. *Scirpus Longii* in North Carolina. Rhodora **45:** 55-56.

________. 1946. A monograph of *Amelanchier*. Rhodora **48:** 129 134.

________. 1950. *Gray's Manual of Botany*, 8th ed. American Book Co., New York, N. Y.

FIELD, M. E., E. P. MEISBURGER, E. A. STANLEY, & S. J. WILLIAMS. 1979. Upper Quaternary peat deposits on the Atlantic inner shelf of the United States. Geol Soc. Amer. Bull. **90:** 618 628.

GRANT, M. C., & J. ANTONOVICS. 1978. Biology of ecologically marginal populations of *Anthoxanthum odoratum*. I. Phenetics and dynamics. Evolution **32:** 822 838.

JONES, G. N. 1946. American species of *Amelanchier*. Ill. Biol. Monogr. **20:** 1 126.

KAYE, C. A.1962. Early post-glacial beavers in southeastern New England. Science **138:** 906 907.

________. 1964a. Outline of Pleistocene geology of Martha's Vineyard, Massachusetts. U. S. Geol. Surv. Prof. Pap. **501-C:** 134-139.

———. 1964b. Illinoian and early Wisconsin moraines of Martha's Vineyard, Massachusetts. U. S. Geol. Surv. Prof. Pap. **501-C:** 140–143.

KEENE, H. W. 1971. Postglacial submergence and salt marsh evolution in New Hampshire. Maritime Sed. **7:** 64–68.

LIVINGSTON, D. A. 1964. The pollen flora of submarine sediments from Nantucket Shoals. Amer. J. Sci. **262:** 479–487.

———. 1968. Some interstadial and Post-glacial pollen diagrams from eastern Canada. Ecol. Monogr. **38:** 87–125.

MACINTYRE, A., N. G. KIPP, A. W. H. BÉ, T. CROWLEY, T. KELLOGG, J. V. GARDNER, W. PRELL, & W. F. RUDDIMAN. 1976. Glacial North Atlantic 18,000 years ago: a CLIMAP reconstruction. *In:* R. M. Cline & J. D. Hays, eds. Investigations of Late Paleoceanography and Paleoclimatology. Geol. Soc. Amer. Mem. **145:** 43–76.

MAXWELL, J. A., & M. B. DAVIS. 1972. Pollen evidence of Pleistocene and Holocene vegetation of the Allegheny Plateau, Maryland. Quatern. Res. **2:** 506–530.

MILLIMAN, J. D., & K. O. EMERY. 1968. Sea levels during the past 35,000 years. Science **162:** 1121–1123.

MUSSELMAN, L., & W. F. MANN, JR. 1977. Host plants of some Rhinantheoideae (Scrophulariaceae) of eastern North America. Plant Syst. Evol. **127:** 45–53.

OGDEN, J. GORDON, III. 1963. The Squibnocket cliff peats: radiocarbon dates and pollen statigraphy. Amer. J. Sci. **261:** 344–353.

PRATT, R. M., & J. SCHLEE. 1969. Glaciation on the continental margin of New England. Geol. Soc. Amer. Bull. **80:** 2335–2342.

PERRY, J. D. 1971. Biosystematic studies in the North American genus *Sabatia* (Gentianaceae). Rhodora **73:** 309–369.

RABINOWITZ, D. 1978. Abundance and Diaspore weight in rare and common prairie grasses. Oecologia **37:** 213–219.

REDFIELD, A. C., & M. RUBIN. 1962. The age of salt-marsh peat and its relation to recent changes in sea level at Barnstable, Massachusetts. Proc. Nat. Acad. Sci. **48:** 1728–1735.

SCHLEE, J., & R. M. PRATT. 1970. Atlantic continental shelf and slope of the United States gravels of the northwestern part. U. S. Geol. Surv. Prof. Paper. **529-H.**

SIRKIN, L. A. 1971. Surficial glacial deposits and post-glacial pollen stratigraphy in central Long Island, New York. Pollen et Spores **13:** 93–100.

———. 1976. Block Island, Rhode Island: evidence of fluctuation of the late Pleistocene ice margin. Geol. Soc. Amer. Bull. **87:** 574–580.

———, C. S. DENNY, & M. RUBIN. 1977. Late Pleistocene environment of the central Delmarva Peninsula, Delaware-Maryland. Geol. Soc. Amer. Bull. **88:** 139–142.

———, J. P. MINARD, & M. RUBIN. 1970. Palynology of some upper Quaternary peat samples from the New Jersey coastal plain. U. S. Geol. Surv. Prof. Paper **700-D:** 77–87.

STEWART, W. G. 1978. *Isotria medeoloides*, the smaller whorled pogonia, new to Canada. Rhodora **80:** 587–590.

TERASMAE, J. 1973. Notes on late Wisconsin and early Holocene history of vegetation in Canada. Arct. Alp. Res. **5:** 201 222.

WHITEHEAD, D. R. 1973. Late-Wisconsin vegetational changes in unglaciated eastern North America. Quatern. Res. **3:** 621 631.

WEIGAND, K. M. 1912. The genus *Amelanchier* in eastern North America. Rhodora **14:** 117 161.

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# VERMONT'S ENDANGERED PLANTS AND THE THREATS TO THEIR SURVIVAL

WILLIAM D. COUNTRYMAN

The major threat to endangered plant species in the Northeast comes not from collection or commercial exploitation but from ever increasing recreation and development pressures. In much of New England today, it is the habitats of these species that are threatened; certainly this is true in Vermont. While it is also true that there are occasional threats to plants by botanists and gardeners who collect specimens for scientific or horticultural purposes, the real concern is with builders and hikers.

For a small non-coastal state, Vermont has a remarkable diversity of habitat types. The many combinations of elevations, slope, aspect, moisture, and soil types support over 1900 species of vascular plants, of which approximately 1400 are indigenous.

The Vermont flora has been studied from the earliest days — since before the state was a state, or even before it was a republic. Samuel de Champlain, who in 1609 reported the chestnut, *Castanea dentata* (Marsh.) Borkh. from the shores of the lake that now bears his name, was one of the first westerners to comment on plants in what is now the State of Vermont (Grant, 1907).

Champlain was followed by the botanist, Luigi Castiglioni, an Italian nobleman, whose concerns, when he visited Vermont in 1785, were more with rattlesnakes than plants (Castiglioni, 1790). Pehr Kalm, André Micheaux and his son François André, Frederick Pursh, and Samuel Rafinesque followed in swift succession. A list of the early visitors to Vermont reads something like a botanical "Who's Who", yet none of these pioneer explorers made any very startling botanical discoveries.

When Kalm visited Vermont in 1749 the weather was very dry and he had little success in plant collecting (Eggleston, 1907). One interesting plant which Kalm did find was *Shepherdia canadensis* (L.) Nutt. He remarked it was flourishing ". . . everywhere on the shore of Lake Champlain." (Kalm, 1753-1761). Today *Shepherdia* is a rare plant in Vermont.

The elder Micheaux spent several days in Vermont in 1792 and listed some 175 species found about Lake Champlain (Eggleston, 1910). Little is known of the botanical discoveries of Francois

Andre Micheaux who visited Vermont in 1806 or of Rafinesque's trip through the State in 1816.

The weather was cold and rainy when Pursh visited Vermont in 1807. He holed up in Rutland where he waited, seemingly in vain, for a letter from his sponsor with funds to continue his journey. He became ill with ". . . a fever & bloody flux." Finally, in desperation, seeing ". . . no other means of getting away from here, than to contrive some way to get money to go on with, & pay my reckoning here, I, with great reluctance, sold my fowling piece this day; God knows whether the money will be enough to bring me on but I must rough it through as well as I can." As fate would have it, the long awaited letter and funds came the following day (Pursh, 1869). In all, Pursh spent approximately three weeks in Vermont during which time he collected some 30 or 40 specimens, mostly weeds and other common species (McVaugh, 1936). His most notable find was *Polystichum Braunii* (Spenner) Fee, the first record of the species in the New World.

It remained for more recent botanists, such as James Watson Robbins, Alphonso Wood, C. C. Frost, and Cyrus Pringle, to make the unusual botanical discoveries in Vermont.

Under circumstances somewhat less rigorous than those encountered by Pursh, James Watson Robbins, M.D., of Uxbridge, Massachusetts, visited Vermont in 1829. Robbins was the first botanist to find many of Vermont's rarest and most interesting plants. *Cornus florida* L., *Floerkea proserpinacoides* Willd., and *Valeriana uliginosa* (Torr. & Gray) Rydb. are a few of the species found by Robbins. Robbins had an eye, a very sharp eye, for discovering the unusual. He was, for example, the first botanist in North America to recognize *Wolffia,* our smallest phanerogam (Gray, 1879). On a limestone ledge only 200 feet long by 50 feet wide along the Winooski River near Burlington, Robbins discovered Vermont's most famous and noteworthy plant, *Astragalus Robbinsii.* The species was named for Robbins by his friend and admirer William Oakes. By 1894 *Astragalus Robbinsii* was extinct (Rydberg, 1924). The circumstances surrounding its demise can at best be called regrettable. The cause of its extinction appears to have been a simple case of over-collection and development. No one, it seems, made any attempt to save the species.

Cyrus G. Pringle, a well known Vermont botanist, made his living as a professional plant collector. He collected plants for Asa Gray, the American Museum of Natural History, and the Smithsonian Institution (Davis, 1936). In addition, he offered plants for sale to private collectors, usually at ten cents per specimen. Asa Gray once called Pringle the "prince of collectors" (Brainerd, 1911). Indeed, Pringle was an assiduous collector with an eye for the unusual. *Astragalus Robbinsii* appears on the trade lists that Pringle circulated to his customers. One can assume it was a "best seller," for the species was never found except at its type station, the tiny river ledge where Robbins first discovered it. That ledge, incidentally, was sufficiently well known to nineteenth century botanists to merit its own special name, "Phaca Ledge" (*Phaca* = *Astragalus*). The name, Phaca Ledge, appears on labels of many early collections of *Astragalus Robbinsii.*

Pringle, when reminiscing about his botanical career, said, there is ". . . a rumor current among botanists that Dr. Robbins' station for *Astragalus Robbinsii* . . . has been obliterated" but, he went on to say, ". . . the rumor proved unfounded." Furthermore, he remarked, there ". . . had been gathered a supply of these plants sufficient for all the herbaria of the world." (Pringle, 1897). And indeed there had — and all from the tiny Phaca Ledge! The ". . . herbaria of the world" abound in Pringle's collections of *Astragalus Robbinsii.* Pringle, however, does not warrant the blame for the extinction of *Astragalus Robbinsii* for he was not, in fact, the last person to see it alive. That distinction, it appears, belongs to W. W. Eggleston and L. R. Jones. Eggleston and Jones, on June 15, 1893 collected several specimens of *Astragalus Robbinsii* and noted on their labels, "last collection ever made." Interestingly, four days later Jones returned to Phaca Ledge and collected at least one more specimen. The reason Eggleston and Jones were inspired to collect these specimens was that a dam was about to be built and the ledge on which *Astragalus* grew was just upstream from the construction site. When the dam was completed, Phaca Ledge was inundated and has been under water ever since. There remains a serious question as to whether or not the extinction of the species was due principally to the dam. The large number of existing herbarium specimens of a species known only from so limited a habitat suggests that its fate may already have been sealed, dam or no dam.

The Endangered Species Act of 1973, P.L. 93 205 (87 Stat. 884), defines an endangered species as ". . . any species which is in danger of extinction throughout all or a significant portion of its range . . ."

If that definition is applied to the flora of Vermont only a few species would meet that criterion. Nonetheless, many species in the State are threatened by habitat destruction and, unless the trend is reversed, the number warranting "endangered" status will increase rapidly. There are many attractive and showy species in Vermont which are in need of protection to avoid commercial exploitation by wildflower nurserymen, but presently fall far short of being considered truly endangered. The white trillium, *Trillium grandiflorum* (Michx.) Salisb., and the moccasin flower, *Cypripedium acaule* Ait., for example, are sufficiently abundant in Vermont to render untenable their inclusion on the state list of endangered species. Another species, the Mayflower, *Epigaea repens* L., has long been the cause of much concern to New England wildflower lovers. It appears on many state lists of protected plants. Yet in Vermont this species is abundant, even along interstate highways on recently disturbed soil.

There are, in contrast, some Vermont species which are truly endangered. These include: *Hydrastis canadensis* L., the goldenseal, a species now known from but a single station in Vermont and a plant that is threatened by housing development; *Cypripedium arietinum* Ait., the ram'shead lady's-slipper, a species formerly found throughout the state but now exceedingly rare and threatened by road-widening and housing development; and *Scirpus ancistrochaetus* Schuyler, a species proposed by the Smithsonian Institution as a candidate for Federal listing as an endangered species, known in Vermont from but a single location, the type station, which is at the edge of a frequently mowed hayfield.

The Virginia chain fern, *Woodwardia virginica* (L.) Sm., is a rare fern in Vermont. It is known in the State from only three or four stations and has not been seen at most of these for many years. Its demise at one station is noteworthy. In the Town of Colchester, the chain fern was once well known along the border of a small pond; so well known, in fact, that botanists dubbed the pond "Woodwardia Pond." This station was destroyed when it was bulldozed under during preparation of the area for a missile launching site. The ground-to-air defense missile, "the Bomark," became obsolete before construction of the launching site was completed, but not before the *Woodwaria* station was destroyed.

While Woodwardia's plight in Vermont is a sad story, it is perhaps appropriate to relate, in a lighter vein, how Vermont lost one population of another rare species.

*Astragulus Jesupi* (Egglest. & Sheld.) Britt. is known from the banks of the Connecticut River at Hartland, Vermont and along the opposite shore in New Hampshire. It is also known from Hart Island which lies between the two areas noted above. Labels of specimens collected from the island read "Hart's Island, Hartland, Vt." The island population of *Astragulus Jesupi* was lost to the State of Vermont when the United States Supreme Court decreed, in its decision *re* Vermont *v.* New Hampshire 289 U. S. 593 (1933), that the boundary between the states was the low water mark along the west bank of the Connecticut River. Vermont's loss, of course, was New Hampshire's gain!

A recent study of Vermont's rare and endangered flora indicates that a high percentage of these species occur only on alpine or subalpine areas (Countryman, 1978). Today Vermont's higher elevations are a good deal less remote than they were a few decades ago. Roads, ski-lifts, radio and television antennas, and an ever increasing number of hikers pose a real and growing threat to alpine and subalpine plants and to the soils which support them. Although Vermont lies roughly between the same latitudes and is approximately the same size as New Hampshire, there is a great difference between the areas of high elevations possessed by the two states. Vermont has only five peaks over 4000 feet. The highest, Mt. Mansfield, is only 4393 feet above sea level. In contrast, New Hampshire has 47 peaks over 4000 feet (AMC, 1979). Of Vermont's 9600 square miles, less than one square mile is above timberline. Only four small areas in Vermont host significant populations of alpine plants: Mt. Mansfield, Smuggler's Notch, Camel's Hump, and the Willoughby area.

While Mt. Mansfield may be dwarfed by peaks in neighboring states, it is high enough to have accumulated several transmitter antennas. Many types of antennas — FM, AM, police, weather, etc.——have been placed on Mt. Mansfield. Even the Bomark missile system mentioned previously was to have included an extensive guidance system installation on Mt. Mansfield. These electronic devices must be maintained in both winter and summer. Ski trails, ski lifts, and other facilities for skiers take up considerable space on Mt. Mansfield. In addition, the mountain has a toll road, a parking lot, and many hiking trails. As a result, much alpine habitat has been destroyed by construction and erosion. *Diapensia lapponica* L. is threatened by hikers in the two small areas where it grows on Mt.

Mansfield. Between Memorial Day and Columbus Day an estimated 40,000 hikers visit Mt. Mansfield (Peet, 1979). Some of the other threatened species which have been found in Vermont only on Mt. Mansfield are *Hierochloë alpine* (Sw.) R. & S., *Salix Uva-ursi* Pursh, *Arenaria rubella* (Wahlenb.) Sw., and *Geocaulon lividum* (Richards.) Fern.

Camel's Hump, a high peak south of Mt. Mansfield, and with a similar flora, has only about ten acres above treeline, yet it hosts some 10,000 hikers a year (Peet, 1979). Obviously such large numbers of hikers cause excessive erosion along trails and trample many rare plants. Both Mt. Mansfield and Camel's Hump are now patrolled during the hiking season by teams of "ranger-naturalists" who attempt to keep hikers on the trails and away from sensitive areas, thus providing some protection to the alpine flora.

Smuggler's Notch is the divide separating Mt. Mansfield from Sterling Mountain to the east. It includes cliffs and ledges on both sides where many interesting plants have been observed. Some of the plants found on Mt. Mansfield and Smuggler's Notch are among Vermont's rarest species. *Deschampsia atropurpurea* (Wahlenb). Scheele, collected by Joseph Torrey on Mt. Mansfield in 1853, has never been seen in the State again (Eggleston, 1895). *Polygonum viviparum* L. and *Geocaulon lividum* (Richards.) Fern. appear not to have been seen in Vermont in this century although many specimens were collected from Mt. Mansfield prior to 1900. In 1878, Thomas Morong found in Smuggler's Notch a single plant of *Primula mistassinica* Michx. in flower, which he collected. The species has never been found there again. *Arnica mollis* Hook. was collected on Mt. Mansfield in 1911 by Charles Schweinfurth and Harold St. John; it has never been found again in the State. Some of the other rarities that occur on Mt. Mansfield and Smuggler's Notch are: *Lycopodium Selago* L., *Woodsia alpina* (Bolton) S. F. Gray, *Dryopteris fragrans* (L.) Schott, *Calamagrostis inexpansa* Gray var. *novae-angliae* Stebbins, *Castelleja septentrionalis* Lindl., *Hedysarum alpinum* L., *Saxifraga aizoides* L., S. *Aizoön* Jacq., and *S. oppositifolia* L.

Lake Willoughby and its associated mountains, Mt. Pisgah and Mt. Hor, comprise a strikingly scenic and botanically unique area in the northeastern part of Vermont. Calcareous cliffs and ledges there rise to elevations of only 2600 feet, far below timberline, yet they support a local population of far northern plant species. Robbins had been in sight of the Willoughby cliffs in 1829, as had John Carey in 1835 or 1836, yet neither explored the area. It remained for Alphonso Wood to discover what the natives called the "Garden of Edom" on his trip to Mt. Pisgah in the summer of 1845. Wood climbed from lake level to the top of the mountain and found *Hedysarum alpinum* L. and *Saxifraga aizoides* L., neither of which had previously been reported as occurring in the United States (Wood, 1847). He also found *Primula mistassinica* Michx., a species then unknown in the United States, save for a single station at Seneca, New York. Five years later, in 1852, C. C. Frost, the "Shoemaker Botanist" from Brattleboro, Vermont, visited Willoughby in company with the Reverend A. H. Clapp. They found *Astragalus Blakei* Egglest. and *Braya humilis* (C. A. Mey.) Robbins (Russell, 1852). The latter species is still known elsewhere in the United States only in northern Michigan. In 1854 William Boott visited the Willoughby area and discovered *Saxifraga Aizoön* Jacq. Boott was followed by Horace Mann, Jr., the Faxon brothers, and Cyrus Pringle. *Woodsia alpina* (Bolton) S. F. Gray and *Asplenium viride* Huds. were added to the list (Eggleston, 1922). Walter Deane and Judge Churchill, both founding members of the New England Botanical Club, spent two weeks botanizing at Willoughby in 1885. Deane prepared a report of their trip for the Botanical Gazette in which he states they traveled via the "Boston and Maine Airline" (Deane, 1886). Judging from the year, 1885, and the travel time from Boston, eight hours, it may be concluded that they traveled by train, not by airplane.

Most of Vermont's alpine and subalpine species have been found at the four classical locations noted above, where the majority were discovered before the turn of the century. There are, however, some other sites for alpine species in Vermont and some more recent discoveries. In 1908, for example, G. Lewis Dutton found *Sedum Rosea* (L.) Scop. on Mt. Horrid in Rochester, Vermont, one of the few inland stations in the country for this species (Dutton, 1908). In 1959, Philip Cook discovered the only known station in the United States for *Arenaria marcescens* Fern. at Haystack Mountain in Lowell, Vermont (Cook, 1959).

What is certainly one of the more exciting and surprising botanical finds in New England in this century was made by Donald White in 1970. White found *Potentilla Robbinsiana* Oakes on a Vermont mountain top. This diminutive species was formerly known only from a limited area on Mt. Washington, New Hampshire (Storks &

Crow, 1978). White's discovery was no accident. Like Robbins, White had sharp and well-trained eyes and a great deal of practice in plant collecting. He was elected to membership in the New England Botanical Club in 1911 and has been collecting plants ever since. His discovery, at age 77, of *Potentilla Robbinsiana* seems a fitting climax to a long career as an enthusiastic and ardent plant collector and should serve as an inspiration to younger botanists.

A cynic might say that the intellectually attractive thing about lists of rare plants is that, in the modern World, they are subject to so much revision. These lists have a purpose beyond the challenge of keeping them current. Their purpose, ultimately, is as an indicator of habitats important to our understanding and appreciation of nature. The responsible botanist knows this and, even in the face of official indifference, will do his part in protecting important species. Vermont's program of ranger-naturalists, whose job it is to inform and, indeed, discipline the considerable crowds that now visit our higher peaks, has worked well. It has been accepted and welcomed by most hikers. As we perceive new needs for protection, the botanist should be willing to accept an active, visible role even beyond the also necessary job of scientific advisor.

## LITERATURE CITED

AMC (Appalachian Mountain Club). 1976. The AMC White Mountain guide, a guide to trails in the mountains of New Hampshire. Appalachian Mountain Club, Boston.

Brainerd, E. 1911. Cyrus Guernsey Pringle (obituary). Rhodora **13:** 225 232.

Castiglioni, L. 1790. Viaggio negli stati-uniti dell America settentrionalis, fatto negli anni 1785, 1786 e 1787 - con alcune osservazziono sui vegetabili piu utili diquel paesse. Milano.

Cook, P. W. 1959. Discovery of *Arenaria marcescens* in the United States. Rhodora **61:** 123 124.

Countryman, W.D. 1978. Rare and endangered vascular plant species in Vermont. U. S. Fish & Wildlife Service, Region 5, Newton Corner, Mass.

Davis, H. B. 1936. Life and work of Cyrus Guernsey Pringle. University of Vermont, Burlington.

Deane, W. 1886. A trip to Willoughby Lake, Vermont. Bot. Gaz. **11:** 112 116.

Dutton, G. L. 1908. Some rare plants of Mount Horrid. Bull. Vermont Bot. Club **2:** 39 39.

Eggleston, W. W. 1895. The flora of Mt. Mansfield. Bot. Gaz. **20:** 72 75.

———. 1907. Peter Kalm's visit to Lake Champlain in July 1749. Bull. Vermont Bot. Club **2:** 23 33.

———. 1910. Early botanists visiting Vermont. Bull. Vermont Bot. Club **5:** 10 14.

———. 1922. Notes on the early botanical explorations of Willoughby Lake. Joint Bull. Vermont Botanical and Bird Clubs **8:** 23 25.

Grant, W. L. 1907. Voyages of Samuel de Champlain, 1604 1618. Charles Scribner's Sons, New York.

Gray, A. 1879. Botanical necrology of 1878 — James Watson Robbins. Amer. J. Sci. & Arts **17:** 180.

Kalm, P. 1853 1861. En resa til Norra America. Volumes I III. Stockholm.

McVaugh, R. 1936. A study of the plant-collections made by Frederick Pursh during a trip to New York and Vermont in the year 1807. Bartonia No. **17:** 24 32.

Peet, H. T., Jr. 1979. Long Trail use figures are useful. The Long Trail News **39**(2): 8 9, 11.

Pringle, C. G. 1897. Remniscences of botanical rambles in Vermont. Bull. Torrey Bot. Club **24:** 350 357.

Pursh, Frederick. 1869. Journal of a botanical excursion in the northeastern parts of the states of Pennsylvania and New York, during the year 1807. Brinkloe and Marot, printers, Philadelphia. Reprinted in 1923 by the Onondaga (New York) Historical Association.

Russell, J. L. 1852. Some of the rarer plants of Vermont. Hovey's Magazine of Horticulture **18:** 481 485. (reprinted in Eggleston, 1922).

Rydberg, P. A. 1924. Some extinct or lost and rediscovered plants — I. Torreya **24:** 98 101.

Storks, I. M., & G. E. Crow. 1979. Rare and endangered vascular plant species in New Hampshire. U. S. Fish & Wildlife Service, Region 5, Newton Corners, Mass.

Wood, A. 1847. Willoughby Lake. Vermont Chronicle **22:** 160.

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# RARE AND ENDANGERED PLANTS OF NEW HAMPSHIRE: A PHYTOGEOGRAPHIC VIEWPOINT[1]

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The native vascular plant flora of New Hampshire is estimated at about 1500 species (Hodgdon, 1973). We regard a total of 398 taxa as sufficiently rare in the state to warrant their protection through habitat preservation, and have enumerated them in our listing of New Hampshire's rare and endangered vascular plants (Storks & Crow, 1978). Of those listed, 144 taxa (36% of list, about 9% of native flora) are considered "endangered," 116 taxa (29% of list, about 8% of flora) "threatened," 127 taxa (32% of list, about 8% of flora) "rare" and 11 taxa (3% of list, about 1% of flora) possibly extinct.

Rare plant species of New Hampshire can be divided into 5 general categories based on distributional patterns within the state: (1) southern New Hampshire, (2) coastal taxa, (3) taxa primarily restricted to the Connecticut River Valley, (4) those of rare, somewhat scattered occurrence in the state, and (5) taxa adapted to the alpine environment of the White Mountains.

## Southern New Hampshire

Over 100 taxa of the state's rare and endangered flora have been found to reach the northern or northeastern limit of their geographical range in the southern portion of the state. A number of taxa, such as *Desmodium marilandicum* (Tick-trefoil), *D. rigidum, D. rotundifolium, Lespedeza procumbens* (Trailing Bush-clover), *L. virginica,* and *Tephrosia virginiana* (Hoary Pea), are found in dry, open woods and slopes. Jeremy Hill in Pelham and the middle summit of the Pawtuckaway Mountains in Nottingham, sites which afford a warm, protected, southern exposure and are too rocky and steep for cultivation, serve as suitable sites for a number of such southern taxa.

*Isotria verticillata* (Whorled Pogonia), a plant of moist or dry acid woods, has been reported from only three stations in southern New Hampshire. *Isotria medeoloides* (Small Whorled Pogonia),

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[1] Scientific Contribution Number 1000 from the New Hampshire Experiment Station

which is extremely rare throughout its geographical range and was under review for federal "threatened" status (Federal Register, 1 July 1975, Vol. 40, No. 127), has been reported from six New Hampshire stations in rich hardwood forests. Both species are difficult to distinguish from *Medeola virginiana* (Indian Cucumber) when lacking flowers.

*Lilium superbum* (Turk's-cap Lily) is represented in New Hampshire by a single station at the edge of a saltmarsh along the Oyster River estuary in Durham. This station marks the northeastern limit of its geographical range.

Table 1 lists taxa of the rare and endangered flora which reach their northern or northeastern range limits in southern New Hampshire (excluding taxa restricted to coastal sites or the Connecticut River Valley).

Table 1. **Southern N.H. (excluding coastal and Conn. R. V.)**

EXTINCT ?
Carex woodii
Prenanthes serpentaria

ENDANGERED
Arisaema dracontium
Aureolaria pedicularia var. intercedens
Bidens laevis
Carex aestivalis
Carex flaccosperma var. glaucodea
Carex polymorpha
Carex seorsa
Cardamine bulbosa
Castilleja coccinea
Desmodium marilandicum
Desmodium rigidum
Eragrostis frankii
Eupatorium sessilifolium
Isoetes foveolata
Isotria medeoloides
Isotria verticillata
Juncus platyphyllus
Lechea tenuifolia
Lespedeza virginica
Lespedeza procumbens
Lilium superbum
Liparis lilifolia
Lygodium palmatum
Panicum longifolium
Panicum sphaerocarpon
Parietaria floridana
Parietaria pensylvanica
Pycnanthemum incanum
Pycnanthemum torrei
Ranunculus ambigens
Ranunculus fascicularis
Rhododendron periclymenoides (=R. nudiflorum)
Rubus cuneifolius
Sericocarpus linifolius (=Aster solidagineus)
Sphenopholis obtusata
Viola palmata

THREATENED
Acalypha virginica
Arabis canadensis
Asclepias purpurascens
Asclepias quadrifolia
Aster patens var. patens
Betula nigra
Bromus kalmii
Carex sparganioides

Table I (continued)

THREATENED, continued

Cyperus houghtonii
Dentaria laciniata
Desmodium cuspidatum
Desmodium rotundifolium
Digitaria filiformis
Galium obtusum var. obtusum
Galium pilosum
Gentiana quinquifolia
Geranium carolinianum var. carolinianum
Glyceria acutiflora
Hemicarpha micrantha
Hypericum adpressum
Isoetes eatoni
Isoetes engelmanni
Isoetes riparia var. riparia
Lemna valdiviana
Muhlenbergia sobolifera
Muhlenbergia tenuiflora
Polygonum tenue
Rhododendron viscosum
Scirpus lineatus
Solidago odorata
Tephrosia virginiana
Triphora trianthophora

RARE

Anemonella thalictroides
Arabis missouriensis
Asclepias amplexicaulis
Asclepias tuberosa
Aureolaria virginica
Carex retroflexa
Cassia hebecarpa
Cenchrus longispinus
Chimaphila maculata
Convolvulus spithamaeus
Gentiana crinita
Hypoxis hirsuta
Iris prismatica
Juncus secundus
Leptoloma cognatum
Lycopus rubellus
Nuphar advena
Panicum philadelphicum
Tovara virginiana
Viola pedata var. lineariloba
Vulpia octoflora var. tenella
Woodsia obtusa
Xanthoxylum americanum
Xyris torta

## Coastal New Hampshire

The coastline of New Hampshire is transitional between the sandy beaches and barrier beach islands with extensive saltmarsh development, characteristic of the South to Middle Atlantic, and the rocky coastline characteristic of the North Atlantic. Although the linear shoreline is a mere 19 miles long, the shoreline of the Great Bay estuarine system is extensive, with several sites along the Piscataqua River having features characteristic of the open coast (Reynolds & Mathieson, 1975). Tidal marshes occupy approximately 7500 acres of the seacoast area (Breeding et al., 1974). A total of 37 taxa of New Hampshire's rare plants are coastal.

In North America *Sagina nodosa* ssp. *nodosa* (var. *pubescens* of *Gray's Manual* (Fernald, 1950)) is restricted to coasts, growing in moist rock crevices along seashores and on sea cliffs from Cape Ann, Massachusetts to Nova Scotia (Crow, 1978). Several specimens were collected by Oakes and Robbins on the Isles of Shoals in the 1800's, but apparently the taxon has not been collected there since, and we regard it as probably extinct in the state.

The coastal region has experienced a continuing intense pressure from development interests. The only recorded site for *Diplachne maritima* (Salt-meadow Grass), a saltmarsh in the town of Seabrook, has been destroyed by development. Seabrook is also the location of a number of state rarities represented by a single New Hampshire station. Most of these are plants of the dune community. Because of coastal development, the foredune and interdune have been replaced by houses and summer cottages and only a remnant of the backdune remains. Several species, such as *Hudsonia tomentosa* var. *tomentosa* (False Heather), *Aristida tuberculosa* (Needlegrass), *Arenaria peploides* var. *robusta* (Seabeach Sandwort), *Cyperus grayii* (Sedge), and *Ammophila brevilgulata* (Beach Grass) occupy this site and their doom is heralded by a large sign announcing "Coming Soon, New Homes."

In contrast, *Iva fructescens* var. *oraria* (Shrubby Marsh-elder), which grows on shores and the upper margins of saltmarshes, appears to be extending its range northward.

Table 2 lists taxa restricted to coastal sites in New Hampshire.

An interior locality which has very strong Coastal Plain affinities is Ossipee Lake, which has very sandy beaches. Hellquist (1971) notes that the southern shore, known as Long Sands, consists of a particularly fine white sand on the shore and in the water, with intermittent "islands" of reeds along the shoreline. Here we have found *Hudsonia tomentosa* var. *intermedia* (False Heather) growing scattered along the entire stretch of beach. *Lycopodium inundatum* var. *bigelovii* (Bigelow's Bog Clubmoss) and *Proserpinaca pectinata* (Mermaid-weed), two additional rarities, grow among the reeds in a sandy-peaty substrate. A dominance of *Pinus rigida* (Pitch Pine) and *Quercus marilandica* (Scrub or Bear Oak) in the adjacent wooded areas is also reminescent of Coastal Plain vegetation.

## Connecticut River Valley

While soils throughout the Granite State are predominately acidic, the alluvial soils of the Connecticut river floodplain and river

Table 2. **Coastal New Hampshire**

EXTINCT?

Diplachne maritima
Elymus mollis
Sagina nodosa ssp. nodosa
Triplasis purpurea

ENDANGERED

Arenaria peploides var. robusta
Aristida tuberculosa
Aster tenuifolia
Chenopodium rubrum
Cirsium horridulum
Cyperus grayii
Eleocharis halophila
Hudsonia tomentosa var. tomentosa
Limosella subulata
Melampyrum lineare var. pectinata
Rumex pallidus
Salicornia virginica
Scirpus robustus
Sclerolepis uniflora
Sporobolus cryptandrus
Triosteum aurantiacum

THREATENED

Ammophila breviligulata
Lilaeopsis chinensis
Lycopodium inundatum var. bigelovii
Polygala cruciata var. aquilonia
Polygonum exsertum
Polygonum prolificum
Potentilla pectinata
Salicornia bigelovii
Samolus parviflorus
Woodwardia areolata

RARE

Agalinis maritima
Artemisia caudata
Chamaecyparis thyoides
Eleocharis parvula
Iva fructescens var. oraria
Puccinellia paupercula
Spartina caespitosa

terraces tend to be neutral to slightly alkaline from the deposition of silty materials derived from calcareous outcroppings upstream (Latimer et al., 1939; Williams et al., 1943). The floodplain and terraces tend to support moist, rich woods and meadows with a flora somewhat different from the rest of the state (Hodgdon & Steele, 1958). A total of 60 taxa on the New Hampshire list of rare and endangered plants are primarily restricted to the Connecticut River Valley.

*Orchis spectabilis* (Showy Orchis) is known from only 10 sites in New Hampshire, 8 of which occur along the Connecticut River, primarily on steep slopes of the river terraces supporting rich, calcareous woods. Indicator plants include *Hepatica acutiloba* (Hepatica), *Asarum canadensis* (Wild Ginger), *Adiantum pedatum* (Maidenhair Fern), and *Caulophyllum thalictroides* (Blue Cohosh) (F. E. Brackley, pers. comm.).

Two orchids reported from the town of Hanover are of particular interest. *Habenaria ciliaris* (Orange-fringed Orchis), represented by a single New Hampshire station, was last collected in 1872 and is now believed to be extinct. *Cypripedium reginae* (Showy Lady's-slipper) was documented from a bog, known as the Bottomless Pit, in 1889, 1890 and 1891, but apparently has not been collected since. The bog is now in the late stages of succession, the open water stage long since passed, and extinction may have been a natural process for this orchid population.

We reported the Hanover station of *Cypripedium reginae* as the single documented station in New Hampshire and probably extinct for the state (Storks & Crow, 1978). During the summer of 1979, F. E. Brackley (1979) located and documented two new stations, one in the town of Lyme and another in the town of Lisbon. This underscores the need for additional field work on the modern status of rare and endangered plants.

Lime Pond in Columbia is located in a calcareous area characterized by bedrock composed of mica schist impregnated with calcareous materials and bands of impure silicious limestone (Pease, 1964). It is one of two documented sites for the exceedingly rare *Calypso bulbosa* (Calypso orchid). This locality, in a wet *Thuja occidentalis* (Northern White Cedar) woods, was discovered in 1934 by T. W. Wallace (letter accompanying photographic specimen in the Hodgdon Herbarium, NHA) and last collected by A. S. Pease in 1946. The site was visited by Pease (1964) in 1952 and 1961, but the orchid was not found, nor were we able to locate it in 1978. A potential threat to the habitat surfaced in 1978 when the State of New Hampshire was approached for permission to mine the lime sediments, estimated at 300,000 tons, to sell to local farmers (Ferriter, 1978). Although the State denied the proposal, the economic value of the lime deposits on the bottom of the pond may pose a threat to the habitat in the future.

Table 3 lists taxa primarily restricted to the Connecticut River Valley.

## Scattered Distribution

A number of taxa are not restricted to a particular region of the state, but occur somewhat widely scattered. Availability of suitable habitat appears to be the primary factor influencing the distribution of these plants.

Several orchids fit this distributional pattern and may be declining due to the vulnerability of their habitats to development and

Table 3. **Primarily restricted to Connecticut River Valley**

EXTINCT

Calypso bulbosa
Habenaria ciliaris

ENDANGERED

Acer nigrum
Amphicarpa bracteata var. comosa
Aster ptarmicoides
Astragalus alpinus var. brunetianus
Astragalus robbinsii var. jesupi
Carex buxbaumii
Carex castanea
Carex garberi var. bifaria
Collinsonia canadensis
Corydalis aurea
Cypripedium reginae
Dentaria maxima
Eleocharis nitida
Equisetum variegatum var. jesupi
Eragrostis hypnoides
Halenia deflexa
Heteranthera dubia
Juniperus horizontalis
Malaxis brachypoda
Polygonatum commutatum
Potamogeton filiformis
Potamogeton foliosus
Potamogeton lateralis
Pycnanthemum virginianum
Ranunculus subrigidus
Rosa acicularis
Salix cordata var. abrasa
Spiranthes lucida
Tofieldia glutinosa
Uvularia grandiflora
Woodsia glabella

THREATENED

Allium schoenoprasum var. sibiricum
Carex amphibola var. rigida
Carex aurea
Carex diandra
Eleocharis pauciflora var. fernaldii
Hypericum pyramidatum
Liparis loeselii
Parnassia glauca
Potamogeton richardsonii
Salix interior
Solidago purshii

RARE

Camptosorus rhizophyllus
Carex bebbii
Celtis occidentalis
Cyperus inflexus
Cystopteris bulbifera
Dicentra canadensis
Dryopteris goldiana
Equisetum pratense
Hepatica acutiloba
Hydrophyllum virginianum
Juncus brachycephalus
Lobelia kalmii
Sanicula gregaria
Senecio pauperculus
Staphylea trifolia
Viola rostrata

destruction. Examples include *Cypripedium calceolus* var. *pubescens* (Large Yellow Lady's-slipper) and var. *parviflorum* (Small Yellow Lady's-slipper), *Listera cordata* (Heartleaf Twayblade), and two which were under review for federal "threatened" status (Federal Register, 1 July 1975, Vol. 40, No. 127), *Habenaria (Platanthera) flava* var. *herbiola* (Pale Green Orchis) and *Cypripedium arietinum* (Ram's-head Lady's-slipper).

Another orchid of particular interest is *Triphora trianthophora* (Nodding Pogonia). This species occurs in nearly pure stands of *Fagus grandifolia* (American Beech) whose soils have a deep humus.

The plants may remain dormant underground for long periods (Lownes, 1920) and therefore may appear to be exceedingly rare in some years and locally abundant in others.

The caryophyllaceous *Paronychia argyrocoma* var. *albimontana* (White Mountain Silverling or Silver Whitlow-wort) occupies bare granitic slopes and ledges and occasionally sandy river banks. This restricted and local taxon, endemic to northern New England, was under review (Federal Register, 1 July 1975, Vol. 40, No. 127) for federal "threatened" status.

Suitable habitat for *Pinguicula vulgaris* (Butterwort), a boreal species of chiefly wet, calcareous sites, is very rare in the state, with only 3 localities known. The plants occupy wet rock cliffs and steep slopes of the Cannon Cliffs and Mt. Lafayette in Franconia, and Butterwort Flume in Crawford Notch, Hart's Location.

## Alpine Environment

The greatest number of taxa (80) listed as rare and endangered for a single habitat in New Hampshire are adapted to the alpine environment of the Presidential and Franconia Ranges of the White Mountains, chiefly Mt. Washington. A detailed account of the status of the rare and endangered alpine species has been given in a report prepared for the White Mountain National Forest, New Hampshire (Storks, 1979; Storks and Crow, 1979). Several sites and taxa are particularly noteworthy. Tuckerman's Ravine, the Great Gulf, and Huntington's Ravine of Mt. Washington are steep, cool, moist ravines in which great amounts of snow accumulate and remain long into the growing season. A number of plants adapted to arctic conditions occur in these locations.

*Sibbaldia procumbens* (Sibbaldia), disjunct from the Gaspé Peninsula, Quebec; the Long Range, Newfoundland; and arctic regions, occurs only in Tuckerman's Ravine and represents a single New England station.

*Oxyria digyna* (Mountain Sorrel) is known in northeastern United States only from the Great Gulf, Tuckerman's Ravine, and Huntington's Ravine on Mt. Washington.

Other arctic-alpine plants which occur chiefly in the cool, wet ravines and along alpine brooks include *Cardamine bellidifolia* (Alpine Cress), *Salix herbacea* (Dwarf Willow), *Arnica mollis* (Arnica), *Phleum alpinum* (Alpine Timothy), *Festuca prolifera* (Prolific Fescue), *Castilleja septentrionalis* (Pale Painted-cup), *Bar-*

*barea orthoceras* (Winter-cress), *Epilobium alpinum* (Alpine Willow-herb), *E. palustris* (Marsh Willow-herb), *E. hornmanni* (Hornmann's Willow-herb), and *Salix planifolia* (Tea-leaved Willow).

Two extremely rare saxifrages occupy moist ledges and cliffs of the headwall of Huntington's Ravine. *Saxifraga aizoön* var. *neogaea* (Live-long Saxifrage) was discovered in 1939 by Dr. John Churchill (1967), and relocated in 1967 (Steele, 1967), in a site accessible only to professional rock climbers. A second site of 30 40 plants was discovered by Irene Storks in 1978 on a ledge just 10 feet up the cliff. This is the only locality known for New Hampshire. Vermont (Countryman, 1978) and Maine (Eastman, 1978a) report the only other New England occurrences of the taxon.

*Saxifraga cernua* (Bulblet Saxifrage) was also discovered by Churchill at the time he first observed *S. aizoön* on the headwall of Huntington's Ravine (Churchill & Hodgdon, 1967). This site represents a single New England station.

Another Huntington's Ravine rarity is *Gnaphalium supinum* (Alpine Cudweed). It grows in unstable coarse gravels just beneath the headwall of the ravine and is therefore vulnerable to disturbance and possible extirpation by activities of hikers and climbers. The population last documented in Tuckerman's Ravine in 1901 by Eggleston appears to be extinct, perhaps as a result of trampling.

The most critically endangered alpine plant is the New England endemic *Potentilla robbinsiana* (Robbins' Cinquefoil). This species, previously believed to be endemic to New Hampshire, has recently been reported by Countryman (1978) from an understandably undisclosed site in Vermont. We have also recently discovered two additional historical records among an unmounted Robbins collection in the New England Botanical Club Herbarium. Both specimens were collected by Tuckerman, one from the north side of the peak of Mt. Washington (1839) and the other from Mt. Mansfield, Vermont (no date).

The original station for *Potentilla robbinsiana* remains the primary site of the species. Its location on the southwest slope of Mt. Washington is well known. The greatest threat to the population comes, not from naturalists wishing to see this rare endemic (although, admittedly, far too many specimens have been collected by our botanical forefathers), but from the cumulative effect of trampling by hikers over the years. Presently the Crawford Path (part of the Appalachian Trail) passes right through the fragile alpine fellfield and several local botanists can remember when plants of *P. robbinsiana* grew on both sides of the trail (F. L. Steele, pers. comm.). The population has become constricted such that plants now occupy only 2/10ths of an acre and only approximately 1800 mature plants remain (Graber, 1980). Often hikers unknowingly wander across the critical site to reach a rock outcrop which affords a magnificent view from the upper rim of Oakes Gulf. The impact is severely altering the habitat by disturbing the stony surface and trampling individual plants, the seedlings being most sensitive (Graber, 1980).

The White Mountain National Forest staff are concerned about the protection of this population and steps are being taken, in cooperation with the Appalachian Mountain Club, to provide a greater measure of protection to the site.

Table 4 lists plants of the alpine and subalpine considered endangered, threatened or rare in New Hampshire.

## PHYTOGEOGRAPHICAL AFFINITIES

The flora of New Hampshire, post-Pleistocene in age, is derived from a number of phytogeographic elements. Many of our species are rare because they are at the edge of their ranges, northern or southern, or are disjunct from areas where they occur in greater abundance and frequency. Some are rare throughout their entire range.

**Widespread/eastern United States element.** A large number of our rarities reach the northern or northeastern limit of their range in New Hampshire. Table 1 includes a list of plants of southern New Hampshire (exclusive of coastal taxa and taxa restricted to the Connecticut River Valley) which fit this pattern.

Major river systems, such as the Connecticut, Merrimack and Saco Rivers, have served as migratory routes by which some taxa have extended their range. *Celtis occidentalis* (Hackberry), for example, which occurs widely in eastern United States primarily in damp woods and alluvial soils, extends its range northward from southern New England into New Hampshire and Vermont along the Connecticut River Valley and into northern Vermont along the Hudson River Valley (Little, 1971). The pattern is similar for *Carya cordiformis* (Bitternut Hickory).

**Atlantic Coastal Plain element.** The Atlantic Coastal Plain provides

Table 4. **Alpine and subalpine New Hampshire**

EXTINCT?
Calamagrostis nubila

ENDANGERED
Barbarea orthoceras
Cardamine bellidifolia
Carex atratiformis
Carex capillaris var. capillaris
Carex capitata
Carex lenticularis var. albimontana
Epilobium alpinum
Euphrasia oakesii
Festuca prolifera
Gnaphalium supinum
Luzula confusa
Oxyria digyna
Poa alpigena
Potentilla robbinsiana
Salix peasei
Saxifraga aizoön var. neogaea
Saxifraga cernua
Sibbaldia procumbens
Silene acaulis var. exscapa
Viola labradorica

THREATENED
Achillea borealis
Arctostaphylos alpina
Arnica mollis
Calamagrostis lacustris
Calamagrostis neglecta
Cassiope hypnoides
Castilleja septentrionalis
Geum peckii
Houstonia caerulea var. faxonorum
Paronychia argyrocoma var. albimontana
Phleum alpinum
Phyllodoce caerulea
Polygonum viviparum
Prenanthes Boottii
Rubus chamaemorus
Salix argyrocarpa
Salix herbacea
Salix planifolia
Saxifraga rivularis
Trisetum spicatum var. pilosiglume
Veronica alpina var. unalaschcensis

RARE
Agrostis borealis var. americana
Agrostis borealis var. borealis
Arenaria groenlandica
Betula glandulosa
Betula minor
Calamagrostis canadensis var. robusta
Calamagrostis pickeringii var. debilis
Calamagrostis pickeringii var. pickeringii
Carex bigelowii
Carex scirpoidea
Deschampsia atropurpurea
Diapensia lapponica
Empetrum atropurpureum
Empetrum nigrum
Epilobium ciliatum
Epilobium hornmanni
Epilobium palustre
Geocaulon lividum
Hierochloe alpina
Juncus trifidus
Loiseleuria procumbens
Luzula spicata
Lycopodium annotinum var. pungens
Lycopodium selago
Poa fernaldiana
Poa glauca
Prenanthes trifoliolata var. nana
Rhinanthus crista-galli
Rhododendron lapponicum
Salix uva-ursi
Scirpus cespitosus var. callosus
Solidago cutleri
Spiraea latifolia var. septentrionalis
Vaccinium boreale
Vaccinium uliginosum var. alpinum
Vaccinium vitis-idaea var. minus
Viburnum edule
Viola palustris

another avenue of migration for a number of plants. Taxa such as *Ammophila breviligulata* (Beach Grass), *Aristida tuberculosa* (Needlegrass), *Chamaecyparis thyoides* (Atlantic White Cedar), *Cyperus grayii* (Sedge), *Hudsonia tomentosa* var. *tomentosa* (False Heather), *Polygonum robustius* (Robust Smartweed) and *Proserpinaca pectinata* (Mermaid-weed) serve as examples.

*Parietaria floridana* (Pellitory) in New Hampshire is somewhat of a puzzle. The taxon is clearly a Coastal Plain species in southeastern United States, occupying maritime forests from Florida to Texas, and north to North Carolina on the outer Coastal Plain (Small, 1933; Radford et al., 1968; Correll & Johnston, 1970). However, the species occurs westward to Arizona and southern California in non-coastal sites (Kearney & Peebles, 1964; Munz & Keck, 1970). It occurs in a disjunct locality in New Hampshire, not on the coast, but on Mt. Pawtuckaway (elevation 1,011 ft.) in Nottingham, Rockingham County. It is possible that this species was more widespread during the post-glacial warming trend which reached a temperature maximum between 5000 and 8000 years ago (Wright, 1972) and that the Mt. Pawtuckaway station may represent a relict population. It has not been collected since A A. Eaton's discovery in 1896.

**Northern coastal element.** This phytogeographic unit is represented by only a few of our rare species. These include *Elymus mollis* (Sea Lyme-grass), *Puccinellia paupercula* (Alkali-grass), and *Sagina nodosa* ssp. *nodosa* (Pearlwort).

**Cordilleran element.** Several taxa of the flora of New Hampshire belong to a Cordilleran element, disjunct from the montane regions of western North America. Of those taxa listed as rare and endangered in New Hampshire, *Arnica mollis* (Arnica), a disjunct from the alpine and subalpine regions of western North America, and *Osmorhiza chilensis* (Sweet Cicely), a woodland plant, fit this distributional pattern.

**Circumboreal element.** Several of our rare species range widely around the world in the boreal forest region. *Calypso bulbosa* (Calypso), *Equisetum palustre* (Horsetail), *Hieracium umbellatum* (Hawkweed), and *Listera cordata* (Heart-leaved Twayblade) are examples of this distribution pattern.

**Circumpolar element.** A large number of arctic-alpine disjuncts are distributed widely around the polar regions of the Northern Hemisphere. Examples include: *Arctostaphylos alpina* (Alpine Bearberry), *Cardamine bellidifolia* (Alpine Cress), *Carex capitata* (Capitate Sedge), *Epilobium alpinum* (Alpine Willow-herb), *Loiseleuria procumbens* (Alpine Azalea), *Lycopodium annotinum* var. *pungens* (Bristly Clubmoss), *Oxyria digyna* (Mountain Sorrel), *Phleum alpinum* (Alpine Timothy) —a bipolar disjunct, *Salix herbacea* (Dwarf Willow), *Saxifraga cernua* (Bulblet Saxifrage), and *Saxifraga rivularis* (Alpine-Brook Saxifrage).

**North American element—transcontinental in the boreal forest region.** Species representing this element include: *Achillea borealis* (Northern Yarrow), *Geocaulon lividum* (Northern Commandra), *Juniperus horizontalis* (Creeping Savin), *Listera convallarioides* (Broad-lipped Twayblade), *Pinus banksiana* (Jack Pine), and *Viburnum edule* (Mooseberry).

**North American element—transcontinental at high latitudes.** Several of our arctic-alpine disjuncts comprise this element: *Castilleja septentrionalis* (Pale Painted-cup), *Saxifraga aizoön* var. *neogaea* (Live-long Saxifrage), and *Vaccinium vitis-idaea* var. *minus* (Mountain Cranberry).

**Northeastern North American element.** Arctic-alpine examples of this group include: *Arenaria groenlandica* (Mountain Sandwort), *Betula minor* (Dwarf Birch), *Empetrum atropurpureum* (Purple Crowberry), *Juncus trifidus* (Three-forked Sedge), *Salix uva-ursi* (Bearberry Willow), and *Vaccinium boreale* (Northern Blueberry). Plants of lower elevations include: *Listera auriculata* (Auricled Twayblade), *Malaxis brachypoda* (Adder's Mouth), and *Myriophyllum farwellii* (Farwell's Water-Milfoil).

**Amphi-Atlantic element.** Several of our arctic-alpine plants have an Amphi-Atlantic distribution, their range including both sides of the Atlantic. Examples are *Carex bigelowii* (Bigelow's Sedge), *Cassiope hypnoides* (Moss Plant), *Diapensia lapponica* (Diapensia), *Festuca prolifera* (Prolific Fescue), *Rhododendron lapponicum* (Lapland Rosebay) and *Silene acaulis* var. *exscapa* (Moss Campion).

**Endemic element.** The endemic element, as one might expect for a recently derived flora in a region completely denuded of vegetation by glacial action, consists of just a few taxa. Endemics which occur in New Hampshire include the following:

*Prenanthes boottii* (Boott's Rattlesnake-root) is restricted to alpine areas in New York, Vermont, New Hampshire, and Maine. The center of distribution appears to be the White Mountains of

New Hampshire, where Pease (1964) considered the species to be common in the alpine zone. The species is known from 3 stations in Maine (Eastman, 1978a), 2 sites in Vermont (Countryman, 1978) and 3 localities in New York (Mitchell, 1979).

*Paronychia argyrocoma* var. *albimontana* (White Mountain Silverling or Silver Whitlow-wort) is likewise primarily distributed in New Hampshire, where it is documented from 19 sites, growing principally on dry, rocky ledges. Eastman (1978b) cites 8 stations in Maine, and a single station is known from Massachusetts on rocky ledges of an island in the Merrimack River (Coddington & Field, 1978).

*Houstonia caerulea* var. *faxonorum* (Alpine Bluet) has a very restricted overall distribution. It occupies meadows and stream margins of alpine and subalpine areas in the Presidential range of the White Mountains, New Hampshire, and along stream borders in the French Territory of St. Pierre et Miquelon, off the southern coast of Newfoundland. This taxon differs from the typical variety on very minor characters and a review of its taxonomic status is in order.

*Geum peckii* (Mountain Avens) occurs in great abundance in moist alpine meadows and subalpine ravines throughout the Presidential and Franconia Ranges of New Hampshire. It is also occasionally found growing on wet rocks in openings at lower altitudes in Coos and Grafton Counties. The species is known only from the White Mountains in New Hampshire and in Nova Scotia from a large bog on Brier Island, Digby County (Roland & Smith, 1969) and two new sites, Cumberland and Pictou Counties (Scoggan, 1978). The species is most closely related to *Geum radiatum*, a rare endemic of balds at upper elevations in North Carolina (Raynor, 1952; Gajewski, 1957).

*Potentilla robbinsiana* (Robbins' Cinquefoil) is our rarest endemic, with only 2 populations believed to be extant in New England, the primary site located on the southwestern slope of Mt. Washington and the small station newly reported by Countryman (1978) in Vermont. Löve and Löve (1966) regard the taxon as an apomictic segregate of the arctic *P. hyparctica* and treat the arctic taxon as *P. robbinsiana* ssp. *hyparctica* (D. Löve, 1968).

## CONCLUSIONS

A complex interrelationship involving environmental, biotic, physical, and historical factors has come to bear on the development of the rare components of the flora of New Hampshire. Of the estimated 1500 native vascular plant species comprising the flora, about 9% are endangered, about 8% are threatened, about 8% are rare and about 1% are possibly extinct. The rare component of the flora appears to consist of 11 phytogeographical groups: Widespread/eastern United States element, Atlantic Coastal Plain element, Northern coastal element, Cordilleran element, Circumboreal element, Circumpolar element, North American Element—transcontinental in the boreal forest region, North American element—transcontinental at high latitudes, Northeastern North American element, Amphi-Atlantic element, and the Endemic element.

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## LITERATURE CITED

Brackley, F. E. 1979. *Cypripedium reginae* rediscovered in New Hampshire. Rhodora **81:** 579 580.

Breeding, C. H. J., F. D. Richardson, S. A. L. Pilgrim. 1974. Soil survey of New Hampshire tidal marshes. N. H. Agric. Exp. Sta. Research Report No. **40.**

Churchill, J. R. 1967. *Saxifraga aizoon* in New Hampshire. Rhodora **69:** 483 484.

Churchill, J. R. & A. R. Hodgdon. 1967. *Saxifraga cernua* in New England. Rhodora **69:** 485 486.

Coddington, J. & K. Field. 1978. Rare and endangered vascular plant species in Massachusetts. The New England Botanical Club in cooperation with the U. S. Fish and Wildlife Service [Region 5, Newton Corner, MA].

Correll, D. S. & M. C. Johnston. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, Texas.

Countryman, W. D. 1978. Rare and endangered vascular plant species in Vermont. The New England Botanical Club in cooperation with the U. S. Fish and Wildlife Service [Region 5, Newton Corner, MA].

Crow, G. E. 1978. A taxonomic revision of *Sagina* (Caryophyllaceae) in North America. Rhodora **80:** 1 91.

Eastman, L. M. 1978a. Rare and endangered vascular plant species in Maine. The New England Botanical Club in cooperation with the U. S. Fish and Wildlife Service [Region 5, Newton Corner, MA].

EASTMAN, L. M. 1978b. Rare vascular Maine plants: a compilation of herbarium and literature citations. Maine State Planning Office, Augusta, Maine.

FERNALD, M. L. 1950. Gray's manual of botany. Corrected printing, 1970. D. VanNostrand Co., New York.

FERRITER, T. 1978. A proposal to Mine Lime Pond has North Country folks up in arms. New Hampshire Times, Vol **7**, no. 47 (May 10 May 16, 1978).

GAJEWSKI, W. 1957. A cytogenetic study on the genus *Geum* L. Monographiae Botanicae **4:** 1–416.

GRABER, R. E. 1980. The life history and ecology of *Potentilla robbinsiana.* Rhodora **82:** 131–140.

HELLQUIST, C. B. 1971. Vascular flora of Ossipee Lake, New Hampshire and its shoreline. Rhodora **73:** 249 261.

HODGDON, A. R. 1973. Endangered plants of New Hampshire. Forest Notes No. **114:** 2–6.

HODGDON, A. R. & F. L. STEELE. 1958. The woody plants of New Hampshire. N. H. Agric. Exp. Sta. Bull. **447.** University of New Hampshire, Durham, NH.

KEARNEY, T. H. & R. H. PEEBLES. 1964. Arizona Flora. 2nd ed. with suppl. University of California Press, Berkeley, CA.

LATIMER, W. J., M. H. LAYTON, W. H. LYFORD, W. H. COATES & P. N. SCRIPTURE. 1939. Soil survey of Grafton County, New Hampshire. USDA Bureau of Chemistry and Soils Series **1935**, No. 6.

LITTLE, E. L. 1971. Atlas of the United States Trees. Vol. 1. Conifers and important hardwoods. Forest Service, USDA Misc. Publ. No. **1146**.

LÖVE, A. & D. LÖVE. 1966. Cytotaxonomy of the alpine vascular plants of Mount Washington. University of Colorado Studies, Series in Biology No. **24.** University of Colorado Press, Boulder, COLO.

LÖVE, D. 1968. Nomenclatural notes of Mt. Washington plants. Taxon **17:** 89.

LOWNES, A. E. 1920. Notes on *Pogonia trianthophora.* Rhodora **22:** 53 55.

MITCHELL, R. S. 1979. Preliminary lists of rare, endangered and threatened plant species in New York State. New York State Museum Leaflet No. **21.**

MUNZ, P. A. & D. D. KECK. 1970. A California flora. University of California Press, Berkeley, CA.

PEASE, A. S. 1964. A flora of northern New Hampshire. The New England Botanical Club, Inc., Cambridge, MA.

RADFORD, A. E., H. E. AHLES, & C. R. BELL. 1968. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill, NC.

RAYNOR, L. A. 1952. Cytotaxonomy of *Geum.* Amer. J. Bot. **39:** 713 719.

REYNOLDS, N. B. & A. C. MATHIESON. 1975. Seasonal occurrence and ecology of marine algae in a New Hampshire tidal rapid. Rhodora **77:** 512 533.

ROLAND, A. E. & E. C. SMITH. 1969. The flora of Nova Scotia. Nova Scotia Museum, Halifax, NS.

SCOGGAN, H. J. 1978. The flora of Canada. Part 3 Dicotyledoneae (Saururaceae to Violaceae). National Museum of Natural Sciences Publ. in Botany, No. 7(3). National Museum of Canada, Ottawa, Ontario.

SMALL, J. K. 1933. Manual of the southeastern flora. Facsimile reprint, Hafner Publ. Co., New York, NY. 1972.

STEELE, F. L. 1967. The *Saxifraga aizoön* station revisited. Rhodora **69:** 484 485.

STORKS, I. M. 1979. Rare and endangered vascular plant species in New Hampshire with special reference to the White Mountain National Forest. M.S. Thesis, University of New Hampshire, Durham, NH.

STORKS, I. M. & G. E. CROW. 1978. Rare and endangered vascular plant species in New Hampshire. The New England Botanical Club in cooperation with the U. S. Fish and Wildlife Service [Region 5, Newton Corner, MA].

STORKS, I. M. & G. E. CROW. 1979. Endangered, threatened and rare vascular plant species in the White Mountain National Forest, New Hampshire. N. H. Agric. Exp. Sta., University of New Hampshire, Durham, NH.

WILLIAMS, B. H., W. H. COATES, & P. N. SCRIPTURE. 1943. Soil survey of Coos County, New Hampshire. USDA Bureau of Plant Industry, Series **1937**, No. 5.

WRIGHT, H. E. 1972. Interglacial and postglacial climates, the pollen record. Quat. Res. **2:** 274 282.

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## *ABSTRACT:*

# THE RARE AND ENDANGERED SPECIES IN MAINE

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The Report on Endangered and Threatened Plant Species of the United States prepared by the Smithsonian Institution in 1975 recommended ten taxa of vascular plants which occur in Maine for federal listing as endangered or threatened. The revised list (1978) recommended listing of an additional seven taxa. Of the 17 taxa, five are endemic or nearly endemic to the state of Maine. Three others are restricted to the Northeast, and the remainder are considered extremely rare throughout the eastern portion of the United States. One species, *Trollius laxus* Salisb., although listed for Maine, does not occur in the state.

The endemic species appear to be the most puzzling in view of the fact that the entire state of Maine experienced extensive glaciation during the Pleistocene. Important questions about this group pertain to the accuracy of identification, the manner in which the taxa survived glaciation, the possibility of a taxon having evolved since the last glacial advance, and the taxonomic validity of the taxa in question.

*Pedicularis furbishiae* S. Wat., *Carex elachycarpa* Fern., and *C. josselynii* (Fern.) Mackenz. are three endemics which occur in the St. John and Aroostook River Valleys of northern Maine. There appears to be no question concerning the taxonomic status of *Pedicularis furbishiae*. However, doubts have arisen as to whether or not *Carex elachycarpa* and *C. josselynii* are good species. Some botanists contend that both may be hybrids.

*Carex oronensis* Fern. is restricted to the Penobscot River Valley of central Maine. Its taxonomic status is also in question. The plant grows in open meadows and clearings in association with other species of section *Ovales* of the genus *Carex* and could well be a hybrid. The sedge was last collected in 1916 by M. L. Fernald and B. Long. Douglas Burdick of Bangor and I relocated the population on July 7, 1978.

The last endemic in question is *Mimulus ringens* var *colpophilus* Fern., which occurs in estuaries from Washington County to Sagadahoc County. This variety differs from the typical variety in that the internodes and principal leaves are smaller. These characters may represent phenological expression in response to submergence by tidal waters twice daily, and thus the plant may represent an ecological form unworthy of taxonomic recognition.

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# LAWS AND INFORMATION NEEDS FOR LISTING PLANTS

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Conservation of plants and their habitats is an ambitious goal which requires the involvement and interaction of the private sector, academia, and government. While federal involvement alone will not insure achievement of this goal, several pieces of national legislation in the last decade have brought increased attention to its importance. The Endangered Species Act of 1973 (Public Law 93-205) was the first federal endangered species legislation to include protection for plants. Previous national legislation had only affected animal species. The 1973 legislation provided the means for conservation of endangered and threatened species of fish, wildlife, and plants, and the ecosystems upon which they depend. Of special importance for plants was section 12 of the Act which instructed the Smithsonian Institution to compile a report on those plants threatened with extinction and to report their findings to Congress within one year. The actions which followed resulted in the formation of a federal plant conservation program. This paper will attempt to review these actions and discuss the information and interaction needed from botanists and conservationists to further plant conservation.

The 1973 Act authorized the Department of Interior to carry out the Act, and this responsibility was delegated to the U.S. Fish and Wildlife Service (hereinafter referred to as the Service). Therefore it is the objective of the Service's Office of Endangered Species to develop a list of taxa, both plants and animals, which are in danger of extinction in their natural habitats and to carry out programs for their conservation. The Act provides two possible categories for listing, Endangered and Threatened. These are defined in section 3 of the Act as follows:

*Endangered* — any species which is in danger of extinction throughout all or a significant portion of its range, and

*Threatened* — any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range.

Determination of whether a taxon is Endangered or Threatened must be related to one or more of the factors set forth in section 4(a)(1) of the Act, which follow:

(**1**) the present or threatened destruction, modification, or curtailment of its habitat or range;
(**2**) overutilization for commercial, sporting, scientific, or educational purposes;
(**3**) disease or predation;
(**4**) the inadequacy of existing regulatory mechanisms; or
(**5**) other natural or manmade factors affecting its continued existence.

The decision to list a species as Endangered or Threatened is made by the Director of the U.S. Fish and Wildlife Service under authority delegated by the Secretary of Interior.

The listing process is a lengthy one with which few people outside the Office of Endangered Species are truly familiar. The process usually starts by either internal initiative or by someone petitioning the Service to list specific taxa under section 4(c)(2) of the Act. After initial consideration of the best available scientific and commercial data and if the taxon appears to warrant further consideration, then either a notice of review or a proposal to add the species to the list is prepared. The procedures for both notices of review and proposals incorporate comment periods and encourge involvement of the affected states, federal agencies, and interested persons and organizations. The notice of review is often not necessary when adequate data is available for a proposal. After a plant is proposed, all comments are reviewed and summarized and a decision is made concerning whether a final rulemaking determining the taxon to be either Endangered or Threatened should be prepared. Designation of a species' critical habitat under the provisions of section 7 of the Act follows basically the same procedures. The Endangered Species Act Amendments of 1978 require that final determination of a species' critical habitat, where prudent, be done simultaneously with the final determination of the species' status, and that economic and other relevant impacts be considered in determining critical habitat. If a final rulemaking is prepared and the Director determines the species to be either Endangered or Threatened, then the determination is published in the *Federal Register* and the species is afforded the protection offered by the Act.

Federal actions which resulted in plants being listed under the 1973 Act began with the Smithsonian's report to Congress in 1975. The Service treated the Smithsonian's report, which contained the names of 3,187 plants, as a petition and published the report as a notice of review in the July 1, 1975 *Federal Register* (U.S. Fish and Wildlife Service, 1975b). One previous notice of review, which contained the names of four plants, had been published in April 1975 (U.S. Fish and Wildlife Service, 1975a) in response to a Wisconsin petition. Later, in 1977 (U.S. Fish and Wildlife Service, 1977c), a third notice involving one plant was published. Based on the information gathered by the Smithsonian and the 1975 notices of review, the Service proceeded with a proposal on June 16, 1976 (U.S. Fish and Wildlife Service, 1976) proposing 1,783 plants to be Endangered. One additional publication (U.S. Fish & Wildlife Service, 1975c) involving plants proposed 45 plant taxa, which appeared on the Convention on International Trade in Endangered Species, as Endangered.

On June 24, 1977 (U.S. Fish and Wildlife Service, 1977a) the final regulations establishing the prohibitions and permit procedures for Endangered and Threatened plants were published and the stage was set for plants to be listed. On August 11, 1977 the first four plants were listed (U.S. Fish and Wildlife Service, 1977b). Since that time (as of June 1979) a total of 24 plants have been listed, 22 Endangered and 2 Threatened (U.S. Fish and Wildlife Service, 1978a, 1978c, 1979a, and 1979b), and for 2 of these plants critical habitat has been determined (U.S. Fish and Wildlife Service, 1978b).

The listing process, which has always been lengthy, was greatly affected by the Endangered Species Act Amendments of 1978. The most publicized effect of the Amendments was the creation of the exemption process and the Endangered Species Committee. The Amendments affect the listing process as well by requiring 1) that critical habitat, where prudent, be determined simultaneously with the species' status; 2) that economic and other impacts be considered in determining critical habitat; 3) that more thorough public notification procedures be employed; and 4) that proposals be withdrawn if not finalized after 2 years (proposals currently over 2 years old must be withdrawn in November 1979, the first anniversary of the passage of the Amendments). These requirements have greatly slowed the listing process for native species. Only 2 native species have been listed from the time the Amendments passed until June, 1979. However, some advantageous changes for plants were included in the Amendments.

What protection is offered plants by the Endangered Species Act of 1973? This is a frequently asked question and the treatment of plants and animals under the Act does differ. The Endangered Species Act Amendments of 1978 included plants equally in sections 5 and 6 which had previously favored animal species. Section 5 of the Act authorizes the Secretary of Interior and the Secretary of Agriculture (U.S. Forest Service) to acquire land for the purpose of conserving fish, wildlife, and plants. Section 6(c) of the Act, which covers state cooperative agreements, enables the Service to provide financial assistance to states to assist them in carrying out programs for conserving Endangered and Threatened species. Through cooperative agreements, funds are available to states to carry out research, management, and recovery efforts for Endangered and Threatened species. Many states already have such agreements for animals and now the same is possible for plants. Botanists should urge their states to qualify for and to seek cooperative agreements for plants.

Plants and animals have always been equally covered under section 7 of the Act which requires federal agencies, in consultation with the Service, to insure that their actions do not jeopardize the continued existence of any Endangered or Threatened species or result in the adverse modification of their critical habitat. Both plants and animals are equally covered under a new section 4(g) of the Act which requires the development and implementation of recovery plans for Endangered and Threatened species. A recovery plan is a guide to justify, delineate, and schedule actions to restore and secure Endangered and Threatened species as viable, self-sustaining members of their ecosystems. These plans often require species biology research in order to obtain information needed for developing sound management plans. Sections 8 and 9 of the Act do differ in the protection they offer plants versus animals. Plants receive limited coverage under section 8 of the Act, which deals with international cooperation. Section 9 of the Act, which prohibits the taking, possession of illegally taken, and commerce in, Endangered fish and wildlife, only prohibits interstate commerce, import, and export of Endangered plants. Although plants are treated less restrictively than animals in the Act, substantial protection is offered plants and their natural habitats.

The U.S. Fish and Wildlife Service needs reliable and documented information on Endangered and Threatened plants in order to carry out plant conservation programs under the Endangered

Species Act. The listing process requires consideration of the best available scientific and commercial data. Information, such as the species' taxonomy, description, and historical range, is certainly basic for listing and is often available from the literature. Other types of necessary information are often not so easily accessible. A species' present known range, the history of its decline, current population numbers and trends, threats to extant populations, and recommendations for critical habitat boundaries are all necessary to determine its status, and must be obtained from current field studies. A knowledge of the species' habitat, applicable state laws, the ownership and current administration of extant populations, and possible economic or other impacts of listing is necessary for satisfying NEPA (National Environmental Policy Act) and the new economic analysis requirements associated with listing. Although certain categories of information constitute the minimum necessary for listing, other types of information are necessary for plant conservation. Information on various aspects of the species' biology is necessary for the development of management and recovery plans. A more detailed discussion of the information required to use the Endangered Species Act for plant conservation is presented by MacBryde (1979). Status report outlines and information systems have also been developed that researchers can follow in gathering needed information. Several of these are presented in the symposium, "Geographical Data Organization for Rare Plant Conservation", proceedings (Morse & Henifin, 1979). The need for good data has prompted the Service as well as other federal and state agencies to initiate contracts for needed research. The data from these contracts, along with those available from interested botanists and conservationists and the increased interest in species biology research, have resulted in adequate data for a large number of species. For other species, necessary information is not available and further contracts and studies will be required.

As federal programs continue to grant contracts and the Service continues to carry out the provisions of the Endangered Species Act, state agencies and private conservationists must continue to play an important role in the plant conservation effort. If this effort is to be successful, botanists and conservationists must help in many areas, such as educating the public, encouraging strong and effective state and federal legislation, and continuing to carry out needed research.

## ACKNOWLEDGEMENTS

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## LITERATURE CITED

MACBRYDE, B. 1979. Information needed to use the Endangered Species Act for Plant Conservation. *In:* Morse, J.L. and M.S. Henifin (Eds.). 1979. Geographical Data Organization for Rare Plant Conservation. New York Botanical Garden, Bronx, New York.

MORSE, L. E. & M. S. HENIFIN (Eds.). 1979. Geographical Data Organization for Rare Plant Conservation. New York Botanical Garden, Bronx, New York.

PUBLIC LAW 93 205. 1973. Endangered Species Act of 1973. 87 Statute 884. 93rd Congress. U.S. Government Printing Office.

U.S. FISH & WILDLIFE SERVICE. 1975a. [Notice of review] Review of Endangered Species Status. Federal Register **40**(77)[April 21]:17612.

_____. 1975b. [Notice of review] Review of Status of Over 3,000 Vascular Plants and Determination of "Critical Habitat". Federal Register **40**(127)[July 1]: 27823 27924.

_____. 1975c. [Proposal] Proposed Endangered Status for 216 Species Appearing on Convention on International Trade. Federal Register **40**(188) [September 26]: 44329 44333.

_____. 1976. [Proposal] Proposed Endangered Status for some 1700 U.S. Vascular Plant Taxa. Federal Register **41**(117)[June 16]: 24523 24572.

_____. 1977a. [Final rule] Prohibitions on Certain Uses of Endangered or Threatened Plants, Permits for Exceptions to Such Prohibitions, and Related Items. Federal Register 42(122)[June 24]: 32373 32381.

_____. 1977b. [Final rule] Determination That Seven California Channel Island Animals and Plants are Either Endangered Species or Threatened Species. Federal Register **42**(155)[August 11]: 40682 40685.

_____. 1977c. [Notice of review] American Ginseng; Review of Status. Federal Register **42**(155)[August 11]: 40823.

_____. 1978a. [Final rule] Determination that 11 Plant Taxa are Endangered Species and 2 Plant Taxa are Threatened Species. Federal Register **43**(81) [April 26]: 17909 17916.

_____. 1978b. [Final rule] Determination of Critical Habitat for Two Endangered California Plants. Federal Register **43**(170)[August 31]: 39041 39044.

———. 1978c. [Final rule] Determination of Five Plants as Endangered Species. Federal Register **43**(189)[September 28]: 44810 44812.

———. 1979a. [Final rule] Determination that *Rhododendron chapmanii* is an Endangered Species. Federal Register **44**(80)[April 24]: 24247 24250.

———. 1979b. [Final rule] Determination that *Echinacea tennesseensis* is an Endangered Species. Federal Register **44**(110)[June 6]: 32603 32605.

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# HABITAT PROTECTION

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Documentation of species destruction has come to the fore in recent years, on both a worldwide (Eckholm, 1976) and national (Barney, 1977) basis. This raising of our collective consciousness that we are indeed stewards of the planet and all that it contains has been a rather abrupt phenomenon in the time-scale of planetary human events (Jackson, 1979). The United States now has rather far-reaching endangered species legislation, even though it was recently amended to provide for override in exceptional circumstances (P.L. 93-205, 1973). Success of the laudble aim of respect for fellow creatures and the realization that we must match our words with physical accomplishments showed clearly most recently in the Snail Darter Case. Even though the fish itself was protected by law, it would soon become extinct unless its habitat was likewise kept in its present natural state. The lesson, then, is that habitat protection is an integral part of species protection (Cahn, 1978). This conclusion may be obvious to ecologically oriented natural scientists, but alas, not so to that great group of "other" individuals who are swayed by reports on the need for more oil quickly, the need for more coal quickly, and the need for more nuclear-generated electricity quickly. Mankind itself may well become an endangered species if our life-support (photosynthetic) systems, the plant ecosystems, are not treated with enough respect to maintain their diversity.

Who should decide on where and how much of the natural ecosystems of a given area ought to be left alone in order to insure a reasonable opportunity for survival to a particular species? And is mere survival enough? As previous speakers have asked us, how do we insure enough genetic diversity in a population? These and many other questions involve often rather intimate knowledge of the biology of the species in question. Fortunately for the main thrust of the group here assembled, there are few known migratory plants. Thus we primarily need consider only specific sites, and not wintering or nesting grounds at distant geographic locations. Really it is the botanists and ecologists who work with these species who are best able to give the best technical advice on just what habitat is critical for their continued survival.

The decisions to save particular habitats, however, are seldom made directly by those who work with the area's biota. The decisions are instead made by often biologically unskilled people in largely governmental frameworks at the local, state, or national levels. Most people concerned with the direct management of private habitat-saving groups, such as land trusts, Audubon societies, and various other wildlife defenders, are often not themselves any better-versed in biology, and must depend upon the knowledge of competent scientists to help frame their decisions. Here, in my opinion, is the place where we as plant biologists, as leaders in studies of natural plant populations, have failed ourselves as well as our fellow humans. We are as much to blame for the endangered status of some of our pet study objects as anyone. Very few of us have demonstrated over the past decade through our individual or collective actions the degree of concern that was and most certainly still is needed to assure even minimal direction to land acquisition programs. Competent biologists we are, yes: but until we, these same biologists, become as concerned as we are competent, most of our endangered species will, in my opinion, continue toward extinction, inexorably joined one by one by other taxa not now even remotely considered as endangered. These endangered species — *our* species, if you will — must have human defenders if they are to survive at all. It is up to us, the botanists and ecologists who work with them, to speak out to assure their survival.

How many times has each of you in this audience participated in giving, without waiting to be asked — giving of your scientific knowledge to your own local conservation commission or planning commission or state natural resources executive department or your state legislative committee on natural resources? Or written to any congressional committee on endangered species? Where do you suppose they can obtain information, which is accurate, sincere, and consistent with ecological principles, if not from people like you? Can't you, as a competent biologist, also become concerned about your own future, your family's future, your students' future? They are all linked, as each of us knows quite well.

I feel compelled to interject a note of caution here. Let's suppose for a moment that you not only *can* become involved, but *do*. From my own personal experience and as observations reported to me, I must warn you that while speaking out regularly and consistently on such causes generates a respect with the listeners who are the immediate beneficiaries and who can translate your concerns into law and strong programs, attitudes ranging from benign neglect to downright hostility are frequently met both from one's colleagues and his or her college administrators. For instance, popular articles, regardless of how convincing they may be and how helpful they may be to the saving of habitats, are often brushed off as "unscholarly" and worthy of mention only as "gray literature", after the manner of certain rather slick corporate brochures which purport to demonstrate no lasting damage at all from some clear environmental disaster. Unless and until every one of us regards as part of his or her responsibility, job description, or incumbent duty, the education of others both inside and outside academic circles, on the needs and values of habitat preservation, our study species, and thus our livelihoods, will continue to march together toward extinction.

How does one accomplish habitat protection? First, each of us should realize that it is seldom a single-person activity. Most of us simply do not own any spare ecosystems we'd like to see preserved; even those who do own land seldom have the means to make gifts of such areas at reduced prices or perhaps with no menetary compensation at all. Yet gifts of land continue to be one of the largest aggregate sources of newly-preserved habitat each year. Gifts occur both to public and to private agencies, and under present tax laws, their value as gifts often represents a substantial tax saving for the giver, as well as to the municipality in which the gift lies through lowered municipal service demands (Ells, 1976).

Restrictions, often called easements, which are made either as gifts or are acquired at less cost than full purchase price, with some or all of the tax advantages listed above, may also be utilized to save habitats. Massachusetts has an excellent restrictions law (Chapter 666 of the Acts of 1969, as amended by Chapter 784 of the Acts of 1977), which recognizes conservation restrictions, historic preservation restrictions, and agricultural preservation restrictions (Dawson & Nickerson, 1978). Each is written as a partial-interest (less-than-fee) deed, registered with the state, and requires that the land on which it is in force be valued separately for tax purposes. Public access is not mandated, and occurs only if the owner so specifies in the instrument which creates the restriction. Local zoning in Massachusetts and such statutes as the Coastal Wetlands Restriction Act, the Scenic Rivers Act, the Scenic Roads Act and the Inland Wetlands Restriction Act further allow habitat preservation (Dawson & Nickerson, 1978). Requirements for public hearings under each law and the Open Meeting Law guarantee opportunity for input. Acquisition of the fee, or total ownership, has been and will continue to be the major means of habitat preservation. Private groups, associations, and trusts again are a potent force in such activities. The Nature Conservancy, active throughout New England, is an excellent example (Anon., 1978). Local land charitable trusts exist in literally dozens of cities and towns, turning gifts of all kinds of assets into tangible purchases of specific habitats. Enabling legislation exists in each New England state to allow formation of city or town conservation commissions, staffed by citizens. In Massachusetts, which invented the concept in 1957, 36 of 39 cities and 299 of 312 towns have established such commissions (Dawson & Nickerson, 1978). Until such legislation was put on the books, acquisition of any land had to be for specific municipal purposes which had never included conservation or habitat preservation for its own sake. These commissions, as arms of local government, can seek funds from town meetings (thus involving many people); can accept land gifts and recommend land purchases, which they will then manage and control; and at least in Massachusetts, these commissions regulate removal, dredging, filling, or altering of wetlands of all kinds. If the town so votes, the selectmen may use eminent domain powers to acquire land for conservation purposes. Eminent domain procedures also permit full acquisition of lands with unknown owners, or of fractional ownerships, often at great savings to the municipality. Conservation commissions in Massachusetts have been responsible for setting aside 50,000 acres of habitat, approximately 1% of the state's area. State parks and forests total 250,000 acres, or about 5% of the total area. We have three laws to encourage municipal acquisition of habitat: (1) the Self-Help Act, which reimburses costs up to 50% of the purchase price for land devoted to passive recreation and maintained in their natural state. This fund has disbursed $18 million over the twelve years of its existence. (2) The Urban Self-Help Act, which received an initial capitalization of $5 million, reimburses up to 80% of the costs of acquisition of parks for active recreation. (3) The Agricultural Preservation Restriction Act, also initially capitalized at $5 million as a pilot program, helps farmers stay in business rather than sell the prime agricultural land for development. These laws, their procedures and sample instruments are all discussed in Dawson and Nickerson (1978).

One of the major concerns today, which we can perhaps diagnose as a variant of Proposition 13 fever, is whether we can afford to purchase and thus withdraw any lands from development. However, habitat preservation has its positive economic values as well. Wetlands, because of their roles in flood control, water storage, adsorption of heavy metals, pesticides, and phosphates, and in denitrification (Nickerson, 1978), perform service conservatively valued at over $140,000 per acre, according to a recent Tufts study (Thibodeau & Ostro, 1979). Open land generates desirability for proximal sites. Dennis, a Cape town in Massachusetts, has acquired nearly 600 acres of a projected 1200 acres conservation program. Its equalized (100%) valuation tax rate is $14 per thousand, stable for the past five years. One of the prime factors keeping that real estate desirable is the proximity of guaranteed open space to many of the town's living areas (Town Clerk of Dennis, 1979).

In a forthcoming book, Robert A. Lemere, Chairman of the Conservation Commission of Lincoln, Mass., discusses open-space acquisition studies which compare costs resultant to municipal acquisition with those following development. He shows that in many Massachusetts towns, purchase costs through taxes are initially less and will continue to drop due to amortization of debt, while such costs will be more and continue to rise with maximum development of the same space, as greater demands are made on municipal school, fire, police, roads, water, and other town services. The economic lesson is clear. Conservation of habitat translates into conservation of the tax rate. Land values will never be any lower: purchases made now recoup their cost rapidly and the benefits of such open space to the surrounding human community, as well as the biological community existing there, continue indefinitely.

## LITERATURE CITED

ANON. 1978. The Land Savers. The Nature Conservancy, Eastern Regional Office, 294 Washington Street, Boston, MA.

BARNEY, J. O. (Ed.). 1977. The Unfinished Agenda. Thomas Y. Crowell Co., New York. 184 pp.

CAHN, ROBERT. 1978. Footprints on the planet. Universe Books, N.Y. 277 pp.

Dawson, Alexandra D. & Norton H. Nickerson. 1978. Environmental Handbook for Massachusetts Conservation Commissioners. Mass. Assn. of Conservation Commissions, Lincoln Filene Ctr., Tufts University, Medford, MA. 118 pp.

Eckholm, Erik P. 1976. Losing Ground; W.W. Norton Co., New York. 223 pp.

Ells, Stephen F. 1976. Gifts of Land for Conservation. Conservation Law Foundation, 3 Joy Street, Boston, MA.

Jackson, Wes. 1979. Man and the Environment, 3rd Ed. W.C. Brown Co. Publishers, Dubuque. 363 pp.

Nickerson, N. H. 1979. Freshwater wetlands their nature and importance to man. Lincoln Filene Ctr., Tufts University, Medford, MA. 8 pp.

Public Law 93 205. (87 Stat. 884). The Endangered Species Act of 1973, and Amendments of 1976 (90 Stat. 724; 90 Stat. 911), 1977 (91 Stat. 1493), and 1978 (92 Stat. 3751).

Thibodeau, Frank R. & Bart D. Ostro. 1979. An economic analysis of wetland protection. Land Economics (Submitted May, 1979).

Town Clerk of Dennis Annual Report. 1978. Town of Dennis, So. Dennis, MA. 280 pp.

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# THE BOTANICAL ASPECT OF MAINE'S CRITICAL AREAS PROGRAM

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Since 1974 the State of Maine has taken an active role in the conservation of rare plant species through its Critical Areas Program. Efforts to identify significant natural areas began in 1971 when Maine participated in the New England Natural Areas Program. This program identified 474 botanical areas in New England, including 157 areas in Maine, and its report recommended that the state continue the natural areas inventory (Hartman, 1972). The Natural Resources Council of Maine and the State Planning Office drafted legislation for a Maine natural areas program. The natural areas bill was defeated in the 1973 regular session, but passed in the special session of 1974 as the Critical Areas Act. The title "Critical Areas" was assigned to the natural areas program so that its name would conform to the name of proposed federal legislation which was never passed.

Under the Critical Areas Act of 1974, the State Planning Office has been working actively on the conservation of Maine's rare plant species. In the absence of a State rare and endangered species law for plants, Maine has been able to accomplish a significant amount of work to protect rare plants with its natural areas program.

## APPROACH

Maine's Critical Areas Act directs that a state-wide inventory be conducted for rare and unusual plant species that are worthy of preservation, and that an official listing of the significant areas be compiled. Further, the Act directs that the State Planning Office coordinate the conservation of "critical areas". The focus of the Act is to collect natural resource data to be used by planners, conservationists, and landowners.

Being essentially non-regulatory, the program uses non-traditional land conservation techniques for rare plant protection. Knowledge of the location of rare plants is essential for providing protection and the program has, therefore, emphasized the identification of critical areas. Ignorance of the exact location of the rare species has been the main destructive threat. Uninformed landowners have, in many cases, destroyed significant stations without realizing what they were doing.

Most of the landowners are unaware of the rare plants on their property and are also unaware of the plants' significance. In most cases government agencies as well are unaware of rare plants on lands they mange. For example, Maine's only station for *Ilex glabra* (Inkberry) was relocated just within the boundary of Acadia National Park, and the three significant stations for *Triphora trianthophora* (Nodding Pogonia) were located within the Evans Notch unit of the White Mountain National Forest.

Because most Maine land is privately owned, the private sector has a major role in protecting rare plants. The program recognizes that the landowner is in a key position to insure the safety of the plants. Since there are no regulatory laws protecting rare plant critical areas, the program depends upon the cooperation and good will of the landowner. One of the fundamental approaches, to which the program devotes a considerable amount of time, is to inform the landowner fully of the significance and location of the rare plant areas. This method has worked very well; most people are receptive to the information and supportive towards rare plant protection. There are few instances where the areas are directly threatened by destruction. Thus, we feel that we have achieved a major conservation accomplishment by identifying sites and informing the landowner.

The positive attitude of Maine's people toward conservation and wise use of the land has helped to create a positive climate for natural areas protection. Over the years the garden clubs in Maine and the New England Wildflower Society have increased the public awareness about rare plant conservation through a variety of educational services. Members of the Josselyn Botanical Society have also encouraged rare plant conservation. In addition, the work of The Nature Conservancy and Maine Coast Heritage Trust has promoted the role of the private sector in protecting unusual pieces of land. The active work and programs of these organizations have been very complementary to the Critical Areas Program's effort.

## CONSERVATION

A number of innovative approaches have been developed for rare plant conservation in Maine. Because Maine does not have a law protecting rare plant species, we have developed our conservation strategy around irrefutable scientific documentation and around working on a cooperative basis with the landowner. Central to the program's success is the verification by field checking of the State's rare plant stations.

The documentation on rare plants that we have assembled with the help of Maine botanists is very powerful information. Planning reports and botanical fact sheets play a major role in transmitting the information from the scientific community to the landowner or conservation interests. Written in non-technical language, these reports usually convince the reader that a particular plant species is rare, and that the areas where it is found are worthy of conservation. The planning reports have been carefully prepared by recognized authorities, and are complete and comprehensive. No one has challenged the data or conclusions of planning reports and fact sheets. These reports are a major factor in the success of Maine's program.

The listing of natural areas on the Register of Critical Areas is a time-consuming process that culminates in official state recognition of an area's significance. Landowners are initially contacted by a letter regarding proposed areas. After land ownership is verified, the planning report, and a description and map of the critical area are mailed to the landowner. After some time, landowners are telephoned or visited by the Critical Areas Program staff to discuss the rare plant species and proposed critical area. An eleven member Critical Areas Advisory Board appointed by the governor reviews the planning report, botanical fact sheets, and related documentation on each area before voting to officially register an area as a critical area. Once an area is registered, landowners are sent a copy of *The Landowner's Option*, jointly prepared by the Maine Coast Heritage Trust and Critical Areas Program. This booklet outlines the variety of land conservation techniques that can be used in Maine.

An overwhelming majority of landowners contacted by the Critical Areas Program support the designation and conservation of rare plant areas. Many people are intrigued by the presence of rare plants on their property, and greatly appreciate the scientific documentation provided by the program. A few landowners are apathetic to protection of rare plants. However, most are pleased and proud to own these areas and many have indicated they will not destroy the areas now that they know of their significance. Such positive response indicates that this approach of voluntary cooperation is an effective conservation technique.

A few landowners have even taken additional action to protect rare plant areas as a result of being contacted by the Critical Areas Program. Upon learning about a very significant old growth white oak forest on their property, landowners in York decided to terminate a pending sale of a portion of the land. The major owners of the Sand Pond Rare Plant Area in Sanford were prompted to offer a donation of the land to a conservation organization.

In 1978, The Nature Conservancy, which works closely with the Critical Areas Program, acquired two rare plant areas in Maine. It purchased 1541 acres of Great Wass Island in Washington County as the result of a major effort to identify and acquire a nationally significant natural area in Maine. Great Wass Island supports a diversity of unusual plant communities and rare plant species, described later in this paper.

The second Nature Conservancy acquisition is the only known Maine station for *Iris prismatica* (Slender blue flag), in Wells, York County, which was registered as a critical area in May 1977. The United States Fish and Wildlife Service had been trying to acquire this strip of salt marsh land as an addition to an existing wildlife refuge. The Critical Areas designation acted as a catalyst and prompted the landowner to donate the land in a bargain sale to The Nature Conservancy, which in turn will transfer it to the United States Fish and Wildlife Service.

In the future, more landowners may offer significant rare plant areas to private conservation organizations or government agencies. As rare plant areas become available, organizations and agencies dedicated to botanical conservation should be prepared to acquire and manage them. In some cases, areas will have to be purchased, and these organizations will have to be prepared to finance the protection of the area.

The Critical Areas Program annually monitors the status of critical areas by sending a letter and prepaid return questionnaire to the landowner inquiring about the status of the rare plant area. The response has indicated that a number of critical areas have changed ownership; in most cases the sellers neglected to inform the buyers about the critical area. Thus, a new task for the program is to inform the new owners about the significance of the recently acquired land.

During the four years of the Critical Areas Program, identification and registration have not created adverse publicity about rare plant areas. While almost all landowners have expressed fears of increased publicity, no landowners have actually complained about receiving any adverse publicity as a result of critical area designation. We do not know of any case where a rare plant locality has been threatened as a result of critical areas designation. While publicity is a natural concern, it has not materialized as a problem.

By maintaining close contact with landowners the program is able to ascertain which areas are threatened by physical destruction. Only a few rare plant areas are threatened by construction or harvesting of natural resources. The vast majority of botanical critical areas are not threatened by destruction because they are in isolated areas such as mountain tops, steep rocky cliffs, ravines, and riverbanks. In addition, the slow pace of the Maine economy has had a protective effect on many areas.

Technical advice regarding critical area management is one service that needs to be provided to landowners. A number of rare plant area owners, both public and private, have requested advice on how to manage their land to best maintain healthy rare plant poulations or old growth forests. The program was able, for example, to arrange for a State forester to write a management plan for a 250 year old white pine stand owned and maintained by the Norway Nature Club. In general, however, technical information on both general management techniques and strategies for certain species is still needed.

Natural area identification programs are also useful to scientists studying plant distribution and the biology of rare species. Maine's program has received several recent requests from biologists for precise site data, which it was able to provide easily. In addition, the comprehensive planning reports are often requested by students and scientists, as well as planning agencies, conservation organizations, libraries, and interested citizens. Active exchange of data with the scientific community should promote more research and a better understanding of our rare plant species.

In order to increase the general public's awareness of a few of Maine's outstanding rare plant species, general reports, usually based upon the planning reports, have been prepared in a brochure format. Brochures have been prepared on orchids, *Kalmia latifolia* (Mountain Laurel), *Rhododendron maximum* (Great Rhododendron), and several uncommon tree species.

## INVENTORY

The program has developed a rigorous and systematic inventory process to identify the rare species in the State of Maine. The first task was the development of a list of rare vascular plant species of at least state significance. In 1975, the Center for Natural Areas compiled the first listing of Maine rare plants in the report, *A Preliminary Listing of Noteworthy Natural Features in Maine* for the Critical Areas Program (Adamus and Clough, 1976). The center consulted with Dr. A. E. Brower, Dr. Charles Richards, Dr. George Rossbach, and Mr. L. M. Eastman, all of whom are active botanists with a working knowledge of Maine flora. The *Revised Check-List of the Vascular Plants of Maine* (Bean et al, 1966), and *The Flora of New England* (Seymour, 1969) were also useful in determining which species should be placed on Maine's rare plant list.

The Center's list, which included 233 species, has been updated several times. L.M. Eastman (1978a) added 16 species, and other additions are being considered based upon recent data from active Maine botanists, including the list of rare Maine plants compiled by L.M. Eastman (1978b) for the United States Fish and Wildlife Service. As the program's inventory brings additional information to light, the working rare plant list will be further revised.

In addition to rare species, the program also searches for unusual plant communities such as alpine-tundra, sand dune, and peatland communities. Dr. Ian Worley of the University of Vermont has prepared a classification of the types of peatlands found in Maine, and has also initiated an inventory of some of the peatlands. Finally, the program also inventories and identifies outstanding areas of common species such as old growth white pine, red spruce, and northern hardwood tree species.

A crucial element in the success of the program's inventory is coordination with botanical inventory work occurring independently throughout the state. The program has drawn heavily, for example, on C.S. Campbell's and L.M. Eastman's recent inventory of the Oxford County flora (Campbell, 1975; Campbell & Eastman, 1978), as well on extensive field work conducted by Eastman, particularly in the southern part of the state. The program also coordinated its inventory of some of the northern elements of Maine's flora with work done by the Army Corps of Engineers in the St. John River area. However, without a systematic, comprehensive, and up-to-date documentation of Maine's flora, the program must also rely on its own resources.

A major difficulty of the rare plant inventory is the lack of recent locational data for many of the state's rare plants. One-hundred thirty-five of Maine's rare plant species have been collected from less than five locations, often at least fifty years ago, and the locational information on the herbarium label is usually limited to county and town. In only a few cases are the collectors still alive, and even then, they may not be able to recall the exact location. In quite a few cases, however, these shortcomings can be overcome by botanical detective work, especially by contact with locally active naturalists.

After selecting certain species for consideration, the program hires Maine botanists to ground check reported areas and to verify the species' presence. After completing their field work, they submit locational data, detailed site maps, a description, and photographs of the area to the Critical Areas Program staff; this material serves as the basis for the Program's documentation of the area.

The official documentation of rare plant areas has, in the past, been based on planning reports prepared by the botanists who conduct the fieldwork. Each report synthesizes all of the pertinent information on a species in Maine, and includes a description of the species, its life history, biology and ecology, and, if applicable, historical background. It also describes the inventory methodology, lists and describes the locations at which it has been found, and recommends significant stations for evaluation as critical areas.

The planning report is often the only up-to-date comprehensive report on the species in Maine or the New England region. As such, it enables the program to select areas which are particularly worthy of conservation.

The planning report system is best suited to **1**) those species for which a large amount of background material is available (e.g. *Kalmia latifolia*) or **2**) those species for which management is especially critical, e.g. those considered endangered or threatened at the federal level (e.g. *Cardamine Longii*). However, their expense in both time and money makes them impractical for many of Maine's rare plant species which are relatively unknown and which occur in only a few locations. To improve the efficiency and effectiveness of the rare plant inventory, a revised methodology has been adopted, eliminating the planning reports for many species and concentrating instead on obtaining accurate and complete locational information (Gawler, 1978).

A cornerstone of the revised system is a compilation of all New England herbaria records for the rare plant species (Eastman, 1978a) which gives locality information on 214 species. The program selects localities from this report, and attempts to relocate these historical localities. As stations for these species are found, the documentation formerly provided by the planning report is condensed into a botanical fact sheet for each species which includes an illustrated technical description, a general description, historical localities and localities which have been verified. As the inventory becomes more complete, the fact sheet can easily be amended to include new locations.

The Critical Areas Program's botanical inventory thus now proceeds on two levels: for those species for which a limited amount of information is available and which are reported from less than 15 locations, the fact sheet approach provides accurate, adequate, and efficient documentation; while for rare species reported from more than 15 locations or for which a greater amount of information is warranted, planning reports may be required for complete documentation (Gawler, 1978).

The inventory work that remains will be the most difficult, since most of the species yet to be located have been reported from obscure, poorly defined areas. Furthermore, many of the collections were made 50 to 100 years ago and rare plant stations of that time may not now exist, due to ecological changes or residential and commercial development.

## RESULTS OF THE BOTANICAL INVENTORY

As of May 1979, the program had verified and described 136 significant plant or old growth forest areas. Thirty-three planning reports (PR) and 36 fact sheets (FS) have been completed for the following species: *Dasya baillouviana* (PR), *Schistostega pennata* (PR), *Lycopodium Selago* (FS), *Adiantum pedatum* var. *aleuticum* (FS), *Cryptogramma Stelleri* (PR), *Dryopteris fragrans* var. *remotiuscula* (FS), *Dryopteris Goldiana* (FS), *Polystichum Braunii* (FS), *Woodsia alpina* (FS), *Woodsia glabella* (FS), *Chamaecyparis thyoides* (PR), *Pinus Strobus* (old growth) (PR), *Phleum alpinum*

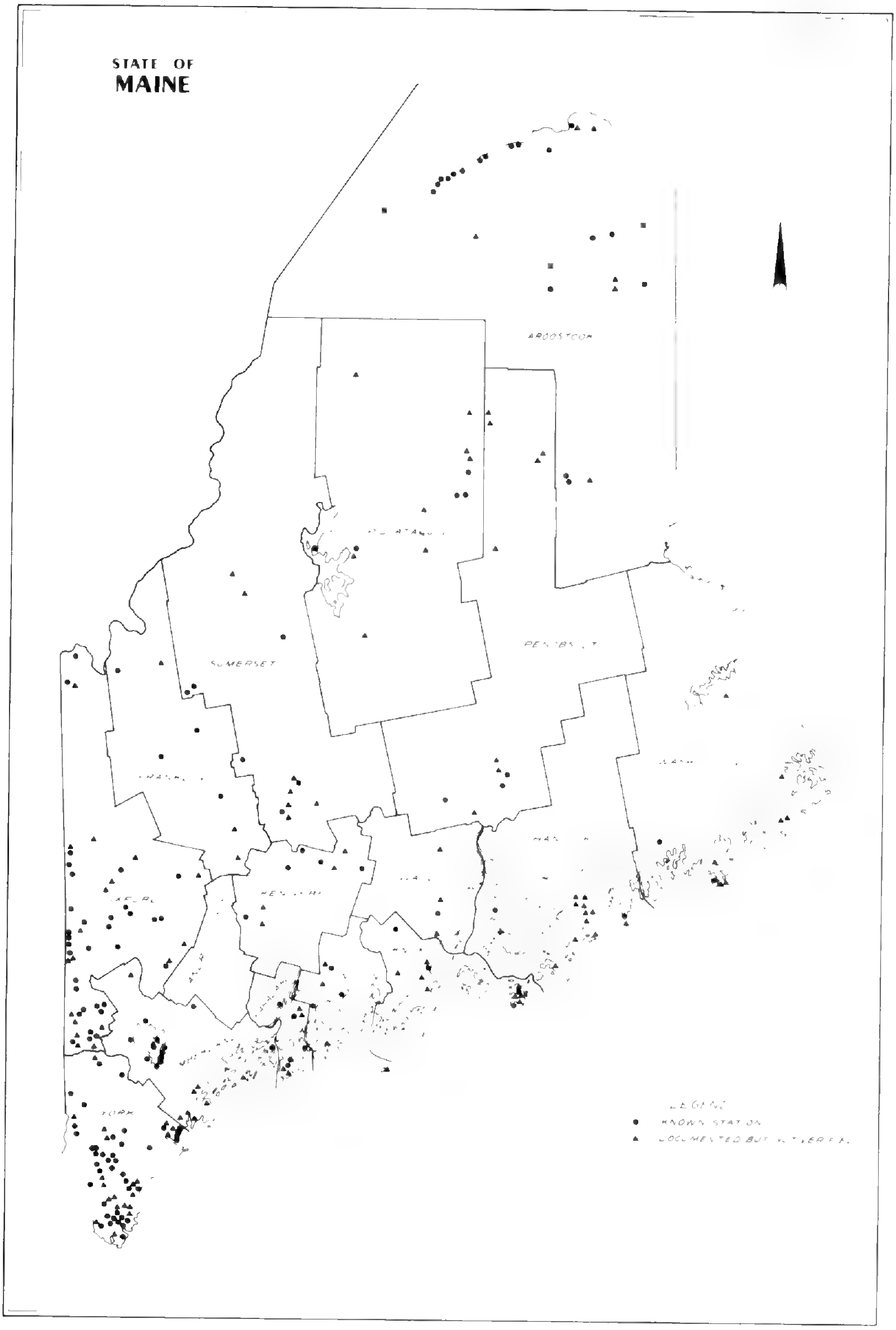

Figure 1. Critical Areas Program's Rare Plant Stations

(FS), *Carex eburnea* (FS), *Carex media* (FS), *Eleocharis tuberculosa* (FS), *Hemicarpha micrantha* (FS), *Peltandra virginica* (FS), *Xyris Congdoni* (FS), *Juncus trifidus* (FS), *Tofieldia glutinosa* (FS), *Iris prismatica* (PR), *Arethusa bulbosa* (FS), *Calypso bulbosa* (FS), *Cypripedium arietinum* (PR), *Habenaria leucophaea* (PR), *Isotria medeoloides* (PR), *Listera auriculata* (PR), *Orchis rotundifolia* (PR), *Triphora trianthophora* (PR), *Salix candida* (FS), *Salix interior* var. *exterior* (FS), *Carya ovata* (old growth) (PR), *Quercus alba* (old growth) (PR), *Quercus coccinea* (PR), *Quercus Prinus* (PR), *Arenaria groenlandica* (FS), *Nelumbo lutea* (FS), *Nuphar microphyllum* (FS), *Anemone multifida* (PR), *Clematis verticillaris* (FS), *Ranunculus lapponicus* (FS), *Lindera benzoin* (PR), *Sassafras albidum* (PR), *Cardamine Longii* (PR), *Draba arabisans* (FS), *Parnassia glauca* (FS), *Saxifraga Aizoön* var. *neogaea* (FS), *Amelanchier gaspensis* (FS), *Oxytropis johannensis* (PR), *Ilex glabra* (PR), *Impatiens pallida* (FS), *Ceanothus americanus* (PR), *Sheperdia canadensis* (PR), *Nyssa sylvatica* (PR), *Panax quinquefolius* (PR), *Cornus florida* (PR), *Chimaphila maculata* (PR), *Kalmia latifolia* (PR), *Rhododendron maximum* (PR), *Rhododendron viscosum* (PR), *Castilleja septentrionalis* (PR), *Pedicularis Furbishiae* (PR), *Lonicera oblongifolia* (FS), *Valeriana uliginosa* (FS), *Lobelia Kalmii* (FS), *Antennaria rupicola* (FS), *Prenanthes Bootii* (FS). The program has officially designated seventy-four botanical critical areas covering 2,463 acres. The remaining 62 areas are currently being described and mapped in detail as part of the official designation process. The program has relatively detailed locality data on another 122 areas, and is currently working towards relocating these stations. Additional localities are expected to come to light as work progresses.

The critical areas for rare plants are found in the floristically rich areas which are also the areas which have been heavily botanized (Figure 1). Many areas of Maine, such as the northwestern part of the State, have not been explored for rare species. A few areas have been botanized but have few rare plants found there. Hill's survey of the Penobscot Bay area (Hill 1919, 1923), and Rand's survey of Mount Desert Island (Rand & Redfield, 1894) found few rare plant stations. The recent field work by Campbell and Eastman in Oxford County, and Eastman in York Country, has resulted in the discovery of a number of new rare plant stations. Older collections by M.L.

Fernald, Kate Furbish, J.C. Parlin, R.C. Bean, A.H. Norton, and G.D. Chamberlain have been very helpful in relocating areas.

Of the 136 known rare plant stations, the majority (74) are significant because of a single rare species. Sixty-two areas harbor more than one rare species. In addition, many of these areas are outstanding examples of different plant communities found in Maine.

To illustrate the current results of the botanical inventory, descriptions of ten areas and two regions which have been documented by the program follow. The selection of areas is necessarily subjective, and the descriptions are meant to serve only as examples of what the program considers Maine's most notable botanical areas. The examples were chosen also to represent the diversity of unusual habitats found in Maine: northern calcareous bogs, arctic-alpine vegetation, coastal vegetation, rich woods, riverbank communities, and communities of southern affinities. These exemplary rare plant stations display a broad geographical and ecological diversity; they are here arranged from south to north.

**Rare Plant Stations in York County.** The numerous rare plant areas in York County (Figure 1) are representative of the southern element of Maine's flora. Many of the species found at these areas are relatively common elsewhere but are considered rare in Maine because they are at the northern periphery of their range. *Quercus Prinus* (Chestnut Oak) for example, is known from but one Maine station. *Q. alba* (White Oak) and *Carya ovata* (Hickory), on the other hand, are relatively frequent in York County but occur few other places in Maine; thus some of the largest York County stands are significant. Three of the four known stands of *Sassafras albidum,* rare in Maine but very common throughout much of its range, occur in York County. *Kalmia latifolia* (Mountain Laurel) and *Rhododendron maximum* (Great Rhododendron) also reach their northern limit in Maine, with significant stands in York County. Maine's one naturally occurring specimen of *Cornus florida* (Flowering Dogwood) is found on Mt. Agamenticus. Other southern species contributing to the uniqueness of the York County flora include *Nyssa sylvatica* (Black Gum), *Ceanothus americanus* (New Jersey Tea), *Iris prismatica* (Slender Blue Flag), *Ilex laevigata* (Smooth Winterberry), *Lindera benzoin* (Spicebush), *Clethra alnifolia* (Sweet Pepperbush), *Peltandra virginica* (Tuckahoe), *Saxifraga pensylvan-*

*ica* (Swamp Saxifrage), and *Liatris borealis* (Northern Blazing Star). In addition to these known southern species, several others have been collected in the past but have not been recently seen. These include *Lespedeza hirta* (Hairy Bush Clover), *Baptisia tinctoria* (Wild Indigo), *Verbena urticifolia* (White Vervain), and *Sericocarpus asteroides* (Northern White Topped Aster). These species serve as indicators of southern plant communities which are infrequent in Maine. These communities, as well as the species themselves, are considered by the program to be significant.

**Seawall Beach, Small Point, Sagadahoc County.** Seawall Beach is one of the most outstanding of several significant sand dune plant communities along the Maine coast. The significance of this sand beach system was documented by the planning report on the geological and botanical aspects of sand beaches (Nelson & Fink, 1978). The extensive backdune area of this beach is made up of high parabolic dunes which support species such as *Ammophila breviligulata* (American Beachgrass) and *Hudsonia tomentosa* (Beach Heather) along with the common *Myrica pensylvanica* (Bayberry), *Lathyrus japonicus* (Beach Pea), *Cakile edulenta* (Sea Rocket), and *Artemisia Stelleriana* (Dusty Miller). The extensive coverage of *Hudsonia*, one of the largest areas in the State, and the occurrence of *Geaster hygrometricus* (Earthstar Puffball) at the northern limit of its range are especially noteable. Also distinctive is the vegetational pattern — a mosaic resulting from the hummocky topography, rather than the more typical zonational pattern. Successional patterns and different successional stages may be observed here, as may the response of dune species to sand accretion and deflation processes. Because of its outstanding geological and botanical features, Seawall Beach was registered in July 1978 Furthermore, the landowners have promoted conservation of the area by granting a conservation easement to The Nature Conservancy.

**Rattlesnake Mountain, Oxford County.** This area is one of several outstanding rare plant areas which have come to light as a result of recent botanical work in the State. It was discovered by L.M. Eastman in 1974, and is currently a candidate critical area. On moist calcareous ledges above the southern hardwood slope of the mountain are found several rare species, many of them disjunct populations. *Ceanothus americanus* (New Jersey Tea), for example, is found here and at only one other location in the State. The mountain is the only known Maine station for *Ranunculus fascicularis* (Early Buttercup), and one of two known Maine stations for *Vitis aestivalis* var. *argentifolia* (Summer Grape) and *Arabis missouriensis* (Missouri Rock-Cress). Several other unusual species, such as *Asplenium trichomanes* (Maidenhair Spleenwort) and *Goodyera pubescens* (Downy Rattlesnake Plantain), occur here as well. The diversity and rarity of the plant species found here make Rattlesnake Mountain a botanically unique area (Eastman, 1977).

**Great Wass Island, Washington County.** A large island near Jonesport, Great Wass Island exemplifies the vegetation of the eastern Maine coast, but is noteworthy for its unique complex of three distinctly different peatlands, a large stand of *Pinus Banksiana* (Jack Pine), and several rare plant species. Most unusual are three maritime species which are found primarily on the eastern coast of Canada, and which reach their southern limit in Maine. *Iris Hookeri* (Hooker's Iris), reported from 20 locations in Maine and as far south as Knox County; *Lomatogonium rotatum* (Marsh Feelwort), which, in Maine, has been collected only at two locations, both in Washington County; and *Primula laurentiana* (Bird's-eye Primrose), reported from five locations in Washington County, seven locations in Aroostook County, and one station (which could not be relocated recently) in Piscataquis County (Pike, 1963). In addition, the Great Wass Heath supports other rare plant species, including *Arethusa bulbosa* and *Rubus chamaemorus* (Baked Appleberry). As more complete locational information becomes available, portions of Great Wass Island will be considered for designation as critical areas. In 1978, The Nature Conservancy purchased 1541 acres of Great Wass Island as a nature preserve.

**Norridgewock Rare Plant Station, Somerset County.** This is a rich deciduous woods area on the bank of the Kennebec River. It is most important as one of three Maine locations for *Cypripedium arietinum* (Ram's-Head Lady Slipper), listed as threatened by the Smithsonian Institution, especially as it is the northernmost natural stand in North America (Brower, 1977). This species has been known from here since 1959. *Chimaphila maculata* (Spotted Wintergreen) also occurs here, at the northern limit of its range; this species is known from only three other areas in the State (Eastman, 1976).

Also found here are *Orchis spectabilis* (Showy Orchis), *Habenaria Hookeri* (Hooker's Orchid), and a wide array of spring wildflowers including *Sanguinaria canadensis* (Bloodroot), *Hepatica americana,* and *Aquilegia canadensis* (Columbine). A small stream running through the lower part of the woods supports a wide diversity of ferns. The Norridgewock Rare Plant Station was registered as a critical area in 1977.

**Twin Peaks, Oxford County.** Twin Peaks is another noteworthy rare plant area which has come to light as a result of recent extensive botanical work in Oxford County. This remote mountain was first explored by C.S. Campbell and L.M. Eastman in 1974, who found the entire area botanically unusual because of its high elevation and the presence of Serpentine outcrops (Campbell & Eastman, 1978). Sites of especial interest are two cliff areas on the eastern side of the mountain. The lower of these, at 2600 feet, is a wet, calcic cliff covered with mosses and liverworts, where *Woodsia glabella* (Smooth Woodsia), *Woodsia alpina* (Alpine Woodsia), *Cystopteris bulbifera* (Bulblet Fern) and other ferns occur, as well as three very rare sedges: *Carex capillaris* var. *major, C. atratiformis,* and *C. media.* At the summit a dry cliff supports other calciphiles: *Lycopodium Selago* (Alpine Clubmoss), *Dryopteris fragrans* var. *remotiuscula* (Fragrant Fern), *Poa glauca, Carex eburnea, Saxifraga Aizoön* var. *neogaea* (Livelong Saxifrage), and *Antennaria rupicola* (Smaller Cat's Foot). The latter three species are particularly significant, being well beyond their previously known range here. Twin Peaks was designated as a critical area in April 1979.

**Mt. Katahdin, Piscataquis County.** Katahdin, Maine's highest mountain, has long been regarded as one of the most, if not the most, significant natural features of the state. Botanical work on Katahdin in the late 1800's and early 1900's established the distinctive character of the mountain; during this time, 32 vascular species now considered rare in Maine were collected from the mountain, 11 of which have been found in Maine only on Mt. Katahdin (Fernald, 1901). More recently, in 1976, an inventory of the part of the mountain above treeline was conducted by Diane Ebert May and Dr. Ronald Davis (1978), which focused on the alpine-tundra communities rather than on specific rare species. Eleven of the thirty-two rare species originally found on the mountain were relocated in the course of this study, including five which are known in Maine only from Mt. Katahdin: *Arctostaphylos alpina* (Alpine Bearberry), *Cassiope hypnoides* (Moss Plant), *Loiseleuria procumbens* (Alpine Azalea), *Phyllodoce caerulea* (Mountain-Heath), and *Rhododendron lapponicum* (Lapland Rosebay). Other recent work has uncovered stations for *Saxifraga stellaris* var. *comosa* (Star Saxifrage), its only known location in Maine, as well as *Saxifraga Aizoön* var. *neogaea* (Livelong Saxifrage) and *Viburnum edule* (Mooseberry). However, many of the rarities originally reported have not been recently relocated, including nine species known in Maine only from Mt. Katahdin: *Carex katahdinensis, C. mainensis, Luzula spicata* (Alpine Woodrush), *L. confusa* (Northern Woodrush), *Polygonum viviparum* (Alpine Knotweed), *Epilobuim alpinum* and *E. anagallidifolium* (Willow-Herb spp.), *Euphrasia Oakesii* (Oakes' Eyebright), and *Gnaphalium supinum* (Alpine Cudweed). Two other species, *Carex saxatilus* and *Cardamine bellidifolia* (Alpine Cress), are known from only one other Maine station, and have not been recently found at either location. In the near future the program hopes to relocate stations of these rare species. In a more general sense, Katahdin is noteworthy because of the many types of alpine-tundra plant communities and the overall extensive coverage of alpine-tundra vegetation.

**Crystal Bog, Aroostook County.** Crystal Bog has been known as one of the most interesting botanical areas in Maine since the turn of the century, when M.L. Fernald and others studied and described its flora (Fernald and Weigand, 1910). Also known as Thousand Acre Bog, the extensive peatland includes acid bogs and calcareous fens.

Botanical interest in the area has been rekindled of late, partially due to the gift of most of the bog to The Nature Conservancy by the J.M. Huber Corporation. As part of this recent work, the several distinct floristic regions of the bog have been described and mapped (Davis & Sawyer, 1978), and documentation of the rare plant species of the bog is being brought up to date. The rediscovery of the only Maine station of *Drosera linearis* (Linear-Leaf Sundew) here, for example, was the culmination of intensive and extended search (Rooney et al, 1978). Another rare species, *Habenaria leucophaea*, has been known from Crystal Bog since at least 1906, but its population has apparently never been extensive or stable. Fernald first described it from a fen on what is now Nature Conservancy property (Fernald and Weigand, 1910), but all recent sightings of this species have been in the fen in the small part of the bog which is privately owned. Also known from the bog are *Tofieldia glutinosa* (False asphodel), *Arethusa bulbosa, Parnassia glauca* (Grass of Parnassus), *Lonicera oblongifolia* (Swamp Fly-honeysuckle), *Valeriana uliginosa* (Northern Valerian), and *Lobelia Kalmii* (Brook Lobelia). Another rare species, *Juncus stygius* var. *americanus,* collected at Crystal Bog in 1907, has not been recently found. Crystal Bog is significant both in overall character and in the number of rare and unusual species which occur there.

**The St. John River Region, Aroostook County.** Botanical interest in the St. John River, long renowned for the many rare plant species found along its shores, has recently been revived as a result of the proposed Dickey-Lincoln hydroelectric power project. *Pedicularis Furbishiae* (Furbish's lousewort), endemic to the river and, until recently, believed extinct, was rediscovered in 1976 by Dr. Charles D. Richards of the University of Maine at Orono, growing along the banks of the river at six locations, all within the township of Allagash. It has since been found at twelve other stations along the St. John River. Also endemic to the river valley is *Carex Josselynii* (Josselyn's Sedge), collected in the past between St. Francis and Fort Kent; recent searches for this sedge have proven fruitless. *Astragalus Blakei* (Blake's Milk-Vetch), while not endemic to the St. John River, is very rare, being restricted to cliffs and talus of northern Maine and northern Vermont. In Maine, it was last collected in 1939, and was not seen in Dr. Richards' 1976 survey. Although these three species are by far the rarest of the St. John plants, the river supports a remarkable assemblage of arctic and boreal species, here at the southern limit of their range. The most frequently encountered of these rare species are *Astragalus alpinus* var. *brunetianus* (Alpine Milk Vetch) and *Tanacetum huronense* var. *johannense* (Huron Tansy), which occur along the lower shores of the river from Allagash to Frenchville, often together. Less commonly found are *Castilleja septentrionalis* (Northern Painted Cup), *Anemone multifida* (Cut-leaved anemone), *Oxytropis johannensis* (Field Oxytrope), *Primula mistassinica* (Bird's-eye Primrose), *Juncus alpinus* and *J. alpinus* var. *rariflorus* (Alpine Rush), and *Hedysarum alpinum* var. *americanum* (Sweet-Broom). Several other nothern species, more widely distributed in Maine than the preceding, but still rare, are found along the river as well. These include *Parnassia glauca* (Grass-of-Parnassus), *Tofieldia glutinosa* (False Asphodel), *Lobelia Kalmii* (Brook Lobelia), *Arnica mollis* (Hairy Arnica), and *Allium schoenoprasum* var. *sibiricum* (Wild Chive). With the wide diversity of rare and unusual plant species found along its banks, the St. John River is truly a unique botanical area.

## FUTURE BOTANICAL ACTIVITIES

The program will continue to search for the rare species not yet located. As the efforts of the program become better known, we hope that botanists and naturalists unfamiliar with the program will cooperate with our inventory. Much hard detective work remains to be done to relocate formerly known stations. In addition, more general inventory work needs to be carried out in regions where there is a very poor data base for rare plants (Figure 1). In 1979, several areas that will qualify as critical areas were reported to the program by interested landowners, a trend which we hope will continue.

Conservation activities for known rare plant areas will increase as more people become concerned about maintaining the areas to protect the plants. The program's staff will continue to monitor the status of rare plant critical areas. Management guidelines will need to be prepared for some species. Autecological studies of rare species should be undertaken to increase our understanding of their ecology and reproduction. The program stands ready to assist botanists and landowners who would like to increase their knowledge of Maine's rare plants.

Land conservation will play an increasing role in the long term protection of some areas. Conservation interests should be prepared to purchase significant areas without delay if threatened areas are offered for sale. However, because of the large number of privately owned areas, the program will have to depend very heavily upon continued cooperation from the private landowners to protect their rare plant stations.

## LITERATURE CITED

ADAMUS, PAUL R., & GARRETT C. CLOUGH. 1976. A Preliminary Listing of Noteworthy Natural Features in Maine. Maine State Planning Office, Augusta, Maine 04333. 397pp.

BEAN, RALPH C., C. D. RICHARDS, & F. HYLAND. 1966. Revised Check-list of the vascular plants of Maine. Bull. Josselyn Bot. Soc. Maine No. **8.** 72pp.

BROWER, A. E. 1977. Ram's-head Ladyslipper (Cyprepedium arietinum R. Br.) in Maine and its Relevance to the Critical Areas Program. Planning Report No. **25.** Maine State Planning Office, Augusta, Maine 04333. 13pp.

CAMPBELL, C. S. 1975. A Flora of Oxford County, Maine. MS Thesis in Botany, University of Maine, Orono. 161pp.

______.,& L. M. EASTMAN. 1978. Contributions to the vascular flora of Oxford County, Maine. Rhodora **80:** 309 317.

DAVIS, RONALD, & MERRYLYN SAWYER. 1978. A Preliminary Ecological Survey of Crystal Bog. Maine Chapter, The Nature Conservancy, Augusta, Maine. 28pp.

EASTMAN, L. M. 1976. Spotted Wintergreen, *Chimaphila maculata* (L.) Pursh. in Maine and its Relevance to the Critical Areas Program. Planning Report No. **21.** Maine State Planning Office, Augusta, Maine 04333. 14pp.

______. 1976. Ginseng, *Panax quinquefolius* L. in Maine and its Relevance to the Critical Areas Program. Planning Report No. **16.** Maine State Planning Office, Augusta, Maine 04333. 19pp.

______. 1977. Notable plants of Rattlesnake Mountain, Porter, Maine. Rhodora **79:** 316.

______. 1978a. Rare Vascular Maine Plants, A Compilation of Herbarium and Literature Citations. Maine State Planning Office, Augusta, Maine 04333. 446pp.

______. 1978b. Rare and Endangered Vascular Plant Species in Maine. The New England Botanical Club in cooperation with the U. S. Fish & Wildlife Service (Region 5, Newton Corner, MA.)

FERNALD, M. L., & K. M. WEIGAND. 1910. A summer's botanizing in Eastern Maine and Western New Brunswick. Part I. Rhodora **12:** 101 121.

GAWLER, S. 1978. A Revision of the Maine Rare Plant Inventory Process. Maine State Planning Office, Augusta, Maine 04333. 23pp.

HARTMAN, HERBERT. 1972. New England Natural Areas Project. Phase II. Natural Areas Protection in Maine. Natural Resources Council of Maine. 25pp. (Unpublished)

HILL, A. F. 1919. Vascular flora of the Penobscot Bay region. Proc. Portland Nat. Hist. Soc., Vol. **III,** part 2.

______. 1923. The vegetation of the Penobscot Bay region, Maine. Proc. Portland Soc. Nat. Hist., Vol. **III,** part 3.

KNOWLTON, C. H. 1904. Notes on the flora of Day Mountain, Franklin County, Maine. Rhodora **6:** 206 209.

MAY, DIANE E., & RONALD DAVIS. 1978. Alpine Tundra Vegetation on Maine Mountains and its Relevance to the Critical Areas Program. Planning Report No. **36.** Maine State Planning Office, Augusta, Maine 04333. 66pp.

MILNE, JANET E. 1978. The Landowner's Option, A Guide to the Voluntary Protection of Land in Maine. Revised Edition. Maine State Planning Office, Augusta, Maine 04333. 43pp.

NELSON, BRUCE W., & L. KENNETH FINK, JR. 1978. Geological and Botanical Features of Sand Beach Systems in Maine and their Relevance to the Critical Areas Program. Planning Report No. **54.** Maine State Planning Office, Augusta, Maine 04333. 269pp.

PIKE, RADCLIFFE B. 1963. Note on Lomatogonium. Rhodora **65:** 364 366.

RAND, EDWARD L., & JOHN H. REDFIELD. 1894. Flora of Mount Desert Island, Maine: A Preliminary Catalogue of the Plants Growing on Mount Desert and the Adjacent Islands. John Wilson & Sons, Cambridge.

ROONEY, S. C., C. S. MCKELLAR, & F. GAFFNEY. 1979. *Drosera linearis* Goldie rediscovered in Crystal Bog, Maine. Rhodora **81:** 145.

SEYMOUR, F. C. 1969. The Flora Of New England. The Charles E. Tuttle Company, Rutland, Vermont. 4596pp.

SMITHSONIAN INSTITUTION. 1975. U.S. House of Representatives Document 94 51. Report on Endangered and Threatened Plant Species of the United States. House Document No. **94-51,** Serial No. 94-A, 94th Congress, 1st session. Government Printing Office. 200pp.

MAINE STATE PLANNING OFFICE
189 STATE STREET
AUGUSTA, MAINE 04333

# MASSACHUSETTS NATURAL HERITAGE PROGRAM

MARTHA N. FISHER AND STEVEN C. BUTTRICK

The growth of our population and its demands upon our natural resources are inevitable. Pressure is continually increasing on our remaining natural areas for expanding agricultural, forestry, industrial, and residential needs. It is thus crucial that we develop ecologically sound planning for our continued growth. We must identify those elements of our natural heritage that are most critical for the preservation of our native flora, fauna, ecological associations, and landscape resources.

In 1978, The Nature Conservancy, in cooperation with the Massachusetts Department of Environmental Management, established the Massachusetts Natural Heritage Program. The purpose of this program is to create a continuing process for the identification of the significant natural areas of Massachusetts.

The goal of The Nature Conservancy is, and always has been, the preservation of natural diversity. Within the New England region, Conservancy acquisition efforts have resulted in the preservation of many important biological habitats, including:

— that of populations of the Plymouth Red-bellied Turtle (*Chrysemys rubriventris bangsi*), which has been recommended for listing as a Federally Endangered Species;

— portions of an island on the Maine Coast, including the largest stand of Jack Pine (*Pinus Banksiana*) in the state, stands of *Iris Hookeri, Sedum rosea, Primula laurentiana*, and *Lomatogonium rotatum* (all considered to be rare species in Maine (Eastman, 1978), and examples of rare coastal-plateau raised and blanket bogs.

For the past two decades, The Nature Conservancy has participated in natural area inventories throughout the United States. Through this involvement and experience have evolved the Conservancy's Natural Heritage Programs (Jenkins, 1975, 1976, & 1977). These programs are a new approach to continuous biological collection and management, one which focuses upon the distribution of *individual elements of diversity* (a rare species, plant community, aquatic habitat, etc.) rather than sites or natural areas. By focusing on elements of diversity which are rare or endangered, this type of inventory concentrates scarce resources on identification and location of examples of those elements that most need protection. Shortcomings of previous natural area inventories such as the New England Natural Areas Project (New England Natural Resources Center, 1972) included (a) a focus upon entire natural area sites, which proved expensive to survey and difficult to compare objectively, and (b) inventories representing only one point in time which quickly became outdated. The Heritage inventory by contrast is ongoing and records alterations in the ever-changing landscape, thus providing a comprehensive data base to meet Massachusetts' growing needs. In conjunction with the element inventory, detailed methods have been developed for determining protection priorities and implementing protection programs.

Since 1974 The Nature Conservancy has established Heritage Programs in twenty-one states (Arizona, Arkansas, California, Colorado, Indiana, Kentucky, Maryland, Massachusetts, Minnesota, Mississippi, New Mexico, North Carolina, Ohio, Oklahoma, Oregon, Rhode Island, South Carolina, Tennessee, Washington, West Virginia, and Wyoming) and the Tennessee Valley Authority, and contracts are being negotiated in a number of other states. Only by combining standard methods and criteria in many state programs can a national perspective on protection needs be achieved.

Natural Heritage Programs are generally conducted in cooperation with state governments, usually under one or two year contracts. The Massachusetts Natural Heritage Program has been established as a unit of the Massachusetts Department of Environmental Management's Office of Planning. Funding for this program has come from the federal Heritage Conservation and Recreation Service, the Commonwealth of Massachusetts, and private donors including the Fund for the Preservation of Wildlife and Natural Areas and the Mabel Louise Riley Trust. The Department of Environmental Management is the major land-managing agency in Massachusetts, administering a quarter of a million acres, and is the only agency with a broad mandate to manage and protect the environment. Species protection is an important part of this effort.

The establishment of a heritage program consists of three phases: program development, pilot inventory, and protection and planning for the preservation of a state's natural heritage. These three phases are briefly outlined below.

## PROGRAM DEVELOPMENT

The program development phase includes the creation of a classification system and file structure that will be used to keep track of the data. The classification consists of lists of elements sorted by class. The classes of elements include the rare plants, rare animals, plant communities, aquatic habitats, and significant landscapes and other natural features (see Figure 1). The analysis of the distribution of these elements serves to pinpoint natural areas needing protection. These element lists are drawn up utilizing existing class lists when available. For the classification to be authoritative and effective, we must rely upon the continuing input of the academic community.

In Massachusetts,we are fortunate to have the carefully researched report "Rare and Endangered Vascular Plant Species of Massachusetts" by Coddington and Field (1978). This well-documented list, coupled with the catalytic impetus of Dick Dyer, Regional U.S. Fisheries and Wildlife Service Endangered Species Botanist, and the guiding influence of the New England Botanical Club's Endangered Species Committee (Countryman, Dowhan, & Morse, 1979: Countryman, et al., 1972) will serve as a firm foundation to the rare plant portion of our Heritage Program.

The Massachusetts Division of Fisheries and Wildlife has formulated a list of Vertebrate "Species for Special Consideration in Massachusetts" (1979) which we will be using as a guideline in our program. Our lists of plant communities, aquatic habitats, and significant landscape features are now being developed and we invite all suggestions and additions. It should be emphasized that these lists are not static, being constantly updated as more data becomes available to us.

### Data Management System

The data management system constitutes a dynamic atlas of information on the existence, characteristics, numbers, condition, protection status, location, and distribution of occurrences of the state elements. This information is organized in a cross-indexed set of *manual, map,* and *computer* files which permit exceptional flexibility in systems use.

*Manual files:* The extensive manual files include the Element

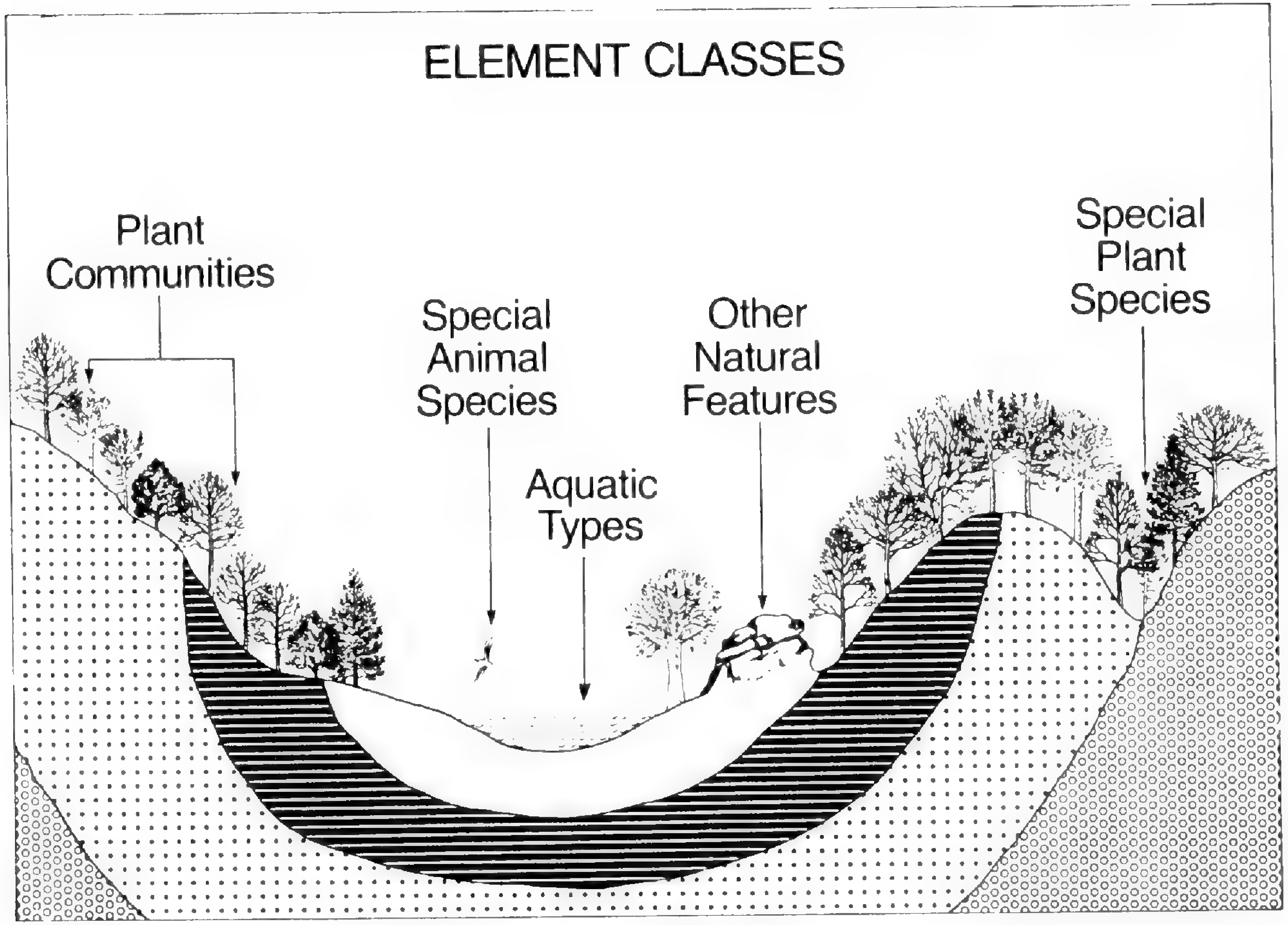

Figure 1. Elements of our natural heritage. (Sanders, 1978)

Files, Element Abstracts, Source Files, Managed Area Files, and Geographic Manual Files. The Element Files contain general monographic information for each rare plant or animal species, plant community type, etc. Any and all information collected by the heritage program for each element is stored or referenced in these files. The Element Abstract contains condensed and summarized information from the Element Files including description, nomenclature, habitat, range, status, proposed management, and sources of information for each element, using the format outlined in the "Guidelines for the Preparation of Status Reports on Rare and Endangered Plant Species" (Henifin, in press; for example, see Morse, in press). The Element Files also include a range map of each element within the 351 cities and towns and 14 counties of Massachusetts.

The Source of Information Files include extensive information concerning the agencies, managed areas, institutions, repositories, societies, knowledgeable individuals, and available literature relating to the elements. The Managed Area Files include maps, aerial photographs, management plans, and species checklists for each managed area in the Commonwealth. This kind of information is essential in determining how well-protected certain occurrences of an element within the state really are, as defined by the management policies of the administering land managing agency.

*Map Files:* The Map Files are the central component of the element occurrence records in the heritage program. This file consists of a complete set of USGS 1:24,000 scale topographic maps for the state, upon which the location of all element occurrences and managed areas are recorded as accurately as the data will allow. Each map will include a record of historically documented and/or field-verified occurrences of the various elements listed in our state. These maps serve as a essential tool in land-use planning and development conflict-avoidance efforts within the state. For instance, if a project were proposed for a particular site, our maps would indicate if there were a population of rare plants there and how they might be avoided. For each map there is a corresponding file which contains all the supporting information pertaining to the element occurrences and managed areas found on that map. Any other material which can be geographically referenced to that map will be found in this file.

*Computer Files:* The computerized LCD (Lowest Common Denominator) file is designed to outline the minimum amount of data necessary for analysis of the locations of occurrences of the elements. These LCD's act as a guide to the more extensive information available in the manual files. The computerized files allow us to sort quickly element occurrence locality information by county, town, physiographic province, owner, watershed, planning region, or various other parameters. The resultant facility in querying, selective retrieving, and editing and purging of the data base greatly aids our efforts to maintain up-to-date information and respond promptly to enquiries.

The computerized component also includes modules for graphic output devices such as X–Y pen plotters and character-mapping programs. These graphic display modules are designed to generate maps depicting the spatial distribution of the occurrences of elements within the state. These distributional range maps can be plotted to any scale, and can be plotted directly on mylars, so that they can easily be used as overlays for base maps.

## INVENTORY

Once the lists of elements of special concern within the state have been drawn up, and the manual, map, and computer files established, the major role of the Heritage Program is the coordination of a *continuously* updated inventory of the occurrences and biology of the elements. The landscape is continually undergoing natural and man-made changes; at the same time our understanding and appreciation of ecological processes and species distribution is always expanding. Thus, the revision of the data base must be an ongoing activity; otherwise the data will grow obsolete and lose its utility.

The inventory process combines an extensive search of the scientific literature and repositories, consultation with authorities in their respective fields and, most important of all, intensive field verification efforts and *de novo* searches. Let us reemphasize that the land-use planning and setting of protection priorities resulting from this inventory are only as good as the data base in the information system. If this inventory of the rare elements of the Massachusetts natural environment is to be of any value, there must be constant involvement and input from the scientific community. We do not see ourselves as "the experts" on rare species or characteristic ecological associations in Massachusetts. Many important aspects of the inventory process—developing meaningful classification systems, generating lists of occurrences, and especially conducting the vital field surveys—can only be accomplished with the enthusiastic support and volunteer efforts of natural scientists, agencies and organizations, and the public at large.

Individuals who would like to participate in the inventory effort are invited to write or call [(617) 749-4565] the Massachusetts Natural Heritage Program for personal "Expertise Survey" forms and for standardized "Observation" forms on which to report populations of rare or endangered species. In the Massachusetts Natural Heritage Program, the continuing inventory process is the product; we are attempting to establish a new program within Massachusetts that will serve as a central clearing house in an extensive inventory of the remaining critical habitats, ecological associations, and landscapes in the state, and so we need the support of the environmental community.

One problem peculiar to rare plant conservation in our region is that *much of the information concerning the distribution and biology of rare species available in the classical botanical literature is unsatisfactory for making critical habitat management decisions.* A majority of our herbarium specimen localities were collected during the New England botanical renaissance about 75 years ago; the New England landscape has changed dramatically since then. Additionally, the New England Botanical Club's Committee on Vascular Plant Distribution has confirmed that there exist areas in our region significantly underexplored botanically (Morse, et al., 1979).

Clearly what is needed is a renewed botanical field effort here in Massachusetts. We need to determine the actual distribution and population status of those species thought to be rare. Last year, Jonathan Coddington and others initiated a field inventory and precise mapping of some older reported rare species localities. Such field verification efforts in Massachusetts should be continued and expanded. By the field season of 1980, our program will have a complete documentation of the historically recorded and presently known populations of Massachusetts' rare species. We will then be in a position to coordinate an extensive field survey effort. The Massachusetts Natural Heritage Program, as part of this coordinated field inventory, needs up-to-date plant occurrence information from knowledgeable botanists across the state.

In addition to distribution field surveys of rare species, there is a need for long term studies of the habitat preferences, population demography, and reproductive biology of the rare and declining portions of our biota (Anderson, 1980; Graber, 1980). In developing management recommendations for these species it is necessary to know their breeding systems, pollen vectors, seed dispersal mechanisms, habitat requirements, predators, etc. For protection purposes, we need to know which stages in a species' life cycle are most vulnerable. Whitson and Massey (1979) have assembled a comprehensive outline of parameters to be investigated when analyzing the status of a rare plant population. Little information of this kind is presently known for most plant species on our Massachusetts list, and yet such knowledge will be essential for developing management and protection plans. Once again, we are not attempting to initiate single-handed research and conservation efforts; we are attempting to coordinate a functioning public/private natural area identification and protection process.

## PROTECTION PLANNING

Periodically the Heritage Program inventory data will be analyzed to determine which natural elements are the most vulnerable in the state. We will tabulate the number of reported occurrences for given elements, and determine which of these occur on adequately protected sites. This analysis will indicate which elements are the rarest in the state and have the fewest protected occurrences and thus are prime candidates for the limited funds that are available for natural area acquisition. This element prioritizing aspect of our information system will feed directly into the acquisition programs of the Department of Environmental Management, The Nature Conservancy, and other land managing agencies and organizations in the state.

A further application of the Heritage Program inventory will be environmental impact review processes, long hindered by a lack of a state, regional, or national perspective. The National Environmental Policy Act (NEPA) requires that environmental impact statements be prepared for all major federal actions. Massachusetts has a similar statute regarding major state actions in the Massachusetts Environmental Policy Act (MEPA). In addition, through the A-95 review process, all states have implemented review procedures for state projects assisted by federal funds, with the state agencies reviewing each others' proposals to eliminate redundancy and conflict (Klein, 1978).

The NEPA and MEPA impact statements and the A-95 reviews are significant for they allow proponents of natural area protection to comment upon poorly sited developments while plans are flexible. The Heritage Program inventory information will allow developers to reduce conflicts before projects are finalized, by avoiding significant sites altogether or by accomodating the natural features involved.

Among potential users for the Massachusetts Natural Heritage Program are the U.S. Fish and Wildlife Service Office of Endangered Species, the Heritage Conservation and Recreation Service National Natural Landmark Program, the U.S. Army Corps of Engineers, the U.S. Department of Transportation, NEPA, the Massachusetts Department of Environmental Management, the Massachusetts Division of Fisheries and Wildlife, the Massachusetts Department of Public Works, MEPA, A-95, regional planning centers, municipal planning boards and conservation commissions, the Trustees of Reservations, the Massachusetts Audubon Society, and The Nature Conservancy.

## SUMMARY

The most important product of the Massachusetts Natural Heritage Program is the continuing inventory of Massachusetts' rare natural elements. Our goal is to establish a cooperative effort between the public and private sectors for the identification and protection of those areas which best represent the state's natural heritage.

## ACKNOWLEDGEMENTS

We would like to express our sincere appreciation to Mr. Ray Angelo, Mr. Jonathan Coddington, Mr. Richard Dyer, Ms. Katharine Field, and Mr. Bruce Sorrie for having so generously supplied the Massachusetts Natural Heritage Program with both historically and presently known rare plant population localities. We also thank Dr. Larry Morse for his support and advice throughout the establishment of this program.

## LITERATURE CITED

ANDERSON, G. J. 1980. The very rare *Prunus gravesii*. Rhodora **82**(829):113 129

CODDINGTON, J., & K. G. FIELD. 1978. Rare and endangered vascular plant species in Massachusetts. U. S. Fisheries & Wildlife Service. Newton Corner, Massachusetts. 52pp.

COUNTRYMAN, W. D., J. J. DOWHAN, & L. E. MORSE. in press. Regional co-ordination of rare plant information synthesis by the New England Botanical Club. *In:* L. E. Morse & M. S. Henefin (eds.), Geographical Data Organization for Rare Plant Conservation. New York Botanical Garden, Bronx, New York.

______., H. E. AHLES, G. L. CHURCH, A. R. HODGDON, G. A. L. MEHLQUIST, & R. B. PIKE. 1972. Guidelines and criteria for the evaluation of natural areas. (A report prepared for the New England Natural Resources Center by the Natural Areas Criteria Committee of the New England Botanical Club, Inc. Cambridge, Massachusetts.) 12pp.

EASTMAN, L. M. 1978. Rare and endangered vascular plant species in Maine. U. S. Fish & Wildlife Service. Newton Corner, Massachusetts. 33pp.

GRABER, R. E. 1980. The life history and ecology of *Potentilla robbinsiana*. Rhodora **82**(829):131 140.

HENEFIN, M. S., L. E. MORSE, J. L. REVEAL, B. MACBRYDE, J. I. LAWYER. In press. Guidelines for the preparation of status reports on rare and endangered plant species. *In:* L. E. Morse & M. S. Henefin (eds.), Geographical Data Organization for Rare Plant Conservation. New York Botanical Garden, Bronx, New York.

JENKINS, R. E. 1975. The preservation of natural diversity. *In:* Humke, J. W., B. S. Tindall, R. E. Jenkins, H. L. Wieting, Jr., & M. S. Lukowski (eds.), The preservation of natural diversity: a survey and recommendations. The Natural Conservancy, Arlington, Virginia.

______.1976. Maintenance of natural diversity: approach and recommendations. pp 441 451. *In:* Transactions of 41st North American Wildlife and Natural Resources Conference, Wildlife Management Institute, Washington, D. C.

______. 1977. Classification and inventory for the perpetuation of ecological diversity. *In:* Classification, Inventory, and Analysis of Fish and Wildlife Habitat, a national symposium. U. S. Fish and Wildlife Service, Washington, D. C.

KLEIN, R. 1978. Long term protection of Maine's critical areas. (A report prepared for Maine's Critical Areas Program by The Nature Conservancy, Arlington, Virginia. 85pp & appendices A Z.

MASSACHUSETTS DIVISION OF FISHERIES AND WILDLIFE. 1979. Species for Special Consideration in Massachusetts. Westboro, Massachusetts. 5pp.

MORSE, L. E. In press. Report on the conservation status of *Hudsonia montana*, a candidate endangered species. *In:* L. E. Morse & M. S. Henefin (eds.), Geographical Data Organization for Rare Plant Conservation. New York Botanical Garden, Bronx, New York.

———, M. Lamson, A. F. Tryon, & R. R. Walton. 1979. Specimen locality indexing by the New England Botanical Club. *In:* L. E. Morse & M. S. Henefin (eds.), Geographical Data Organization for Rare Plant Conservation. New York Botanical Garden, New York.

New England Natural Resources Center. 1972. New England Natural Areas Project. Boston, Massachusetts.

Sanders, R. 1978. The state natural heritage programs: a partnership to preserve natural diversity. The Nature Conservancy News **28:** 13–19.

Whitson, P., & J. R. Massey. In press. Information systems for use in studying the population status of threatened and endangered plants. *In:* L. E. Morse & M. S. Henefin (eds.), Geographical Data Organization for Rare Plant Conservation. New York Botanical Garden, Bronx, New York.

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*The Proceedings of the Symposium*

## "RARE AND ENDANGERED PLANT SPECIES IN NEW ENGLAND"

4, 5 May 1979

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Cover illustration
*Geum Peckii* Pursh

This rare species is a Northeastern endemic, known from the White Mountains of New Hampshire and from three sites in Nova Scotia.

Original artwork by Lisa Bandazian

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Vol. 82 April, 1980 No. 830

# CONTRIBUTIONS TO THE VASCULAR FLORA OF BOREAL SASKATCHEWAN, CANADA[1]

VERNON L. HARMS, JOHN H. HUDSON,
AND JUDY HEILMAN-TERNIER

The flora of boreal Saskatchewan is poorly known, especially of the region north of 55° latitude. Despite collections by various persons dating back to the early 19th Century, adequate floristic inventories have been limited to very few areas in northern Saskatchewan, with most of the region remaining botanically unexplored. Among the earliest plant collections from boreal Saskatchewan were those made by John Richardson and Thomas Drummond, while with the First (1819–22) and or Second (1825–27) Franklin Arctic Expeditions respectively, with their results largely published in Hooker (1829–1840). Some plant specimens were acquired from the southern fringe of the boreal forest by N. Bourgeau, a botanist on the Captain John Palliser Expedition of 1857–59. During 1872–1881, John Macoun, and in 1888 his son, James M. Macoun, collected plants on the Upper Churchill and the Clearwater Rivers, especially at Methy Portage and areas somewhat upstream, while with expeditions of the Geological Survey of Canada. In 1891, J. B. Tyrell obtained some botanical samples between Lake Athabasca and the Churchill River. Quite comprehensive collections were made in 1926 by Hugh M. Raup in the Lake Athabasca area (Raup, 1936). Largely in the decade preceding 1943, numerous plant

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[1] This work has been supported directly or indirectly from a variety of sources, including, in particular, grants from the Institute for Northern Studies and President's Fund of the University of Saskatchewan, The Saskatchewan Department of the Environment, the National Research Council of Canada, Gulf Minerals Canada, Ltd., and the Saskatchewan Research Council. The Saskatchewan Youth Employment Program was helpful in its support for summer student assistants.

collections were accumulated by W. P. Fraser and R. C. Russell, primarily from the general Prince Albert-Prince Albert National Park-Montreal Lake region of Saskatchewan's southern boreal forest. The following decade saw extensive plant collecting undertaken by A. J. Breitung, especially in the Melfort-Bjorkdale-Nipawin region on the southern boreal forest fringe of east-central Saskatchewan. During 1953-54, John H. Hudson made a comprehensive collection in the Amisk Lake area. Over a span of about 20 years, George F. Ledingham, who has collected primarily in southern Saskatchewan, also gathered plant samples from various boreal Saskatchewan areas, including, in particular, Lac la Ronge, the Montreal Lake-La Ronge Road, and Wollaston Lake Post. G.W. Scotter (1961 & 1964) obtained botanical voucher specimens in conjunction with his caribou range studies in the region of Black Lake northward to the boundary of the Northwest Territories. During various boreal Saskatchewan expeditions in the 1960s, George W. Argus collected at Lake Athabasca, Carswell Lake, and Hasbala-Patterson Lakes region in the northeastern corner, and along the Hanson Lake Road (Argus, 1964, 1966, & 1968). Relatively thorough collections have been obtained from the Candle Lake area by the cumulative efforts of G. W. Argus, J. M. A. Swan (1966), J. K. Jeglum (1972), and H. K. Anderson (1976). In conjunction with a vegetation study of the Saskatchewan River delta marshes near Cumberland House, numerous voucher specimens were collected by H. J. Dirschl (1972) and his assistants. Further ecological studies and collections have been made in the sand-dune area south of Lake Athabasca by Hermesh (1972) and more recently by G. W. Argus.

Since 1970, the present authors, along with students and associates, have conducted various botanical field studies in boreal Saskatchewan, and made quite extensive plant collections. The results of a floristic survey along the Green Lake-La Loche Road were published by Harms (1974). Other boreal Saskatchewan areas surveyed and collected by the authors include the La Ronge-Southend and Wollaston Lake Roads (Hwys. 102 and 105, respectively), west side of Wollaston Lake, Reindeer and eastern Churchill Rivers, Sandy Bay-Island Falls vicinity, the Pelican Narrows-Sandy Bay Road, Meadow Lake Provincial Park, Greenwater Lake, Porcupine Hills, and elsewhere. Some of the above were the focus of environmental baseline and impact assessment investigations preceding proposed hydroelectric or mining developments, including the lower Churchill and Reindeer Rivers, the Collins Bay-Hidden Bay area of Wollaston Lake, and the Cluff Lake area. Although the relatively detailed information from the latter botanical surveys has been the subject of various reports (Heilman-Ternier & Harms, 1974; Harms, 1977a and 1977b), unfortunately these have very limited distribution and availability to the scientific community.

Recent plant collections have often added considerably to the distributional knowledge of the flora of boreal Saskatchewan. Other earlier collections of phytogeographical significance frequently had been filed in herbaria without having been reported in the literature, and other such specimens have been forwarded to the Fraser Herbarium for identification. These additional records from recent and earlier unreported collections have helped to fill in or to amplify the known distributions of various plant species in Saskatchewan, and sometimes have represented significant range extensions. The intent of this article is to share with interested naturalists, taxonomists, ecologists, and phytogeographers some of the phytogeographically more significant distributional data now available concerning various vascular plant species in boreal Saskatchewan. This supplements several earlier papers (Harms & Hudson, 1978; Harms, 1978) which respectively reported 13 vascular plant species new to the flora of Saskatchewan, and range amplifications for various orchid taxa.

For each of the species' entries below, the citations of our more recent collections are followed by a review of previous literature reports for the taxon in Saskatchewan and a listing of other herbarium records seen, concluding with brief distributional or taxonomic comments if appropriate. The names of collectors in the specimen citations have mostly been shortened to surnames. These include those of the authors, our primary field assistants (Marie A. Jasieniuk, Sheila M. Lamont, N. Andy Skoglund, Rob A. Wright, and John Polson), as well as others among the more frequently cited collectors (including George F. Ledingham, G. W. Argus, Zoheir Abouguendia, J. S. Maini, Howard G. Anderson, Tom F. Cameron, Luc Delanoy, Don Dabbs, Reinhard Hermesh, Herman J. Dirschl, J. M. A. Swan, J. B. Millar, Robert A. Godwin, & J. R. Caldwell). The collections of Judy Heilman-Ternier prior to 1974 are cited as "Ternier", while her 1974 collections, which were jointly made with Jim Heilman and labeled "J. & J. Heilman" on the specimen sheets, are cited simply as "Heilman". Unless otherwise indicated, all specimens cited have been deposited in the Fraser Herbarium (SASK) of the University of Saskatchewan. For brevity in the citations of collections, abbreviations are used for directions, units of distance, and such place name words as lake, river, creek, island, point, etc. The 95 species entries below are alphabetically arranged under genera and families, with the families taxonomically arranged according to the traditional Engler-Prantl sequence. To aid readers in better comprehending the locality information, a map (fig. 1) showing the general vegetation zones, larger lakes and rivers, important place names, and latitude-longitude coordinates in Saskatchewan is included. In addition, Table 1 provides the latitude-longitude coordinates for the other localities most frequently cited in this report, to avoid the repetition of these throughout the paper.

Table 1. Latitude and Longitude Coordinates for Various Cited Localities in Boreal Saskatchewan

| | |
|---|---|
| Amisk L.: Denare Beach | 54°40′N; 102°05′W |
| Beaupre L. | 54°32′N; 107°10′W |
| Besnard L. | 55°20 30′N; 105°45′ 106°15′W |
| Big Sandy L. | 54°27′N; 104°06′W |
| Carrot R. Prov. Forest | 53°22′W; 103°30′W |
| **Churchill R.:** | |
| Devil L. | 55°40′N; 104°45′W |
| Island Falls | 55°32′N; 102°21′W |
| Keg L. | 55°24′N; 104°00′ 05′W |
| Keg Falls | 55°23′N; 103°54′W |
| Missinipe | 55°36′N; 104°46′W |
| Otter L. | 55°35′N; 104°46′W |
| Otter Rapids | 55°38′N; 104°44′W |
| Pita L. | 55°29 36′N; 102°43 46′W |
| Sandy Bay | 55°33′N; 102°18′W |
| Sokatisewin L. | 55°27 30′N; 102°23 28′W |
| Trade L. | 55°20½ 24′N; 103°40 49′W |
| Wapumon L. | 55°35 36′N; 102°56′W |
| Wintego L. | 55°32 33′N; 102°52 55′W |
| Cluff L. | 58°19½ 22′N; 109°31′ 35½′W |
| Clut L. | 59°24′N; 105°48′W |
| Cumberland House | 53°57′N; 102°15′W |

Table I (continued)

| | |
|---|---|
| Duck Mtn.: Madge L. | 51°35′N; 101°00′W |
| Garthland, 5 mi. NNW | 52°58′N; 106°28′W |
| Green L. | 54°17′N; 107°47′W |
| Greenwater L. | 52°30′N; 103°31′W |
| **Highway 102 (La Ronge — Southend Road):** | |
| Bervin L. | 55°47′N; 104°33′W |
| Brabant L. | 56°00′N; 103°43′W |
| Dickens L. | 55°45′N; 104°40′W |
| Jaysmith L. | 55°59′N; 104°07′W |
| Jct. with Hwy. 105 | 56°15′N; 103°30′W |
| Lynx L. | 55°21′N; 104°58′W |
| McKay L. | 55°27′N; 104°56′W |
| McLennan | 55°53′N; 104°22′W |
| Wierzycki L. | 56°01′N; 103°56′W |
| **Highway 105 (Wollaston L. Road):** | |
| Atwater L. | 56°48′N; 103°37′W |
| Bothwell L. | 57°03′N; 103°36′W |
| Courtenay L. | 57°24′N; 103°58′W |
| David L. | 56°38′N; 103°33′W |
| Davin L. | 56°50′N; 103°40′W |
| Geikie R. Crossing | 57°41½′N; 103°59½′W |
| Peter L. | 57°15′N; 103°53′W |
| Swift Cr. of Lightning Bolt | 56°34′N; 103°34′W |
| Wathaman R. | 57°06′N; 103°43′W |
| Island Falls | 55°32′N; 102°23′W |
| Island L. | 58°21′N; 109°33′W |
| Jan L. | 54°56′N; 102°55′W |
| Lac la Plonge: Weber Bay | 55°10′N; 107°27′W |
| **Lac la Ronge:** | |
| English Bay | 55°13′N; 105°17′W |
| La Ronge | 55°06′N; 105°17′W |
| Nemeiben Cr. | 55°17′N; 105°10′W |
| Waden Bay | 55°17′N; 105°05′W |
| La Loche | 56°29′N; 109°26′W |
| Leaf Rapids | 54°50′N; 102°38′W |
| Little Amyot L. | 55°11′N; 107°50′W |
| Little Bear L. | 54°20′N; 104°35′W |
| Limestone L. | 54°38′N; 103°13′W |
| MacDonald Cr., of MacDonald L. | 57°12′N; 105°35′W |
| MacDowall, 5 mi. SSW | 52°57′N; 106°05′W |
| Macoun L. | 56°32′N; 103°50′W |

Table 1 (continued)

| | |
|---|---|
| **Meadow L. Prov. Pk.:** | |
| Greig L. | 54°27′N; 108°41½′W |
| Kimball L. | 54°24′N; 108°48½′W |
| 1st Mustus L. | 54°27½′N; 108°48½′W |
| 2nd Mustus L. | 54°25½′N; 108°58½′W |
| 3rd Mustus L. | 54°26′N; 108°54′W |
| Methy Portage | 56°38′N; 109°45′W |
| Mirond L. | 55°00–13′N; 102°48½–103°07′W |
| Nipawin Prov. Pk.: Lower Fishing L. | 54°02′N; 104°38′W |
| Pasquia Hills | 53°07–14′N; 102°24–41′W |
| Pelican Narrows | 55°10′N; 102°56′W |
| Porcupine Hills, 14 mi. S of Armit | 52°38′N; 101°48′W |
| **Reindeer R.:** | |
| Atik Falls | 55°36′N; 103°11′W |
| Devil L. | 55°40′N; 104°45′W |
| Devil Rapids | 56°12′N; 103°10′W |
| McDonald Cr. | 56°02–04′N; 103°02–05′W |
| Royal L. | 56°01½′N; 103°06′W |
| Steephill L. | 55°55–59′N; 103°04–11′W |
| Steephill Rapids | 55°56½′N; 103°17′W |
| The Two Rivers | 55°45–47′N; 103°07–10′W |
| White L. | 56°00′N; 103°16′W |
| **Reindeer L.:** | |
| N end at D.T.R.R. Fisheries Camp | 57°46′N; 102°06′W |
| Numabin Bay | 56°18–26′N; 103°15–23′W |
| Southend | 56°20′N; 103°12′W |
| Sandy Bay, at Nemei R. | 55°29′N; 102°19′W |
| Taylor L. | 56°03′N; 108°34′W |
| Turnor L. | 56°28′N; 108°41′W |
| Waskesiu L. (in Pr. Albert Nat'l. Pk.) | 53°54′–55°01′N; 106°04–26′W |
| Wheeler R., near Russell L. | 57°22′N; 105°26′W |
| White Gull L. | 53°56′N; 105°04′W |
| Wilson L. | 57°17′N; 105°33′W |
| **Wollaston L.:** | |
| Collins Bay | 58°14½–16½′N; 102°38–41′W |
| Hidden Bay | 58°02½–07½′N; 103°41–47½′W |
| Minor Bay | 57°56′N; 103°50′W |
| Nekweaga Bay | 57°44–52½′N; 102°38–47½′W |
| Pow Bay | 58°12½–14′N; 103°37–39′W |
| Rabbit L. | 58°12′N; 103°43′W |
| Umpherville R. | 58°06′N; 103°47′W |

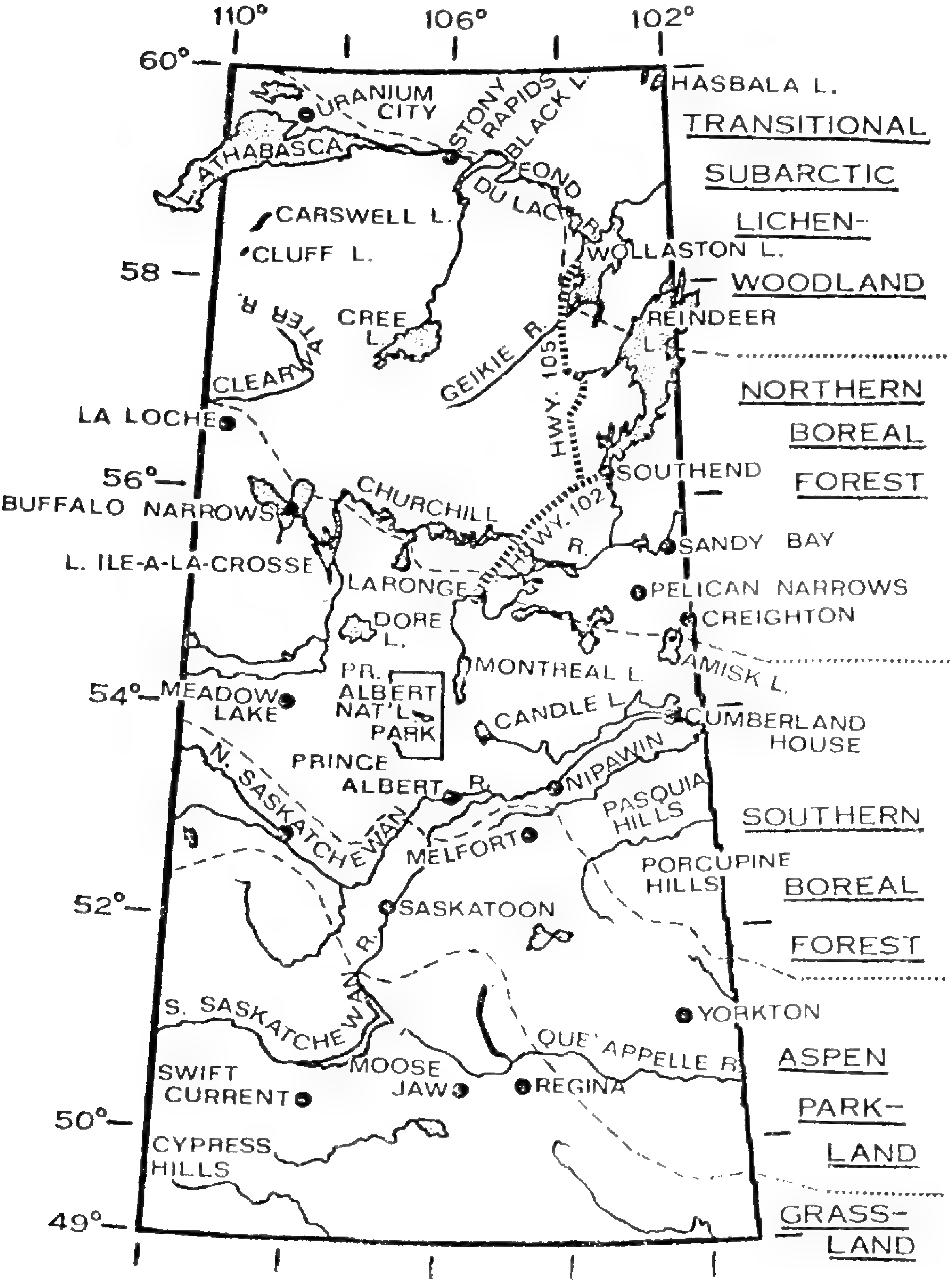

Figure 1. Map of Saskatchewan showing general vegetation zones, larger lakes and rivers, other important place names, and latitude longitude coordinates.

## LYCOPODIACEAE

**Lycopodium inundatum** L.

Cluff L., very wet open fen, *Hudson & Polson 3698.* Previously recorded in Saskatchewan only from Windrum L. (Boivin, 1967b).

**Lycopodium sitchense** Rupr. [*L. sabinaefolium* Willd. var. *sitchense* (Rupr.) Fern.].

Cluff L., mesic black spruce-jack pine forest, *Hudson & Polson 3675.* An apparently rare species previously reported in the province only from Portage La Loche (= Methy Portage; Macoun, 1890), the L. Athabasca S shore (Raup, 1936), and Hasbala L. (Argus, 1966).

**Lycopodium selago** L.

SW end of Hidden Bay of Wollaston L., rare on dense moss in white birch-black spruce-river alder gallery mixedwoods, *Harms 22160.* 2 mi. W of Southend, near Numabin Bay of Reindeer L., jack pine-lichen forest with rock outcrops, *Ternier & Lamont 533.* This arctic-subarctic clubmoss seems rare in Saskatchewan, where it was previously reported only in the northernmost part of the province (L. Athabasca, Raup, 1936; Hasbala L., Argus, 1966). The present collections multiply the number of known localities for it and extend the known range of the species in Saskatchewan southward nearly 200 miles. Thus, this clubmoss is not strictly subarctic in the province but apparently occurs at least sporadically in the northern boreal forest region as well.

## ISOETACEAE

**Isoetes echinospora** Dur. var. **braunii** (Dur.) Engelm. [*I. braunii* Dur.; *I. muricata* Dur. var. *braunii* (Dur.) Reed].

Cluff L., *Hudson & Polson 3668;* Hidden Bay of Wollaston L., *Harms 21687, 21815 & 22089;* Collins Bay of Wollaston L., *Harms 21959;* NE arm of Davin L., *Harms 22553;* Little Bear L., *Harms 20235B.* The plants were relatively frequent and often locally abundant on the lake bottom at 0.5 1.5 m below the water surface. The species had been considered uncommon in the province. Previous reports from Saskatchewan include: Creighton (Breitung, 1957), Hasbala-Patterson L. area (Argus, 1966), Little Gull L. on the S shore of L. Athabasca (Argus, 1968), and the following localities along the Hanson Lake Road: Limestone L., Jan L., Kistapisken L., and Sturgeon-Weir R. (Argus, 1968; the latter as *I. muricata* var. *hesperia* Reed). Although Argus (1968) stated that the species was widespread throughout Saskatchewan on the Precambrian Shield, evidence of this from available collections was then lacking for the region between the far northern stations and sites along the Hanson Lake Road at the southern edge of the shield.

## OPHIOGLOSSACEAE

**Botrychium matricariifolium** Braun [includ. ssp. *hesperium* Maxon & Clausen].

Between Davin L. & Bothwell L., uncommon at edge of shallow pool in esker valley, *Ternier & Jasieniuk 1747;* Pita L. on Churchill R., rare on rock outcrops, *Heilman 2227.* Breitung (1957) reported this species in Saskatchewan from the Cypress Hills, Mortlach, Amisk L., and Beechy. Additional herbarium specimens have been seen from near Fox Valley (*Ledingham & Jones 5676,* USAS). The present records amplify the few previous ones for Saskatchewan, extending about 150 miles northward the known range of this species. Surprisingly, while this grape-fern is now known in Saskatchewan from the Cypress Hills forest, mixed grassland, and northern boreal forest zones, it has not yet been recorded from either the aspen parkland or the southern boreal forest zones. It remains uncertain whether this apparent gap is a collecting artifact.

**Botrychium multifidum** (Gmel.) Rupr. [includ. var. *multifidum* and var. *intermedium* (D.C. Eaton) Farw.].

Cluff Lake, mesic black spruce-jack pine forest, *Hudson & Polson 3704;* McDonald Cr. of Reindeer R., rare on creek banks, *Heilman 2556;* Churchill R., at Trade L., rare on exposed beach point, *Heilman 2353.* Generally considered a rare and sporadically occurring, although quite widespread, species, it was previously known from Big River, McKague, Saskatoon (Breitung, 1957), Cypress Hills (*Newsome 528-62*), Lac Ile-a-la-Crosse (Harms, 1974), Amisk L. (*Hudson 1571,*JHH), and Mortlach (*Hudson 1902,* DAO).

**Botrychium virginianum** (L.) Sw. [includ. var. *europaeum* Angstr.].

Cluff L. area: Germaine L., rare on wet mossy shore, *Harms, Skoglund & Wright 24272.* This most commonly encountered grape-fern in Saskatchewan is characteristic of the aspen parkland and southernmost boreal forest zones, but was previously recorded from no farther north in the province than Meadow L. Prov. Park, Waskesiu L., and Candle L. The present Cluff L. collection appears to be the first from the northern half of Saskatchewan and represents an over 250-mile northward range extension. However, since this species has been reported from Keewatin and Mackenzie Districts, N.W.T. (Boivin, 1967b), its occurrence at least sporadically throughout northern Saskatchewan is expected. The fronds of the Cluff L. specimens were unusually small-sized even for the smaller var. *europaeum*. Most Saskatchewan specimens, however, do not appear readily separable into the usually recognized varieties.

## POLYPODIACEAE

**Gymnocarpium robertianum** (Hoffm.) Newm. [*Dryopteris robertianum* (Hoffm.) C. Chr; *Phegopteris robertianum* (Hoffm.) A. Br.].

Ca. 5 mi. N of La Ronge, vertical rock outcrop face, *Harms 21134;* Midway L., 8.5 mi. N of La Ronge, rock outcrop cliff side, *Ternier & Lamont 114;* Reindeer R., midway between Steephill L. and The Two Rivers, occasional on rock cliff, *Heilman 1539;* near David L., common on rock outcrops, *Ternier & Jasieniuk 1971;* 1.5 mi. S of Bothwell L., uncommon on rock outcrops, *Ternier & Jasieniuk 1783;* N side of Wathaman L., uncommon on rock outcrops in jack pine forest, *Ternier & Jasieniuk 1683;* 7.5 mi. S of Geikie Crossing, SW end of Wollaston L., uncommon on rocky slope in mixed forest, *Ternier & Jasieniuk 2418.* A rarely collected plant in Saskatchewan, where it was previously reported only from L. Athabasca (Raup, 1936) and the Hasbala-Patterson L. area (Argus, 1966). Herbarium specimens have also been seen from Limestone L. (mossy limestone outcrops, lake shore, *Argus & Hudson 4575*) and from Clut L. (*Campbell 3 Aug. 1935*). The present locality records suggest that this fern is much more widespread and frequent in the province than was once believed, at least on the metamorphic rocks of the Precambrian Shield in eastern boreal Saskatchewan. It appears both morphologically and ecologically distinct from the similar *G. dryopteris* (L.) Newm., and we cannot concur with Boivin (1967b) who considered the two species conspecific.

**Matteuccia struthiopteris** (L.) Todaro var. **pensylvanica** (Willd.) Morton [*Onoclea struthiopteris* (L.) Fern. var. *pensylvanica* (Willd.) Boivin].

About 15 mi. W of Numabin Bay of Reindeer L., birch-alder woods along stream, *Ternier & Jasieniuk 2097;* Courtenay L., alder-birch woods, *Ternier & Jasieniuk 1476.* Conspicuous, frequent and often locally abundant in the southern boreal forest and aspen parkland zones of Saskatchewan, this fern was not recorded previously from the northern half of the province. The present records represent northward range extensions.

**Thelypteris phegopteris** (L.) Slosson [*Dryopteris phegopteris* (L.) Christensen; *Phegopteris polypodioides* (L.) Fee].

5 mi. S of Geikie R. Crossing, moist gallery birch woods, *Ternier & Jasieniuk 2353;* Geikie R., rocky creek in boggy marsh, *Ternier & Jasieniuk 2543;* Hidden Bay of Wollaston L., moist lush white birch-black spruce-river alder gallery mixed woods, *Harms 21604, Harms & Wright 23756.* This species was previously recorded in Saskatchewan by Raup (1936) from Axis L. at the E end of L. Athabasca and by Breitung (1957) from Clut L. and Porter L. (E. of Frobisher L.). However, the voucher specimens for the latter citations, which were reportedly filed in the Fraser Herbarium, have not been located. Thus Boivin (1967) listed only Axis L. as a verified locality for the Saskatchewan distribution of this species, and further cited only a single locality in each of the neighboring provinces. More recently, Looman (1973) reported its discovery at McLennan L., a locality where it also had been found previously by us (*Ternier & Lamont 1111*). The present Geikie R.-Wollaston L. collections add substantially to the known distribution of this fern in Saskatchewan and western Canada. Its occurrence should be expected elsewhere in the northern boreal forest region on the Precambrian Shield of especially northeastern Saskatchewan. Based upon the known Saskatchewan distribution, it might also be expected in southern Keewatin or southeastern Mackenzie Districts, N.W.T., where neither Boivin (1967) nor Porsild & Cody (1968) recorded it.

## NAJADACEAE

**Potamogeton amplifolius** Tuckerm.

Churchill R., W side of Sokatisewin L., flooded inlet, water depth ½ m, *Heilman 1700.* Breitung (1957) cited this species from Waskesiu L. based upon a collection filed in the Fraser Herbarium that has since been revised. Boivin (1966–67) listed Saskatchewan only parenthetically, indicating that he had not verified any Saskatchewan reports. Unfortunately, our specimens are sterile, but their identification based on foliage characters seems quite certain.

**Potamogeton epihydrus** Raf.

Churchill R., Keg L., *Polson 6 & 14;* Ca. 5 mi. W of Reindeer R. & 5 mi. N of White L., *Heilman 2478;* Reindeer R., between Steephill L. & Royal L., *Heilman 2427;* Jaysmith L., *Ternier & Jasieniuk 2576;* 7½ mi. S-SE of La Loche, *Harms & Skoglund 19679;* Dickens L., *Ternier & Lamont 1326;* McKay L., *Ternier & Jasieniuk 2725;* 12 mi. W of Numabin Bay of Reindeer L., *Harms 22638, Ternier & Jasieniuk 2244;* Atwater L., *Ternier & Jasieniuk 1835;* Peter L., *Ternier & Jasieniuk 2308, 2309;* Geikie R. Crossing, *Ternier & Jasieniuk 2479, 2549;* Cluff L. area: Snake L., *Hudson & Polson 3683.* An often abundant aquatic in shallow quiet water of lakes, ponds, creeks, marshes and very wet sedge fens. This species was first recorded for Saskatchewan from Denare Beach, Amisk L. (*Hudson 1735,* DAO). However, it was not listed for Saskatchewan by Fraser & Russell (1944 & 1953) nor Breitung (1957). Boivin (1966 67) included Saskatchewan at the western limit of its eastern Canadian range from New Brunswick, presumably on the basis of the Amisk L. collection. To our knowledge, the new records represent the only subsequent collections of this species in the province. Although formerly thought to be rare in Saskatchewan because of the dearth of collections, this pondweed now appears likely to be common in the northern boreal forest zone.

**Potamogeton natans** L.

Alcott Cr., 26 mi. N of Glaslyn, *Hudson 3660;* Meadow L. Prov. Park, N shore of Kimball L., *Harms 20627;* McKay L., *Ternier & Jasieniuk 2710;* Bervin L., *Ternier & Lamont 1161;* Jaysmith L., *Ternier & Jasieniuk 2581;* McDonald Cr. of Reindeer R., *Heilman 2397b;* Garvin Bay of Steephill L. on Reindeer R., *Heilman 2436;* Cluff L. area, Claude L., *Hudson & Polson 3718.* The plants occurred in shallow water marshes along shores of protected lake bays and sluggish streams. Breitung (1957) reported the species from only Prince Albert Nat'l. Park and McKague; Jeglum (1972) from Candle L.; and Harms (1974) from Lac la Plonge and Turnor L. There are also specimens of this species in the Fraser Herbarium from Cumberland House (*Argus 4029, Dabbs 89-66*), Sled L.

(*Caldwell, 19 July 1963*), and Big Sandy L. (*Hudson & Argus 4535-6, 4540*). The present records extend its known Saskatchewan range considerably northward.

**Potamogeton obtusifolius** Mert. & Koch.

Ca. 5 mi. W of Reindeer R. & 5 mi. N of White L., in fen pond, *Heilman 2515;* Devil L., 1.5 mi. N of Otter Rapids, rock outcrop shore, *Ternier & Jasieniuk 2626;* Ballantyne Bay of Deschambault L., ½-1 m water, *Harms 22960.* The only previous records for this apparently rare aquatic in Saskatchewan are from L. Athabasca (Raup, 1936; Breitung, 1957), Candle L. (Jeglum, 1972), and Amisk L. (*Hudson 1550*). Presumably this pondweed is scarce throughout the western Canadian provinces.

**Potamogeton pusillus** L. [including *P. berchtoldii* Fieber].

Devil L., *Ternier & Jasieniuk 2626;* Trade L. on Churchill R., *Ternier & Jasieniuk 2590 & 2594;* Wintego L. on Churchill R., *Heilman 1947 & 2065;* McDonald Cr. on Reindeer R., *Heilman 2396 & 2450.* Cluff L. area: Douglas R., *Hudson & Polson 3713.* The plants were frequent and often abundant in sedge fen ponds and shallow water marshes of protected lake bays and sluggish streams. Previously thought to be infrequent in Saskatchewan where it was recorded from the L. Athabasca region (Raup, 1936), Spur Creek (sic) and Fort Carleton (Breitung, 1957), Candle L. (Jeglum, 1972), and from Little Amyot L. and Lac Ile-a-la-Crosse (Harms, 1974). In addition, we have verified specimens in the Fraser Herbarium from Amisk L. (*Hudson 1550*), Carnduff (*Bolton 8*), Prince Albert (*Furniss, 5 Aug. 1936*), Melfort (Millar 65-252), Cadillac (*Garton 13454*), and Saskatoon (*Coupland & Middleton 462; Millar 65-275*). This pondweed is now known to occur throughout the parkland and southern boreal forest regions of Saskatchewan.

**Potamogeton robbinsii** Oakes.

Cluff L.: Sandy L. north of Douglas R., aquatic, *Hudson & Polson 3714, Polson et al 26-7-78.* Apparently rare in Saskatchewan where it has previously been recorded only from Nemeiben L. (Caldwell, 1960) and Limestone L. (*Hudson & Argus 4579*).

**Potamogeton zosteriformis** Fern.

Otter L. at Missinipe, aquatic in ½-2 m water depths, *Ternier & Jasieniuk 2667;* Devil L., aquatic in water ½-1½ m deep near shores of protected bays and inlets, *Ternier & Jasieniuk 2634;* Churchill R., between Keg Falls and Grand Rapids, aquatic, *Polson 62;* Trade L. on Churchill R., aquatic in 2 5 m water depths in protected bay, *Heilman 2582;* Ray Bay of Wintego L. on Churchill R., small creek entering bay, *Heilman 1960b & 2063;* Sokatisewin L. on Churchill R., aquatic in flooded inlet, Heilman *1702.* Breitung (1957) reported this species from Pike L. and Waskesiu L. It was recorded by Jeglum (1972) from Candle L. and by Harms (1974) from the Canoe R. There also are specimens in the Fraser Herbarium from the Cumberland House vicinity (*Argus 4030B & 4066*), Limestone L. (*Argus & Hudson 4585*), Big Sandy L. (*Hudson & Argus 4543*), Lower Fishing L. in Nipawin Prov. Park (*Argus & Hudson 4408 & 4452*), Dore L. (*Caldwell July 1963*), Sled L. (*Caldwell July 1963*), Beaupre L. (*Caldwell, 17 July 1963*), Waterhen R. in Meadow L. Prov. Park (*Hudson 2430*), and Melfort (*Millar 63-64*). This pondweed may be more frequent in the aspen parkland and southern boreal forest regions of Saskatchewan than once thought.

### SCHEUCHZERIACEAE

**Scheuchzeria palustris** L. var. **americana** Fern.

Ca. 12 mi. W of Numabin Bay of Reindeer L., wet sedge bog, *Ternier & Jasieniuk 2220;* Ca. 10 mi. E of Macoun L., wet sedge bog, *Ternier & Jasieniuk 2085;* David L., wet semi-treed bog, *Ternier & Jasieniuk 1978;* Peter L., wet sedge bog, *Ternier & Jasieniuk 1555;* 7.5 mi. S of Geikie R. Crossing, wet boggy sedge area, *Ternier & Jasieniuk 2428;* Cluff L., very wet open fens, *Hudson & Polson 3697;* Wheeler R. near Russell L., wet *Carex-Sphagnum* fen, *Godwin, Aug. 1978.* Recorded previously from only L. Athabasca (Raup, 1936), Prince Albert Nat'l. Park (Breitung, 1957), Candle L. (Jeglum, 1972), Little Amyot L. (Harms, 1974), and the Cumberland House area (*Dirschl & Dabbs 210-62,* SASK), the present records indicate a more widespread occurrence in the province for this species than was formerly realized.

### POACEAE

**Calamagrostis lapponica** (Wahl.) Hartm.

Cluff L. area, semi-stabilized disturbance and natural sandy clearings, open mossy shores, and "drier" treed bogs, *Harms 23813 & 23957; Harms, Skoglund & Wright 24230, 24396 & 24297.* This primarily arctic species was only recently reported by us (Harms &

Hudson, 1974) as new to Saskatchewan, based on collections from William River, S of L. Athabasca and the La Loche area. Thus the present collections document the third locality in Saskatchewan, lessening somewhat the distributional gap between the previous records. The three stations are all located on the western edge of the province north of 56° latitude.

**Calamagrostis purpurascens** R. Br.

Cluff L. area: 1.5 mi. W of Island L., thin soil in open dolomite outcrop areas, *Harms 23896 & 23942; Harms, Skoglund & Wright 24422 & 24428*. This rarely collected arctic species has been recorded elsewhere in Saskatchewan only from the N shore of L. Athabasca (Raup, 1936), Dodge L. (Scotter, 1961), Carswell L. (Argus, 1964), and the Hasbala L. area (Argus, 1966). In northwestern Saskatchewan it is known only from dolomitic sites.

**Festuca brachyphylla** Schultes [*F. ovina* var. *brachyphylla* (Schultes) Piper].

Cluff L., natural sand-blowout clearing, *Harms 24332*. We have also revised to this species the following collection in the Fraser Herbarium: Stony Rapids, N of Fond-du-Lac R., open aspen stand, *Maini & Swan 517*. An apparently rare arctic species in Saskatchewan, it is recorded elsewhere only from rock crevices on the N shore of L. Athabasca (Raup, 1936).

**Poa alpigena** (Fr.) Lindm. [*P. pratensis* L. var. *alpigena* Fries].

Meadow L. Prov. Park, E side of Kimball L., *Harms 20479;* La Ronge, *Harms 21034;* 3 mi. N of La Ronge, *Ternier & Lamont 488;* Wierzycki L., *Ternier & Lamont 1029;* near Southend, Numabin Bay of Reindeer L., *Harms 22715;* ca. 10 mi. E of Macoun L., *Harms 22635;* Huggins L. outlet to Minor Bay of Wollaston L., *Harms 22176;* NE end of Cluff L., *Harms 24154*. At these places the plants occurred either on dry open stream shores or in disturbed clearings. The species was not included for Saskatchewan by Fraser & Russell (1937 & 1954) or Breitung (1957), and Boivin (1966–67) listed both Saskatchewan and Manitoba in parentheses to indicate the existence of reports not verified by him. Harms (1974) recorded it from Green L., Little Amyot L. and La Loche. An additional specimen of this species has been identified in the Fraser Herbarium (cleared forest, N end of Cree L., *Maini 78*). Possibly overlooked or not usually distinguished from the more common *P. pratensis* L. in Saskatchewan.

**Poa nemoralis** L.

Mirond L., open jack pine woods, *Harms 23076;* Opawikusehikan Narrows, 3 mi S of Pelican Narrows, dry roadside, *Harms 20128;* English Bay of Lac la Ronge, lake shore sedge meadow, *Harms 21255.* This species was listed by Fraser & Russell (1954) for the eastern mixed prairie and aspen parkland regions of Saskatchewan but without citation of any specific localities. Breitung (1957), who probably included the species under *P. palustris* L., did not list it. Boivin (1966–67) included Saskatchewan within its range. It was recorded by Harms (1974) from Green and Taylor Lakes. In the Fraser Herbarium there also are Breitung collections from McKague, Wallwort, and Golburn, as well as a specimen from 5 mi. S of Candle L. (wet-mesic balsam poplar-black spruce forest, *Swan 65-35*). A grass probably not rare in Saskatchewan but perhaps overlooked or not usually distinguished from the more common *P. palustris.*

**Torreyochloa pallida** (Torr.) Church [*Glyceria pallida* (Torr.) Trin.; *Puccinellia pallida* (Torr.) Clausen].

3 mi. SW of Otter L. of Churchill R., emergent in small marshy creek pond, *Harms 22735;* McDonald Cr. of Reindeer R., aquatic in shallow marsh delta wetlands, *Heilman 2472, Polson 103;* ca. 5 mi. W of Reindeer R. & 5 mi. N of White L., shore sedge fen along creek, *Heilman 2499;* Northern Reindeer L., D.T.R.R. Fishing Camp, *Polson 96.* This, a presumably rare species in Saskatchewan, was first reported for the province by Argus (1968) from Stony Rapids and from Yakow L. at the SE end of L. Athabasca. A grass found mostly in more eastern North America, it is known otherwise in western Canada from several disjunct sites in northern Alberta and British Columbia.

**Trisetum spicatum** (L.) Richt. var. **molle** (Michx.) Beal.

Cluff L., open dolomite outcrops, *Abouguendia 7-8-78.* Previously recorded in Saskatchewan from the Cypress Hills (Breitung, 1954 & 1957), and the far north at L. Athabasca (Raup, 1936) and Hasbala L. (Argus, 1966).

## CYPERACEAE

**Carex abdita** Bicknell.

W side of Trade L. on Churchill R., rock outcrops, *Heilman 2645;* S end of Sokatisewin L., on Churchill R., rock outcrops in pine forest, *Heilman 1804, 1805;* near Steephill L. on Reindeer R., rock outcrops, *Heilman 2374;* Reindeer R., below Steephill Rapids, rock outcrops in open jack pine forest, *Heilman 1425;* near David L., dry rocky creek bed, *Ternier & Jasieniuk 1944.* Cluff L. area: Snake L., sandy disturbed clearing in jack pine forest, *Harms, Skoglund & Wright 24542C.* Although this sedge was once considered rare in Saskatchewan, known only from Hasbala L. (Argus, 1966), L. Athabasca (*Ledingham 3346 & 3365,* USAS) and Lac la Ronge (*Ledingham 48-280 & 49-331,*USAS), the present records show that it occurs across the boreal forest zone. The distribution of this and other *Carex* species in Saskatchewan is mapped by Hudson (1977).

**Carex concinna** R. Br.

Cluff L. area: W of Island L., frequent on dolomite cliffs, *Harms, Skoglund & Wright 24455A.* This species, which is characteristic of the aspen parkland and more southern boreal forest regions of the province, is disjunct in northwestern Saskatchewan, where it has been recorded from the N shore of L. Athabasca (Raup, 1936) and the Cluff L. area. This apparent disjunction may be artificial due to inadequate collecting in western boreal Saskatchewan.

**Carex eburnea** Boott.

Cluff L. area: 1.5 mi. W of Island L., dolomite cliffs, *Harms 23897 & 23902; Harms, Skoglund & Wright 24427.* A rare calciphile in Saskatchewan, this sedge grows mainly in the valleys of the N. and S. Saskatchewan and Qu'Appelle Rivers in the grassland and aspen parkland zones. It is disjunct in northwestern Saskatchewan, where it has been recorded from the N shore of L. Athabasca (Raup, 1936), Carswell L. (Argus, 1964), and Cluff L. This gap in range is likely due to the rarity of suitable calcareous sites in the intervening boreal forest region.

**Carex garberi** Fern.

Missinipe, forest trailside, *Ternier & Lamont 297;* Cluff L., semi-open shrub shores, *Harms, Skoglund & Wright 24177 & 24212.* These reports, the first records from the mid-boreal forest and from northwestern Saskatchewan, are for a sedge that was known previously from only about five places in southern Saskatchewan and from Hasbala L. in the NE corner of the province.

**Carex houghtonii** Torr.

Atwater L., roadside, *Ternier & Jasieniuk 1884;* SE end of

Nekweaga Bay of Wollaston L., shrubby streambank, *Harms 22375.* Cluff L. area: 1.5 mi. N of Island L., semi-open jack pine woods & trailside, *Harms 23987;* NW of Snake Lake, *Harms, Skoglund & Wright 24536A.* These records represent an approximately 100-mile northward range extension of the species in Saskatchewan.

**Carex lanuginosa** Michx.

Cluff L. area, 1.5 miles N of Island L., "drier" open bogs and jack pine forest clearings, *Harms, Skoglund & Wright 24371 & 24405B.* For a sedge known mainly in the grassland and aspen parkland zones, with a few scattered records northward into the southern boreal forest, but none from north of 55° latitude, the Cluff Lake collection represents a 230-mile northward range extension in Saskatchewan.

**Carex lenticularis** Michx.

Collins Bay of Wollaston L., moist shrub shore, *Harms 21928;* Hidden Bay of Wollaston L., frequent on moist open and shrub shores, *Harms 21610, 21802-3, & 21882;* Royal L. on Reindeer R., mud-boulder beach, *Heilman 2465;* McLennan L., wet sandy lake shore, *Ternier & Lamont 1093.* Previously, this species was recorded in Saskatchewan only from L. Athabasca (Raup, 1936), Lac la Ronge, (Breitung, 1957), Reeves L. NW of Black L. (*Campbell, 12 July 1936,* CAN) and Amisk L. (*Hudson 1513,* DAO). Our present records indicate a greater frequency for the species in boreal Saskatchewan than formerly believed.

**Carex leptalea** Wahl.

Campbell Is. in Sokatisewin L. on Churchill R., sedge fens, *Heilman 1838;* ca. 15 mi. W of Southend, Numabin Bay of Reindeer L., moist disturbance areas, *Ternier & Jasieniuk 2188;* about 12 mi. W of Numabin Bay of Reindeer L., swamp horsetail marsh, *Ternier & Jasieniuk 2232;* Wathaman R., moist mixedwoods, *Ternier & Jasieniuk 1666, 1777;* N of Geikie R., boggy creek shore, *Ternier & Jasieniuk 2544;* Cluff L. area, moist gallery mixedwoods, lake shores, and natural sand-blowout clearings, *Harms, Skoglund & Wright 24208, 24304, & 24334B.* These collections narrow the apparently wide gap between the species' previously known occurrence in the aspen parkland and southernmost boreal forest region (north only to Waskesiu L. and Candle L. at ca. 54° N lat.) and far northern Saskatchewan [L. Athabasca (Raup, 1936), Carswell L. (Argus, 1964), Hasbala L. (Argus, 1966)].

**Carex livida** (Wahl.) Willd.

7 mi. S of Geikie R., wet sedge fen, *Ternier & Jasieniuk 2427;* Courtenay L., boggy lake shore, *Ternier & Jasieniuk 1529;* ca. 12 mi. W of Numabin Bay of Reindeer L., wet marsh, *Ternier & Jasieniuk 2238.* These records partly fill a previous gap in the range of this infrequently collected species between its main area of occurrence in the aspen parkland and southern boreal forest, and the far northern records at Hasbala L. (Argus, 1966) and L. Athabasca (S shore E of William R., *Argus 337-62,* distributed as *C. limosa* L.).

**Carex loliacea** L.

Geikie R., SW of Wollaston L., moist black spruce willow bog, *Ternier & Jasieniuk 2522;* Courtenay L., birch woods along creek, *Ternier & Jasieniuk 1517;* Atwater L., birch woods along stream, *Ternier & Jasieniuk 1869;* ca. 12 mi. W of Numabin Bay of Reindeer L., wet black spruce-tamarack treed bog, *Ternier & Jasieniuk 2296;* Wapumon L. on Churchill R., wet forest along stream, *Heilman 1990;* Pita L. on Churchill R., creek bank, *Heilman 2193;* Lynx L., willow marsh, *Ternier & Lamont 412A, 421 & 427.* This subarctic sedge of wet habitats, formerly thought to be rare in Saskatchewan, was known only from the northernmost region of the province at L. Athabasca (Raup, 1936), Oblate L. and Faraud L. N of Black L. (Scotter, 1961), and Patterson L. (Argus, 1966), except for a collection (*Ledingham 49-337,* USAS, DAO) from Lac la Ronge (Breitung, 1957) and a more recent one from the Porcupine Hills (Hudson, 1974). The presently cited collections suggest a more or less continuous boreal distribution for this sedge at least in eastern Saskatchewan.

**Carex michauxiana** Boeckl.

Ca. 12 mi. W of Numabin Bay of Reindeer L., wet marsh, *Ternier & Jasieniuk 2237.* A species of eastern Asia and eastern North America first discovered in Saskatchewan by Argus (1968) on the S shore of L. Athabasca. The present collection represents only the second record for Saskatchewan and apparently also for the western Canadian provinces, since Boivin (1966–1967) did not report it from west of Ontario.

**Carex oligosperma** Michx.

Cluff L., very wet open fens, *Hudson & Polson 3690;* Collins Bay of Wollaston L., dominant in wet sedge pond fen, *Harms 21998;* 7.5

mi. S of Geikie R. Bridge, boggy sedge area, *Ternier & Jasieniuk 2421;* Peter L., wet sedge bog, *Ternier & Jasieniuk 1553;* David L., wet black spruce-tamarack bog, *Ternier & Jasieniuk 1977;* ca. 12 mi. W of Numabin Bay of Reindeer L., "boggy" sedge area, *Ternier & Jasieniuk 2212, Harms 22641.* These include the first records from northeastern Saskatchewan. It is otherwise known in Saskatchewan from Methy Portage (Breitung, 1957), the S side of L. Athabasca (Raup, 1936; Argus, 1968), and Buffalo Narrows (*B. Nelson S58044,* SASKP).

**Carex pauciflora** Lightf.

Ca. 13 mi. W of Numabin Bay of Reindeer L., open sedge bog, *Ternier & Jasieniuk 2199 & 2215;* Courtenay L., moist tamarack bog, *Ternier & Jasieniuk 1532;* Cluff L. area. 1½ mi. N of Island L., *Harms, Skoglund & Wright 24406.* This apparently rare species has been otherwise recorded in Saskatchewan from only three sites: L. Athabasca (Argus, 1968), Candle L. (Jeglum, 1972), and Porcupine Hills (Hudson, 1974).

**Carex richardsonii** R. Br.

W side of Sokatisewin L. on the Churchill R., aspen forest, *Heilman 1788;* Reindeer R. near The Two Rivers, aspen forest, *Heilman 1573;* 2 mi. below Steephill Rapids on Reindeer R., aspen forest, *Heilman 1523;* Cluff L. area, dolomite outcrops, cliffs, and disturbed area, *Harms 23814, 23927 & 23938.* These collections extend the known range of the species well north of the previous records from Amisk L., Candle L., Waskesiu L., and Nipawin Provincial Park, with the Cluff L. collections representing a 300-mile northwestward range extension.

**Carex saxatilis** L. [includ. var. *rhomalea* Fern.; var. *miliaris* (Michx.) Bailey; var. *major* Olney; ssp. *laxa* Kalela; & *C. physocarpa* Presl.].

Courtenay L., sedge meadow and wet shore, *Ternier & Jasieniuk 1501 & 1506.* Cluff L. area, trailside clearing near small stream, in jack pine forest, *Harms, Skoglund & Wright 24259.* This subarctic sedge was previously recorded in Saskatchewan only from the N shore of L. Athabasca (Raup, 1936) and Hasbala L. (Argus, 1966).

**Carex trisperma** Dewey.

Ca. 13 mi. W of Numabin Bay of Reindeer L., black spruce bog, *Ternier & Jasieniuk 2251.* This species was first reported for

Saskatchewan by Hooker (1829 1840), who cited a Drummond collection from Cumberland House. The species was erroneously reported by Breitung (1957) from Candle L. based upon specimens now revised to *C. brunnescens* (Pers.) Poir. Argus (1968) found it at Little Gull L. south of L. Athabasca.

**Eleocharis nitida** Fern.

Hidden Bay of Wollaston L., shallow mossy pool in black spruce forest, *Harms 21445;* ca. 12 mi. N of Geikie R., rocky stream edge, *Harms 22442;* Davin L., open bouldery stream edge, *Harms 22571;* near David L., rocky creek bed and open disturbance area, *Ternier & Jasieniuk 1942 & 1960;* Nemei R., at S end of Sandy Bay on Churchill R., 5 mi. S of Island Falls, moist sandy edge of black spruce woods, *Harms 20013B;* W of Reindeer R., 5 mi. N of White L., sedge fen-bog, *Heilman 2512.* This represents the second report for this apparently rare species in Saskatchewan. It was first recorded for the province by Argus (1968) based upon a collection from Stony Rapids. The species' occurrence in Saskatchewan is phytogeographically quite interesting, since this northern species had formerly been thought to be widely disjunct in North America (Newfoundland, New England, the Great Lakes area, and the Alaskan-British Columbia Pacific coast). However, the overall distribution of this species remains somewhat uncertain, because taxonomists have not always distinguished it from *E. elliptica* Kunth or from *E. tenuis* (Willd.) Schultes.

**Rhynchospora alba** (L.) Vahl.

Cluff L., wet open fen, *Hudson & Polson 3695.* Previous records from Saskatchewan include Dahlton, Prince Albert, Nipawin (Breitung, 1957), L. Athabasca S side at Little Gull L. (Argus, 1968), Wallwort (*Breitung, 1372*), and Garthland (*Hudson 3037 A,* JHH). The Saskatchewan range appears disjunct from the species' main eastern North American (Ontario and eastward) and Pacific Coast distributional areas.

**Rhynchospora fusca** (L.) Ait. f.

Cluff L., wet open fen, *Hudson & Polson 3692.* The first Saskatchewan record for this eastern bog plant, which was not previously reported from west of Ontario and southern Michigan.

**Scirpus acutus** Muhl.

Cluff L. area, Germaine L., shallow water to 5 dm depths, *Harms,* *Skoglund & Wright 24280.* This collection probably represents the northernmost record in Saskatchewan. However, literature reports are untrustworthy in delineating the range of the species because of its frequent confusion with *S. validus.*

**Scirpus fluviatilis** (Torr.) A. Gray.

Churchill R., between Keg Falls and Grand Rapids, shallow marsh, *Polson 51;* Trade L. on Churchill R., shallow off-shore marshes, *Heilman 2576;* on Churchill R., Wintego L., shallow off-shore marsh, *Heilman 1946;* Elcott, marshy RR ditch, *Hudson 3644.* An infrequently collected, apparently rare species that was reported from only Pike L. and Indian Head (Breitung, 1957), although a specimen from Birch River S of Cumberland House (*Dabbs 112-66*) is also filed in the Fraser Herbarium. Our new collections extend the known range of the species over 100 miles northward to the eastern Churchill R. region. The few Saskatchewan stations for this bulrush are widely spaced.

**Scirpus hudsonianus** (Michx.) Fern. [*Eriophorum alpinum* L.].

Ca. 12 mi. W of Numabin Bay of Reindeer L., wet marshy *Carex-Lysimachia-Andromeda* bog, *Ternier & Jasieniuk 2221;* Cluff L., moist mossy shores and drying sandy stream bed, *Harms, Skoglund & Wright 24019 & 24293.* Infrequently collected and previously reported from L. Athabasca (Raup, 1936), Golburn, McKague, Nipawin, Peesane, Lac la Ronge (Breitung, 1957), Hasbala L. (Argus, 1966), and MacDowall (Hudson, 1971), our new records expand its area of known occurrence in the more northern boreal forest region of the province and suggest that it may be fairly widespread in northern Saskatchewan.

## JUNCACEAE

**Juncus longistylis** Torr.

Cluff L., moist sandy "dry" stream bed, *Harms 24018.* This collection seems to represent an approximately 300-mile northward extension of range, since we are unaware of any previous records for it from north of the grassland and parkland regions of Saskatchewan where it is quite frequent.

**Juncus stygius** L. subsp. **americanus** (Buch.) Hult.

Ca. 12 mi. W of Numabin Bay of Reindeer L., wet open and treed bogs, *Ternier & Jasieniuk 2223 & 2225;* near David L., wet treed bog, *Ternier & Jasieniuk 1979;* Cluff L., very wet open fen, *Hudson & Polson 3694;* S of MacDowall, wet open spots in marl bog, *Hudson 3069*. To our knowledge this rush was known previously in Saskatchewan only from the S side of L. Athabasca (Raup, 1936; Argus, 1968) and near Garthland (Hudson, 1976). The present records help narrow by at least 250 miles the apparent midcontinental gap between the known western and eastern North American stations.

**Juncus tenuis** Willd. var. **multicornis** E. Mey. [*J. macer* S. F. Gray].
Meadow L. Prov. Park, SW of Greig L., abandoned trail in aspen-pine woods, *Hudson 2410;* Nipawin Prov. Park, Lower Fishing L., trailside in black spruce forest, *Harms 22903;* English Bay of Lac la Ronge, disturbed trailsides, *Harms 21241;* Otter Rapids of Churchill R., disturbed roadside, *Ternier & Jasieniuk 2645;* McLennan L., disturbed roadside, *Ternier & Jasieniuk 1241;* S end of Sandy Bay of Churchill R., 5 mi. S of Island Falls, trailside in aspen woods, *Harms 23345*. Although probably not rare in Saskatchewan, this rush is infrequently collected. Breitung (1957) cited it only from Prince Albert Natl. Park and Montreal L. More recently Harms (1974) recorded it from Green L., Lac la Plonge and Taylor L. The present collections more than double the recorded stations for the species in Saskatchewan, while extending its known range in the province northeastward.

**Luzula acuminata** Raf. [*L. saltuensis* Fern.].
McDonald Cr. NE of Steephill L. on Reindeer R., sedge shore fens, *Heilman 2337, 2447;* Pasquia Hills, dry open pine-spruce forest, *Hudson 2896;* Porcupine Hills 14 mi. S of Armit, black spruce woods on high ground, *Hudson 2927*. The only previous report is from Meadow Lake (Breitung, 1957). Boivin (1966–67) included Saskatchewan within the Canadian range of this woodrush (i.e., Newfoundland to Alberta), although we do not know any basis for this other than the above-mentioned record by Breitung. In Alberta, it has been reported only from the Swan Hills by Packer & Dumais (1972).

**Luzula parviflora** (Ehrh.) Desv.
Brabant L., open roadside, *Ternier & Lamont 823;* Pasquia Hills, at Bankside L., *Felske & Pegg, 11 Aug. 1971;* Porcupine Hills, 14 mi. S of Armit, wet clearing in black spruce forest, *Hudson 2867*. To our knowledge, this species was previously recorded in Saskatche-

wan only from Candle L., Meadow L., Lac Ile-a-la-Crosse, and Lac la Ronge (Breitung, 1957), Hasbala L. (Argus, 1966), Taylor L. and La Loche (Harms, 1974), and Big Sandy L. (*Hudson & Argus 4459*). From the present records, it would appear quite widespread but sporadic, especially in the southern half of Saskatchewan's boreal forest.

## POLYGONACEAE

**Rumex orbiculatus** A. Gray.

Inlet to Numabin Bay of Reindeer L., *Heilman 2767;* ca. 3.5 mi. N of Courtenay L., *Ternier & Jasieniuk 1435;* SW end of Hidden Bay of Wollaston L., *Harms 20893.* At each of these stations, the plants were shallow water emergents in wet sedge fens. These collections represent the northernmost records in Saskatchewan of a species formerly believed to be common only in the wetlands of the southern boreal forest region of the province. Making the new records somewhat less surprising is the recent report of this species from southern Mackenzie District, N.W.T., by Cody (1978).

## CARYOPHYLLACEAE

**Arenaria macrophylla** Hook.

Near Jct. Hwys. 102 & 105, ca. 14–15 mi. W of Numabin Bay of Reindeer L., open aspen woods and open willow disturbed area, *Ternier & Lamont 702, Ternier & Jasieniuk 2182.* Previously known in Saskatchewan only from L. Athabasca (Raup, 1936) and Hasbala L. (Argus, 1966).

**Arenaria rubella** (Wahl.) J. E. Smith [*Minuartia rubella* (Wahl.) Graebn.].

Cluff L. area, 1½ mi. W of Island L., rare on dolomite cliff and outcrops, *Harms 23926B.* This arctic-subarctic and cordilleran species is known elsewhere in Saskatchewan only from the N shore of L. Athabasca (Raup, 1936) and the Cypress Hills (Breitung, 1954 & 1957).

## NYMPHAEACEAE

**Nymphaea tetragona** Georgia ssp. **leibergii** (Morong) Porsild.

NW side of Peter L., *Ternier & Jasieniuk 2332;* Cluff L. area, Sandy L., *Hudson & Polson 3710.* At these places, the plants occurred in shallow water (5–15 dm deep) of wave-sheltered lake edges and mouths of sluggish streams. Previously recorded from near Cumberland L. (Breitung, 1957), Hudson Bay Jct. (Kujt, 1959), S side of L. Athabasca (Argus, 1968), Candle L. (Jeglum, 1972), and Little Amyot L. (Harms, 1974). The new records amplify somewhat the known distribution of this rare species in Saskatchewan.

## RANUNCULACEAE

**Anemone parviflora** Michx.

White Gull Creek near White Gull L., black spruce muskeg, *Anderson 1280;* Cluff L., moist jack pine burn, *Abouguendia 30-7-78.* This apparently rare species was previously recorded only in northernmost Saskatchewan from the N shore of L. Athabasca (Raup, 1936), Hasbala L. (Argus, 1966), and Carswell L. (Argus, 1964). The present White Gull L. collection represents a 300-mile southward extension of range in Saskatchewan. This suggests the possibility that the species might be expected almost anywhere in our boreal forest region. However, other subarctic species also appear disjunctly in the Candle Lake area and/or sometimes in the Pasquia and Porcupine Hills. Perhaps these represent isolated, relict populations of a subarctic element which once existed along the receding shores of post-glacial Lake Agassiz.

**Coptis trifolia** (L.) Salisb. [*C. groenlandica* (Oeder) Fern.].

David L., disturbance area, *Ternier & Jasieniuk 1959;* Atwater L., dry black spruce bog, *Ternier & Jasieniuk 1812;* Wathaman R., moist birch woods, *Ternier & Jasieniuk 1670;* Peter L., moist disturbance area with *Alnus* and *Myrica, Ternier & Jasieniuk 1575;* 15 mi. S of Geikie R. crossing, jack pine regrowth woods, *Ternier & Jasieniuk 1378;* W of Hidden Bay of Wollaston L., dry black spruce forest, *Harms & Wright 23727;* Cluff L. area, 1½ mi. N of Island L., "drier" treed bog, *Harms, Skoglund, & Wright 24403a.* This species, which is more characteristic of the aspen parkland and southern mixedwood section of the boreal forest, was previously known in more northern Saskatchewan from only Wolverine Pt. on the S shore of L. Athabasca (Raup, 1936) and Patterson L. in the northeastern corner of the province (Argus, 1966). The present records help to fill the northern boreal distributional gap which was formerly apparent in the province.

## BRASSICACEAE

**Draba lanceolata** Royle.

Cluff L. area, W of Island L., dolomite cliffs, *Harms 23920; Harms, Skoglund & Wright 24434*. This represents the third station for this apparently rare calciphile in Saskatchewan. It is known elsewhere in the province only from dolomitic rock crevices N of L. Athabasca (Raup, 1936) and from a similar habitat at Carswell L. (Argus, 1964; reported as *D. cinerea* Adams, based on *Argus 596-62*, SASK).

**Subularia aquatica** L. ssp. **americana** Mull. & Cald.

English Bay of Lac la Ronge, *Harms 21295A;* ca. 3 mi. W of Southend, *Harms 22666;* Northern Reindeer L: D.T.R.R. Fisheries Camp, *Polson 120;* Hidden Bay of Wollaston L., *Harms 20857, 20940, 20957 & 21857;* Cluff L., *Hudson & Polson 3670*. The plants grew submerged on lake bottoms in relatively shallow water. Previously reported from only Amisk L. (Breitung, 1957) and near Stony Rapids (Argus, 1968). Of note was its surprising abundance at Hidden Bay of Wollaston L., where it represented a codominant lake bottom plant with *Eleocharis acicularis* var. *submersa* (Nils.) Svens. at depths of 0.5–1.5 m.

## DROSERACEAE

**Drosera anglica** Huds.

Ca. 12 mi. W of Numabin Bay of Reindeer L., wet marsh, *Ternier & Jasieniuk 2239;* Courtenay L., "boggy" lake shore, *Ternier & Jasieniuk 1526;* 7.5 mi. S of Geikie R. crossing, wet sedge bog, *Ternier & Jasieniuk 2426;* Cluff L. area, N shore of Germaine L., emergent in mossy inlet spring, *Harms, Skoglund & Wright 24285;* 2 km E of Silver Grove, ca. 24 km S of Shellbrook, high-mineral spring area, *Cameron 553*. This sporadically occurring species has been considered rare in Saskatchewan, where it was known only from the southernmost boreal forest region at Prince Albert and McKague (Breitung, 1957), Big Sandy L. on the Hanson Lake Road (*Hudson & Argus 4515*), the MacDowall area (Hudson, 1976), L. Athabasca (Raup, 1936), and the Hasbala L. area (Argus, 1966). Very recently, it has also been found at two localities in the Qu'Appelle Valley. The present records amplify significantly the few known localities for the province.

SARRACENIACEAE

**Sarracenia purpurea** L.

Ca. 12 mi. W of Numabin Bay of Reindeer L., open bog, *Ternier & Jasieniuk 2219, Harms 22645;* ca. 10 mi. E of Macoun L., bog, *Ternier & Jasieniuk 2080;* Buffalo Narrows, boggy area, *Delanoy 62.* Also filed in the Fraser Herbarium are previously unreported northern Saskatchewan collections from bogs at Cree L. (Middleton Is., *Maini 39;* Lazy Edward Bay, *Maini 170*). Previously known from about a dozen different localities in the more southern boreal forest region of eastern Saskatchewan, the most northern of which were Candle L. and Amisk L.; also recorded from L. Athabasca by Raup (1936) and subsequent collectors. The present collections add some mid-boreal records and help to narrow somewhat the wide distributional gap formerly apparent in the province. This species is of sporadic occurrence in Saskatchewan but is usually locally abundant where found.

ROSACEAE

**Potentilla pensylvanica** L. var. **litoralis** (Rydb.) Boivin [*P. pectinata* Raf.].

Pita L. on Churchill R., open rock outcrops, *Heilman 2222;* N end of Methy Portage at Clearwater R., old campground on river floodplain, *Cameron 319.* In the Fraser Herbarium is another specimen from Saskatchewan (3 mi. N of Hudson Bay Jct., *Breitung 732*). This variety was reported by Breitung (1957 & 1959) from L. Athabasca, and by Harms (1974) from Turnor L. Boivin (1967b) parenthetically listed NW Saskatchewan, indicating that he had not verified any reports. The *Potentilla pensylvanica* complex in Saskatchewan needs careful study. It now appears that most, although not all, specimens of the species (sensu lat.) from boreal Saskatchewan belong to this variety.

RHAMNACEAE

**Rhamnus alnifolia** L'Her.

Cluff L., moist gallery mixedwoods, *Harms, Skogland & Wright 24079.* This collection appears to represent an approximately 250-mile northward extension of the known range of this species in Saskatchewan. However, its reported range in Manitoba and

Alberta suggests that the distributional gap is likely artificial due to inadequate collecting. Also, Raup (1936) reported the species as common in the lower Athabasca R. region of Alberta, less than 75 miles SW of the Cluff L. area.

## OENOTHERACEAE

**Circaea alpina** L.

Ca. 1 mi. N of La Ronge, birch-alder-willow shrub zone bordering stream, *Ternier & Jasieniuk 2096;* Numabin Bay of Reindeer L. near Southend, rocky creek bank, *Ternier & Lamont 599;* Geikie R. SW of Wollaston L., *Ternier & Jasieniuk 2547;* inlet stream from Parks L. to Hidden Bay of Wollaston L., moist lush birch-black spruce-river alder gallery mixedwoods, *Harms 21595, Harms & Wright 23746.* The plants were locally abundant at most of the above sites. We are unaware of any previous collections of this species from the northern half of Saskatchewan, *i.e.* north of known sites at Waskesiu L., Candle L. and Big Sandy L. Thus, the Wollaston L. collections appear to represent a 250-mile northward range extension in Saskatchewan, although the species is known from equally as far north in Alberta.

## HALORAGACEAE

**Myriophyllum alterniflorum** DC.

McLennan L., *Ternier & Lamont 1106;* Jaysmith L., *Ternier & Lamont 2570;* Wierzycki L., *Ternier & Lamont 970 & 971;* Cluff L. area, Sandy L., *Hudson & Polson 3715.* The plants were growing submerged in shallow lake water (less than 0.5 m depths). This species was not cited by Breitung (1957) for Saskatchewan. Boivin (1968) listed the following records for the Prairie Provinces: Axis L. (Saskatchewan), and Cochrane R. and Reindeer L. (Manitoba). Harms & Hudson (1974) recorded it from Little Amyot L. at SW end of Lac Ile-a-la-Crosse. Three of the new collections were made within 20 miles of each other, but these, plus the Cluff L. record, add significantly to the known distribution of this sporadically occurring aquatic in the Prairie Provinces.

**Myriophyllum verticillatum** L. var. **pectinatum** Wallr.

Ca. 5 mi. W of Reindeer R. & 5 mi. N of White L., submerged in shallow water of creek shore fen, *Heilman 2490.* To our knowledge, this apparently rare aquatic has been recorded elsewhere in Saskatchewan only from Prince Albert and Yorkton (Breitung, 1957), Candle L. (Jeglum, 1972), Nipawin Prov. Park (*Argus & Hudson 4440*), Melfort (*Millar 65-168*), and SE of Big Beaver (*Ledingham 4986*, USAS). The present collection extends northward of the formerly known range of the species in the southern boreal forest region of the province. However, since the species has been recorded from much of the Mackenzie District, N.W.T. (Porsild & Cody, 1968), our northern Saskatchewan record is hardly surprising. The species should be looked for throughout boreal Saskatchewan. The variety appears well-marked, and we cannot concur with Boivin (1968), who considered it a taxonomic synonym of *M. spicatum* (Watt.) B.S.P. (including *M. exalbescens* Fern.).

## APIACEAE

**Cicuta mackenzieana** Raup.

Cluff L. area: 1.5 mi. N of Island L., open bog pools, *Harms, Skoglund & Wright 24380*. Hidden Bay of Wollaston L., wet sedge shore fen, *Harms 21724 & 22121*. Ca. 4 mi. N of Courtenay L., shallow water off lakeshore, *Ternier & Jasieniuk 1404*. 1.5 mi. S of Bothwell L., aquatic in small lake, *Ternier & Jasieniuk 1786*. S end of Sandy Bay on Churchill R., shallow water off lakeshore, *Harms 23098*. McDonald Cr., NE of Steephill L. on Reindeer R., aquatic and shallow marsh, *Heilman 2415*. W of Reindeer R., 5 mi. N of White L., shore sedge fen bordering creek, *Heilman 2480*. Jaysmith L., boggy lakeshore, *Ternier & Lamont 882*. Meadow L. Prov. Park: SE shore of First Mustus L., shallow water, *Harms 20644;* S shore of Greig L., shallow water edge, *Harms 20373*. We have also revised to this species the following specimens in the Fraser Herbarium: Stony Rapids, *Maini 294;* and Lazy Edward Bay of Cree L. *Maini 148*. This was once thought to be a subarctic species restricted to northernmost Saskatchewan (L. Athabasca, Raup, 1936; Carswell L., Argus, 1964; Hasbala L., Argus, 1966), but recent collections have shown it to extend sporadically nearly throughout the boreal forest region of the province.

## PYROLACEAE

**Chimaphila umbellata** (L.) Bart. [includ. var. *occidentalis* (Rydb.) Blake, & var. *cisatlantica* Blake].

E shore of Pita L. on Churchill R., moist mixed forest, *Heilman 2151*. 4 mi. N of Denare Beach at NE end of Amisk L., rock outcrops of open woodland, *Skoglund 441*. Cluff L. area: Sandy L., mesic white birch-Jack pine forest, *Hudson & Polson 3711*. This species has usually been considered rare in Saskatchewan where it was known only from the S shore of L. Athabasca (Raup, 1936), White Fox, Birch L., and the Cypress Hills (Breitung, 1957). There is also a specimen in the Fraser Herbarium from La Ronge (*Maini 172*). Specimen labels indicate a scarcity of the plants at most Saskatchewan sites. It does not appear meaningful to attempt a varietal separation of material of this species, but if such a distinction was made, Saskatchewan specimens seem nearest to var. *occidentalis* on the basis of its conspicuous leaf venation.

**Pyrola elliptica** Nutt.

Meadow L. Prov. Park: E side of Kimball L., white birch forest, *Harms 20511*. Otter Rapids of Churchill R., black spruce-aspen forest, *Ternier & Jasieniuk 2587*. Reindeer R., midway between The Two Rivers & Steephill L., aspen-white birch forest, *Heilman 1505*. Cluff L., aspen forest, *Harms, Skoglund & Wright 24126*. Previously this species was known in Saskatchewan primarily from the aspen parkland region. The present collections from the Churchill and Reindeer Rivers, plus the recently reported ones from Lac Ile-a-la-Crosse (Harms, 1974), extend its more southern Saskatchewan main range nearly 200 miles northward into the boreal forest region. However, the present Cluff L. collection, together with Raup's (1936) much earlier report from the L. Athabasca region, still indicate a disjunct area in northwestern Saskatchewan that is separated from a southern area by a 200-mile gap.

## MONOTROPACEAE

**Monotropa uniflora** L.

Bervin L., *Ternier & Jasieniuk 1172*. McLennan L., *Ternier & Lamont 1086; Harms 22780*. SW side of Wintego L. of Churchill R., *Heilman 1964*. Pita L. of Churchill R., *Heilman 2152*. W side of Sokatisewin L. of Churchill R., *Heilman 1795*. S end of Sandy Bay of Churchill R., 5 mi. S of Island Falls, *Harms 23190*. Reindeer R. near The Two Rivers, *Heilman 1696*. Meadow L. Prov. Park: land strip between Kimball L. & Raspberry L., *Harms 24696*. At most of the above sites, the plants were scarce in rich mixedwood forests.

This conspicuous saprophyte, which once was considered rare in Saskatchewan, had been reported from L. Athabasca (Raup, 1936), Big River, Emma, Waskesiu and Amisk Lakes (Breitung, 1957). There are also specimens in the Fraser Herbarium from Lac la Ronge (*Argus 182-61; Maini 596*), Candle L. (*Swan 62-285*), and White Gull Creek (*Anderson 1308*). The known records show the species to be quite widespread, though sporadic, in the southern boreal forest of Saskatchewan south of 56° latitude, but with an apparent 200-mile gap separating the southern area from the L. Athabasca locality. This disjunction is probably an artifact due merely to inadequate collecting in northern Saskatchewan, since the species has been recorded from almost throughout the boreal forest zone of the other western Canadian provinces and Mackenzie District, N.W.T. (Boivin, 1966-67; Porsild & Cody, 1968).

## ERICACEAE

**Arctostaphylos alpina** (L.) Spreng. subsp. **rubra** (Rehd. & Wilson) Hult.

Cluff L. area: 1½ miles W of Island L., "boggy" black spruce woods and treed bog, *Harms, Skoglund & Wright 24438*. Pasquia Hills, on sphagnum moss in black spruce woods, *Hudson 2897*. This arctic-subarctic plant was previously known in Saskatchewan only from the N shore of L. Athabasca (Raup, 1936), Hasbala L. in the NE corner of the province (Argus, 1966), and Candle L. (Argus, 1968). The Candle L. and Pasquia Hills records are quite far south in the boreal forest region, therefore suggesting the possible sporadic presence of *A. alpina* elsewhere in the Saskatchewan boreal forest zone. However, this seems another example of the possible distribution pattern referred to under *Anemone parviflora*, — *i.e.* a subarctic element surviving disjunctly in the Candle L.-Pasquia Hills area.

**Ledum palustre** L. ssp. **decumbens** (Ait.) Hult. [*L. decumbens* (Ait.) Lodd.].

Hidden Bay of Wollaston L., treed bogs and moist black spruce forests, *Harms 21563 & 21869*. Cluff L. area: open and treed bogs, *Harms 23784 & 23969; Harms, Skoglund & Wright 24097*. Wheeler R. near Russell L., *Sphagnum* bog, *Godwin, Aug. 1978*. This arctic species has been infrequently collected in Saskatchewan, where it was reported previously from L. Athabasca (Raup, 1936), Reeves L.

(Breitung, 1957), Grove L. and Offset L. (Scotter, 1961), and the Hasbala L. area (Argus, 1966). At some bog sites it was found to be an abundant and codominant low shrub. There are earlier collections filed in the Fraser Herbarium from Stony Rapids (*Maini 549*) and Cree L. (*Maini 31, 41, 217*). Although Breitung (1957) indicated that *L. palustre* occurred only "in the extreme northern part of our area", the present collections extend its range in the province over 100 miles southward. It may be frequent throughout the subarctic transitional lichen-woodland region of Saskatchewan, but also extends somewhat farther southward in favorable bog sites where it occurs with the more abundant *L. groenlandicum* Oeder. In our experience the two species always appear quite well-marked with no obvious evidence of intergradation. Thus, we must disagree with Boivin's (1967b) statement that the "bog phase" (=*L. groenlandicum*) grades northward into the "tundra phase" (=*L. p.* ssp. *decumbens*), and with his conclusion that *L. groenlandicum* should be treated as a variety of *L. palustre.*

**Vaccinium uliginosum** L.

Collins Bay of Wollaston L., common in moist-drier black spruce forests, *Harms 21919.* Above Pow Bay of Wollaston L., common in regenerating black spruce burns, *Harms & Wright 23774.* Hidden Bay of Wollaston L., common on shrub shores, black spruce woods and burns, *Harms 21463, 21550, 21632 & 21800.* Minor Bay of Wollaston L., common in open dry black spruce-lichen woods, *Harms 22265.* 15 mi. S of Geikie R. Crossing, dry burned-over spruce bog, *Ternier & Jasieniuk 1358.* Courtenay L., willow-birch-*Ledum* shrub zones, *Ternier & Jasieniuk 1500.* Peter L., common in wet shrubby area near shores, *Ternier & Jasieniuk 1564.* Wathaman R., uncommon in burned jack pine forest, *Ternier & Jasieniuk 1767.* Cluff L., mesic cut-over black spruce forest, *Hudson & Polson 3689.* Wilson L., in *Carex*-shrub *Betula-Chamaedaphne* fen, *Godwin, Aug. 1978.* A largely sub-arctic species, previously known in Saskatchewan only from the far north, where it was reported at L. Athabasca (Raup, 1936), Offset L. (Scotter, 1961), and Hasbala L. (Argus, 1966), and is also represented in the Fraser Herbarium by collections from Clut L. (*Campbell, July 31, 1935*), Hatchet L. (*Maini 89*), and the Stony Rapids area (*Maini 324, 443, & 524*). Present information indicates that *V. uliginosum* is a common and characteristic species throughout the subarctic transitional lichen-woodland region of northern Saskatchewan and also occurs sporadically somewhat to the south in suitable habitats of the northern boreal forest zone.

## PRIMULACEAE

**Primula mistassinica** Michx.

Cluff L., rare on moist shaded shorelines, *Harms 23856; Harms, Skoglund & Wright 24175.* Carrot R. Prov. Forest, wet open black spruce-tamarack forest, *Hudson 3173.* To our knowledge, this boreal species has been recorded elsewhere in Saskatchewan from only L. Athabasca (Raup, 1936), Amisk L., Prince Albert and Nipawin (Breitung, 1957), and the Hasbala L. area (Argus, 1966). The species is widespread, but sporadic, in its distribution.

## SCROPHULARIACEAE

**Euphrasia subarctica** Raup [*E. arctica* Lange var. *dolosa* Boivin; *E. hudsoniana* Fern. & Wieg.; *E. disjuncta* auct. of Sask. reports].

Pita L. on Churchill R., moist crevices of rock outcrops, *Heilman 2229.* Birch Rapids Portage, N of Leaf Rapids, ca. 38 mi. W of Creighton, rock outcrops, *Skoglund 420.* Buffalo Narrows, wet roadside in town limits, *Delanoy 1.* This apparently rare species in Saskatchewan was first recorded for the province by Raup (1936) from L. Athabasca and Clut L. Only the L. Athabasca locality was listed by Breitung (1957). Boivin (1972) parenthetically listed NW Saskatchewan as the range of this taxon, implying that he had not verified Raup's records. Harms & Hudson (1974) recorded it from La Loche. An earlier collection from Stony Rapids (*Maini 520*) is in the Fraser Herbarium. Our additional records amplify considerably the known localities for this sporadically occurring species and extend southward its known range in the province to Buffalo Narrows and the Leaf Rapids area.

**Pedicularis labradorica** Wirsing.

W side of Pow Bay of Wollaston L., burnt black spruce forest, *Harms & Wright 23775.* W-SW of Hidden Bay of Wollaston L., open dry black spruce forest, *Harms 22144 & 22240; Harms & Wright 23729.* Geikie R., *Ternier & Jasieniuk 2515.* 15 mi. S of Geikie R. Crossing, burnt jack pine forest, *Ternier & Jasieniuk 1381.* This presumably rare species was previously recorded only from northernmost Saskatchewan: McKeever L., (Scotter, 1961) and the Hasbala L. vicinity (Argus, 1966). The present records represent a southward extension of the known range of this lousewort and suggest that it may occur throughout the subarctic transitional lichen-woodland zone of northeastern Saskatchewan.

**Pedicularis parviflora** J. E. Smith. [*P. macrodonta* Richards.].

Hidden Bay of Wollaston L., wet sedge shore fens, *Harms 20967 & 22135*. Collins Creek, near mouth into Collins Bay of Wollaston L., wet sedge shore fen, *Harms 21976*. Ca. 5 mi. S-SW of MacDowall, open tamarack-shrub birch fen, *Hudson 2714*. Previously recorded in Saskatchewan from L. Athabasca (Raup, 1963), McKague, Candle L., and Prince Albert (Breitung, 1957), and also by a specimen in the Fraser Herbarium from Big Sandy L. (tamarack-dwarf birch fen, *Hudson & Argus 4509*). Widespread though sporadic in Saskatchewan and apparently scarce at all known sites.

**Rhinanthus crista-galli** L.

Churchill R., Wintego L., open disturbed area on small island, *Heilman 2049*. Churchill R., Pita L., open disturbed water edge, *Heilman 2092*. S end of Sandy Bay on Churchill R., open area above sandy beach, *Harms 20055; Harms 23117*. Island Falls Dam on Churchill R., partially overgrown trail, 3 Sept. 1975, *Harms 23231B*. Thomson Bay, S side of L. Athabasca, white spruce forest along beach, *Hermesh 442*. Buffalo Narrows, roadside ditch, *Delanoy 4*. The species was reported in Saskatchewan from the Cypress Hills (Breitung, 1954), Ile-a-la-Crosse and Carnduff (Breitung, 1957). However, the Carnduff report is based on a T. N. Willing collection in the Fraser Herbarium with dubious locality data and should be discounted as unverified. The present collections extend the known range of this species in Saskatchewan east to the eastern Churchill R. area and north to L. Athabasca. It is noteworthy that, except for the Cypress Hills and L. Athabasca collections, all Saskatchewan records of the plant are from along the upper or lower Churchill River.

## LENTIBULARIACEAE

**Pinguicula villosa** L.

Geikie R., SW end of Wollaston L., *Ternier & Jasieniuk 2523*. 15 mi. S of Geikie R. Crossing, black spruce treed bog, *Ternier & Jasieniuk 1391*. Courtenay L., moist tamarack-sphagnum bog, *Ternier & Jasieniuk 1533.* David L., wet treed bog, *Ternier & Jasieniuk 1982.* Previously known along the north shore of L. Athabasca (Raup, 1936), Offset L. (Scotter, 1961), and Hasbala L. (DeVries, 1977). The present records represent a 200-mile southward extension of its known range in Saskatchewan. This inconspicuous plant may often have been overlooked by the few collectors in northern Saskatchewan.

**Pinguicula vulgaris** L.

Near Mennon, N of Langham, calcareous bog, *Hudson 2623.* 2 km E of Silver Grove, ca. 24 km S of Shellbrook, mineral spring, *Cameron 552.* Cluff L., moist shorelines, *Harms, Skoglund & Wright 24174.* This was included by Argus & White (1975) on their preliminary list of rare and endangered species in Saskatchewan. It has been recorded from Prince Albert (Breitung, 1957), Strawberry L. S of Indian Head (Jones, 1964), Hasbala L. (Argus, 1966), and Candle L. (Jeglum, 1972). The more northern Saskatchewan localities are not isolated since the species has been recorded from Keewatin and Mackenzie Districts, N.W.T. (Boivin, 1966 67; Porsild & Cody, 1968). It appears to be absent in boreal Saskatchewan between latitudes 54° and 58° N. This butterwort seems widespread but rather sporadic in Saskatchewan. However, the local populations are usually quite large.

**Utricularia cornuta** Michx.

Ca. 13 mi. W of Numabin Bay of Reindeer L., *Ternier & Jasieniuk 2230 (in part).* 7.5 mi. S of Geikie R., *Ternier & Jasieniuk 2404B.* Cluff L., very wet open quaking fen, *Hudson & Polson 3691.* The habitat of the plants was very shallow water of sheltered, marshy or "boggy" shores. The only previous report was from the S shore of L. Athabasca (*Argus 461-62;* Boivin, 1972). This may be a very rare species in Saskatchewan, but is possibly overlooked because vegetatively it is difficult to detect, especially when intermixed with *U. intermedia* Hayne as it was at the above sites.

**Utricularia minor** L.

SW side of Trade L. on Churchill R., creek channel, *Heilman 2597.* Between Davin L. and Wathaman L., aquatic at edge of small lake, *Ternier & Jasieniuk 1788.* An infrequently collected species in Saskatchewan previously reported from L. Athabasca (Raup, 1936), Dahlton and Nipawin (Breitung, 1957), Candle L. (Jeglum, 1972), and from S. of La Loche (Harms, 1974). In the Fraser Herbarium there are also specimens from Nipawin Prov. Park (*Argus 4426*), Arelee (*Hudson 2552*), and Mennon (*Hudson 2622*). Including these new records, it is known from at least 10 scattered localities in the boreal and aspen parkland regions of the province. However, it may often be overlooked by collectors because of infrequent flowering and confusion in the field with depauperate plants of the more common *U. vulgaris* L.

## LOBELIACEAE

**Lobelia dortmanna** L.

Near Steephill L. on Reindeer R., *Heilman 2438*. Reindeer R. between Atik Falls and The Two Rivers, *Polson 95*. Devil Rapids on Reindeer R., *Polson 160*. Geikie R., *Ternier & Jasieniuk 2474*. Wollaston L. area: North L., N of Rabbit L., *Harms 22029; Harms & Wright 23665*. Cluff L. area: Germaine L. & Snake L., *Harms Skoglund & Wright 24084 & 24566*. This largely submersed to sometimes emergent aquatic plant occurred at 0.5–8 dm water depths off quiet wave-sheltered shores. It was previously considered rare in Saskatchewan, being known only from Windrum L. (Breitung, 1957), Little Gull L. S. of L. Athabasca and Carswell L. (Argus, 1964), Methy Portage (Boivin, 1972), and Little Amyot L. SW of Lac Ile-a-la-Crosse (Harms & Hudson, 1974). The present collections increase considerably the number of recorded stations in Saskatchewan, and expand its known range across the boreal forest belt in eastern Saskatchewan.

**Lobelia kalmii** L. [*L. strictiflora* (Rydb.) Lunell].

Cluff L. area: Snake L., moist mossy open shore, *Harms, Skoglund & Wright 24289*. We are not aware of any previous records for this species in boreal Saskatchewan from north of Prince Albert Nat'l. Park, Candle L., and Big Sandy L. Thus, the present collection appears to represent a 250-mile northward extension of the Saskatchewan range and the first record from the northern half of the province. However, the reported occurrence of the species in the Mackenzie District (Boivin, 1966–67; Porsild & Cody, 1968; Cody, 1978) makes our Cluff Lake area collection expected. The present record is near the midpoint of the 500-mile gap reported by Cody (1978) between the northern and southern areas of this species. The species should be looked for at least throughout western boreal Saskatchewan.

## ASTERACEAE

**Anaphalis margaritacea** (L.) Benth. & Hook.

Cluff L.: Sandy L., scarce on beach & roadside, *Abouguendia 29-7-78; Polson, et al. 13-6-78.* Now known from the Cypress Hills (Breitung, 1954 & 1957), and very rare at three other widely spaced localities in westernmost Saskatchewan: Cutknife (Breitung, 1957; but in SCS not SASK); Buffalo Narrows (Harms & Hudson, 1974), and the Cluff L. area.

**Antennaria neodioica** Greene [*A. neglecta* Greene var. *attenuata* (Fern.) Cronq.].

Devil L., Churchill R., uncommon on rock outcrops above lake, *Ternier & Jasieniuk 2630.* Previously reported in the province only from the Cypress Hills (Breitung, 1957). The present record represents an over 400-mile northeastward range extension within Saskatchewan. The species has been recorded from Wekusko L. and Riding Mtn., as well as various other Manitoba localities, and also from Alberta. In addition, we have tentatively revised to this taxon a vegetative specimen from south of Big Muddy L. (*Morrison 68-493*), but better verification is needed for the latter.

**Arnica lonchophylla** Greene var. **lonchophylla.**

Ca. 1 mi. SW of Hidden Bay of Wollaston L., open black spruce woods and roadside, *Harms 22233.* Cluff L. area: 1½ mi. W of Island L., occasional on semi-open aspen-wooded and open dolomitic ridges and cliffs, *Harms 23889A&B; Harms, Skoglund & Wright 24418.* To our knowledge, this primarily subarctic plant is known elsewhere in Saskatchewan only from three widely separated localities: the N shore of L. Athabasca, Amisk L. (Breitung, 1957), and Hasbala L. (Argus, 1966). A depauperate specimen from Candle L. (*Anderson 1157*) has also been tentatively revised by us to this species, but the latter locality record requires better verification. Some of our northern Saskatchewan specimens morphologically approach the arctic *A. alpina* (L.) Olin ssp. *attenuata* (Greene) Maguire, which has been reported from the N shore of L. Athabasca (Raup, 1936) and Hasbala L. (DeVries, 1977).

**Bidens beckii** Torr. [*Megalodonta beckii* (Torr.) Greene].

Ca. 3 mi. W-SW of Missinipe, aquatic in pond in small tributary of Otter L., *Harms 22734.* This represents the third locality for this apparently rare species in Saskatchewan. It was previously reported in the province from the Cumberland L. area (Breitung, 1957; Boivin, 1972) and from Little Amyot L. (Harms & Hudson, 1974). The three Saskatchewan localities are widely spaced across the southern boreal forest belt.

**Erigeron elatus** (Hook.) Greene [*E. acris* L. var. *elatus* (Hook.) Cronq.].

Ca. 5 mi. S-SW of MacDowall, wet boggy black spruce woods, *Harms 22853*. Meadow L. Prov. Park: S side of Greig L., disturbed aspen-bordered gravel pit, *Harms 20381*. "Height of Land", 28 mi. S of Meadow Lake, moist grassy open edge of spruce forest, *Hudson 3410*. Raup (1936) first reported this species from Saskatchewan (N shore of L. Athabasca, as *E. acris* var. *arcuans* Fern.). However, the species was not included for the province by Fraser & Russell (1937 & 1953) or Breitung (1957). Boivin (1972) listed Saskatchewan only parenthetically indicating that reports were unverified by him. Jeglum (1972) reported the species from Candle L. Harms (1974) recorded it from Taylor L. It represents an infrequently collected if not a rare species with the known stations being widely spaced. Probably the species has been much overlooked in the field because of its general similarity to the more common *E. acris* var. *asteroides* (Andrz.) DC.

**Erigeron glabellus** Nutt.

Cluff L. area: 1.5 mi. W of Island L., open dolomite cliff summit and ridges, *Harms, Skoglund & Wright 24423B*. This record, and a collection from a similar habitat at Carswell L. (Argus, 1964), suggests a disjunct area of occurrence in northwestern Saskatchewan that is separated by a gap of nearly 250 miles from the main range of the species farther south in the province, where it is quite frequent in the grassland, aspen parkland, and southern boreal forest regions. The above statement is based on a restudy of available herbarium specimens, discounting literature reports, since there has been confusion between this species and *E. asper* Nutt.

**Erigeron hyssopifolius** Michx.

Cluff L. area, moist jack pine-black spruce forest on dolomitic outcrops, *Abouguendia, 7-8-78*. Swift Creek of Lightning Bolt, E of Macoun L., wet tamarack bog, *Ternier & Jasieniuk 2020*. Gull Creek Crossing of Hwy. 120, near Gull L., 15 mi. NE of Candle L., black spruce muskeg, *Anderson 1049*. Carrot R. Prov. Forest: N of

Carrot R., open black spruce-tamarack fen forest over limy till, *Hudson 3168*. This rare species has been reported elsewhere in the province from only Amisk L. (Breitung, 1957), Hasbala L. (Argus, 1966), and Carswell L. (Argus, 1964). The cited collections double the known Saskatchewan stations for the species and help somewhat to narrow the gaps in its distribution.

**Gnaphalium uliginosum** L.

S end of Sandy Bay of Churchill R., 5 mi. S of Island Falls, dirt trail in aspen woods, *Harms 23346*. SW side of Candle L., mineral soil of road depression, *Anderson 1433*. Near Court, W of Kerrobert (SW ¼ Sect. 26, T34 N, R28 W 3rd M), disturbed mud of slough, *Hudson 3235*. This introduced species is known from only a few scattered localities in Saskatchewan, including Loon Lake (Breitung, 1957), Saskatoon, Rosetown and Paradise Hill (Boivin, 1972). Although it is similar to the native *G. palustre* Nutt., our material would appear well enough marked.

**Senecio streptanthifolius** Greene [*S. cymbalarioides* Nutt. var. *borealis* (Torr. & Gray) Greenm.].

Cluff L. area: 1.5 mi. W of Island L., open dolomite outcrops and cliff, *Harms, Skoglund & Wright 24416 & 24437*. ¼ mi. N of Cluff L., open disturbed areas over metamorphic bedrock, *Harms 23803; Harms, Skoglund & Wright 24372B*. The Cluff L. area represents the third general Saskatchewan locality known for this rare subarctic and alpine plant. It was earlier reported in the province from northwestern Saskatchewan at calcareous sites on the N shore of L. Athabasca (Raup, 1936) and Carswell L. (Argus, 1964).

**Solidago multiradiata** Ait.

Cluff L. area: 1.5 mi. W of Island L., dolomite outcrops of pine-wooded ridge, *Harms, Skoglund & Wright 24468*. White Gull L. area, 2 mi. SW of White Gull Cr. Bridge, rare in cleared jack pine-black spruce stand, *Anderson 1262*. This predominantly arctic-subarctic and subalpine species was previously reported in Saskatchewan only from widely separated stations at Ile-a-la-Crosse and Waskesiu L. (Breitung, 1957). Raup (1936) recorded it from the lower Athabasca R. in NE Alberta. More recently, Harms (1974) reported it from Lac la Plonge, La Loche, and several localities N of Buffalo Narrows. The present collection from the Cluff L. area represents the northernmost record for the species in Saskatchewan, and apparently is the only one to date on the Precambrian Shield in this province.

**Other species:** Various additional vascular plant species, which in the past had been only infrequently collected and often presumed to be rare or at least relatively uncommon in the province, have recently been found to be much more frequent in boreal Saskatchewan than once believed. Although the individual collections upon which their new status is based are far too numerous to cite here, these taxa at least deserve a brief listing as follows: *Carex adusta* Boott., *Cypripedium acaule* Ait., *Juncus brevicaudatus* (Engelm.) Fern., *J. filiformis* L., *Lycopus uniflorus* Michx., *Oxycoccus quadripetalus* Gilib., *Poa interior* Rydb., *Polygonum cilinode* Michx., *Pyrola minor* L., *Scirpus microcarpus* Presl., *Sparganium angustifolium* Michx., *S. chlorocarpum* Rydb., *S. minimum* (Hartm.) Fries, *Viola palustris* L. and *V. renifolia* A. Gray.

## LITERATURE CITED

Anderson, H. K. 1976. Vegetation and Land Forms in the Candle Lake, Saskatchewan, Area. Ph.D. Thesis, University of Saskatchewan, Saskatoon.

Argus, G. W. 1964. Plant collections from Carswell Lake and Beartooth Island, northwestern Saskatchewan, Canada. The Canad. Field-Naturalist, **78:** 139 149.

______. 1966. Botanical investigations in northeastern Saskatchewan: The subarctic Patterson-Hasbala Lakes region. The Canad. Field-Naturalist, **80:** 119 143.

____. 1968. Contributions to the flora of boreal Saskatchewan. Rhodora, **70:** 200 214.

______, & D. White. 1975. A preliminary list of the rare plants of Saskatchewan. National Museums of Canada, Ottawa. 14 pp.

Boivin, B. 1966 1967. Enumeration des Plantes du Canada, I VI. Naturaliste Canadien, **93 & 94.** Reprinted as Provancheria, No. **6,** Mém. de l'Herbier Louis-Marie, Univ. Laval, Qué.

______. 1967b. Flora of the Prairie Provinces, Part I Pteroids, Ferns, Conifers and Woody Dicopsids. (Reprinted from Phytologia, **15 & 16**). 202 pp.

______. 1968. Flora of the Prairie Provinces, Part II Digitatae, Dimerae, Liberae. (Reprinted from Phytologia, **16–18**). 185 pp.

______. 1972. Flora of the Prairie Provinces, Part III Connatae. (Reprinted from Phytologia, **22 & 23**). 224 pp.

Breitung, A. J. 1954. A botanical survey of the Cypress Hills. The Canad. Field-Naturalist, **68:** 55 92.

____. 1957. Annotated catalogue of the vascular flora of Saskatchewan. The Amer. Mid. Naturalist, **58:** 1 72.

______. 1959. Supplement to "Flora of Saskatchewan". The Amer. Mid. Naturalist, **61:** 510 512.

CALDWELL, B. 1960. A new pondweed for Saskatchewan, *Potamogeton robbinsii*. The Blue Jay **18:** 129.

CODY, W. J. 1978. Range extensions and comments on the vascular flora of the continental Northwest Territories. The Canad. Field-Naturalist, **92:** 144-150.

DEVRIES, B. 1977. Further notes on the vascular flora of the Hasbala Lake region, Saskatchewan. The Blue Jay, **35:** 74-76.

DIRSCHL, H. J. & R. T. COUPLAND. 1972. Vegetation patterns and site relationships in the Saskatchewan River delta. The Canad. J. Bot., **50:** 647-675.

ERSKINE, A. J. 1974. Off into the wet green yonder: birds and plants of a boreal bog. The Blue Jay, **32:** 33-37.

FRASER, W. P. & R. C. RUSSELL. 1944. An Annotated List of the Plants of Saskatchewan. University of Saskatchewan, Saskatoon, Sask. 64 pp.

———. 1953. An Annotated List of the Plants of Saskatchewan. University of Saskatchewan, Saskatoon, Sask. (Rev. by R. C. RUSSELL, G. F. LEDINGHAM & R. T. COUPLAND). 55 pp.

HARMS, V. L. 1974. Botanical studies in the boreal forest along the Green Lake-La Loche Road, northwestern Saskatchewan. The Musk-Ox **14:** 37-54.

———. 1977a. Wildlife and Vegetation Survey at Gulf Minerals Uranium Operation at Wollaston Lake. III. Vegetation Survey. Saskatchewan Research Council, Report **C76-2.** Saskatoon, June, 1977. 182 pp. and infold map.

———. 1977b. Review of the Vegetation Assessment of the Proposed Cluff Lake Uranium Mining Operations. Part 2 — A Baseline Survey of the Flora and Vegetation of the Cluff Lake Area. The Cluff Lake Board of Inquiry and Saskatchewan Department of the Environment. Regina, October, 1977. 151 pp and infold map.

———. 1978. Additional records for some rare or uncommon native orchids in Saskatchewan. The Blue Jay, **36:** 130-136.

———, & J. H. HUDSON. 1974. Some new and noteworthy vascular plant records from northwestern Saskatchewan. Rhodora, **76:** 39-44.

———, & ———. 1978. Some vascular plants new to the flora of Saskatchewan. The Canad. Field-Naturalist, **92:** 389-391.

HEILMAN-TERNIER, J., & V. L. HARMS. 1975. Plant Ecology-Taxonomy, Final Report **5.** Churchill River Study (Missinipe Probe). Gov't. of Saskatchewan, Saskatoon, Saskatchewan. 126 pp.

HERMESH, R. 1972. A Study of the Ecology of the Athabasca Sand Dunes with Emphasis on the Phytogenic Aspects of Dune Formation. M.Sc. Thesis, University of Saskatchewan, Saskatoon. 158 pp.

HOOKER, W. J. 1829-1840. Flora Boreali-Americana. London. Vol. I - 351 pp. Vol. II - 328 pp.

HUDSON, J. H. 1971. Of *Eragrostis* and range extensions; 1970 botanical remarks. The Blue Jay, **29:** 96-98.

———. 1974. Plant records for Saskatchewan — 1973 version — starring Porcupine Mountain. The Blue Jay, **32:** 210-214.

———. 1976. 1974 plant records from Saskatchewan: rediscoveries, discoveries and other curiosities. The Blue Jay, **34:** 9-13.

———. 1977. *Carex* in Saskatchewan. Bison Press, Saskatoon, Sask. 193 pp.

HULTÉN, E. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford, California. 1008 pp.

JEGLUM, J. K. 1972. Boreal forest wetlands near Candle Lake, Central Saskatchewan. I. Vegetation. The Musk-Ox, **11:** 41 58.

JONES, G. J. 1964. *Pinguicula vulgaris* in southern Saskatchewan. The Blue Jay, **22:** 117 118.

KUJI, E. 1959. New record of small white water-lily. The Blue Jay, **17:** 162.

LOOMAN, J. 1973. Some new and interesting plant records for the prairie provinces. The Blue Jay, **31:** 176 179.

MACOUN, J. 1890. Catalogue of Canadian Plants, Part V Acrogens. Wm. Foster Brown & Co., Montreal, pp. 249 398.

MORRISON, H. 1969. A preliminary botanical survey of the Big Muddy Valley in southern Saskatchewan, 1968. The Blue Jay, **27:** 42 53.

MOSS, E. H. 1959. Flora of Alberta. University of Toronto Press, Toronto, Ontario. 546 pp.

NEWSOME, R. D. & R. L. DIX. 1968. The forests of the Cypress Hills, Alberta and Saskatchewan, Canada. The Amer. Midl. Naturalist, **80:** 119 185.

PACKER, J. G. & M. G. DUMAIS. 1972. Additions to the flora of Alberta. The Canad. Field-Naturalist, **86:** 269 274.

PORSILD, A. E. & W. J. CODY. 1968. Checklist of the Vascular Plants of Continental Northwest Territories, Canada. Canada Dept. of Agriculture, Ottawa, Ontario. 101 pp.

RAUP, H. M. 1936. Phytogeographical studies in the Athabasca-Great Slave Lake region. I. Catalogue of the Vascular Plants. Journal Arnold Arbor. **17:** 180 315.

SCOGGAN, H. J. 1957. Flora of Manitoba. National Museum Canada Bulletin **140,** Ottawa. 619 pp.

SCOTTER, G. W. 1961. Botanical collections in the Black Lake region in northern Saskatchewan (1960). The Blue Jay, **19:** 28 33.

___. 1964. Effects of forest fires on the winter range of Barren-Ground Caribou in northern Saskatchewan. Canadian Wildlife Service, Wildlife Management Bulletin, Ser. 1, No. **18.**

SWAN, J. M. A. & R. L. DIX. 1966. The phytosociological structure of upland forest at Candle Lake, Saskatchewan. J. Ecol. **54:** 13 40.

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# INTROGRESSION IN CANADIAN POPULATIONS OF *LYCOPUS AMERICANUS* MUHL. AND *L. EUROPAEUS* L. (LABIATAE)

J. M. WEBBER AND P. W. BALL

The genus *Lycopus* was the subject of an extensive taxonomic monograph by Henderson (1962). He recognized fourteen species, of which eight are native to North America. A ninth species, *L. europaeus* L., is naturalized in eastern North America and is now well established in a number of localities. A detailed account of the distributional history of this species was given by Stuckey and Phillips (1970), who concluded that the species is established on the eastern coast of the United States and is probably actively spreading through the Great Lakes region.

This investigation was initiated in 1971 when the second author examined a population of *Lycopus* occurring on the shore of Lake Ontario at Rattray Marsh, about 30 km west of Toronto. Although apparently consisting of only a single species, *L. europaeus,* this population showed variation in some diagnostic characters which extended beyond the range limits previously recorded for this species (Fernald, 1950; Gleason, 1952; Henderson, 1962; Ball, 1972).

A more detailed investigation was carried out by the first author in 1973 and was further expanded in 1974. At an early stage of the investigation it became apparent that the descriptions and key given by Henderson (1962) did not afford a satisfactory means of distinguishing between *Lycopus europaeus* and *L. americanus* Muhl. It was therefore necessary to make a critical reassessment of the features that can be utilized to separate these two species before any conclusions could be reached regarding the Canadian material of *L. europaeus.*

Ruttle (1932) published chromosome counts of $2n = 22$ for specimens of *Lycopus europaeus* (from Buckow, Germany) and *L. americanus* (from Kashong Glen, near Geneva, New York, U.S.A.). Several more counts for European specimens of *L. europaeus* have supported Ruttle's report (Tischler, 1934; Rohweder, 1937; Ehrenberg, 1945; Gadella and Kliphuis, 1963; Hindakova and Cincura, 1967).

## MATERIALS AND METHODS

Samples of 66 specimens of *Lycopus americanus* and 53 specimens of *L. europaeus* were examined from the following herbaria (abbreviations according to Holmgren & Keuken, 1974): BM, DAO, HAM, RNG, TRT, and TRTE. The sample of *L. americanus* included specimens collected from localities where *L. europaeus* did not occur. The sample of *L. europaeus* included only European collections. The specimens were selected to cover, as far as possible, both geographical and morphological variation. Taxonomic characters and the range of variation of discriminating characters were evaluated from these two samples.

Mass collections were made from the following Canadian mixed populations of *Lycopus americanus* and *L. europaeus*: Toronto Island, York Co., Ont. (25 specimens); Rattray Marsh, Peel Co., Ont. (39 specimens); Levis, Levis Co., Que. (23 specimens); Portneuf, Portneuf Co., Que. (13 specimens); and Berthierville, Berthier Co., Que. (10 specimens). Measurements of the useful taxonomic characters, as determined from the herbarium material of *L. americanus* and of European *L. europaeus,* were recorded for the specimens from the five Canadian populations. The data were subjected to a principal components analysis. Pictorial scatter diagrams were also constructed. Specimen citations and the original data have been sent to the National Research Council of Canada, Ottawa.

In addition, smaller samples were collected from populations at the following Ontario localities: along the Grand River at Galt, Waterloo Co.; Oakville, Halton Co.; Etobicoke, York Co.; and High Park, York Co. As these samples each consisted of fewer than 10 individuals, the data from these populations was not analyzed by the methods mentioned above.

Live specimens of *Lycopus europaeus* were grown from seed obtained through seed exchange with the following European Botanic Gardens: *Austria*, Botanischer Garten und Arboretum der Stadt Lizt Danau; *France*, Jardin Botanique, Rouen; *Germany*, Gottingen, Jena, Friedrich Schiller Universitat; Munchen-Nymphenberg Botanischer Garden; *Switzerland*, Geneve, Conservatoire et Jardin Botanique. Specimens of *L. americanus* were transplanted or grown from seed gathered at localities where *L. europaeus* had not been reported. Live specimens of *Lycopus* from the Canadian mixed populations were transplanted or grown from seed. The live specimens were used to compare pollen viability and

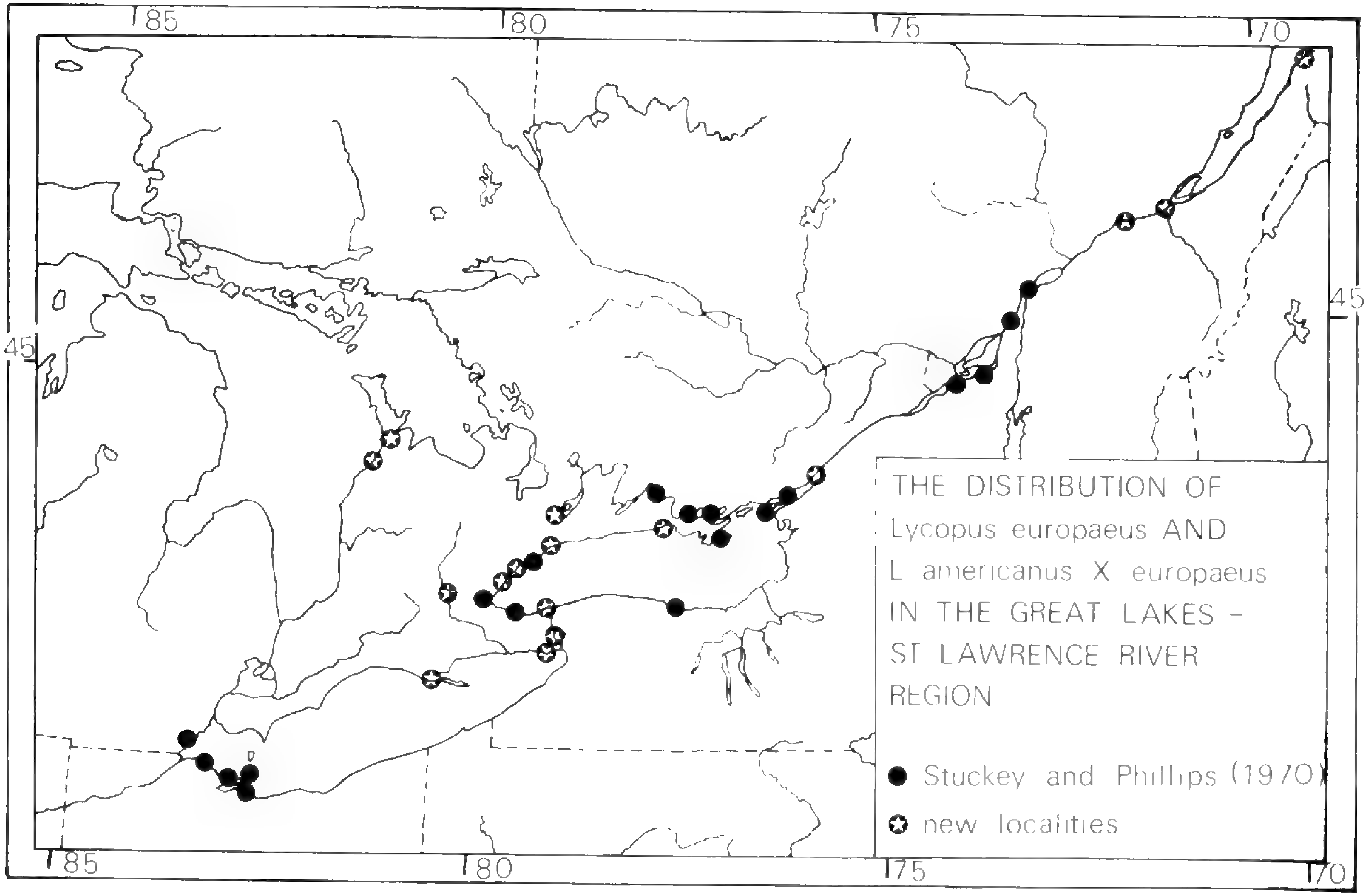


Figure 1. The distribution of *Lycopus europaeus* and *L. americanus* × *europaeus* hybrids in the Great Lakes–St. Lawrence region.

characters which proved to be difficult to observe satisfactorily on dried plant material. A few specimens were examined cytologically.

Slides of root tip and anther preparations were made according to the methods outlined by Radford *et al.* (1974; pp. 251–257). Chromosome counts for specimens of *Lycopus americanus* and *L. europaeus* were determined. Voucher specimens were deposited in the Erindale College Herbarium (TRTE).

## TAXONOMIC CHARACTERS

A general review of the taxonomic characters of *Lycopus* was given by Henderson (1962). It is not intended to repeat this review but to consider in some detail the characters which distinguish *L. americanus* from *L. europaeus*. The observations made in this section were based on European specimens of *L. europaeus* and specimens of *L. americanus* collected from localities in which *L. europaeus* had not been recorded in North America.

1) **Stem habit.** Henderson (1962) defined a stolon as an underground, horizontal stem and a runner as an overground, horizontal stem. *Lycopus americanus* was said by Henderson to possess stolons. *L. europaeus* was said to have runners. Moreover, Henderson (1962) used this as an important character in his key to species. However, he stated (p. 103) that *L. americanus* may produce stolons at the first or second node which then grow downward, entering the soil at the base of the plant. In such instances the stolons of *L. americanus* are not strictly underground.

In practice, the type of horizontal stem produced is a difficult character to utilize. As many herbarium specimens are collected without the base, evaluation of this character is often impossible on herbarium material. In addition, observations of plants in the field and in cultivation suggest that horizontal stems are often not present. Both species may produce stolons and runners, although the latter were not commonly seen on specimens of *Lycopus americanus*. Furthermore, the runners of *L. europaeus* are not always strictly overground. In some instances the type of stem produced may be explained by movement of an unstable substrate.

2) **Stem Angles.** In his key to species, Henderson (1962, p. 105) included *L. americanus* with species having stems ". . . acutely 4-angled", whereas he included *L. europaeus* with species having

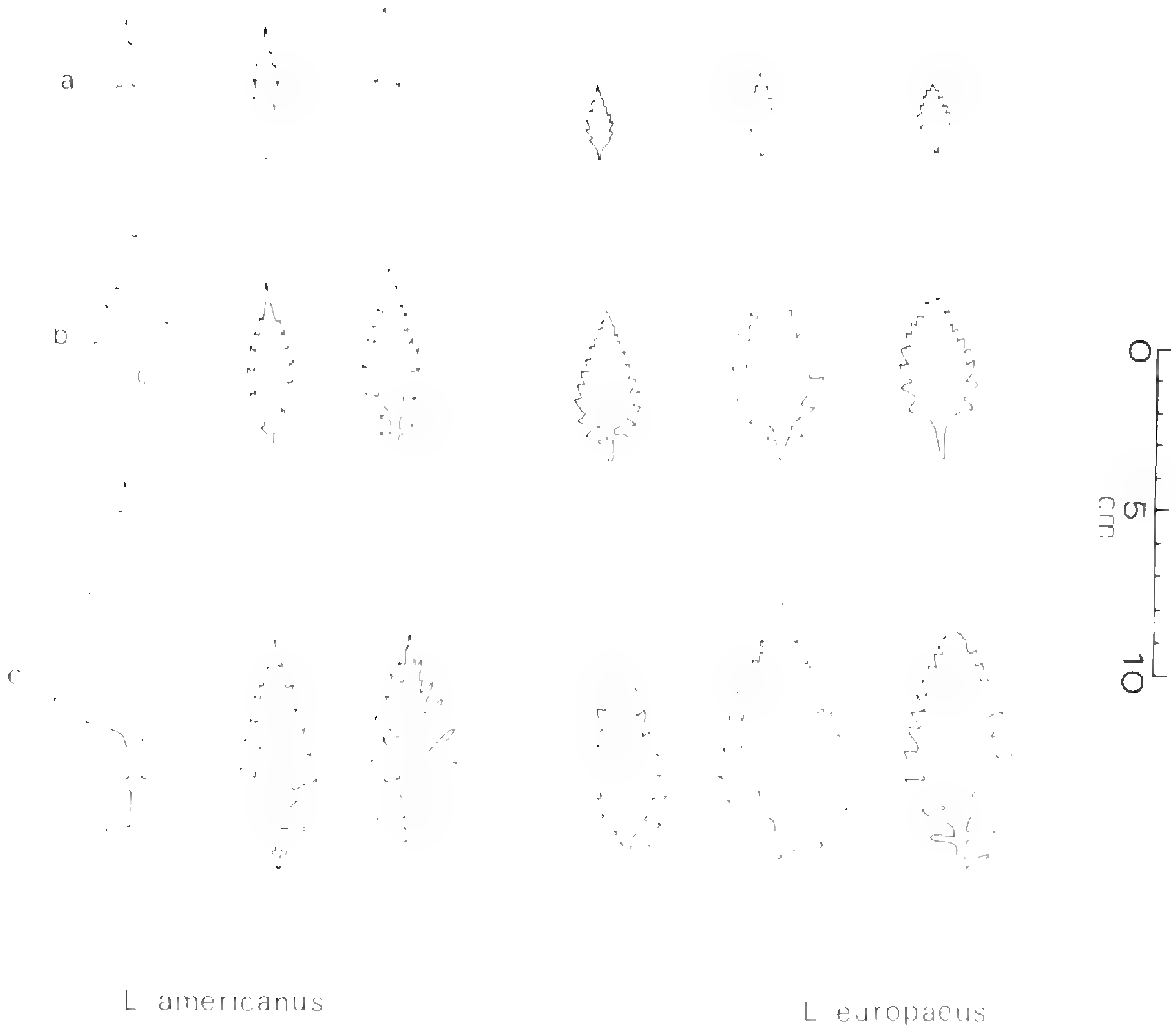


Figure 2. The shape of upper (a), middle (b), and lower (c) leaves of *Lycopus americanus* and *L. europaeus*.

stems ". . . obtusely 4-angled or rounded angles, not ridged or winged." This separation is contradicted by his description of *L. americanus,* in which he claimed that the stem angles of this species are ". . . rounded or with a prominent ridge." (p. 113).

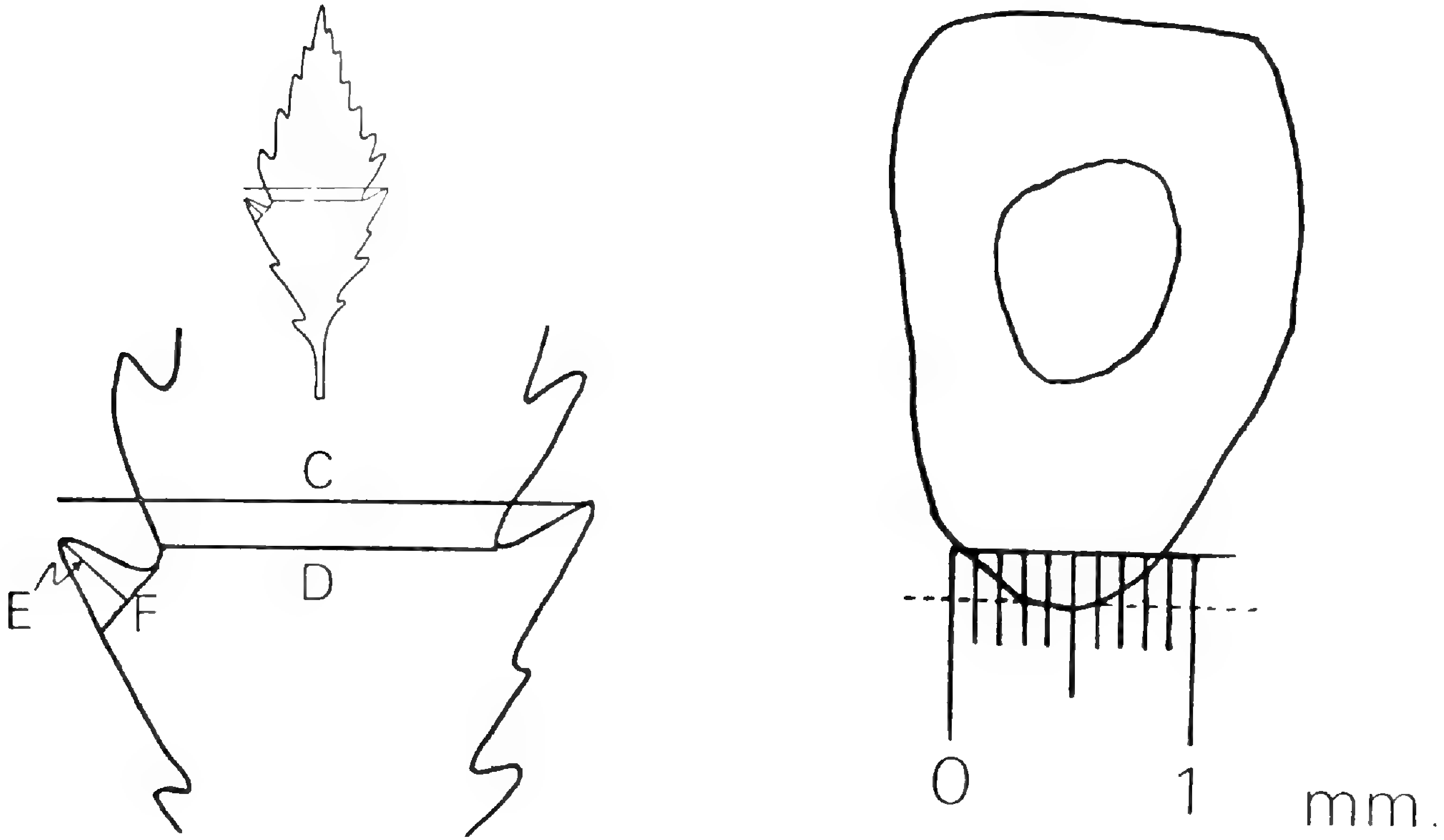
The shape of the stem angles is a difficult character to observe on dried, pressed specimens. Sections of living stems were cut from the internode below the lowest verticil. No difference in stem shape between the two species was observed. Both developed small ridges on the rounded corners of the stem to varying degrees. With increase in size, the stems lost their square shape, and rounded corners and ridges became more pronounced.

3) **Leaves.** The leaves of *Lycopus* are extremely variable. Both species have deeply lobed lower leaves and shallowly toothed upper leaves (Fig. 2). Despite this variation, the leaves do afford useful characters.

A difference in leaf shape between the species was implied by previous authors; however, these differences were not always based on comparable material. Fernald (1950) described the "lower primary leaves" of *Lycopus americanus* as ". . . lanceolate, narrowly ovate or oval . . ." and the "leaves" of *L. europaeus* as ". . . broadly lanceolate to narrowly ovate . . .". Gleason (1952) described the "leaves" of *L. americanus* as ". . . lanceolate or narrowly oblong . . ." and the "principal leaves" of *L. europaeus* as ". . . ovate or ovate-oblong . . .". Henderson (1962) described the "leaves" of *L. americanus* as ". . . linear to ovate-lanceolate . . ." and those of *L. europaeus* as ". . . ovate, ovate-lanceolate or narrowly lanceolate . . .".

In this study, leaves at the node below the lowermost verticil on the main stem were utilized. No significant differences in the leaf length or the distance from the base to the widest part of the leaf were found. The leaves of *Lycopus europaeus* were found to be significantly wider than those of *L. americanus.* However, there was considerable overlap in the ratio of leaf width divided by leaf length (Fig. 5a).

Subtle differences in the shape of the leaf teeth and the degree of lobing of the leaves were observed (Fig. 2). These characters were measured at the widest part of the leaf as shown in Fig. 3. The leaf teeth of *Lycopus europaeus* were observed to be wider and more blunt than those of *L. americanus.* This difference was quantified by the ratio EF (tooth length divided by tooth width). A histogram of



Figures 3 & 4.

**3** (Left) Location of leaf measurements used in this study: **C** maximum leaf width at widest point of the leaf, **D** minimum leaf width at widest point of the leaf, **E** leaf tooth length and, **F** leaf tooth width.

**4** (Right) Position of scale used to measure the width of the nutlet base and distance between the ends of the nutlet 'collar' (when present). The scale was positioned in such a way that the bottom of the nutlet was at the midpoint of the 0.1 mm division lines of the scale (here indicated by the dotted line). The width of the base of the nutlet was therefore measured about 1/4 mm above the actual base.

this character (Fig. 5b) shows that tooth shape afforded a good, but not complete, separation of the two species.

The leaves of *Lycopus americanus* were observed to be more deeply lobed than those of *L. europaeus*. The ratio CD (width of the leaf at the widest point of the leaf divided by the width between the lobes) was used to compare the degree of lobing, or division, of the leaves. As shown by the histogram (Fig. 5c), this character afforded some separation of the two species.

In his description of the species, Henderson (1962) noted that the leaf surface of *Lycopus americanus* is glandular-punctate whereas that of *L. europaeus* is closely glandular-punctate. No difference in the degree of this condition was observed in this study.

Another character which is difficult to observe on dried material is the leaf texture. Leaves of live *Lycopus europaeus* are rugose; those of *L. americanus* are smooth. As insufficient live material was examined, this character was not used in this study.

4) **Indumentum.** Little attention has been given to indumentum differences between these two species. Both species are variable in the density of the indumentum, but *Lycopus americanus* is most frequently sparsely hairy, whereas *L. europaeus* is often densely hairy. Both species may be nearly glabrous.

The full range of variation found in *Lycopus europaeus* does not appear to be present in Canada. Nothing resembling the very densely hairy plants described as *L. europaeus* subsp. *mollis* (Ball, 1972) has been found in this investigation. We therefore disagree with Fernald (1950), who claimed that this plant (which he called a variety) was present in the United States and southern Ontario. As *L. europaeus* subsp. *mollis* is restricted to the southeastern part of the range of the species, the populations found in Canada are most likely to have originated from northern or western Europe.

The substantial variation in density of indumentum found in both species has tended to obscure a difference in the nature of the hairs. Fernald (1950) possibly hinted at the difference when he described the upper surface of the lower and median primary leaves of *Lycopus europaeus* as strigose and the lower surface as slightly pubescent to glabrescent whereas the lower primary leaves of *L. americanus* were said to be glabrous or minutely pubescent on the veins beneath.

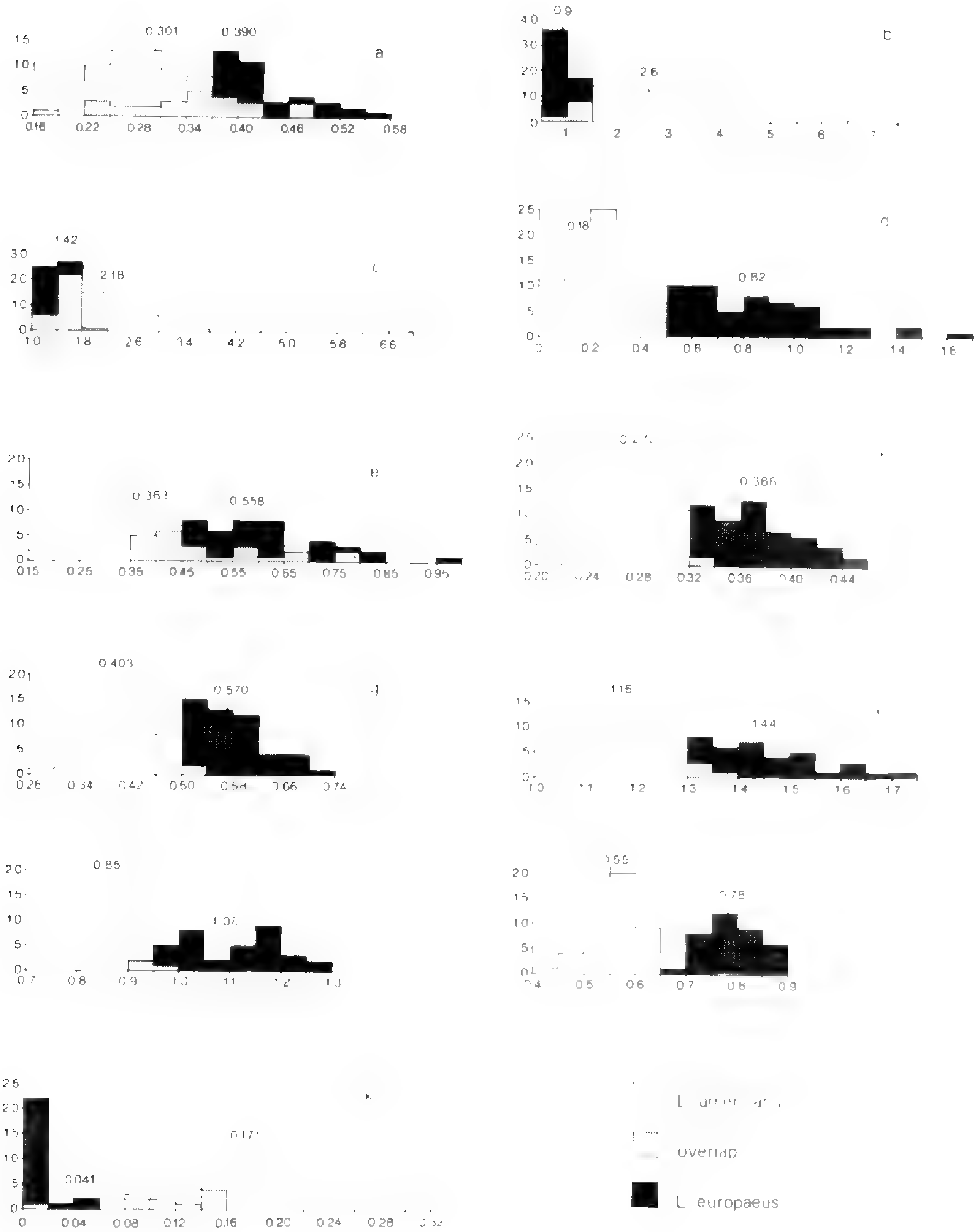


Figure 5. Histograms of characters in which *L. americanus* and European *L. europaeus* were found to differ: (a) ratio C:A — leaf width C, divided by leaf length A; (b) ratio E:F — leaf tooth length E, divided by leaf tooth width F; (c) ratio C:D maximum leaf width C, divided by minimum leaf width D; (d) hair length in mm, (e) bracteole length in cm, (f) calyx length in cm, (g) anther length in mm, (h) nutlet length in mm, (i) nutlet width in mm, (j) width of nutlet base in mm, (k) distance between ends of nutlet collar in mm.

The difference that has been observed in this study is in the length of the hairs on the lower surface of the leaf below the lowest verticil. Measurements of hair length afforded a complete separation of the species (Fig. 5d). The hairs of *L. americanus* were 0.01–0.50 mm long whereas those of *L. europaeus* were 0.50–1.60 mm long.

5) **Bracteole Length.** The structures referred to here as bracteoles are identical with the 'inflorescence bracts' of Henderson (1962) and the 'bracts' of Gleason (1952) and Fernald (1950). The term bracteole is used here to avoid confusion with the leaves subtending the verticils, which are also sometimes referred to as bracts. Henderson (1962) reported the bracteoles of *Lycopus americanus* to be ". . . up to 3 mm long . . . at least as long as the calyx lobes of the outermost flowers . . ." and those of *L. europaeus* to be ". . . 3–5 mm long . . . slightly shorter than the calyx lobes of the outermost flowers . . .". Gleason (1952) stated that the bracteoles of *L. americanus* are ". . . about equaling the calyx . . .", whereas those of *L. europaeus* are ". . . much like *L. americanus* . . .". Fernald (1950) mentioned only that the bracteoles of *L. americanus* are "short".

In this investigation, considerable difficulty was experienced in obtaining strictly comparable material. The bracteoles were found to vary substantially, even in the same verticil. The longest bracteole of the lowest verticil was measured. Often the bracteoles are deciduous in older individuals. In such instances the longest bracteole at a higher node was measured. The mean bracteole length of *Lycopus americanus* was 3.6 mm, whereas the mean bracteole length of *L. europaeus* was 5.6 mm. Although these means are statistically different, there is considerable overlap in the measurements (Fig. 5e).

6) **Calyx and Calyx Lobe Length.** Henderson (1962) described the calyx of *Lycopus americanus* as ". . . reaching to the sinuses of the corolla . . ." and the calyx of *L. europaeus* as ". . . 2.8–3.2 mm long, almost as long as the corolla tube . . .". Henderson's (1962) failure to state the calyx or calyx lobe length for *L. americanus* is surprising, as Gleason (1952) used the length of the calyx lobes as a key character to separate the two species.

Some problems exist in utilizing this lobe length character because of the zygomorphic structure of the calyx. To avoid this problem, the overall length of the calyx, from the base to the tip of the longest lobe, was measured. Calyx measurements were taken from the lowermost verticil of the main stem. As the calyx was observed to expand as the nutlets mature, calyces containing mature or only slightly immature nutlets were measured.

A significant difference in calyx length was found between the two species with only a minimum of overlap (Fig. 5f). The calyces of *Lycopus americanus* were found to be 0.20–0.33 cm long; those of *L. europaeus* were 0.30–0.45 cm long. The greater lengths of the calyces of *L. europaeus* are, in part, due to the comparatively longer subulate tips of the calyx lobes.

7) **Corolla.** Henderson (1962) stated that the corolla tube of *Lycopus americanus* expanded ". . . abruptly into a campanulate throat . . ." whereas that of *L. europaeus* expanded "gradually". A problem with this character arises from the tendency of the species to produce small female flowers later in the season, the corolla tubes of which expand very slightly, as well as perfect flowers which are usually produced early in the season. Only perfect flowers were compared in this study. Although a tendency of the corolla tubes of *L. americanus* to expand more abruptly than those of *L. europaeus* was observed, much overlap was found.

The corollas of both species are strikingly similar. No differences in corolla tube length, shape of the corolla lobes and pattern of purple dots at the mouth were found.

8) **Anthers.** No previously published data on the anther length of these two species has been traced. Examination of live material showed that there was a difference in anther length between the species, and that the character was not correlated with the size of the corolla tube or the position of the verticil on the plant.

As the anthers of dried specimens shrivel, care was taken to soak the anthers in a soap-water solution prior to measurement. Due to the difficulty of obtaining mature nutlets and flowers on a single specimen, anthers measured generally came from upper verticils. The longest anther lobe of a flower was measured. Anther length gave an almost complete separation of the species (Fig. 5g). The anthers of *Lycopus americanus* were 0.26–0.50 mm long, those of *L. europaeus* were 0.50–0.70 mm long.

9) **Nutlets.** The value of nutlet characters as a means of distinguishing species of Lycopus was noted by Hermann (1936). How-

ever, the nutlets of *L. europaeus* were not discussed in this article. Fernald (1950), Gleason (1952) and Henderson (1962) noted that the nutlets of *L. europaeus* are larger than those of *L. americanus*. This difference was confirmed in this study.

Nutlets of *Lycopus americanus* were 1.00–1.37 mm long, by 0.73–0.95 mm wide; those of *L. europaeus* were 1.30–1.73 mm long, by 0.93–1.25 mm wide. The variation of these characters is shown in Figs. 5h and 5i.

The shape of the base of the nutlet is a useful character which is difficult to quantify. Nutlets of *Lycopus americanus* have a narrow base, which gives them a wedge-shaped appearance. Those of *L. europaeus* have a broader base, and are comparatively more square. Comparable measurements were made by placement of a scale on the nutlet, as shown in Fig. 4. The bases of the nutlets of *L. americanus* were between 0.42 and 0.64 mm wide; those of *L. europaeus* were 0.69 and 0.80 mm wide (Fig. 5j).

The 'collar' shape, which is visible on the margins of the abaxial surface of the nutlets (cf. Fig. 6) is another useful character. The distance between the ends of the 'collar' for nutlets of *Lycopus americanus* was 0.10–0.30 mm. In comparison, the ends of the 'collar' are thicker and the resultant distance between the ends, 0–0.20 mm, was less for *L. europaeus* (Fig. 5k). The ends of the 'collar' on the nutlets of this species are confluent (cf. Fig. 6a), so that a ring, rather than a 'collar' appears.

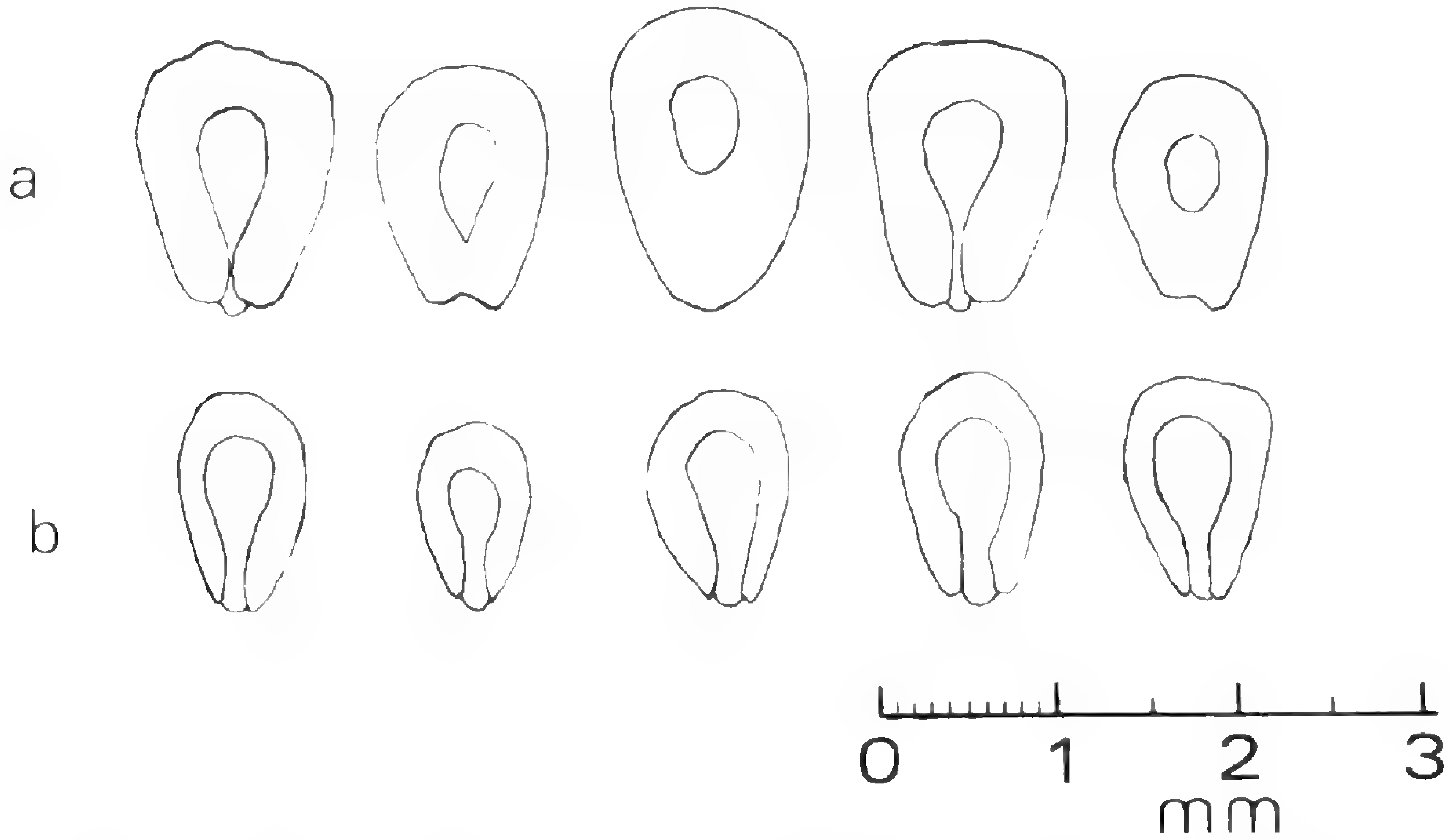


Figure 6. Shape of nutlets of *Lycopus europaeus* (a) and *L. americanus* (b).

10) **Chromosome Counts.** Despite difficulty in interpretation due to the persistence of oil droplets, the chromosome number of one specimen of *Lycopus americanus* (Erindale College Campus, Peel Co., Ont., 9 Aug., 1973, *J. Webber No. 6*) is $n = 11$. This number confirms Ruttle's (1932) count of $2n = 22$.

The chromosome number of Canadian *Lycopus europaeus* (Toronto Island, York Co., Ont., 15 Sept., 1973, *J. Webber No. 332*) is $2n = 22$. This count is identical to the number previously reported for this species from Europe, as discussed above. As the chromosome numbers of the two species are identical, chromosome number was not further utilized in this study.

## CHARACTER ANALYSIS

### Principal components analysis

The thirteen characters used in the principal components analysis are listed in Table 1. The principal components analysis programme contained in the NTSYS '74 programme package (Rohlf, F. J. et al. 1974) was utilized. The R technique was applied to the data matrix of 13 rows (characters) and 229 columns (specimens of *Lycopus americanus*, European *L. europaeus* and *Lycopus* from the five Canadian populations). Data was standardized before the calculation of Pearson correlation coefficients.

Table 1. **Characters used in Principal Components Analysis.**

1. leaf tooth width (cm)
2. ratio of leaf tooth length divided by leaf tooth width
3. ratio of maximum leaf width (at widest point of leaf) divided by minimum leaf width (at widest point of leaf)
4. leaf hair length (mm)
5. bracteole length (cm)
6. calyx length (cm)
7. anther length (mm)
8. nutlet length (mm)
9. nutlet width (mm)
10. nutlet base width (mm)
11. distance between ends of nutlet 'collar' (mm)
12. maximum leaf width (cm)
13. leaf length (cm)

Eight principal components were extracted. Components 1, 2 and 3 accounted for 48.47%, 15.17% and 7.87% of the trace, respectively. Subsequent principal components accounted for smaller percentages of the trace. The steep drop in variance of the first, second and third principal components is in keeping with analyses which show good separation of groups (Blackith & Reyment, 1971).

As the first principal component accounts for nearly half of the variance, the best separation was expected to be shown by this axis. This expectation is confirmed by examination of the projection of the first and second principal components (Fig. 7). This projection shows that *Lycopus americanus* is completely separated from *L. europaeus* on the first axis. The majority of the individuals from the Canadian populations are intermediate between *L. americanus* and *L. europaeus,* although some individuals fall into the ranges of the clusters of the parent species. The intermediates tend to resemble *L. europaeus* more than *L. americanus.*

## Pictorial Scatter Diagrams

Pictorial scatter diagrams were constructed following the techniques of Anderson (1949). Five characters which showed the greatest separation between *Lycopus americanus* and *L. europaeus* were chosen. Two of these characters were used as the axes. The three remaining characters were scored, symbolized, and added to the appropriate points of the scatter diagrams. Data from Canadian populations of *Lycopus* were similarly analyzed and compared with the data from specimens of *L. americanus* and *L. europaeus* (Fig. 8). Unlike the principal components analysis, specimens with missing characters could not be included in the pictorial scatter diagrams. Therefore, many specimens from the Canadian populations are excluded from the pictorial scatter diagrams.

The results obtained by applying conventional Andersonian techniques to the data agree with the findings of the principal components analysis. As shown by Fig. 8, the majority of the individuals from the Canadian populations are intermediate between *Lycopus americanus* and *L. europaeus,* although some individuals fall within the clusters of the parent species. The intermediates tend to resemble *L. europaeus* more than *L. americanus.*

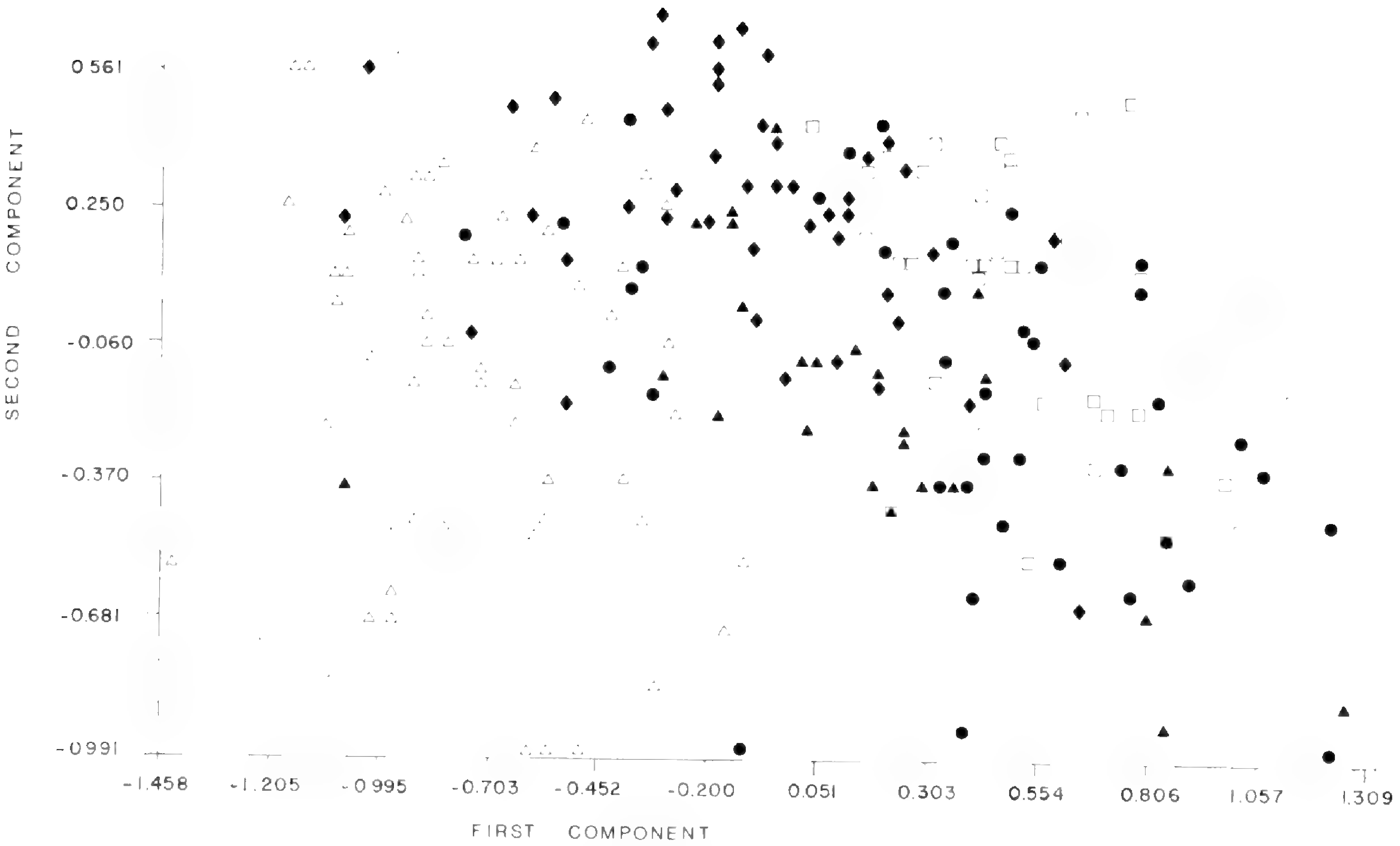


Figure 7. Bivariate plot of specimen scores on the first and second principal components: △ *L. americanus* (collected from areas in Ontario and Quebec where *L. europaeus* had not been reported); □ *L. europaeus* (collected from Europe); ● specimens of Lycopus from Rattray Marsh; ▲ specimens of *Lycopus* from Toronto Island; ◆ specimens of *Lycopus* from Quebec populations.

## ANALYSIS OF CANADIAN POPULATIONS OF LYCOPUS

In most cases the sample sizes gathered from five localities in Ontario and Quebec were small. Although there was often apparently a large number of individuals, many of these were found to be clones and therefore only one part of the clone was taken. As mentioned previously, difficulty in obtaining specimens with both fruit and anther characters was a problem.

All of the Canadian populations examined contained individuals with principal component scores (in the case of principal components analysis) or combinations of characters (in the case of pictorial scatter diagrams) which extend beyond the ranges for *Lycopus americanus* and *L. europaeus*. All populations contained at least one individual with principal component scores within the range for *L. europaeus*. Specimens resembling *L. americanus* were much less frequent, although at least one individual of this species was found in each population. The intermediate nature of many specimens is also shown by both the principal components analysis (Fig. 7) and the pictorial scatter diagrams (Fig. 8). The populations examined from Ontario and Quebec are discussed as follows:

### Toronto Island population

*Lycopus europaeus* was first collected from Toronto Island in 1903 (*Scott*, TRT), and appears to have become established. The species now occurs scattered over most of the shoreline. Seedlings readily become established in lawns which are inundated in the spring. *L. americanus* is present in the same habitats, although it is not nearly so common. The population sampled was a patch on 0.1 hectare, 20 m west of the Island School.

Although both *Lycopus americanus* and *L. europaeus* occurred in this population, the majority of the individuals showed combinations of characters which place them intermediate between the two species. For example, most individuals had nutlets not more than 1.30 mm long (a *L. americanus* character), whereas the leaf hairs of these individuals were generally more than 0.40 mm long (a *L. europaeus* character). In general appearance, especially in the shape and division of the leaves, most specimens resembled *L. europaeus*, and for this reason they generally have been uncritically determined as that species. This determination is contradicted by an examination of smaller, less obvious characters.

## Rattray Marsh populations

This population occupied a comparatively small area. There is a strong possibility that the population originated from only a few individuals with extensive vegetative reproduction accounting for much of the spread through the locality. The first record of *Lycopus europaeus* from this locality appears to be 1959 (*A.F. Coventry*, TRTE). However, little significance can be attached to this date, there being no record of any plant collections made there prior to the late 1950's (Macdonald, 1970), although the area may have been visited by naturalists in the early 1900's (Faull, 1913).

As with the Toronto Island population, a small number of individuals fell within the ranges of *L. americanus* and *L. europaeus*, whereas the majority appeared to be intermediates.

## Other Ontario populations

The remaining Ontario populations of *Lycopus europaeus* examined were restricted to marshes and riverbanks close to the shoreline of Lake Ontario. One notable exception was a population of *L. europaeus* occurring inland along the banks of the Grand River at Galt (Waterloo Co.). The sample from this locality, like the samples from High Park (York Co.), Etobicoke Creek (Peel Co.), Port Credit (Peel Co.) and Oakville Creek (Halton Co.), consisted of fewer than 14 individuals. Despite the small size of these populations, analysis by Andersonian techniques showed that these populations are similar in structure to those analyzed by principal components analysis.

## Quebec populations

All localities where samples of *Lycopus europaeus* were gathered in Quebec occurred within the geographical range of *L. laurentianus* Rolland-Germain (1945), which had been collected at only a few localities along the St. Lawrence River. This species is distinguished from *L. americanus* and *L. europaeus* by the presence of conspicuous wings along the stem angles. As none of the specimens collected had winged stem angles, it was assumed that the populations sampled contained only plants of *L. europaeus* and *L. americanus*.

As shown by the principal components analysis (Fig. 7) and pictorial scatter diagrams (Fig. 8), the population samples from Levis, Portneuf, and Berthierville were similar to the Toronto Island

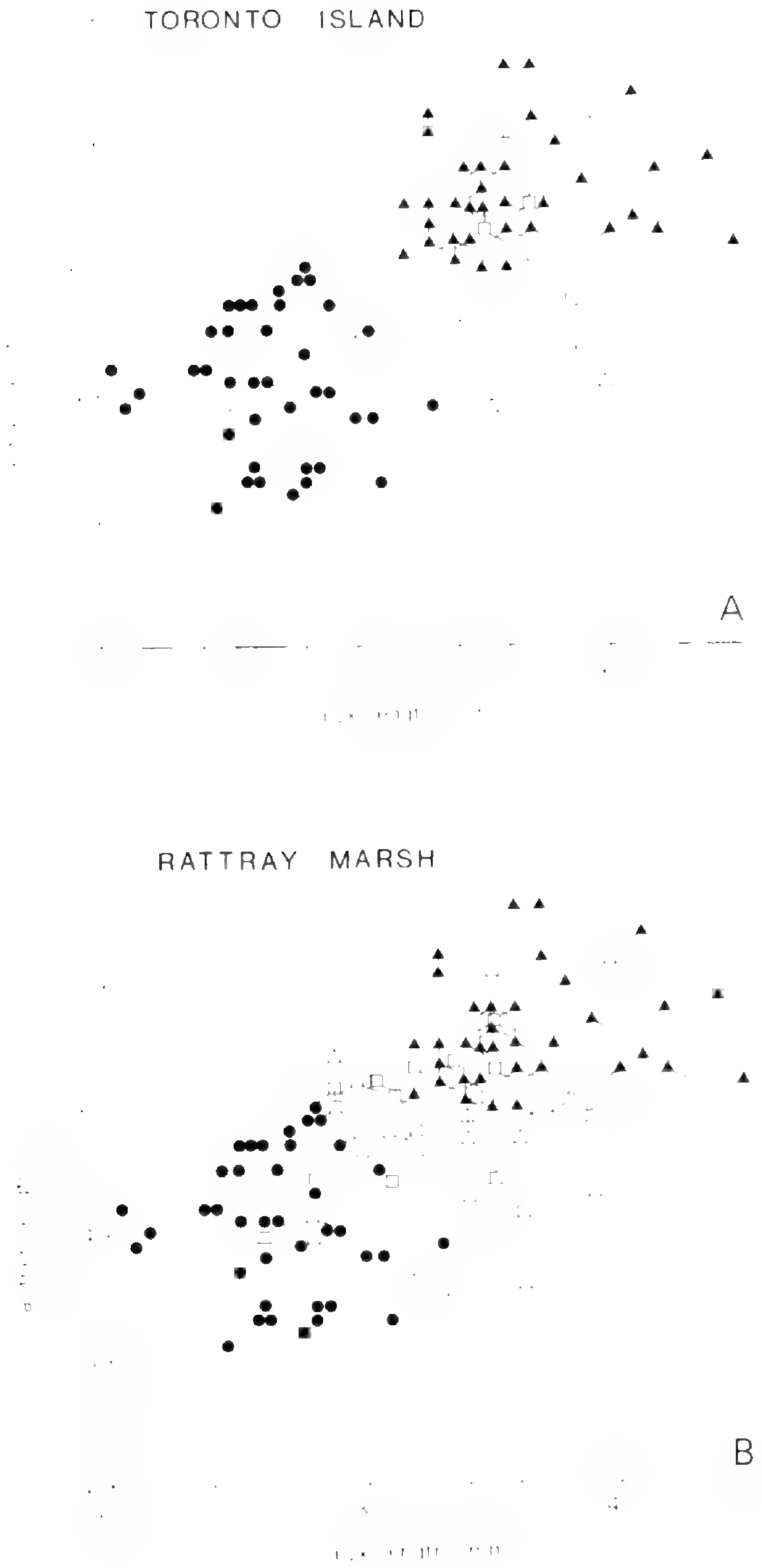
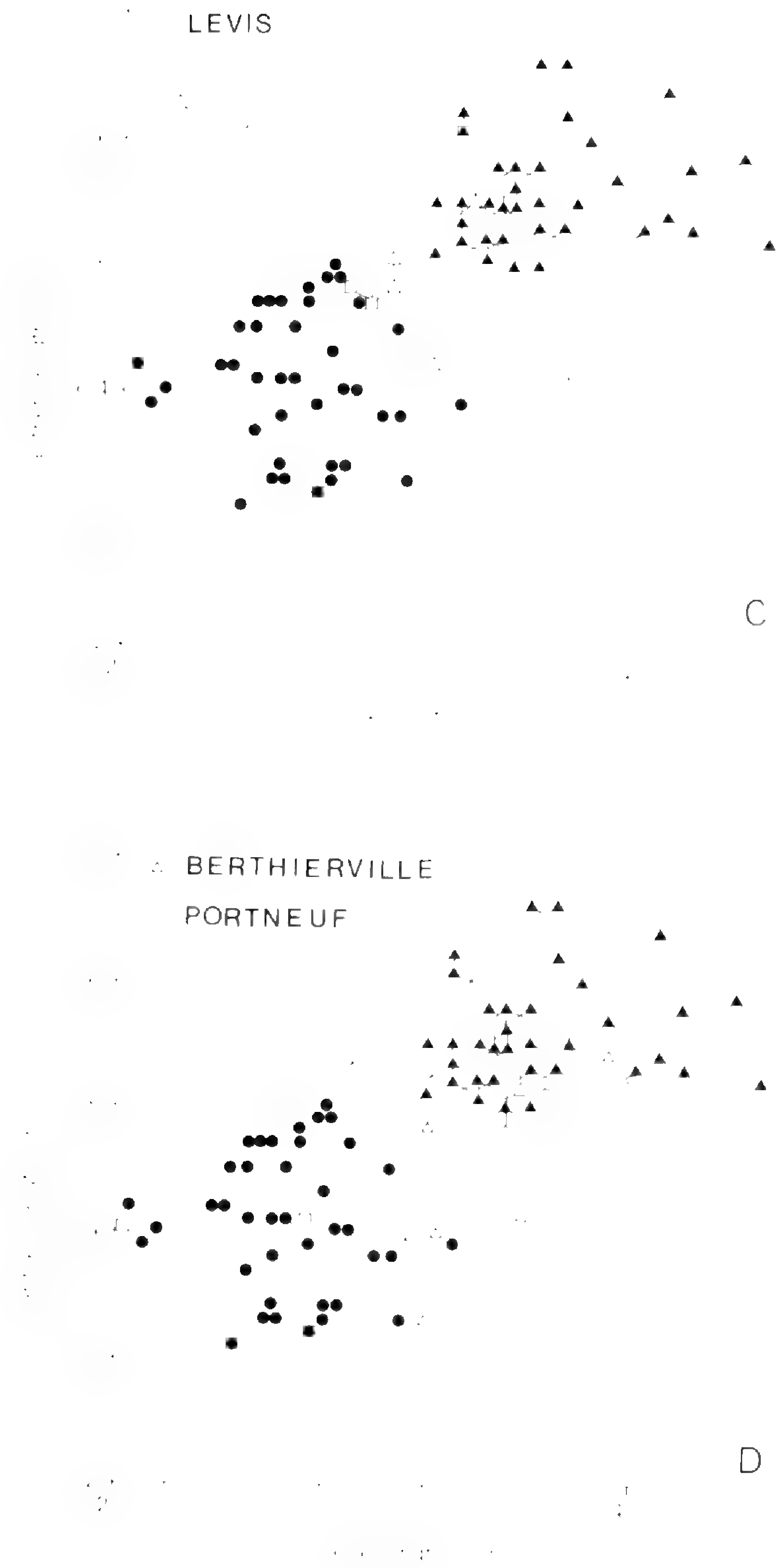


Figure 8. Pictorial Scatter diagrams of samples of *L. americanus* collected from areas where *L. europaeus* is absent and samples of European *L. europaeus* compared

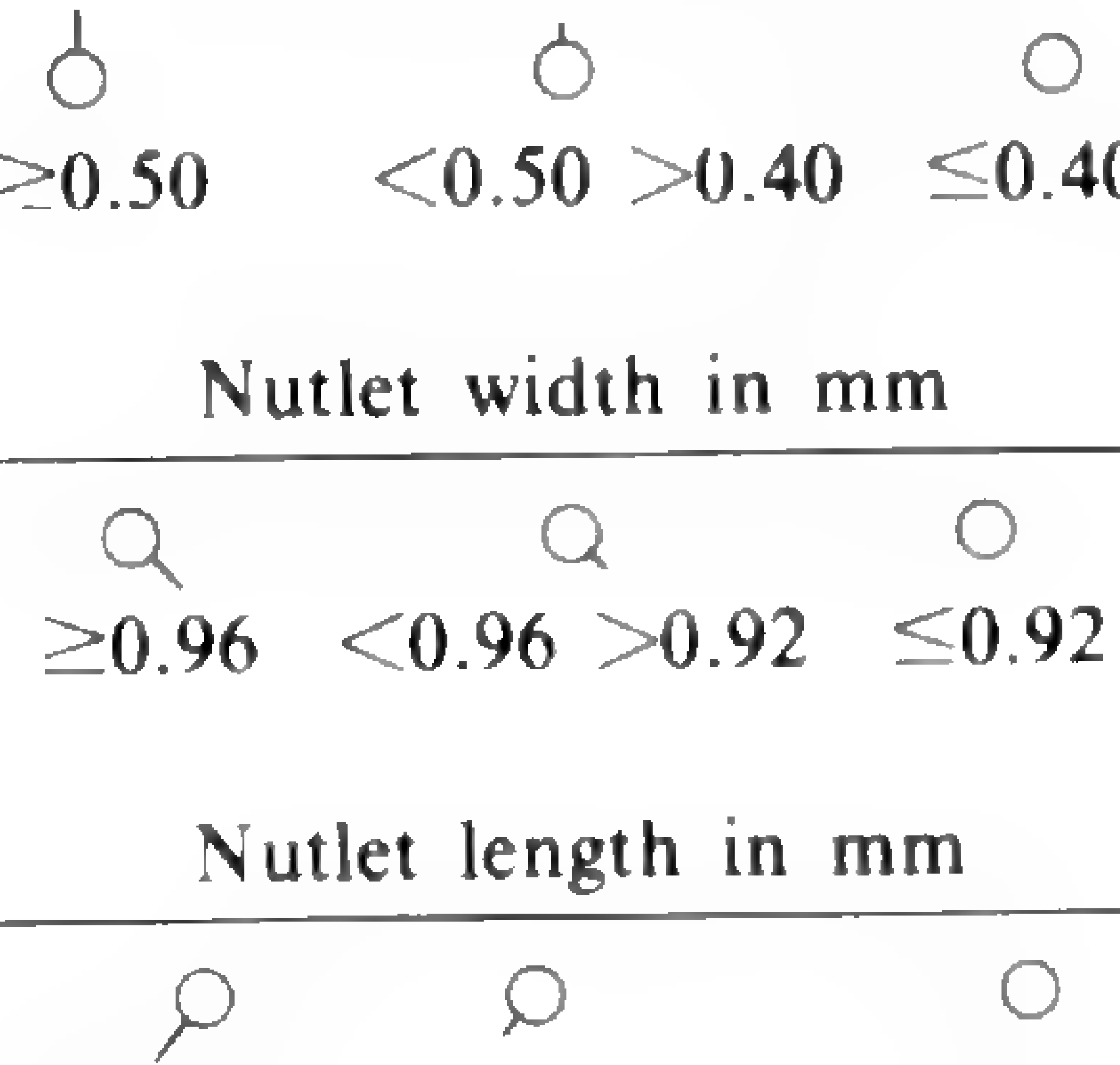


with individuals from *Lycopus* populations at (A) Toronto Island, (B) Rattray Marsh, (C) Levis and (D) Portneuf and Berthierville. (see page 300 for legend)

Legend for Figure 8.

*L. europaeus* ▲

*L. americanus* ●



| *Hair length in mm* | | |
|---|---|---|
| ≥0.50 | <0.50 >0.40 | ≤0.40 |

| Nutlet width in mm | | |
|---|---|---|
| ≥0.96 | <0.96 >0.92 | ≤0.92 |

| Nutlet length in mm | | |
|---|---|---|
| ≥1.35 | <1.35 >1.30 | ≤1.30 |

and Rattray Marsh samples. A few specimens of *Lycopus americanus* were observed, as well as specimens which resembled *L. europaeus*. The majority of the intermediate specimens resembled *L. europaeus* more than *L. americanus*.

## ADDITIONAL EVIDENCE

Besides the above analysis of morphological characters, the effective fertility of *Lycopus europaeus, L. americanus* and intermediate individuals was investigated as an aid to understanding the nature of the Canadian populations. The pollen of all three taxa appeared to be identical in size and shape, and staining with methylene blue indicated a high level (more than 90%) of pollen viability in all specimens examined. Fruit characters were used extensively in this study, but no evidence of sterility was detected in any specimen that was examined. All evidence indicates that the intermediate plants show no reduction in effective fertility compared with *L. europaeus* and *L. americanus*.

## DISCUSSION

The results indicate that the plants named *Lycopus europaeus* in Canada are hybrid swarms derived from *L. europaeus* and *L. americanus*. In most cases, the populations examined contained a few individuals that can be referred to *L. europaeus*. Specimens of *L. americanus* were not so common in the populations examined. Usually the majority of individuals were variously intermediate between these two species with the intermediate individuals showing no reduction in effective fertility compared with *L. europaeus* and *L. americanus*. Although many known examples of the formation and establishment of hybrid swarms are in disturbed habitats, this particular example is noteworthy as it involves a native North American species hybridizing with a European species, apparently enabling the latter to spread more rapidly into eastern Canada.

*Lycopus europeaus* and *L. americanus* × *europaeus* hybrids have been spreading rapidly in the Great Lakes–St. Lawrence region of Canada in recent years. They occur frequently along the shores of the St. Lawrence River and along the north-western shore of Lake Ontario. They are much less frequent along the north shore of Lake Erie and appear to have only recently spread into this area. For example, no specimens were observed at Long Point (Norfolk Co.) in 1974, but in 1975 there were many individuals on landfill sites by the marinas. Two recent records from the Bruce Peninsula in Lake Huron (*Bezdek & McAskie, 1975,* TRTE; *Johnson, 1976,* HAM), one of the few areas in Ontario frequently visited by botanists, indicate that the plants have recently spread into this lake. Collections are also known from two inland localities, Port Perry, Ontario Co. (*Leadbeater et al., 1973,* TRT) and Galt, Waterloo Co. (*Campbell, 1970*; *Webber, 1974,* TRTE), but the spread inland seems to be much slower than along the shores of the Great Lakes.

The recent establishment and spread of the hybrid swarms of *Lycopus americanus* × *europaeus* in the Great Lakes-St. Lawrence region cannot readily be explained. *L. europaeus* has been well established in a few localities, such as Toronto Island, for at least 70 years, but showed little tendency to spread from there. The recent rapid spread along the St. Lawrence River appears to have started soon after the opening of the St. Lawrence Seaway in 1955 and it could be attributed to the invasion of new stocks of *L. europaeus* directly from Europe into the St. Lawrence and Great Lakes.

It is not clear whether there have been a large number of independent invasions of *Lycopus europaeus* from Europe or whether the established populations have been the source of the spread. Many of the populations examined contain at least a few individuals that can be identified as *L. europaeus* so that the hypothesis of frequent invasion from Europe is a possibility. On the other hand, it seems more likely that there have been few invasions from Europe and that the spread through the Great Lakes–St. Lawrence region has been derived mainly from established local populations.

The plants which are now established show many of the attributes of a good colonizing species (cf. Baker & Stebbins, 1965). They are perennials capable of extensive vegetative reproduction, and also capable of growing in and stabilizing disturbed soil and sand, and even gravel and shingle. They show a high degree of phenotypic plasticity. Small individuals, flowering when no more than 5 cm high, have been observed growing in cracks and crevices in rocks and concrete and between wooden boards of docks in many places. In sheltered, more shaded and moist areas, much branched individuals over 2 m tall have been seen. These facts, together with the high level of fertility that has been observed, could explain the success of the hybrid swarms.

The fluctuations in water level in the Great Lakes may also have assisted in the spread of these plants. This phenomenon, together with a considerable increase in human activity, has created a great many more disturbed sites along the shores in recent years.

Although it has not been possible to determine the extent to which hybridization has been an essential component in the success of these plants, the fact that all the populations examined contain a high proportion of intermediate individuals makes it clear that hybridization is undoubtedly important to the success of these plants.

Possible factors which may have contributed to the success of the hybrids (as compared to *Lycopus europaeus*) are: (1) increased phenotypic plasticity, (2) increase in the production of stolons as well as runners, and (3) improved adaptation to the climate of eastern North America. Only extensive comparative cultivation experiments are likely to determine which factors are the most significant.

## ACKNOWLEDGEMENTS

The authors express appreciation to the curators of the various herbaria from which specimens were borrowed. Mrs. M. Riley, of the University of Toronto seed exchange, and all those who sent seed of *Lycopus europaeus* from various European seed exchange institutions, are gratefully acknowledged. Dr. T. Carleton and Prof. A. Baker are thanked for their assistance and advice on the principal components analysis. Dr. J. McNeill's comments on the manuscript are also acknowledged. Previous taxonomy students of the University of Toronto, David Bezdek and Sandy Harris also made a contribution to this investigation.

## LITERATURE CITED

ANDERSON, E., 1949. Introgressive Hybridization. John Wiley and Sons, New York. 109pp.

BAKER, H. G. & G. L. STEBBINS (ed.), 1965. The Genetics of Colonizing Species. Academic Press, New York. 588pp.

BALL, P. W., 1972. *Lycopus*. *In*: Tutin, T. G. et al. (eds.) Flora Europaea. Cambridge University Press, Cambridge. Vol. **3:** 183.

BLACKITH, R. E. & R. A. REYMENT, 1971. Multivariate Morphometrics. Academic Press, New York.

EHRENBERG, L., 1945. Kromosomtalen nos nagra Karlvaxter. Bot. Notiser **4:**430–437.

FAULL, J. H., 1913. The Natural History of the Toronto Region. Can. Inst., Toronto. 419pp.

FERNALD, M. L., 1950. Gray's Manual of Botany, 8th ed. American Book Company, New York. pp. 1245–1247.

GADELLA, T. W. J. & E. KLIPHUIS, 1963. Chromosome numbers of flowering plants in the Netherlands. Acta. Bot. Neerlandica **12:** 195–230.

GLEASON, H. A., 1952. The New Britton and Brown Illustrated Flora of the northeastern United States and adjacent Canada. Hafner Press, New York, Vol. **3:** 182–185.

HENDERSON, N. C., 1962. A Taxonomic Revision of the Genus *Lycopus* (Labiatae). The Amer. Midl. Naturalist **68:** 95–138.

HERMANN, F. J., 1936. Diagnostic Characters in *Lycopus*. Rhodora **38:** 373–375.

HINDAKOVA, M. & F. CINCURA, 1967. Angaben uber die Zahl und Morphologie der Chromosomen einiger Pflanzenarten aus dem Territorium der Ostslowakei. Acta Fac. Rer. Nat. Univ. Comen. **14:** 181–227.

HOLMGREN, P. K., & W. KEUKEN. 1974. Index Herbariorum, 6th Ed. (F. A. Stafleu, general editor).

MACDONALD, I., 1970. The Vegetation and Plant Species of Rattray Marsh in Mississauga Tp., Peel Co., Ontario. Fowler Herbarium of Queen's University, Kingston, Ont. 44pp.

RADFORD, A. E., W. C. DICKISON, J. R. MASSEY & C. R. BELL, 1974. Vascular Plant Systematics. Harper & Row, Publishers, New York. 891pp.

ROHLF, F. J., J. KISHPAUGH, & D. KIRK, 1974. NTSYS. Numerical Taxonomy System of Multivariate Statistical Programs.

ROHWEDER, H., 1937. Versuch zur Erfassung der mengenmassigen Bedeckung des Darss und Zingst mit polyploiden Pflanzen. Ein Beitrag zur Bedeutung der Polyploidie bei der Eroberung neuer Lebenstraume. Planta **27:** 501–549.

ROLLAND-GERMAIN, F. E. C., 1945. Un *Lycopus* endemique de l'estuaire du Saint-Laurent. Nat. Canad. **72:** 177–184.

ROUSSEAU, C., 1968. Historie, habitat et distribution de 200 plantes introduites au Quebec. Nat. Canad. **95:** 49–169.

RUTTLE, M. L., 1932. Chromosome number, embryology and inheritance in the genus *Lycopus*. Gartenbauwissenschaft **7:** 154–177.

STUCKEY, R. L. & W. L. PHILLIPS, 1970. Distributional history of *Lycopus europaeus* (European water-horehound) in North America. Rhodora **72:** 351–367.

Tischler, G., 1934. Die Bedeutungen der Polyploidie fur die Verbreitung der Angiospermen erlautert an den Arten Scheswig-Holsteins, mit ausblicken auf andere Florengebiete. Bot. Jahrb. **69**: 1–36.

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# THE FRESHWATER AND BRACKISH-WATER DIATOMS OF PENIKESE ISLAND, MASSACHUSETTS:
## 1923 and 1973

ROBERT K. EDGAR

In 1873 Penikese Island was the site of the establishment by Louis Agassiz of the Anderson School of Natural History — the spiritual forerunner of the Marine Biological Laboratory at Woods Hole and the impetus for significant changes in the conduct of American science (Lurie, 1974). The flora and fauna of the island were investigated in that year in keeping with the Agassizian tradition of studying "nature, not books." Since then, in 1923 and 1947, the flora and fauna have been reinvestigated in commemoration of Agassiz' original effort. In 1973 a centennial commemoration was held at the Marine Biological Laboratory; this report on the diatom flora is part of the survey of the island conducted at that time.

The only previous investigation of the diatom flora of Penikese was conducted by Conger (1924) in the summer of 1923 during the fiftieth anniversary of the Anderson School's founding. His survey of the freshwater, brackish, and marine habitats listed 96 diatom species and varieties of which over 60% were recorded from euhaline Penikese Harbor. This 1973 reinvestigation was confined to the freshwater and brackish habitats. All ponds and the marsh sampled by Conger were reexamined in 1973 except Dry Pond which had become extinct. Three additional habitats were sampled for their diatoms for the first time: the northernmost of the reservoirs, Leper Pond, and Zinn's Pond. The locations and descriptions of the ponds and the marsh have been presented by Croasdale (1935, 1948).

## METHODS

Penikese Island (41° 27′ N, 70° 55′ W) is part of the Elizabeth Islands chain, which forms the southern boundary of Buzzards Bay, Massachusetts, U.S.A. On 16 August 1973 the ponds and the marsh of the island were sampled for their planktonic, epilithic, epipelic, and epiphytic diatom assemblages. Samples were prepared for microscopic examination using the acid-dichromate-Hyrax procedure of Patrick and Reimer (1966). Taxonomic determinations were made using both brightfield oil-immersion optics with parallel and oblique illumination and phase-contrast optics at a magnification of 1000×. Also, the light microscope structure of some individuals, especially small ones in problematical taxa, was pursued using the scanning electron microscope to facilitate the determinations. Primarily the common diatoms, those having greater than about 1% relative abundance in a sample, have been determined in this survey. All samples and slides have been deposited in the Hellerman Diatom Herbarium (HDSM) at Southeastern Massachusetts University under the reference numbers *HDSM 722–748*.

Selected physicochemical measurements of each pond's surface water were made at the time of the survey and were provided to me by Dr. Peter H. Rich of the University of Connecticut. His water samples were collected near the center of each pond between late-morning and mid-afternoon; their temperature (Whitney Underwater Thermometer Model TC-5C), dissolved oxygen concentration (unmodified Winkler procedure), pH (analytical means unknown), and specific conductance (Yellow Springs Conductivity Cell Model 3402 and Bridge Model 31) were measured. Light penetration was estimated with a Secchi disc.

## RESULTS AND DISCUSSION

### Pond water quality

Selected measurements of the physicochemical characteristics of the ponds taken at the time of the survey are presented in Table 1. Generally the ponds were warm (21–27° C), slightly alkaline and turbid, with low dissolved oxygen concentrations (2 4 mg $O_2 \cdot l^{-1}$) and low oxygen percent saturations (*ca.* 20–50%). Typha Pond was exceptional in being supersaturated (*ca.* 125%) with oxygen. Based on my own past observations South Pond is characteristically mesohaline, as the specific conductance measurement indicates, and Tub Pond, although not measured, is usually at least as saline, being at a lower elevation and closer to the exposed coast. All the other ponds had a relatively low specific conductance and were freshwater or possibly slightly oligohaline. The Marsh had about twice the specific conductance of the other freshwater habitats.

### The flora

Seventy-nine diatom species and subspecific taxa were determined from the ponds during this survey (Table 2). Although sam-

Table 1. **Physicochemical characteristics of the surface waters of Penikese Island ponds on 16 August 1973.**

| *Locations* | *Temperature* (°C) | *Secchi Depth* (cm) | *Specific Conductance* (umhos· cm$^{-1}$) | pH | *Dissolved Oxygen* (mg $O_2 \cdot l^{-1}$) |
|---|---|---|---|---|---|
| Reservoir | 23.1 | 80 | 363 | — | 2.0 |
| The Marsh | 24.9 | 15 | 607 | — | 4.0 |
| Zinn's Pond | 26.3 | 15 | 219 | — | 4.0 |
| Leper Pond | 27.4 | 30 | 245 | 7.8 | 4.3 |
| Tern Pond | 24.4 | 10 | 355 | 7.8 | 3.5 |
| Typha Pond | 21.4 | 13 | 339 | 7.8 | 11.4 |
| South Pond | 21.3 | 40 | 9,716 | 7.0 | 3.2 |
| Tub Pond | — | — | — | — | — |

ples of several microhabitats within each pond were collected and examined separately, qualitative differentiation of these microhabitats based on the diatoms was not usually apparent, and consequently the presentation in Table 2 segregates the taxa solely by their larger scale distribution among the ponds. The surveys of 1923 and 1973 have 18 species in common, but only 9 of them were recorded from the same ponds. Neither survey attempted to deal quantitatively with the flora; however, a qualitative comparison of the common diatoms from the two surveys does reveal substantial differences.

Conger reported from brackish South and Tub Ponds several species which are frequent along the southern New England coast, but he noted particularly that *Caloneis oregonica* (Ehr.) Patr. (synonym: *Navicula formosa* Greg.) in South Pond and *Navicula peregrina* in Tub Pond were predominant. During the recent survey of these two species only *N. peregrina* was found, but in South Pond and it was not abundant. In 1973 South Pond contained also large populations of *Plagiotropis lepidoptera,* which was recorded by Conger from both ponds, *Amphora coffeiformis* including both var. *coffeiformis* and var. *perpusilla, Nitzschia frustulum* var. *subsalina,* and *N. fonticola.* Tub Pond was dominated by the same two varieties of *Amphora coffeiformis* as were found in South Pond. Species of *Amphora* and *Nitzschia* were not recorded from either pond in 1923, but they constituted major components of the flora of each during this survey. The collection of *Coscinodiscus excentricus,* *Paralia sulcata,* and *Stauroneis amphioxys* occurred also during both surveys from these ponds.

Typha Pond in 1923 had an abundant population of *Navicula elegans,* but in 1973 this species was rare in an assemblage dominated by *Nitzschia kutzingiana.* Both surveys of this pond found *Navicula cuspidata, N. rhynchocephala, N. capitata* var. *hungarica* (synonym: *N. nanella* Conger) and *Stauroneis phoenicenteron* f. *gracilis.*

The Marsh contained large populations of *Gomphonema parvulum, Navicula calida, N. cuspidata, Nitzschia palea,* and *Pinnularia viridis* in 1973. It was dry during Conger's visit but he did record *Navicula elegans* from its mud; this was the only species common to our lists from The Marsh.

Tern, Leper, and Zinn's Ponds, which are clustered just north of the remains of the leper village, were dominated by *Nitzschia kutzingiana.* Also, Leper and Zinn's Ponds supported large populations of *Nitzschia obtusa* var. *scalpelliformis* f. *nipponica,* while Tern Pond contained mostly populations of *Synedra pulchella* var. *lacerata, Gomphonema parvulum,* and *Stauroneis phoenicenteron* f. *gracilis.* None of the six species reported in 1923 from Tern Pond was found in it during this survey.

The northernmost reservoir on the hilltop at the southern end of the island was sampled for the first time during this survey and contained predominantly planktonic populations of *Nitzschia kutzingiana* and *Navicula cuspidata.*

A survey of the diatom flora of Penikese was not conducted in 1947 during the "seventy-fifth" anniversary of the Anderson School's founding because the floristic changes were expected to be minimal over only twenty-five years. However, in the results of the two surveys which span 50 years major qualitative differences do exist. To what extent these differences are functions of the seasonally variable nature of the ponds and the succesional changes in the environment over the past few decades is unassessed. Conger's observations indicate he sampled the flora during a dry period in mid-summer, while in 1973 I found no indications of a drought. The successful identification of future changes in the diatom flora over ecological time spans will have to be linked to a quantiative analysis of the flora and its seasonal variability.

*Table 2.* **The distribution of diatom taxa on Penikese Island during the 1923 and 1973 surveys.** C = recorded only in 1923, E = recorded only in 1973, and B = recorded in both surveys. The harbor was not sampled in 1973.

| Taxa | Tub Pond | South Pond | Typha Pond | Tern Pond | Leper Pond | Zinn's Pond | The Marsh | Reservoir | Harbor |
|---|---|---|---|---|---|---|---|---|---|
| COSCINODISCACEAE | | | | | | | | | |
| *Melosira varians* Ag. | | | | | E | | | | |
| *Paralia sulcata* (Ehr.) Cl. | | B | | | | | C | | C |
| *Cyclotella comta* (Ehr.) Kütz. | | | C | C | E | | | E | |
| *C. meneghiniana* Kütz. | | | | | | E | E | | |
| *C. striata* (Kütz.) Grun. | E | | | | | | | | |
| *Coscinodiscus excentricus* Ehr. | B | B | | | | | | | C |
| *Thalassiosira decipiens* (Grun. *ex* V.H.) Jørg. | E | | | | | | | | |
| *Hyalodiscus scoticus* (Kütz.) Grun. | E | | | | | | E | | |
| ACTINODISCACEAE | | | | | | | | | |
| *Actinoptychus senarius* (Ehr.) Ehr. | E | | | | | | C | | C |
| CHAETOCERACEAE | | | | | | | | | |
| *Chaetoceros decipiens* Cl. | | E | | | | | | | C |
| FRAGILARIACEAE | | | | | | | | | |
| *Diatoma tenue* var. *elongatum* Lyngb. | | | E | | | | | | |
| *Fragilaria vaucheriae* (Kütz.) Peters. | | | | | | | E | | |
| *F. construens* var. *venter* (Ehr.) Grun. | | E | | | | E | E | E | |
| *Rhaphoneis minutissima* Hust. | E | | | | | | | | |
| *R. surirella* (Ehr.) Grun. | E | | | | | | | | |
| *Synedra fasciculata* var. *truncata* (Grev.) Patr. | | E | | | | | | | |
| *S. pulchella* var. *lacerata* Hust. | | | E | E | E | | E | | |
| *Grammatophora serpentina* (Ralfs) Ehr. | E | | | | | | | | |
| *Rhabdonema adriaticum* Kütz. | E | C | | | | | | | C |
| EUNOTIACEAE | | | | | | | | | |
| *Eunotia curvata* (Kütz.) Lagerst. | E | | | | | | | | |
| *E. pectinalis* var. *minor* (Kütz.) Rabh. | E | | | | E | | E | | |
| ACHNANTHACEAE | | | | | | | | | |
| *Achnanthes hauckiana* Grun. | | | | | | | E | | |
| *A. lanceolata* (Bréb.) Grun. | | | | | | | E | | |
| *A. minutissima* Kütz. | | | E | | | | | | |
| *A. wellsiae* Reim. | | E | | | | | | | |
| *Cocconeis dirupta* Greg. | E | | | | | | | | |
| *C. pellucida* Grun. | | | | | | | E | | |
| *C. peltoides* Hust. | E | | E | | | | | | |
| *C. placentula* var. *euglypta* (Ehr.) Cl. | E | | | E | | | | E | |

Table 2. Continued.

| Taxa | Tub Pond | South Pond | Typha Pond | Tern Pond | Leper Pond | Zinn's Pond | The Marsh | Reservoir | Harbor |
|---|---|---|---|---|---|---|---|---|---|
| *C. placentula* var. *lineata* (Ehr.) V.H. | | E | | | E | | | | |
| *C. scutellum* Ehr. var. *scutellum* | E | | E | | E | | E | | C |
| *C. scutellum* var. *parva* Grun. *ex* Cl. | E | E | | E | | | E | | |
| *C. Stauroneiformis* (V.H.) Okuno | E | | | | | | | | |
| NAVICULACEAE | | | | | | | | | |
| *Navicula arenaria* Donk. | E | E | | | | | | | |
| *N. calida* Hend. | E | | | | | | E | | |
| *N. capitata* var. *hungarica* (Grun.) Ross | | | B | E | | | E | | |
| *N. crucicula* (W. Sm.) Donk. | E | E | | | | | | | |
| *N. cryptocephala* var. *veneta* (Kütz.)Rabh. | | | E | | | | E | E | |
| *N. cuspidata* Kütz. | | | B | | | | E | E | |
| *N. elegans* W. Sm. | | | B | | | | B | E | |
| *N. gregaria* Donk. | E | E | E | | | | E | | |
| *N. lagerheimii* var. *intermedia* Hust. | E | | | | | | | | |
| *N. mutica* Kütz. | E | | | | E | | | | |
| *N. pelliculosa* (Bréb. *ex* Kütz.) Hilse | | | E | E | E | E | E | | |
| *N. peregrina* (Ehr.) Kütz. | C | B | | | | | C | | |
| *N. pupula* Kütz. var. *pupula* | | | E | | | | | | |
| *N. pupula* var. *elliptica* Hust. | | | | | E | | | | |
| *N. pusilla* W. Sm. | | | | | | | E | | |
| *N. pygmaea* Kütz. | E | E | E | | | | | | |
| *N. rhynchocephala* Kütz. | | E | B | | | | E | | |
| *N. salinarum* Grun. | E | E | | | | | E | | |
| *N. salinicola* Hust. | E | E | | | | | | | |
| *Stauroneis amphioxys* Greg. | | B | C | | | | | | |
| *S. phoenicenteron* f. *gracilis* (Ehr.) Hust. | E | | B | E | E | E | E | | |
| *S. producta* Grun. | E | | E | E | | | E | E | |
| *Caloneis bacillum* (Grun.) Cl. | | | E | E | | | E | | |
| *C. lenzii* Krass. | | | E | | | | | | |
| *Pinnularia borealis* Ehr. | | | C | | E | E | | | |
| *P. obscura* Krass. | E | E | | E | E | E | E | | |
| *P. subcapitata* Greg. var. *subcapitata* | E | | E | | E | E | E | E | |
| *P. subcapitata* var. *hybrida* (Grun.) Freng. | E | E | E | | E | E | E | E | |
| *P. viridis* (Nitz.) Ehr. | E | | E | C | E | E | E | | |
| *Entomoneis pulchra* (J.W. Bail.) Reim. | | E | | | | | | | |
| *Plagiotropis lepidoptera* (Cl.) Reim. | B | B | | | | | | | |
| GOMPHONEMACEAE | | | | | | | | | |
| *Gomphonema parvulum* Kütz. | E | | E | E | E | E | E | E | |

Table 2. Continued.

| Taxa | Tub Pond | South Pond | Typha Pond | Tern Pond | Leper Pond | Zinn's Pond | The Marsh | Reservoir | Harbor |
|---|---|---|---|---|---|---|---|---|---|
| CYMBELLACEAE | | | | | | | | | |
| *Amphora coffeiformis* (Ag.) Kütz. var. *coffeiformis* | E | E | | | | | | | |
| *Amphora coffeiformis* var. *perpusilla* (Grun.) Cl. | E | E | | | | | | | |
| BACILLARIACEAE | | | | | | | | | |
| *Nitzschia bilobata* var. *minor* Grun. | E | | | | | | | | |
| *N. fonticola* Grun. | | E | E | | | | E | | |
| *N. frustulum* (Kütz.) Grun. var. *frustulum* | | | | | | E | | | |
| *N. frustulum* var. *perminuta* Grun. | | E | C | | | | E | E | |
| *N. frustulum* var. *subsalina* Hust. | | E | | | | | | | |
| *N. kutzingiana* Hilse | E | | E | E | E | E | E | E | |
| *N. lanceolata* var. *minima* Grun. | | | E | | | | | | |
| *N. obtusa* var. *scalpelliformis* f. *nipponica* Negoro | E | E | E | E | E | E | E | E | |
| *N. palea* (Kütz.) W. Sm. | E | | | E | E | E | E | E | |
| *N. parvula* Lewis | | | | | | E | | | |
| *N. subtilis* var. *paleacea* Grun. | | | E | E | E | E | E | E | |
| *Hantzschia amphioxys* (Ehr.) Grun. | E | | | | | E | E | | |

## NOTES ON SELECTED TAXA

**Navicula capitata** var. **hungarica** (Grun.) Ross Figures 1–3
Distribution: Typha Pond (*HDSM 727, 728*), Tern Pond (*HDSM 733, 734, 736*)), The Marsh (*HDSM 743, 744*)

Conger (1924) described a single new species from his investigation of the island — *Navicula nanella*, which he found in Typha Pond. He noted its resemblance to Cleve's (1895) description of *Navicula hungarica* Grun. but described it as a new species because of 1) differences in his interpretation of the "strongly marked striae" of Cleve, 2) the absence of a strongly dilated central region of the valve, which he mistakenly said Cleve figured, and 3) his contention, for which I can find no basis in Cleve, that Cleve implied "that the costae are striate" while in *N. nanella* they were not.

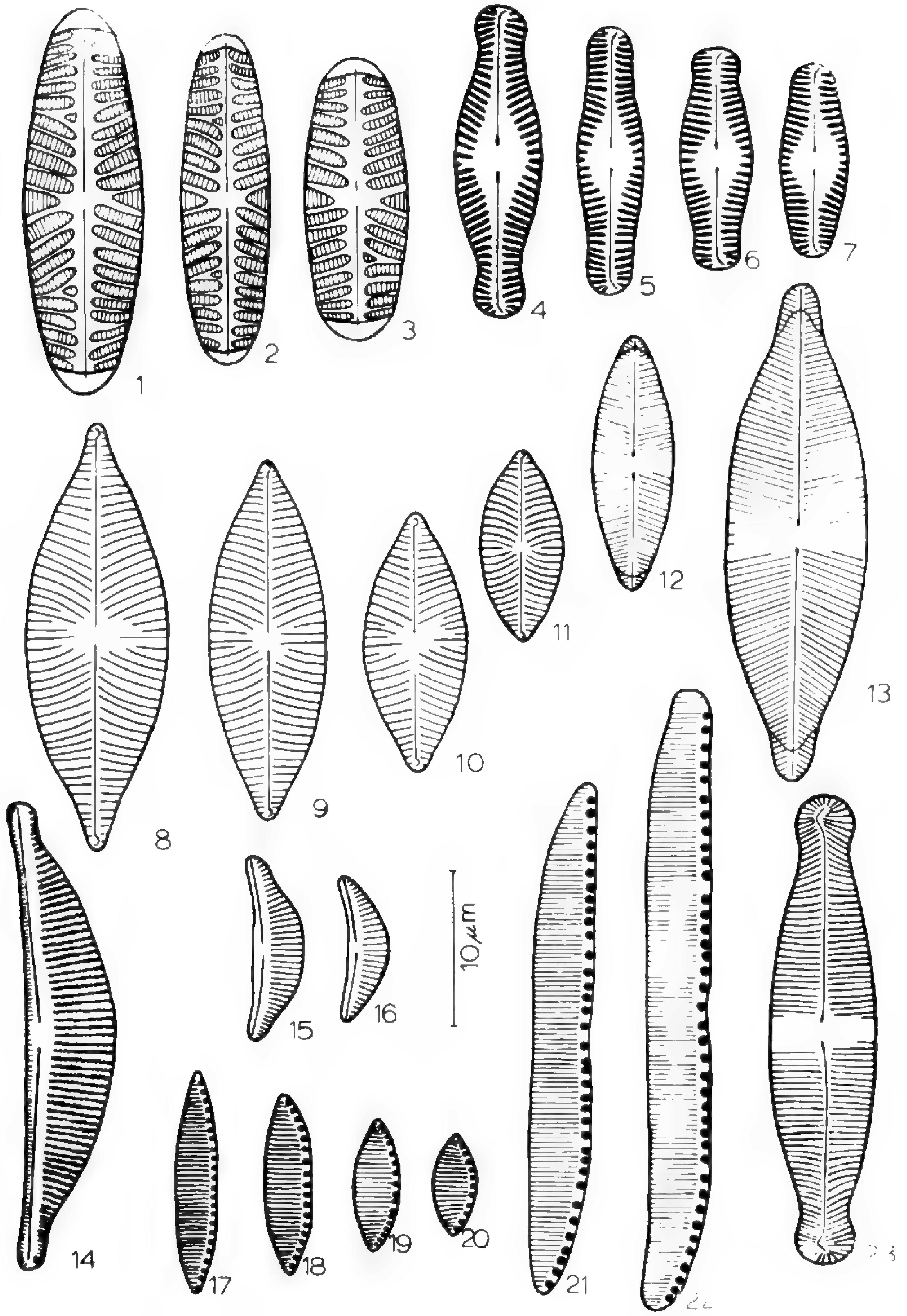
My observations on the Typha Pond population using both light and scanning electron microscopy indicate that the "strongly marked terminal striae" of most authors is due to an internal, apically widened and thickened costa which occurs either at the junction of the valve face and mantle or just apical to that junction and consequently on the mantle. The interpretation of this internal thickening as a costa and not as a transapically expanded terminal nodule is supported by two different sets of observations. First, the terminal pore of the raphe on the valve face ends proximally to the thickening and between the two terminal striae, which may be shorter than other striae due to the presence of a terminal nodule. In the light microscope some views of the valve suggest the raphe extends into the thickening but this view is produced by the curvature of the valve resulting in the superimposition of this thickening, which is at the junction or on the mantle, and the raphe, which is "above" it on the valve face. Different viewing angles could either accentuate or diminish this superimposition. The costa resembles a pseudoseptum, but it is nonmembranous and does not project far from the valve. Conger (1924) illustrated this costa based on girdle views of his material but its projection in his illustration appears exaggerated. Second, on the valve mantle apical to the thickening there are two lineolate (*ca.* 4 punctae/$\mu$m) striae, which are continuous across the pervalvar axis and which have punctae only 20–50% as long as those on the valve face. In favorable girdle views in the light microscope their presence is indicated although their interpretation as striae is not apparent. These mantle striae have been described previously using the transmission electron microscope in *Navicula hungarica* (Helmcke and Kreiger, 1953, taf. 70) and *N. hungarica* var. *capitata* (Helmcke et al., 1974, pl. 878). The presence of striae on both sides of this thickening supports the idea that it is a costa which has undergone additional thickening and apical widening compared to those of the valve face. Other non-Penikese populations of *N. capitata* var. *hungarica* that I have examined show the same junctional costae and apical mantle striae. Additionally, none of the costae in the Penikese populations or other populations of var. *hungarica* that I have examined contains punctae or striae.

The only morphological basis for the separation of the Penikese population from *Navicula capitata* var. *hungarica* that merits additional consideration here is valve shape. However, Conger's description of *N. nanella* conforms in this respect to that of both *N.*

*oestrupi* f. *elliptica* Schulz and *N. hungarica* var. *genuina* f. *elliptica* (Schulz) Cleve-Euler. VanLandingham (1975) has placed each of these latter names in synonymy with *N. capitata* var. *hungarica* (Grun.) Ross, but confirmation of his decisions regarding these names should be based on an examination of the respective types, and this I have not done. The description of the valve shape of var. *hungarica* has been consistent in the literature: valves linear-lanceolate to rhombic-lanceolate with broadly rounded to obtuse ends (Cleve, 1895; Hustedt, 1930; Patrick and Reimer, 1966). Conger's characterization of *N. nanella* as "elliptical with broad obtuse ends" is consistent with this.

I have seen only photographs sent to me by Dr. Conger of the type of *Navicula nanella*, but I am certain nevertheless that we have observed the same population from Typha Pond. His taxon carrying the specific epithet *nanella* has been recorded in no survey other than the 1923 one of Penikese; presumably, populations which have been observed and conformed to the description of *nanella* have been determined to be confined within the description of *N. hungarica* or its synonyms. Also, about three-quarters of all individuals in the Penikese population display the "défauts réguliers" of Voigt (1943), in this case, symmetrically disposed, disjunct striae segments on the valve face, usually on the same side of the raphe at opposite ends of the valve (Figures 1 and 2). Conger illustrated this same phenomenon in his original description of *nanella* and his photographs of the type show the same irregularity. Additionally, Helmcke et al. (1974) point out that in *N. capitata* var. *hungarica* "misarrangement of the loculi occasionally occurs." Based upon all the above considerations, *Navicula nanella* Conger falls within the range of morphological variation exhibited by *N. capitata* var. *hungarica* (Grun.) Ross, and I do not consider it a distinct species.

Finally, Patrick and Freese (1960) described a new variety from Alaska which displays the same kind of "défauts réguliers" — *Navicula hungarica* var. *arctica*. A survey of populations of var. *arctica* at the Academy of Natural Sciences of Philadelphia (PH: *GC'8251C & GC'8241A*) indicates that this irregularity is a general characteristic of this variety, at least in those samples. "Défauts réguliers" are observable in many different diatom species as anomalies, but in these closely related populations from Massachusetts and Alaska they are more the rule.



Figures 1–23. Selected Diatoms of Penikese Island, Mass. **1–3,** *Navicula capitata* var. *hungarica;* **4–7,** *Navicula calida;* **8–11,** *Navicula salinarum;* **12–13,** *Stauroneis producta;* **14,** *Amphora coffeiformis* var. *coffeiformis;* **15–16,** *Amphora coffeiformis* var. *perpusilla;* **17–20,** *Nitzschia frustulum* var. *subsalina;* **21–22,** *Nitzschia obtusa* var. *scalpelliformis* f. *nipponica;* **23,** *Caloneis lenzii.*

**Navicula calida** Hendey Figures 4–7

Distribution: The Marsh (*HDSM 741, 742*), Tub Pond (*HDSM 747*).

Hendey's (1964) original description and illustration of this species agree with that segment of the Penikese populations illustrated in Figure 4, except he indicated that frustule length was limited to 14–16 μm and Penikese individuals were frequently either larger or smaller than that. Among all populations I observed the following ranges in valve measurements: length (8–21 μm), breadth (4–6 μm), and striae (18–22 in 10 μm in the center to 22–26 in 10 μm at the ends). Smaller individuals have valve ends less constricted than what he indicted for *Navicula calida.* The smallest individuals in these populations (Figure 7) strongly resemble *N. justa* Hustedt (Hustedt, 1955), except *justa*'s valves are larger for the same shape (length: 14–18 μm; breadth: 5–6 μm) and its striae are a little finer than those of the Penikese individuals (24–26 in 10 μm). Also, Hustedt's illustration of *justa* indicates striae on the valve face apical to the terminal pore of the raphe; such striae are not observable in the light microscope in the Penikese populations. Hustedt reported *N. justa* "on mud from piles in (Beaufort, North Carolina) harbor," which is euhaline; the Penikese populations are from oligohaline to polyhaline habitats and are also epipelic. I have been unable to obtain samples of *N. justa* for comparison with *N. calida,* but based on the small magnitude of differences in frustule size, striae density and configuration, the similarity of the raphe systems and asymmetrical central areas, and the variability shown in the Penikese populations, I doubt the distinctness of these two nominal species.

**Navicula salinarum** Grun. Figures 8–11

Distribution: South Pond (*HDSM 722–726*), The Marsh (*HDSM 743*), Tub Pond (*HDSM 745–747*).

The larger individuals in these populations (Figure 8) conform to the general description of the species. Intermediate size individuals, ones around 20 μm long, approximate the description of *N. salinarum* f. *minima* Kolbe, except their striae are finer (18–20 in 10 μm as compared to 16–17 in 10 μm). But the smallest individuals (length: 12.5 μm; breadth: 5.5 μm; striae: 20 in 10 μm in the center to 24 in 10 μm at the ends) are not congruent with any of the described variants of *N. salinarum* or any other species of *Navicula* (Figure

11). The raphe systems and lineolate striae are the same in all size individuals as viewed in the scanning electron microscope. The central area is variable in both size and in the irregularity of the adjacent striae, and in the smallest individuals the central area may be vestigial. The full range of variation observed in these populations was: length (12.5–38 μm), breadth (5–13 μm), and striae (16–20 in 10 μm in the center to 18–24 in 10 μm at the ends).

**Stauroneis producta** Grun. Figures 12 and 13

Distribution: Typha Pond (*HDSM 727, 728*), Reservoir (*HDSM 729*), Tern Pond (*HDSM 732*), The Marsh (*HDSM 741–744*), Tub Pond (*HDSM 747*).

Hustedt (1959) gave a minimum valve length of 30 μm and minimum breadth of 8 μm for this species. The range in the Penikese populations was a length of 13.5–38.2 μm and a breadth of 4.5–10.2 μm. As the size of the individuals decreases there is a continuous reduction in the rostrateness of the valve ends, until in the smallest individuals the ends are very slightly produced or just rounded (Figure 12).

**Amphora coffeiformis** (Ag.) Kütz. var. **coffeiformis** and var. **perpusilla** (Grun.) Cl. Figures 14–16

Distribution: South Pond (*HDSM 722–726*), Tub Pond (*HDSM 745–747*).

In var. *coffeiformis* the dorsal striae of the valve in these populations varied from 19 in 10 μm (center) to 28 in 10 μm (ends); the ventral striae were about 40 in 10 μm. Also, the raphe is not in the center of the axial area but displaced toward the ventral striae and separated from the dorsal striae by a thick external ridge of silica running the entire length of the valve. Recognition of var. *perpusilla* in the light microscope is replete with uncertainty. Only the valve and frustule shape, the presence of a raphe and the general orientation and density of the dorsal striae can be seen. Its relationship to *A. coffeiformis* is not apparent. Under the scanning electron microscope, however, the ultrastructure of the striae, the position of the raphe and the elongated ridge of silica that runs dorsal to the raphe indicate its affinity. In the Penikese populations individuals of var. *perpusilla* were as small as 7.5 μm in length with dorsal striae around 30 in 10 μm. Although ventral striae are not resolvable in the light microscope, they are present at a density of 55–60 in 10 μm.

**Nitzschia frustulum** var. **subsalina** Hust. Figures 17–20
Distribution: South Pond (*HDSM 722–726*).

This variety was quite variable in the Penikese collections. Individuals ranged from 6.8–14.6 μm long to 3.0–3.3 μm broad with 14–18 fibulae (= keel punctae) in 10 μm and 32–36 striae in 10 μm. The striae were a little finer than the 29 in 10 μm that Hustedt (1930) originally indicated for var. *subsalina.* Aleem (1949) illustrated a population he described as "*Nitzschia frustulum* (Kütz.) Grun. var. ? (*cf.* var. *subsalina* Hust.)" which conforms to the Penikese populations except the striae are coarser (27–29 in 10 μm). The smallest individuals in the populations (Figure 20) agree with the description of *N. frustulum* var. *indica* Skvortz. (Skvortzow, 1935) except his individuals are not as broad (length: 5.0–8.5 μm; breadth: 2.0–2.5 μm; fibulae: 18 in 10 μm; striae: 30–35 in 10 μm). Also, Hohn and Hellerman (1966) described *N. barca* (length: 8.9 μm; breadth: 3.6 μm; fibulae: 17 in 10 μm; striae: 30 in 10 μm) which is not different from my Figure 19, except the striae are slightly coarser. I find the distinctness of all these taxa questionable.

**Nitzschia obtusa** var. **scalpelliformis**
f. **nipponica** Negoro Figures 21–22
Distribution: South Pond (*HDSM 722, 723*), Typha Pond (*HDSM 727, 728*), Reservoir (*HDSM 729*), Tern Pond (*HDSM 730, 731*), Leper Pond (*HDSM 733–736*), Zinn's Pond (*HDSM 737–739*), The Marsh (*HDSM 742, 743*), Tub Pond (*HDSM 747*).

*Nitzschia obtusa* var. *scalpelliformis* is a common diatom along the western Atlantic coast; however, forma *nipponica* Negoro (Negoro, 1944) is unreported from this region. This may be more an artifact of the general unavailability of Negoro's literature than the absence of the taxon from the area. The concept of var. *scalpelliformis* in the literature (Hustedt, 1930; Peragallo & Peragallo, 1897–1908; Van Heurck, 1880–1885) circumscribes a group of relatively large diatoms (60–110 μm long by 6–13 μm broad) with coarse fibulae (5–9 in 10 μm) and moderately dense striae (26–30 in 10 μm). The variation observed in the Penikese populations was: length (23–46 μm), breadth (4.0–4.5 μm), fibulae (9–11 in 10 μm) and striae (36 in 10 μm). Larger individuals have subrostrate ends (Figure 22) while smaller ones are more rounded but unilaterally attenuated at the ends (Figure 21). These Penikese individuals are quite comparable to f. *nipponica,* which was described as having a length of 17–40 μm, a breadth of 3–4 μm, 9-11 fibulae in 10 μm, and striae "resolved only with extreme difficulty" (Negoro, 1944). Manguin (1942, p. 155, pl. 4, fig. 82) illustrated an unnamed form of *N. clausii,* which is identical to my Figure 22, and he indicates its similarity to *N. obtusa* var. *scalpelliformis*.

**Caloneis lenzii** Krasske Figure 23
Distribution: Typha Pond (*HDSM 727, 728*)

This species which was originally described from South America (Krasske, 1951) is reported here for the first time in North America.

## LITERATURE CITED

ALEEM, A. A. 1949. Distribution and ecology of marine littoral diatoms. Consideration of the littoral diatom-flora with special reference of forms living in gelatinous tubes. Bot. Notiser [**1949**]:414–440.

CLEVE, P. T. 1895. Synopsis of the naviculoid diatoms. K. Svenska Vetensk-Akad. Handl. **27**(3):1–219, pl. 1–4.

CONGER, P. C. 1924. Diatoms. p. 191–195, 215–218. *In:* I. F. Lewis, Ed. The flora off Penikese Island, fifty years after. Rhodora **26**(310): 181–195, 211–219, 222–229

CROASDALE, H. T. 1935. The freshwater algae of Woods Hole, Massachusetts. Published by the author, Philadelphia. 134 p. 8 pl.

______. 1948. II. Fresh and brackish water algae of Penikese Island. Rhodora **50:** 269–279.

HELMCKE, J. G., & W. KREIGER. 1953. Diatomeenschalen im electronenmikroscopischen bild. Teil **I.** Transmare-Photo G. M. B. H., Berlin.

______, ______, & J. GERLOFF. 1974. Diatomeenschalen im electronenmikroscopischen bild. Teil **VIII.** J. Cramer, Lehre.

HENDEY, N. I. 1964. An introductory account of the smaller algae of British coastal waters. Vol. V. Bacillariophyceae (Diatoms). Minist. Agric., Fish & Food, Fish. Invest., Ser. **IV:**1–317. 45 pl.

HOHN, M. H., & J. HELLERMAN. 1966. New diatoms from the Lewes-Rehoboth Canal, Delaware and Chesapeake Bay area of Baltimore, Maryland. Trans. Amer. Microsc. Soc. **85**(1):115–130.

HUSTEDT, F. 1930. Bacillariophyta (Diatomeae). Heft 10. 466 s. 875 abb. *In:* A. Pascher, Ed. Die Süsswasser-Flora Mitteleuropas. G. Fischer, Jena.

______. 1955. Marine littoral diatoms of Beaufort, North Carolina. Duke Univ. Mar. Station Bull. **6:**1–67.

______. 1959. Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. Band VII, Teil 2, Leif. 6, p. 737–845. *In:* L. Rabenhorst. Kryptogamen-Flora von Deutschland, Österreich und der Schweiz. Akad. Verlagsgesellschaft, Geest & Portig, K.-G., Leipzig.

KRASSKE, G. 1951. Die Diatomeenflora der Açudas Nordostbrasiliens. Arch. Hydrobiol. **44**:639–653.

LURIE, E. 1974. Nature and the American mind: Louis Agassiz and the culture of science. Science History Publications, New York. 121 p.

MANGUIN, E. 1942. Contribution à la connaissance des Diatomées d'eau douce des Açores. Trav. Algol., ser. 1. (Revue Algol., t. 13) **2**:11–160, 4 pl.

NEGORO, K. 1944. Untersuchungen über die Vegetation der mineralogenazidotrophen Gewässer Japans. Sci. Rep. Tokyo Bunrika Daig. **6**(101):231–374.

PATRICK, R., & L. R. FREESE. 1960. Diatoms (Bacillariophyceae) from northern Alaska. Proc. Acad. Nat. Sci. Phila. **112**(6):129–293.

———, & C. W. REIMER. 1966. The diatoms of the United States exclusive of Alaska and Hawaii. Vol. 1. Fragilariaceae, Eunotiaceae, Achnanthaceae, Naviculaceae. Acad. Nat. Sci. Phila. Monogr. **13**. 699 p. 64 pl.

PERAGALLO, H., & M. PERAGALLO. 1897–1908. Diatomées Marines de France et des Districts Maritimes Voisins. Texte, 491 p. Atlas, 137 pl. Micrographe-Ed., à Grèz-sur-Loing.

SKVORTZOW, B. W. 1935. Diatoms from Calcutta, India. Philipp. J. Sci. **58**(2):179–192, 1 pl.

VAN HEURCK, H. 1880–1885. Synopsis des Diatomées de Belgique. Atlas, (1880–1883), 132 pl., Ducajeut Cie., Anvers. Texte, (1885), 235 p., Brouwers & Co., Anvers.

VANLANDINGHAM, S. L. 1975. Catalogue of the fossil and recent genera and species of diatoms and their synonyms. Part V. *Navicula*. p. 2386–2963. J. Cramer, Vaduz.

VOIGT, M. 1943. Sur certaines irrégularités dans la structure des diatomées. Revue Algol., N'lle ser., **2**:85–97.

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# NORTH CAROLINA MARINE ALGAE. VIII. THE REPRODUCTIVE MORPHOLOGY OF *CALLITHAMNION CORDATUM* BØRGESEN (RHODOPHYTA, CERAMIACEAE)

CRAIG W. SCHNEIDER

Since the time of its collection in March, 1906 and its description from 27m in the sound off Cruz Bay in the Virgin Islands (Børgesen, 1909), only one previous report (Børgesen, 1915) has added information to the morphology of *Callithamnion cordatum* Børgesen, and that contained only vegetative data. This taxon has subsequently been collected only from the continental shelves of Bermuda (Collins & Hervey, 1917; Howe, 1918[1]), Southern California and Pacific Baja California (both as *Aglaothamnion cordatum* (Børg.) Feldm.-Maz.; Abbott & Hollenberg, 1976; Dawson, 1962), Florida (Humm, 1964; Croley & Dawes, 1970), Curazao (Díaz-Piferrer, 1964), and Antigua (Taylor, 1969).

During a June 9, 1975 Scuba dive on the wreck of the cargo ship *Suloide*[2] in Onslow Bay, North Carolina, this writer observed a great amount of this pale pink species on macroscopic algae as well as on the hard substrate of the sunken ship. Male, female, and tetrasporic specimens were all present (*CWS 990*).

Two tiny samples of *Callithamnion cordatum* had been collected previously by dredging from R/V *Eastward* in Onslow Bay[3] (June 22, 1970, ♂; June 24, 1971, ♀) and several plants most recently by Scuba[4] (*CWS 78-5*-15, June 16, 1978, ⊕, ♂). Subsequent dives on the *Suloide* in June, as well as other months of 1976, 1977, and 1978 have provided only one additional collection of *C. cordatum* (CWS #78-3-6, June 11, 1978, ⊕). This report adds yet another offshore species to the flora of North Carolina (Searles & Schneider, 1978).

## MATERIALS AND METHODS

The collections of *Callithamnion cordatum* made by diving and

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[1] Taylor (1960) erroneously reported this as Howe (1920), in which no report of *C. cordatum* was made.

[2] WR-13, 34° 32′48″N, 76° 53′43″W, depth top 13m, bottom 21.5m, sunk March 26, 1943.

[3] Station No. 14553, June 22, 1970, 34° 19.6′N, 77° 18.2′W, depth 19m, ♂; Sta. No. 17309, June 24, 1971, 34° 19.4′N, 76° 53.2′W, depth 28m, ♀.

[4] *CWS 78-5*, June 16, 1978, 34° 19.0′N, 76° 53.0′W, depth 32m, ⊕, ♂.

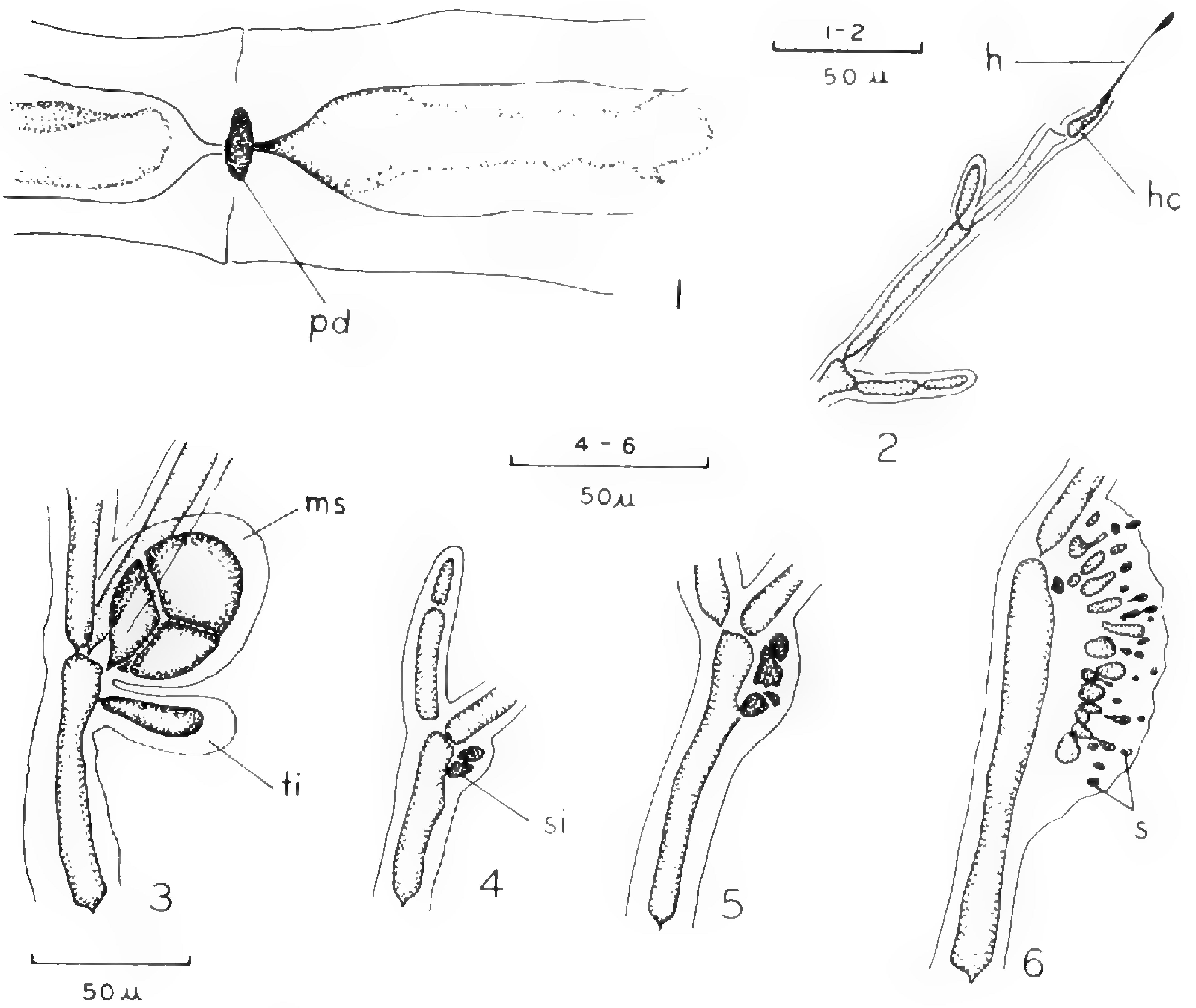
dredging (see Schneider, 1976) were preserved in 10% formalin-seawater. For microscopic examination, the specimens were stained with 1% aniline blue, fixed with 1% HCl, and mounted in 20% Karo-distilled water with phenol added as a preservative. Drawings were made utilizing a camera lucida. Comparative dried material was borrowed from the Botanical Museum, Copenhagen (including type material) and the New York Botanical Garden (Collins & Hervey, as well as Børgesen material). The Carolina specimens are liquid preserved and are deposited in the Duke University Algal Herbarium and the C. W. Schneider Herbarium at Trinity College.

## MORPHOLOGY

**Vegetative.** The Onslow Bay specimens differ slightly from Børgesen descriptions (1909, 1915). These newly collected plants display little, if any, incurving of the branches, as opposed to the marked curvature as drawn by Børgesen (Fig. 202, 1915). Because the type and other borrowed material was dried, it was difficult to discern whether the Virgin Island and Bermudan specimens always showed the habit elucidated by Børgesen (1909, 1915). In the lower portions of the main axis, the large cells have large pit discs (to 25 μm) between them (pd, Fig. 1). Børgesen (1915) observed that unicellular hairs are found most abundantly in the younger portions of the plants (Fig. 2); however, I have observed hairs of nearly twice the length he previously reported, to 250 μm long.

*Callithamnion cordatum* can easily be distinguished from *C. byssoides* Arnott ex Harvey in Hooker, the commoner species of this genus in North Carolina from the intertidal, as well as shelf waters (Schneider, 1974, 1976). *C. cordatum* branches alternately in the lowermost portions and pseudodichotomously or its near approach above, including the ultimate segments. *C. byssoides* is alternately pinnately branched throughout (Harvey, 1846, pl. 262; Taylor, 1960) unlike the habit illustration provided by Børgesen (1915). The overall habit of *C. byssoides* is plumose and much more dense than that of *C. cordatum.*

**Tetrasporic plants.** Tetrasporangia are borne singly, or occasionally in pairs (Fig. 3) or groups of three, distally and adaxially on cells of ultimate or penultimate branches, usually in the upper portions of the plant. The sporangia are obovate (rarely orbicular), evenly or unequally tetrahedrally divided, and 47–50 µm in diameter (including the cell wall) by 55–63 µm long. Although Børgesen (1909) reported sporangia as about 27 × 40 µm (probably not including the cell wall), I have observed a range of 37–43 × 52–55 µm from his Virgin Island specimens. This non-overlap of figures might show significant population differences, but it should be recognized that the Carolina plants were liquid preserved and the Virgin Island plants were dried. Usually, rehydration of dried specimens does not restore full natural cell sizes. No tetrasporangia were found on gametophytic plants from Onslow Bay, as was reported by Børgesen (1909).



Figures 1–6. *Callithamnion cordatum* Borg. **1.** Two lower axial cells of the main axis with a pit disc (pd) between them. **2.** Tip segment with a terminal hair (h) and hair cell (hc). **3.** Tetrasporangial mother cell with a mature sporangium (ms) and a second tetrasporangial initial (ti). **4-6.** Development of the spermatangial cluster and spermatia (s) from the dividing spermatangial initial (si).

**Male plants.** *Callithamnion cordatum* is dioecious. Spermatangia are always produced distally and adaxially on cells of ultimate or penultimate branches of Onslow Bay plants. The developmental sequence from the spermatangial initial cell to spermatia (Figs. 4–6) is similar to the ontogenetic scheme most recently elucidated for other species of *Callithamnion* by Tazawa (1975). Division of the spermatangial initial is distal in early stages (Figures 4–5), but eventually divisions are produced in all directions of 1 plane, making the cluster hemispherical. Each cluster is enclosed in a gelatinous matrix (Fig. 6). Occasionally two spermatangial clusters become confluent due to the more abbreviated branch cells in ultimate portions of the plant, however, the spermatangial initial is always cut off in a distal position. In contrast to North Carolina plants, Dawson (1962) illustrates median, as well as distal, spermatangial clusters from Pacific Baja specimens. Dawson does not discuss or illustrate the position of the spermatangial initial. The development of the spermatangial cluster by repeated division of a single initial, specially formed from a vegetative cell and not incorporated within the plant's vegetative structure, was unique for *Callithamnion* among the many genera studied by Tazawa (1975).

**Female plants.** Although Børgesen (1909) illustrated the 4-celled carpogonial branch and the mature cordate carposporophytes of *Callithamnion cordatum*, the pre- and post-fertilization stages of the female system were not additionally illustrated or elucidated. Onslow Bay specimens allowed for a complete study of these features (Figures 7–18).

Early development of the procarp occurs only a few cells from the

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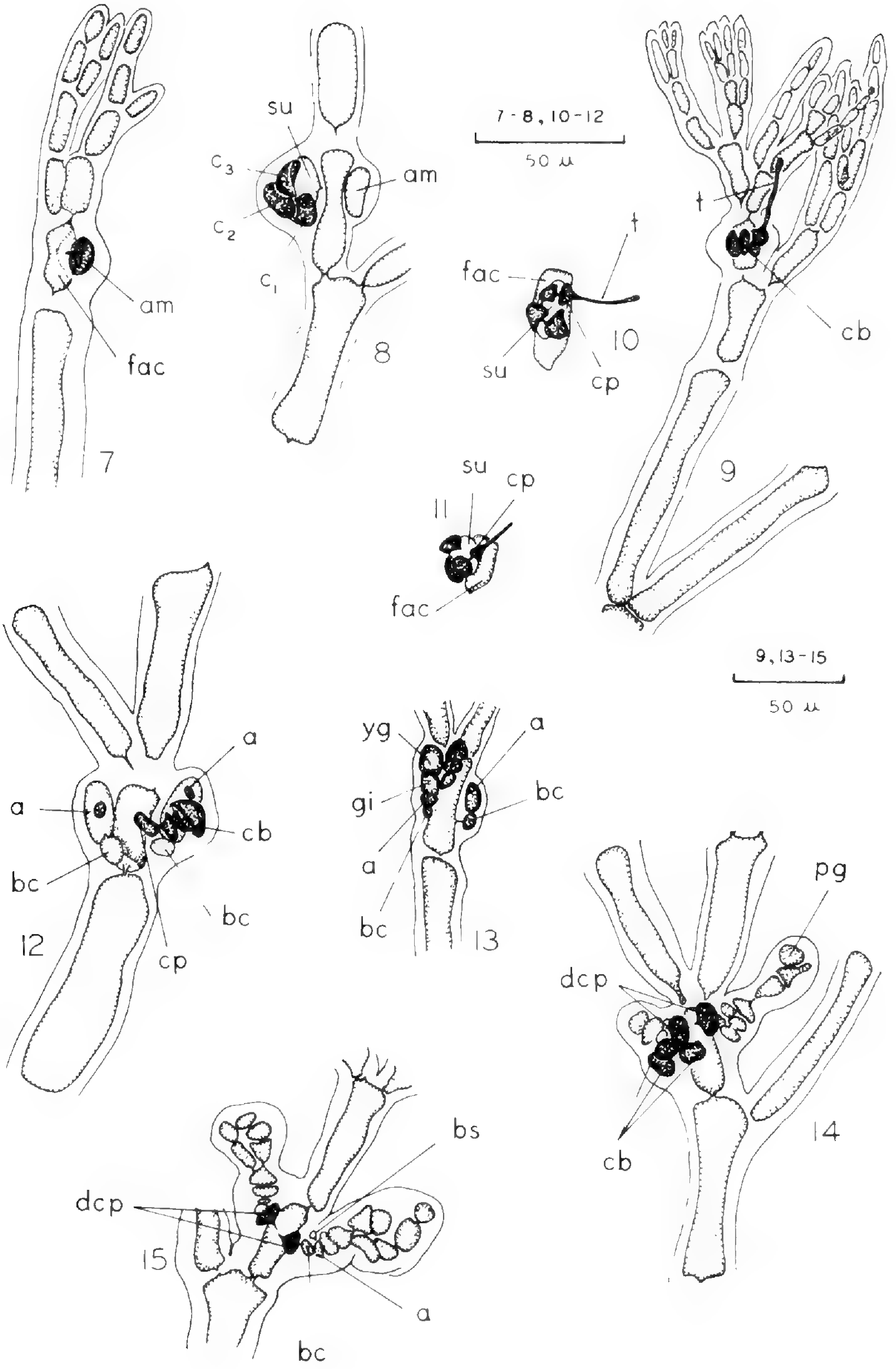
Figures 7–15. *Callithamnion cordatum* Børg. **7.** First auxiliary mother cell (am) being cut off the fertile axial cell (fac). **8.** Supporting cell (su) and first 3 cells of carpogonial branch (c1-c3). The second auxiliary mother cell cut off in an adjacent position. **9.** Four celled straight carpogonial branch (cb) with trichogyne (t). **10 & 11.** Carpogonial branches on supporting cells (su) and fertile axial cells (fac) in a curved arrangement. Carpogonia (cp) with trichogynes (t). **12.** Post-fertilization carpogonial branch, the carpogonium (cp) without a trichogyne. Auxiliary cells (a) cut off the basal cells (bc). **13.** Young gonimoblast (yg) cut off the gonimoblast initial (gi) of one auxiliary cell (a). Second auxiliary cell branch not yet producing gonimoblasts. Basal cell = bc. **14.** Primary gonimoblasts (pg) developing while carpogonial branch (cb) and divided carpogonium (dcp) remain intact. Note early fusion in right hand gonimoblast. **15.** Branching pattern of 1° gonimolobes. Basal septum (bs) cut off the auxiliary cell (a).


am
fac
7
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$c_3$
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7-8, 10-12
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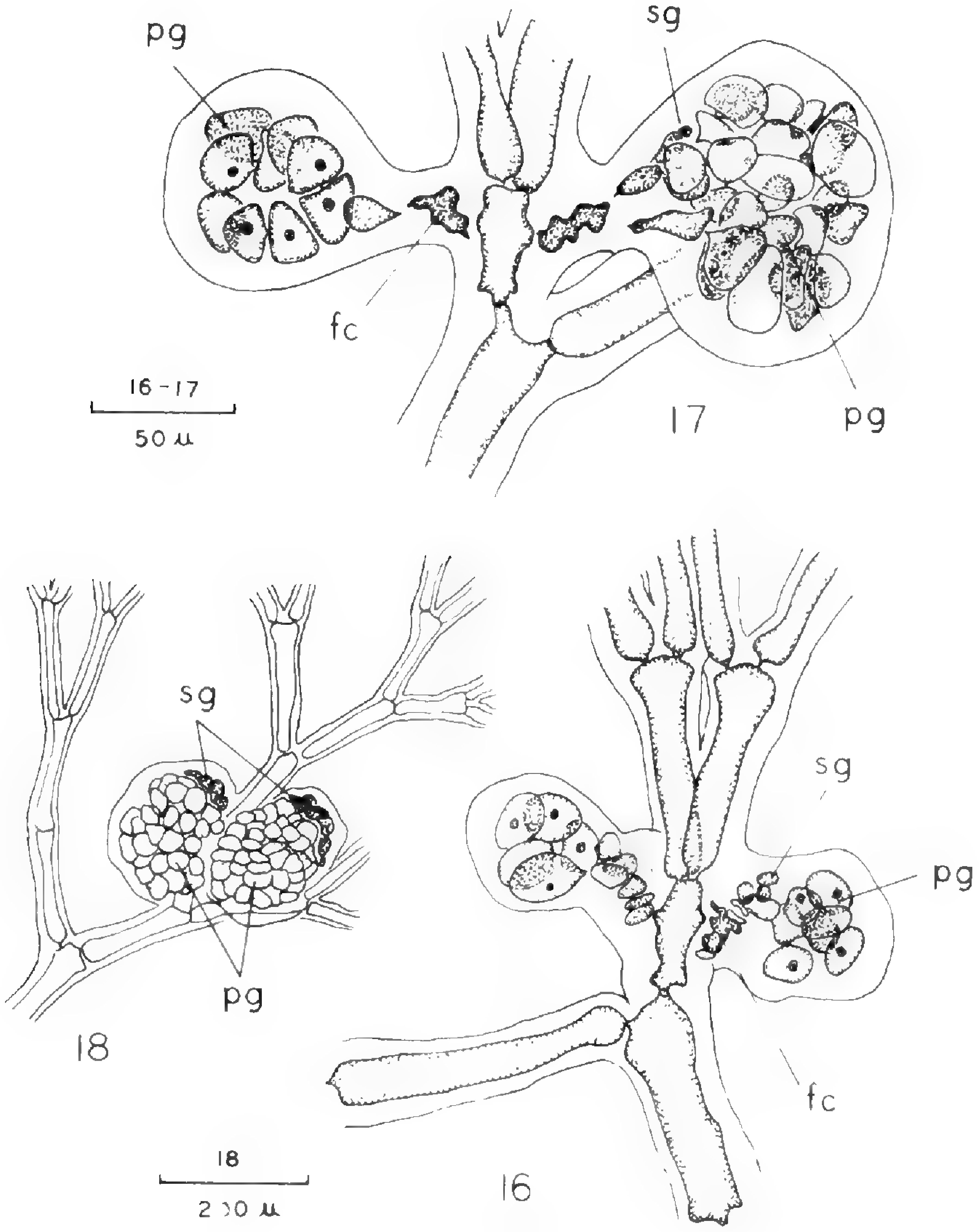
apex of the branches. An auxiliary mother cell (am), or pericentral cell (Fritsch, 1945), is cut off from an intercalary fertile axial cell, usually shorter in length than the cells contiguous with it (fac, Fig. 7). Shortly thereafter, this auxiliary mother cell acts as a supporting cell (su) and sequentially cuts off a four-celled carpogonial branch (c1-c3, Fig. 8; cb, Figs. 9–11). This fertile branch is cut off in a straight (Fig. 9) or curved arrangement (Figs. 10–11). Trichogynes of terminal carpogonia (cp) are oriented in various directions relative to the vegetative axis. The second auxiliary mother cell is cut off the same fertile axial cell in an adjacent position early in carpogonial branch development, similar in sequence to one other species, *Callithamnion reductum* Baardseth (1941). This timing is, however, inconsistent with typical *Callithamnion* development (Oltmanns, 1898; Westbrook, 1927), where both auxiliary mother cells are cut off prior to carpogonial branch formation. Once fertilization occurs, the trichogyne withers and the auxiliary mother cells divide unequally into distal auxiliary cells (a) and proximal basal cells (bc, Fig. 12). The fertilized carpogonium enlarges and equally divides longitudinally into two cells (dcp, Figs. 14–15). In the typical post-fertilization *Callithamnion* scheme (Oltmanns, 1898 for *C. corymbosum* (J. E. Sm.) C. Ag.), these divided carpogonial cells each form a connecting cell which ultimately fuses with the respective auxiliary cell. I have not observed such connecting cells for *C. cordatum,* but do not doubt their existence. Once the diploid nucleus is received, each auxiliary cell forms a primary (1°) gonimoblast, though not at the same time (yg, Figure 13). Cells of the carpogonial branch usually persist into the gonimoblast stage (Figures 14–15). As the gonimoblasts form distally, the haploid auxiliary cell nucleus, no longer necessary for post-fertilization development, is isolated in a basal septum (bs, Figure 15). The basal and auxiliary cells begin to fuse as the 1° gonimoblast forms (Figure 14) and these eventually fuse with a few early gonimoblast cells to form a large fusion cell (fc, Figures 16–17). Sometime after the 1° gonimolobe has developed, a secondary (2°) gonimolobe is produced from a differentiated, unfused primary gonimoblast member (sg, Figures 16–17). The 1° and 2° gonimoblasts are ovoid (Figures 16–17) and each cell of the gonimolobe eventually becomes a viable carpospore. Carpospores of the 1° gonimolobe range in size from 30–50 μm in diameter with 2° gonimolobe carpospores being somewhat smaller. The carposporophyte, then, from its respective fertile axial cell is composed of four major gonimolobes (Fig. 18). Each half is often cordate in shape (Børgesen, 1909, Figures 5G, 6; 1915, Figures 202, 203G, 204) but occasionally they are irregularly ovoid (Figure 18).

## DISCUSSION

The reproductive ontogeny for the genus *Callithamnion* was outlined by Oltmanns (1898) and later summarized by Fritsch (1945). This typical sequence of pre- and post-fertilization stages has been



Figures **16–18**. *Callithamnion cordatum* Børg. **16.** Primary (pg) and secondary gonimoblasts (sg), early fusion cell formation (fc). **17.** Later carposporophyte development with 1° (pg) and 2° (sg) gonimolobes and late fusion cells (fc). **18.** Mature irregularly ovoid lobes of carposporophyte.

elucidated for a number of *Callithamnion* species by Kylin (1923), Rosenvinge (1923), Westbrook (1927, 1930), and Levring (1937). One taxon, *C. reductum* has been shown to deviate distinctly from this typical scheme by producing only one auxiliary cell, that being derived from the auxiliary mother cell opposite to the supporting cell which produces the carpogonial branch (Baardseth, 1941). Although *C. cordatum* parallels the typical Oltmanns' stages in most respects, this species initiates its auxiliary mother cells in a fashion similar to *C. reductum.*

*Callithamnion cordatum* was transferred to a newly erected genus, *Aglaothamnion* Feldmann-Mazoyer (1941), a change accepted by Dawson (1962) and Abbott and Hollenberg (1976), but not by all (e.g., Taylor, 1960). The straight/curved carpogonial branches and irregular carposporophytes of *C. cordatum* support previous criticisms (Harris, 1962) of some criteria on which *Aglaothamnion* was based. *C. cordatum* would fall between the two genera, *Callithamnion* and *Aglaothamnion.* Further data on the nuclear status of mature *C. cordatum* vegetative cells are required to relate the present situation to all the criteria used, but this species seems to support retention of *Callithamnion sensu lato.*

The report of *Callithamnion cordatum* from North Carolina adds another northernmost distributional record for an algal species centered in the Caribbean and another species to the subtropical offshore flora of the Carolinas (Schneider, 1976). This species is known from deep water throughout its range, with few exceptions from shallow waters (Díaz-Piferrer, 1964; Humm, 1964). Including this report, 22 species of Ceramiales have now been added to the North Carolina flora since the offshore project began in 1968 (Schneider, 1975). As to the circumstances surrounding the abundance of *C. cordatum* in June, 1975 and its subsequent disappearance from the *Suloide* nothing is known.

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## REFERENCES

ABBOTT, I. A. & G. J. HOLLENBERG, 1976. *Marine Algae of California.* Stanford Univ. Press, Stanford.

BAARDSETH, E. 1941. The marine algae of Tristan da Cunha. Results Norw. Sci. Exped. to Tristan da Cunha, **9**:1–173.

BØRGESEN, F. 1909. Some new or little known West Indian Florideae. Bot. Tidsskr., **30**: 1–19.

———. 1915–1920. The marine algae of the Danish West Indies. Vol. 2, Rhodophyceae. Dansk. Bot. Arkiv., **3**: 1–498.

COLLINS, F. S. & A. B. HERVEY. 1917. The algae of Bermuda. Proc. Am. Acad. Arts. Sci., **53**: 1–195.

CROLEY, F. C. & C. J. DAWES 1970. Ecology of the algae of a Florida Key. I. A preliminary checklist, zonation, and seasonality. Bull. Mar. Sci., **20**: 165–185.

DAWSON, E. Y. 1962. Marine red algae of Pacific Mexico, Part 7. Ceramiales: Ceramiacae, Delesseriaceae. A. Hancock Pac. Exped. **26**: 1–208.

DÍAZ-PIFERRER, M. 1964. Adiciones a la flora marina de Las Antillas Holandesas Curazao y Bonaire. Carib. J. Sci. **4**: 513–543.

FELDMANN-MAZOYER, G. 1941. *Recherches sur les Céramiacées de la Méditerranée Occidentale.* Minerva, Algiers.

FRITSCH, F. E. 1945. *The Structure and Reproduction of the Algae,* Vol. **2**. Cambridge Univ. Press, London.

HARRIS, R. E. 1962. Contribution to the taxonomy of *Callithamnion* Lyngbye emend. Naegeli. Bot. Notiser, **115**: 18–28.

HARVEY, W. H. 1846–1851. *Phycologia britannica . . .* 4 vols. London.

HOWE, M. A. 1918. Algae. *In:* Britton, N.L., *Flora of Bermuda,* 489–540. Scribner, New York.

———. 1920. Algae. *In.:* Britton, N. L. & C. F. Millspaugh, *The Bahama Flora,* 553–618. Scribner, New York.

HUMM, H. J. 1964. Some new records and range extensions of Florida marine algae. *Bull. Mar. Sci.,* **13**: 516–526.

KYLIN, H. 1923. Studien über die Entwicklungsgeschichte der Florideen. Kgl. Svensk. Vetensk.-Akad. Handl., **63**: 1–139.

LEVRING, T. 1937. Zur kenntnis der algen flora der Norwegischen Westkuste. Lunds Univ. Arsskr. N.F., Avd. 2, **33**: 1–147.

OLTMANNS, F. 1898. Zur Entwicklungsgeschichte der Florideen. Bot. Zeitung, **lvi**.

ROSENVINGE, L. K. 1923–4. The marine algae of Denmark. — III. Kgl. Dansk Vidensk. Selsk. Skrifter. vii, Naturvidensk. Og. Mathm. Afa., **7**: 287–486.

SCHNEIDER, C. W. 1974. North Carolina marine algae. III. A community of Ceramiales (Rhodophyta) on a glass sponge from 60 meters. Bull. Mar. Sci. **24**: 1093–1101.

______. 1975. North Carolina marine algae. VI. Some Ceramiales (Rhodophyta), including a new species of *Dipterosiphonia*. J. Phycol., **11**: 391–396.

______. 1976. Spatial and temporal distributions of benthic marine algae on the continental shelf of the Carolinas. Bull. Mar. Sci., **26**: 133–151.

SEARLES, R. B., & C. W. SCHNEIDER. (1978). A checklist and bibliography of North Carolina seaweeds. Bot. Mar. **21**: 99–108.

TAYLOR, W. R. 1960. *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas.* Univ. of Mich., Ann Arbor.

______. 1969. Notes on the distribution of West Indian marine algae particularly in the Lesser Antilles. Contr. Univ. Mich. Herb., **9**: 125–203.

TAZAWA, N. 1975. A study of the male reproductive organ of the Florideae from Japan and its vicinity. Sci. Pap. Algol. Res., Fac. Sci. Hokkaido Univ., **6**: 95–179.

WESTBROOK, M. A. 1927. *Callithamnion scopulorum* C. Ag. J. of Bot., Lond. **65**: 129–139.

______. 1930. *Callithamnion tetricum* (Dillw.) Ag. Ibid., **68**: 193–203.

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# CORRELATION OF ALKALINITY AND THE DISTRIBUTION OF *POTAMOGETON* IN NEW ENGLAND[1]

C. BARRE HELLQUIST

The abundance of lakes and streams in New England provides for a wide variety of aquatic plants. The two main drainage areas in the region are the coastal watershed, with the major rivers draining to the Atlantic Ocean, and the St. Lawrence River watershed. The chemical quality of these waters varies due to the general substrate of a specific area, farming runoff, and pollution. Much of the region lacks any calcareous substrate, hence the waters are often acidic or neutral. The acidic areas occur mainly in the sandy regions of the coastal drainage and the granitic regions inland. This includes all of Rhode Island, most of New Hampshire and Massachusetts, and parts of Maine, Vermont, and Connecticut. Alkaline areas occur over the limestone regions of northeastern Maine, most of Vermont, extreme western Massachusetts and parts of western and southern Connecticut.

The many floristic publications (Fernald, 1950; Gleason, 1952; Fassett, 1957) and some monographs on the genus *Potamogeton* (e.g. Hagström, 1916; Fernald, 1932; Ogden, 1943) indicate that some species of *Potamogeton* occur mainly in acid, alkaline, or brackish waters. A survey of the literature revealed only two studies on the distribution of aquatic macrophytes and water chemistry in the United States. These were carried out by Steenis (1932) in Wisconsin and by Moyle (1945) in Minnesota. Spence (1967) noted plants commonly found in waters of different alkalinities from Scotland.

This investigation was conducted in an attempt to define the ranges of the species of *Potamogeton* in New England in relation to the chemical properties of the waters in which they grow. Initially, pH, total alkalinity, free carbon dioxide, nitrates, total phosphates and chlorides were tested (Hellquist, 1975). Total alkalinity presented the highest correlation with the other factors tested and *Potamogeton* distribution, hence will be discussed here.

The nomenclature in this paper follows Fernald (1950), with modifications of some taxa by Haynes (1974) and Reznicek and Bobette

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[1] Portion of a Ph.D. dissertation written at the University of New Hampshire.

(1976). These authors recognize 40 taxa in northeastern United States and southeastern Canada, while in New England 37 varieties of 30 species are identified.

## SAMPLING AND STATISTICAL PROCEDURES

Field work was conducted at 321 locations throughout New England (Figure 1). Total alkalinity tests followed the procedure of Theroux et al. (1943). Total alkalinity was expressed as mg $CaCO_3$ per liter and converted to mg $HCO_3^-$ per liter to correspond with results indicated in Hutchinson (1975). Many of the sites and regions were chosen beforehand by consulting the herbaria of the University of New Hampshire, Harvard University, and the New England Botanical Club. In these herbaria, specimens noted by many authors (e.g. Fernald, 1932; Ogden, 1943) as alkaline ("hard") or acidic ("soft") water plants were utilized to determine water-quality regions of New England. This procedure was of particular value for locating rarer plants of such regions.

Means, medians, and ranges of the alkalinity were calculated for each species found in at least five field locations. Separations or cluster formation was sought by placing all data into a distribution of difference between means on the basis of alkalinity. A one-way design analysis was conducted to test for significant differences among the six resulting clusters on means other than that on which they had been segregated. A second analysis showed that real difference among the means were present after the clusters were made (Hellquist, 1975).

## RESULTS AND DISCUSSION

The means, medians, and ranges of the alkalinities for all taxa are found in Table 1. *Potamogeton filiformis* var. *macounii, P. vaginatus, P. hillii, P. lateralis, P. diversifolius,* and one hybrid *P.* × *longiligulatus,* were not found at a sufficient number of locations to make computation of the summary data meaningful. Figure 3 indicates the alkalinity range of *Potamogeton* taxa found in New England waters.

Statistical means for the major watersheds studied in New England (Figure 2) reveal that the alkaline regions occur in western New England and the St. John River drainage of Aroostook County, Maine. A comparison of these values with plant distribution discloses a marked effect of alkalinity in the range of *Potamogeton* in New England.

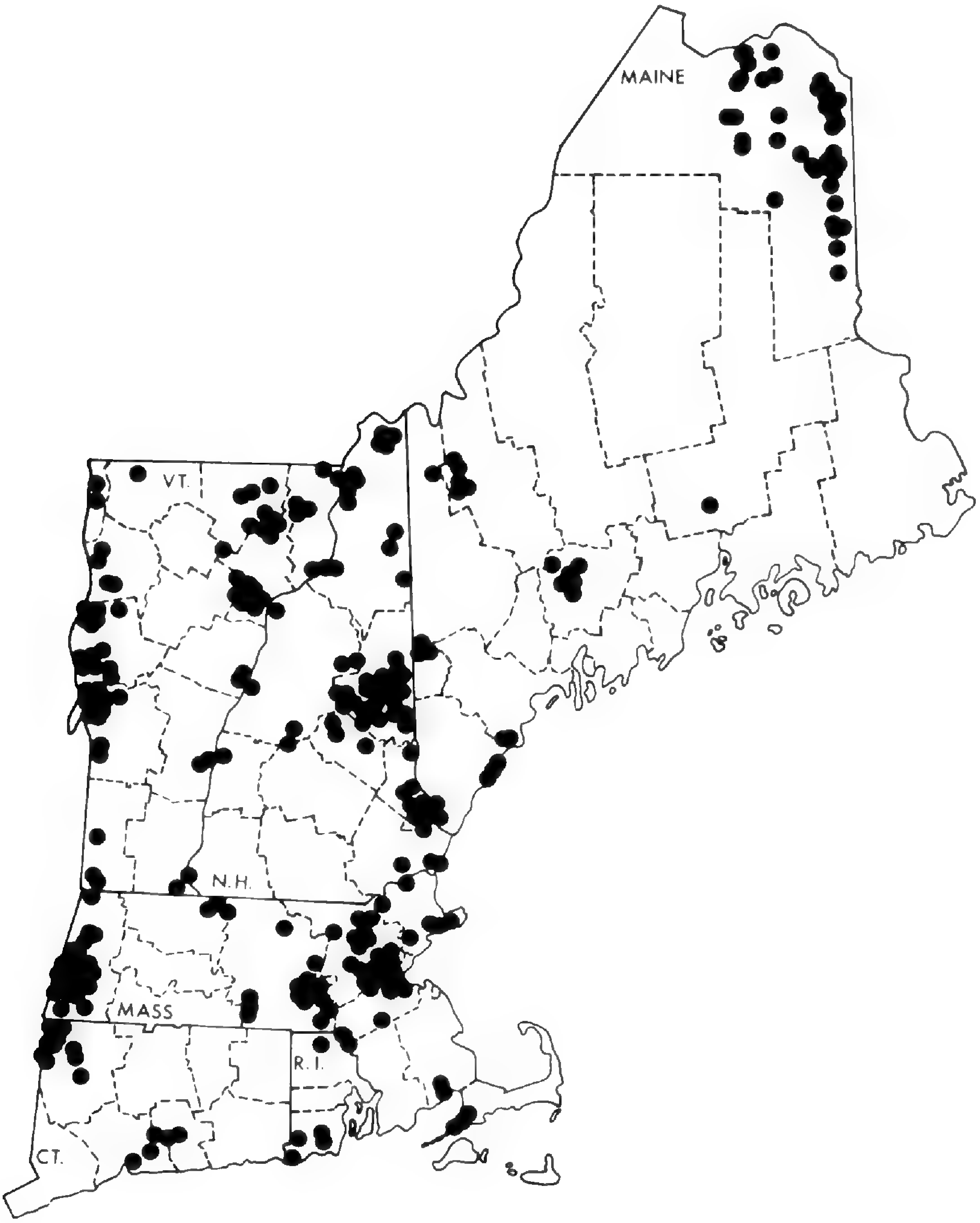


Figure 1. Sampling locations in New England.

Table 1.

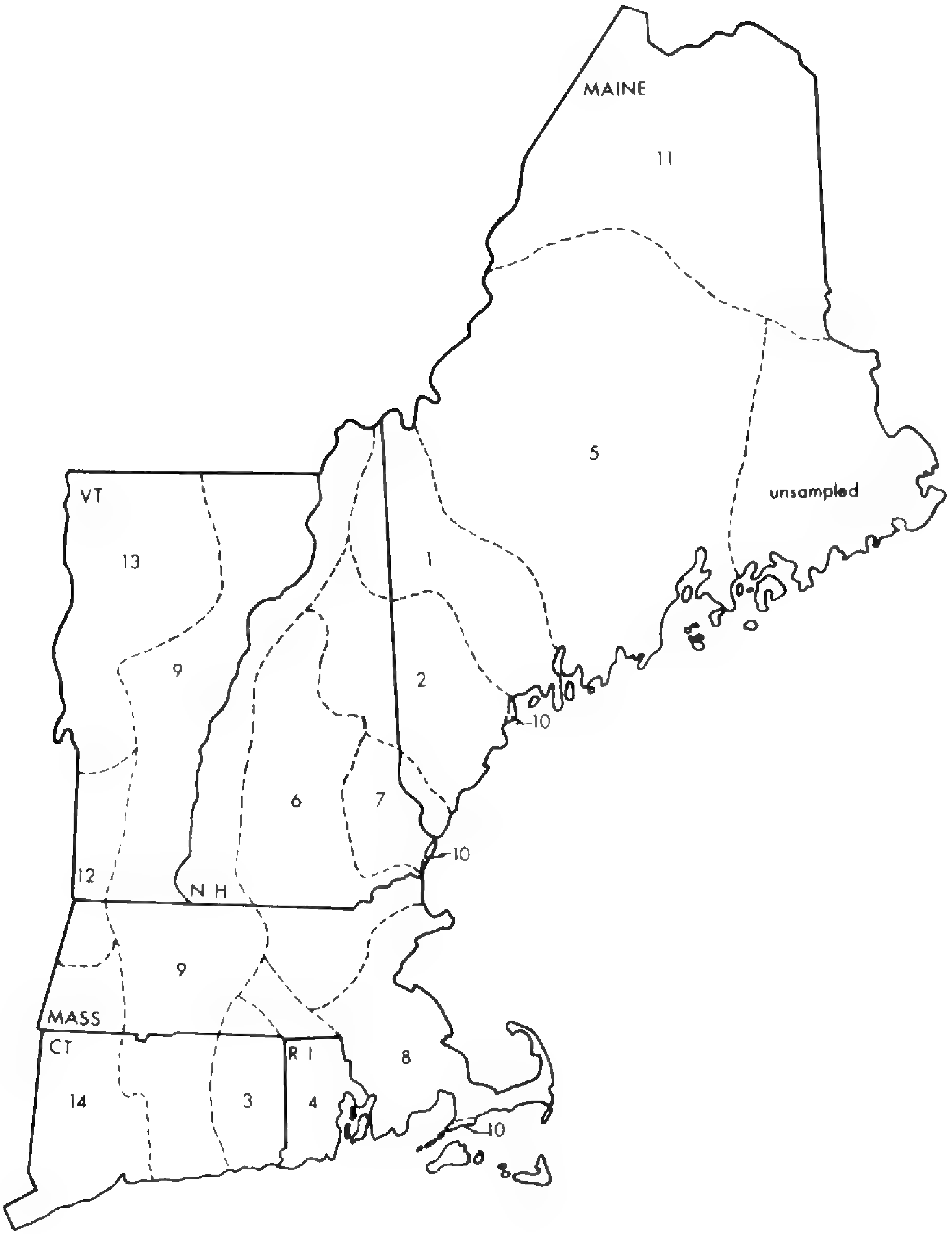
**Occurrence of New England *Potamogeton* and observed alkalinity in lake and stream waters.***

| Species | Alkalinity (mg $HCO_3^-$ liter$^{-1}$) Mean | Median | Range | Number Analyses |
|---|---|---|---|---|
| *P. filiformis* Pers. var. *borealis* (Raf.) St. John | 80.5 | 77.5 | 29.3–107.4 | 10 |
| *P. filiformis* Pers. var. *macounii* Morong | 92.8 | 103.7 | 67.1–107.4 | 3 |
| *P. vaginatus* Turcz. | 125.7 | 125.7 | | 1 |
| *P. pectinatus* L. | 114.5 | 112.9 | 36.6 282.5 | 26 |
| *P. robbinsii* Oakes | 28.8 | 25.6 | 3.7–122.0 | 49 |
| *P. crispus* L. | 84.9 | 93.4 | 14.6–207.5 | 31 |
| *P. confervoides* Reichenb. | 4.2 | 4.3 | 0.6 - 8.5 | 12 |
| *P. zosteriformis* Fern. | 60.2 | 48.8 | 5.5–150.7 | 74 |
| *P. foliosus* Raf. | 77.1 | 73.2 | 17.1–167.8 | 62 |
| *P. friesii* Rupr. | 86.9 | 84.8 | 42.7–150.7 | 11 |
| *P. strictifolius* Ar. Benn. | 84.8 | 87.3 | 67.1–109.8 | 5 |
| *P. pusillus* L. var. *pusillus* | 74.5 | 68.3 | 30.5–139.7 | 21 |
| *P. pusillus* L. var. *gemmiparus* Robbins | 10.5 | 11.0 | 3.1 - 15.9 | 8 |
| *P. pusillus* L. var. *tenuissimus* Mert. & Koch | 36.9 | 19.5 | 3.1–206.3 | 143 |
| *P.* × *longiligulatus* Fern. | 103.3 | 109.8 | 87.3–112.9 | 3 |
| *P. hillii* Morong | 148.6 | 135.5 | 135.5–161.7 | 2 |
| *P. obtusifolius* Mert. & Koch | 58.3 | 58.5 | 16.5–127.5 | 18 |

Table 1 (continued)

| | | | | |
|---|---|---|---|---|
| *P. lateralis* Morong | 16.5 | 16.5 | | 1 |
| *P. vaseyi* Robbins | 26.6 | 25.6 | 8.5- 54.9 | 11 |
| *P. spirillus* Tuckerm. | 19.2 | 13.4 | 3.1- 70.2 | 78 |
| *P. diversifolius* Raf. | 2.4 | 2.4 | | 1 |
| *P. bicupulatus* Fern. | 7.6 | 5.5 | 1.8- 25.6 | 32 |
| *P. epihydrus* Raf. var. *epihydrus* | 65.6 | 70.2 | 11.0-122.0 | 15 |
| *P. epihydrus* Raf. var. *ramosus* (Peck) House | 21.6 | 13.4 | 2.4-161.7 | 154 |
| *P. alpinus* Balbis var. *tenuifolius* (Raf.) Ogden | 41.0 | 23.8 | 4.9-140.3 | 24 |
| *P. alpinus* Balbis var. *subellipticus* (Fern.) Ogden | 60.8 | 59.8 | 12.2-127.5 | 18 |
| *P. amplifolius* Tuckerm. | 35.6 | 28.1 | 4.3-150.7 | 78 |
| *P. pulcher* Tuckerm. | 11.7 | 10.4 | 3.7- 46.4 | 21 |
| *P. nodosus* Poir. | 88.8 | 75.7 | 6.1-282.5 | 20 |
| *P. gramineus* L. var. *gramineus* | 39.0 | 25.0 | 3.1-150.7 | 85 |
| *P. gramineus* L. var. *maximus* Morong | 18.9 | 15.3 | 3.7- 67.1 | 15 |
| *P. gramineus* L. var. *myriophyllus* Robbins | 22.9 | 20.1 | 4.3 95.2 | 17 |
| *P. illinoensis* Morong | 82.9 | 79.9 | 24.4-150.7 | 24 |
| *P. natans* L. | 41.4 | 20.7 | 3.1-161.7 | 152 |
| *P. oakesianus* Robbins | 8.8 | 6.1 | 2.4- 24.4 | 33 |
| *P. praelongus* Wulfen | 56.4 | 43.9 | 9.8-150.7 | 39 |
| *P. richardsonii* (Ar. Benn.) Rydb. | 53.2 | 43.9 | 16.5-130.6 | 27 |
| *P. perfoliatus* L. var. *bupleuroides* (Fern.) Farw. | 36.3 | 23.8 | 6.1-167.8 | 46 |
| total of sampling locations | 43.0 | 24.2 | 0.6-282.5 | 321 |

**Taxa with less than five observations are not included in the statistical analysis*



| | | | |
|---|---|---|---|
| 1 | Androscoggin River | 6 47 | $HCO_3^-$ (mg liter$^{-1}$) |
| 2 | Saco River | 6 59 | |
| 3 | Thames River | 8 13 | |
| 4 | Rhode Island – southeastern Massachusetts | 9 64 | |
| 5 | Kennebec and Penobscot Rivers | 10 92 | |
| 6 | Merrimac River | 11 69 | |
| 7 | New Hampshire seacoast | 20 54 | |
| 8 | eastern Massachusetts | 27 11 | |
| 9 | Connecticut River | 37 28 | |
| 10 | coastal ponds and streams | 40 44 | |
| 11 | St John River | 56 38 | |
| 12 | Hudson River | 74 11 | |
| 13 | St Lawrence River | 81 04 | |
| 14 | Housatonic River | 95 33 | |

Figure 2. Mean alkalinities of major New England watersheds from present study.

The clusters (Table 2) determined in this study provide a basis for the classification of New England waters. Many *Potamogeton* species may occur over a wide range of alkalinities (Figure 3) encom-

*Table 2*

**Classification of New England waters determined by clusters of *Potamogeton* taxa most commonly found in them.**

**Group I**—alkalinity 0.0–18.3 mg $HCO_3^-$ liter$^{-1}$
- *P. confervoides*
- *P. bicupulatus*
- *P. oakesianus*
- *P. pusillus* var. *gemmiparus*
- *P. pulcher*

**Group II**—alkalinity 18.4–30.5 mg $HCO_3^-$ liter$^{-1}$
- *P. gramineus* var. *maximus*
- *P. spirillus*
- *P. epihydrus* var. *ramosus*
- *P. gramineus* var. *myriophyllus*
- *P. vaseyi*
- *P. robbinsii*

**Group III**—alkalinity 30.6–48.8 mg $HCO_3^-$ liter$^{-1}$
- *P. perfoliatus* var. *bupleuroides*
- *P. amplifolius*
- *P. pusillus* var. *tenuissimus*
- *P. gramineus* var. *gramineus*
- *P. alpinus* var. *tenuifolius*
- *P. natans*

**Group IV**—alkalinity 48.9–73.2 mg $HCO_3^-$ liter$^{-1}$
- *P. richardsonii*
- *P. praelongus*
- *P. obtusifolius*
- *P. zosteriformis*
- *P. alpinus* var. *subellipticus*
- *P. epihydrus* var. *epihydrus*

**Group V**—alkalinity 73.3–109.8 mg $HCO_3^-$ liter$^{-1}$
- *P. pusillus* var. *pusillus*
- *P. foliosus*
- *P. filiformis* var. *borealis*
- *P. illinoensis*
- *P. strictifolius*
- *P. crispus*
- *P. friesii*
- *P. nodosus*

**Group VI**—alkalinity greater than 109.8 mg $HCO_3^-$ liter$^{-1}$
- *P. pectinatus*

passing many groups. The statistical means indicate the possibility of this classification which is similar to that of Spence (1967), except that Spence had three rather than six groups.

**Group I** (alkalinity 0.0–18.3 mg $HCO_3^-$ liter $^{-1}$)

Group I in New England includes *Potamogeton* of "soft" waters, but under extreme circumstances ranging up to 48.8 mg. per liter with a mean less than 10.0 mg. per liter. All of the plants in this group are found mainly along the coastal plain.

*Potamogeton confervoides* is a plant of peaty ponds and soft water regions along the New England coastal plain. High altitude ponds of low alkalinity also contain this species. This is the only pondweed to be found in *Sphagnum* bog ponds in this study. The highest alkalinity encountered was 8.5 mg. per liter. *Potamogeton bicupulatus* (*P. capillaceus* Poiret) was abundant in the sandy-bottomed ponds of eastern New England, where only one location occurred with an alkalinity above 18.3 mg. per liter, the calculated upper limit for group I. *Potamogeton oakesianus* and *P. pulcher* were found in similar waters. The former was located at two areas where the alkalinity was above 18.3 mg. per liter, the highest being 23.8 mg. per liter. *Potamogeton pulcher* is the species which is most often found above the "soft" water limits of 18.3 mg. per liter, the highest being 46.4 mg. per liter. *Potamogeton pusillus* var. *gemmiparus* belongs in this group and tends to support the opinions of some botanists that this is an ecological variety. The narrow foliage of *P. pusillus* var. *gemmiparus* may be a growth form due to the low alkalinity, high acidity, or low nutrient content of the water. Steenis (1932) and Moyle (1945) in their studies did not include any of the above mentioned species from group I except *P. bicupulatus* (*P. capillaceus*). Steenis reported *P. bicupulatus* as occurring in very soft water.

Moyle (1945) and Hutchinson (1975) indicate that the pH may have an important role in plant distribution. Hutchinson (1975) notes that some species of *Potamogeton* do not occur perennially in waters with a pH below 6.0 whatever the calcium content. Hydrogen ion concentration data collected in New England indicates that 12 species of *Potamogeton* occur in some waters with a pH below 6.0. Most of these species are from group I or the ubiquitous group III (Hellquist, 1975)

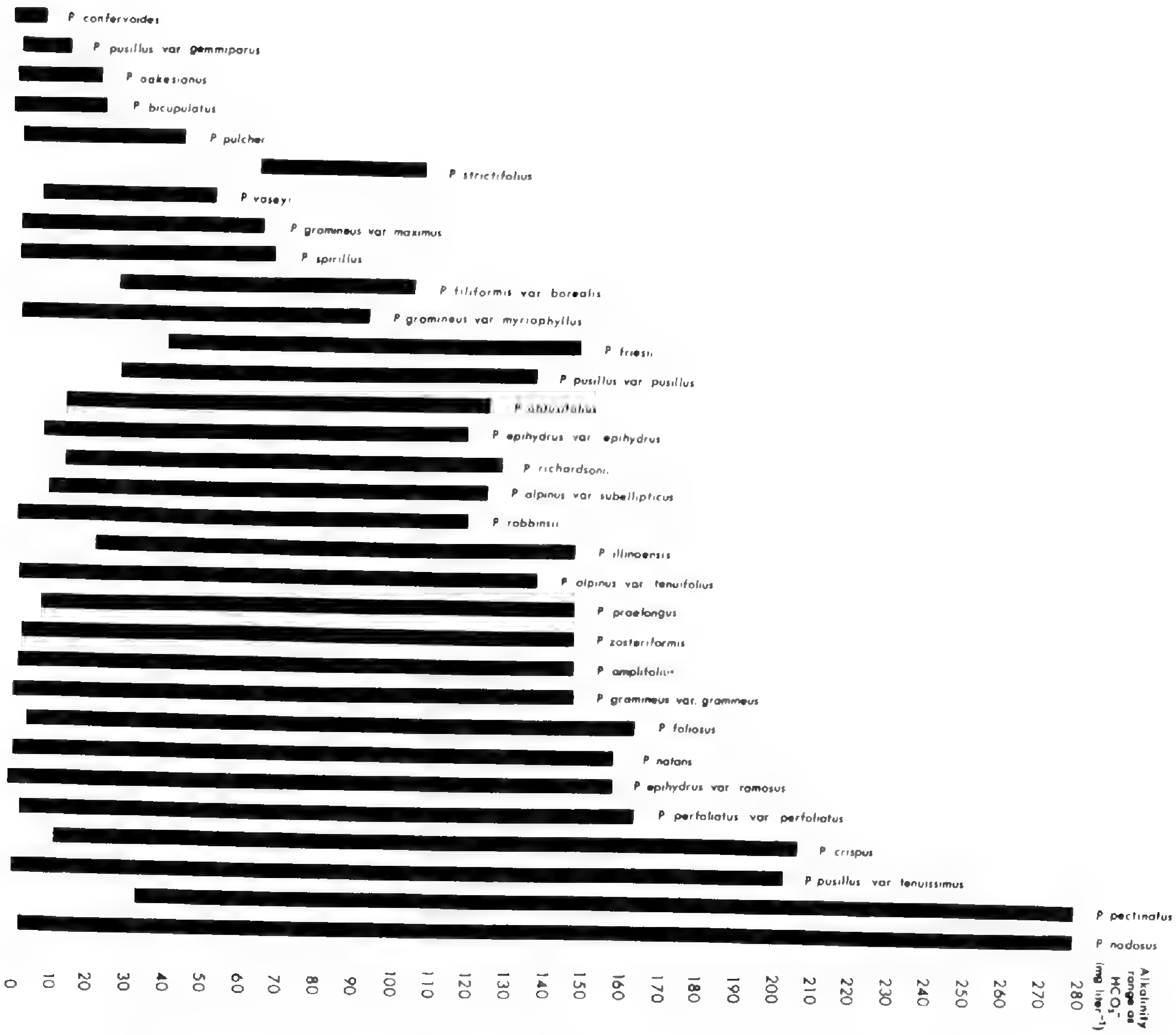


Figure 3. Alkalinity range of *Potamogeton* taxa from New England waters.

**Group II** (alkalinity 18.4–30.5 mg $HCO_3^-$ liter$^{-1}$)

Plants found in groups II–IV are considered to be of moderately alkaline waters. Moyle (1945) in Minnesota found *Potamogeton spirillus* to be the pondweed of the softest water and included it in the soft-water sub-group I of his classification. He included it with the soft-water plants *Eriocaulon septangulare* With. and *Lobelia dortmanna* L. Generally in New England, *P. spirillus* and *P. epihydrus* var. *ramosus* are considered plants of low alkalinity, but they may be found in harder waters, e.g. 60.4 and 69.9 mg. per liter for *P. spirillus* and many above 30.5 mg. per liter for *P. epihydrus* var. *ramosus*. Two of the three varieties of *P. gramineus* are in this group with *P. gramineus* var. *gramineus* in the next group. This may indicate an ecological difference, but the range of means for all three varieties has a width of only 20.1 mg. per liter. Moyle (1945) reported *P. gramineus* var. *graminifolius* f. *myriophyllus* (*P. gramineus* var. *myriophyllus*) from waters above 48.8 mg. per liter. This is considerably higher than found in New England except for one location (95.2 mg/l).

*Potamogeton vaseyi* and *P. robbinsii* are plants of wide geographical distribution in New England. *Potamogeton vaseyi* is confined to waters of a lower alkalinity range (8.5–54.9 mg/l) than *P. robbinsii* (3.7–122.0 mg/l).

**Group III** (alkalinity 30.6–48.8 mg $HCO_3^-$ liter$^{-1}$)

Four of the most commonly encountered taxa in New England occur in this group. These are *Potamogeton natans, P. gramineus* var. *gramineus, P. pusillus* var. *tenuissimus,* and *P. amplifolius.* These plants Moyle (1945) notes are common at all alkalinities in Minnesota. Ogden (1943) notes *P. amplifolius* as a plant of both alkaline and acid waters. Spence (1967) refers to *P. gramineus* as a ubiquitous plant. These statements hold true for these two plants in New England. The other two common pondweeds found throughout New England are in group II. These are *P. epihydrus* var. *ramosus* and *P. robbinsii.*

*Potamogeton perfoliatus* var. *bupleuroides* and *P. alpinus* var. *tenuifolius* are also included in this group. *Potamogeton perfoliatus* is more common along the coastal plain where it is found in waters with an alkalinity as low as 6.1 mg. per liter or in brackish ponds and streams. In western New England it occurs in harder waters up to 167.8 mg. per liter, often with the closely related *P. richardsonii.* *Potamogeton alpinus* has two poorly defined varieties in New England. *Potamogeton alpinus* var. *tenuifolius,* the more common variety, is found in waters with a lower alkalinity than is *P. alpinus* var. *subellipticus* of group IV. Both varieties are found in the northern portions of Maine, New Hampshire and Vermont.

**Group IV** (alkalinity 48.9–73.2 mg $HCO_3^-$ liter$^{-1}$)

This group includes many of the hard-water plants of Moyle (1945), e.g. *Potamogeton richardsonii, P. praelongus,* and *P. zosteriformis.* In New England, plants of this group may occasionally occur in waters of lower alkalinity.

*Potamogeton obtusifolius* is common in northern Maine and northeastern Vermont where it occurs with *P. alpinus* in waters of moderate alkalinity usually below 67.1 mg. per liter. *Potamogeton epihydrus* var. *epihydrus* is also a plant of northern and western New England. This broad-leaved variety has an extremely limited distribution when compared with *Potamogeton epihydrus* var. *ramosus.*

**Group V** (alkalinity 73.3–109.8 mg $HCO_3^-$ liter$^{-1}$)

*Potamogeton* of group V were found almost exclusively in alkaline waters of western New England and northern Maine, in the drainages of the Housatonic, St. Lawrence, Hudson, St. John rivers, and from regions of the Connecticut River drainage (Fig. 3). Moyle (1945) and McCombe and Wile (1971) found *P. crispus* in waters of high nutrients and high alkalinity. In Middlesex County, Massachusetts, *P. crispus* was found in waters with high nutrient levels but with an alkalinity of 24.4 mg. per liter or less. This plant evidently needs high alkalinity and/or high nutrient levels to survive.

*Potamogeton nodosus* is generally found in flowing water (Ogden, 1943). Moore and Clarkson (1967) found *P. nodosus* common in acid streams but not reproducing sexually. Clapham *et al.* (1962) indicate that in England it is found in deeper water along gravelly shores, or in slow-flowing alkaline waters. Moyle (1945) found it in waters of an alkalinity of 50.3–380.8 mg. per liter. In New England *P. nodosus* is common and often fertile in the Lake Champlain valley, especially in pasture streams and rivers of slow current. In eastern New England it is usually found in rivers of swift current with alkalinities below 18.3 mg. per liter. Here the plants are usually sterile. This pondweed appears to favor swift current if a higher alkalinity is not available, possibly because flowing waters are constantly delivering nutrients to the plants.

The remaining taxa in group V were mostly from waters of western New England. Three of these, *Potamogeton filiformis* var. *borealis, P. foliosus,* and *P. friesii* were also from northern Maine. *Potamogeton pusillus* var. *pusillus,* the third variety of this species, is found in this group. Wiegand and Eames (1925) indicate that *P. pusillus* var. *pusillus* is a plant chiefly of brackish or limey waters. It appears that in New England *P. pusillus* var. *gemmiparus* is of acid water, var. *tenuissimus* mainly of acid but also alkaline and brackish waters. Spence (1967) indicated that *P. filiformis* and *P. lucens* of Europe, the latter closely related to *P. illinoensis* of North America, were from calcareous lochs with alkalinities ranging from 42.7–191.6 mg. per liter. This is within the range of *P. illinoensis* in New England. *Potamogeton strictifolius* is rare in New England. During the present study it was found in quiet waters of only five ponds in Vermont. In two of the ponds it appears to have hybridized with *P. zosteriformis* to form the uncommon *P.* × *longiligulatus* (Hellquist, 1977).

**Group VI** (alkalinity greater than 109.8 mg $HCO_3^-$ liter$^{-1}$)

*Potamogeton pectinatus* was statistically isolated to group VI at higher alkalinities. This species occurs in alkaline and brackish water of New England. The two areas where it was found below an alkalinity of 48.8 mg. per liter were brackish ponds along the coast. Many authors (e.g. Metcalf, 1931; Moyle, 1945; Spence, 1967) have indicated that this plant is found in waters of extremely high alkalinity. In North Dakota, Metcalf (1931) found *P. pectinatus* mainly in brackish waters and did not consider it to be a fresh-water indicator. *Potamogeton pectinatus* in Minnesota occurs in waters with alkalinities ranging fromn 38.8 to 458.9 mg. per liter, and is considered a plant of hard and alkali water (Moyle, 1945).

Field studies conducted since this study indicate that *Potamogeton hillii* also belongs to this group. Ten locations as discussed by Hellquist (1977) and one additional site from 1978 field work indicate an alkalinity range of 105.8–316.7 mg. per liter with a mean of 174.5 mg. per liter and a median of 142.7 mg. per liter. Data from the one location in Maine and others in New York and Michigan indicate that *P. vaginatus* also belongs in group VI (Hellquist, 1977).

## SUMMARY

The ranges of the alkalinities for New England taxa were found to compare favorably with those of Moyle (1945) from Minnesota. Certain New England taxa tolerated alkalinity ranges as low as, or lower than, their Minnesota counterparts, especially *Potamogeton robbinsii, P. zosteriformis, P. friesii, P. obtusifolius,* and *P. natans. Potamogeton nodosus* and *P. crispus* occurred at much lower alkalinities than previously reported. Taxa not reported from Minnesota or in sufficient numbers to be reported by Moyle were studied in New England. Plants of the acid water group I may not occur in Minnesota since its waters are not of a low enough alkalinity or pH. A few of these coastal plain species have been reported from Wisconsin and Michigan where favorable conditions exist.

A point that should be remembered is that the results from this study are statistically determined and in some cases offer excellent information to help further the knowledge of *Potamogeton* distribution. Plants in the field may often be found in habitats which seem completely alien to them but seem to do quite well, hence many exceptions exist.

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## LITERATURE CITED

CLAPHAM, A. R., I. G. TUTIN, & E. F. WARBURG. 1962. Flora of the British Isles. 2 ed. Cambridge Univ. Press. Cambridge. 1269 pp.

FASSETT, N. C. 1957. A manual of aquatic plants. Univ. Wisconsin Press. Madison. 405 pp.

FERNALD, M. L. 1932. The linear-leaved North American species of *Potamogeton* section Axillaries. Mem. Am. Acad. Arts. Sci. **17**: 1–183.

———. 1950. Gray's manual of botany. 8 ed. American Book Co., New York. 1632 pp.

Gleason, H. A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. V. 1. Hafner Publishing Co., Inc. New York. 482 pp.

Hagström, J. O 1916. Critical researches on the Potamogetons. Kong. Avenska Vetenskapsakad. Handl. **55:** 1-281.

Haynes, R. R. 1974. A revision of the North American *Potamogeton* subsection Pusillii (Potamogetonaceae). Rhodora. **76:** 564-649.

Hellquist, C. B. 1975. Correlation of selected dissolved substances and the distribution of *Potamogeton* in New England. Ph. D. thesis. Univ. New Hampshire. 269 pp.

______. 1977. Observations on some uncommon vascular aquatic plants in New England. Rhodora **79:** 445-452.

Hutchinson, G. E. 1975. A treatise on limnology V. 3. Limnological botany. Wiley Press, New York. 660 pp.

McCombe, A. M., & I. Wile. 1971. Ecology of aquatic vascular plants in southern Ontario impoundments. Weed Sci. **19:** 225-228.

Metcalf, F. P. 1931. Wild-duck food on North Dakota lakes. U. S. Dep. Agric. Tech. Bull. no. **221.**

Moore, J. A., & R. B. Clarkson. 1967. Physical and chemical factors affecting vascular aquatic plants in some acid stream drainage areas of the Monongahela River. Proc. W. Va. Acad. Sci. **39:** 83-89.

Moyle, J. B. 1945. Some chemical factors influencing the distribution of aquatic plants in Minnesota. Am. Midl. Nat. **34:** 402-420.

Ogden, E. C. 1943. The broad-leaved species of *Potamogeton* of North America north of Mexico. Rhodora. **45:** 57-105, 119 163, 171-214.

Reznicek, A. A. & R. S. W. Bobbette. 1976. The taxonomy of *Potamogeton* subsection Hybridii in North America. Rhodora. **78:** 650-673.

Spence, D. H. N. 1967. Factors controlling the distribution of freshwater macrophytes with particular reference to the lochs of Scotland. J. Ecol. **55:** 147-170.

Steenis, J. H. 1932. Lakes of Sawyer County. Bull. Wis. Dep. Agric. and Markets. no. **138.**

Theroux, F. R., E. F. Eldridge, & W. L. Mallman. 1943. Laboratory manual for chemical and bacterial analysis of water and sewage. McGraw-Hill Book Co., Inc. New York. 274 pp.

Wiegand, K. M., & A. J. Eames. 1925. The flora of the Cayuga Lake basin, New York, vascular plants, Memoir **92.** Cornell Univ. Agric. Exp. Sta.

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# THE GENERIC RELATIONSHIP OF *SARACHA* AND *JALTOMATA* (SOLANACEAE; SOLANEAE)[1]

TILTON DAVIS IV

The genus *Saracha* R. & P. has been confused with other genera in the tribe Solaneae, namely *Bellinia, Jaltomata, Poecilochroma, Hebecladus,* and *Dunalia.* This confusion has resulted from the misinterpretations of a complex nomenclatural history, and until recently (Gentry 1973, 1974) has not received serious attention. This paper elucidates the nomenclature of *Saracha* with respect to these genera. A key to *Saracha* and *Jaltomata* and some other closely related genera is included.

## NOMENCLATURAL HISTORY

The original description of the genus *Saracha* R. & P. in the "Florae Peruvianae et Chilensis Prodromus" (1794) included a diagnosis of unique characters separating it from other genera in the family, but did not include the description of any species. In 1799, five species were described in the second volume of the "Florae Peruvianae et Chilensis". A comparison of the original description and plate of *Saracha,* and the description of these five species shows that the first described species, *S. punctata,* clearly typifies the genus. Morton (1938) and Gentry (1973, 1974) reached a similar conclusion.

Roemer and Schultes (1819) changed the name *Saracha* to *Bellinia.* This change was made in order to prevent confusion of *Saracha* R. & P. with the earlier genus *Saraca* L. (Caesalpiniaceae). I do not recognize *Saracha* R. & P. as a later homonym of *Saraca* L. and therefore, *Bellinia* is placed in synonymy with *Saracha.*

Similarly, Miers (1848) described the genus *Poecilochroma* with *Saracha punctata* R. & P. as its type. In 1853, Miers suppressed *Poecilochroma* and placed all the species into *Saracha,* but later (1857) he again changed his opinion, and preserved *Poecilochroma* as he had originally established it. Because *Poecilochroma* was based on the type of the genus *Saracha,* it is illegitimate and must be placed in synonymy.

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[1] Based on part of a thesis submitted to the Graduate School of the University of Missouri, St. Louis in partial fulfillment of the requirements for the degree of Master of Science.

Further consideration was not given to *Saracha* until Macbride (1930, 1962) and Morton (1938) attempted to resolve the nomenclatural difficulties created by Miers. Both recognized that the establishment of *Poecilochroma* was erroneous. Nevertheless, Macbride (1930) suggested a continuation of Miers' nomenclature by applying the name *Saracha* to those species other than the type *S. punctata* R. & P., and implied that the latter was to serve as the type of *Poecilochroma*. Morton (1938) believed, ". . . both genera [were] relatively unimportant, [and] no great confusion would result from changes of name [in order to correct the nomenclature]," but concurred with Macbride by naming still another species, *Saracha confinis* Morton. Later, Macbride (1962) confused *Hebecladus* Miers with *Saracha* R. & P., but I consider the former a distinct genus, and regard it as a close relative of the non-typical species of *Saracha*.

The most recent treatment of *Saracha* was by De Rojas (1974). She placed *Poecilochroma* into synonymy with both *Saracha* R. & P. and *Dunalia* H. B. K. This placement of *Poecilochroma* with *Dunalia* by implication also places *Saracha* with *Dunalia* since *Poecilochroma* is based on the type of *Saracha*. Consideration of the type description (Humbolt, et al., 1818) and the plate (tab. CXCIV) suggests that *Saracha* and *Dunalia* are best treated as different genera.

The elucidation of the nomenclature now establishes the correct name for *Poecilochroma* as *Saracha*, and the correct name for those species believed to be atypical of *Saracha* R. & P. as *Jaltomata* Schlechtendal (Gentry, 1973).

In 1838, Schlechtendal described *Jaltomata* with one species, *J. edulis*, from Mexico. In 1839, he reduced the genus to synonymy with *Saracha*, and changed the epithet *edulis* to *jaltomata*. This procedure resulted in an illegitimate name when placed in synonymy with *Saracha*. I recognize *Jaltomata* as a distinct genus, and therefore *J. edulis* must serve as the type species.

Gentry (1973, 1974) also recognized the genus *Jaltomata* and transferred two species that were previously aligned with *Saracha* as *J. procumbens* (Cav.) Gentry and *J. confinis* (Morton) Gentry. Many species (ca. 60) have been described for *Saracha*, and preliminary evidence indicates most of these should be referred to *Jaltomata*. A biosystematic study of *Jaltomata* now in progress will

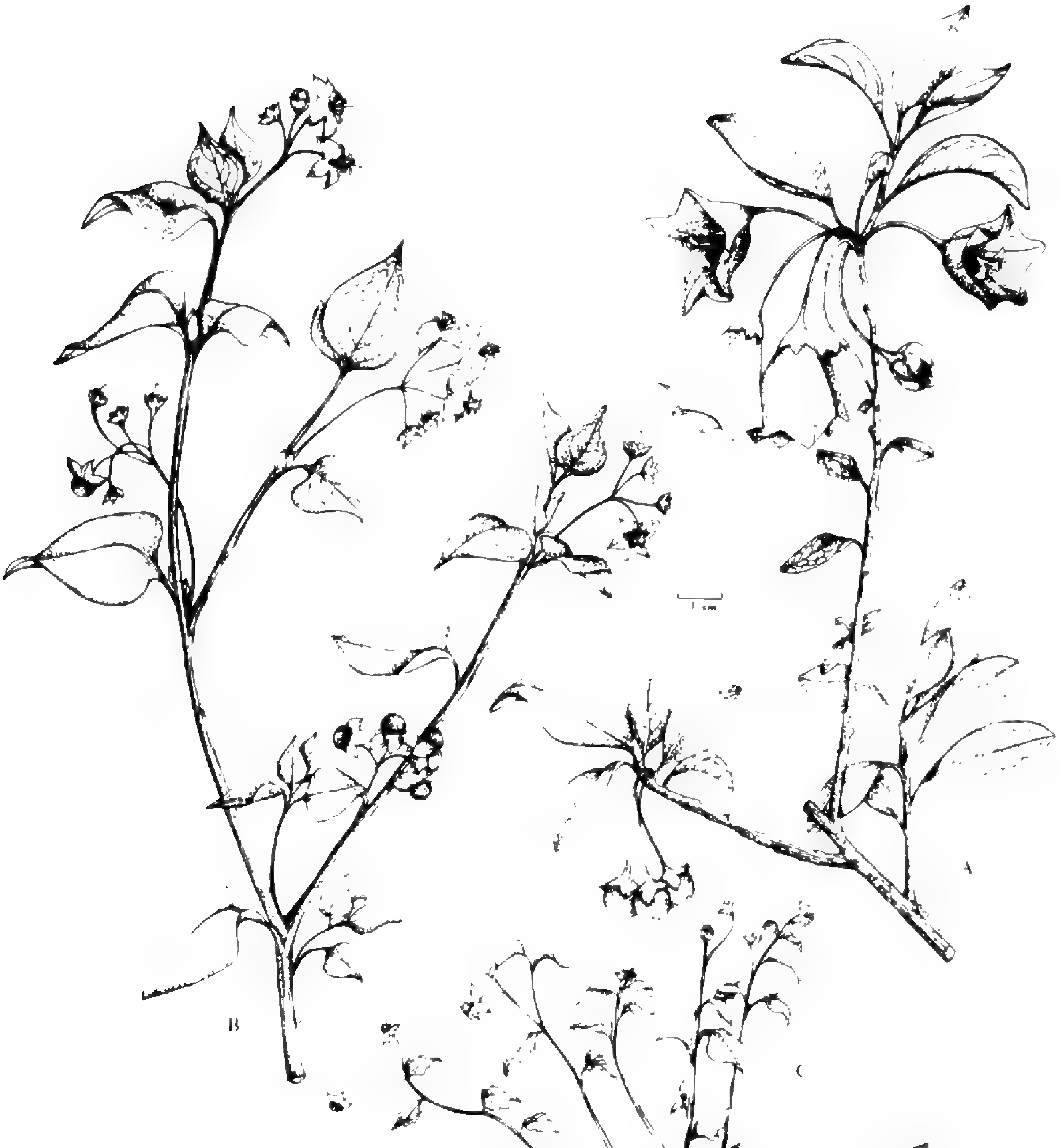

Figure 1. A. *Jaltomata procumbens* (Cav.) Gentry. B. *Saracha punctata* R. & P. C. *Jaltomata confinis* (Morton) Gentry. Note the different inflorescences and floral size and shape.

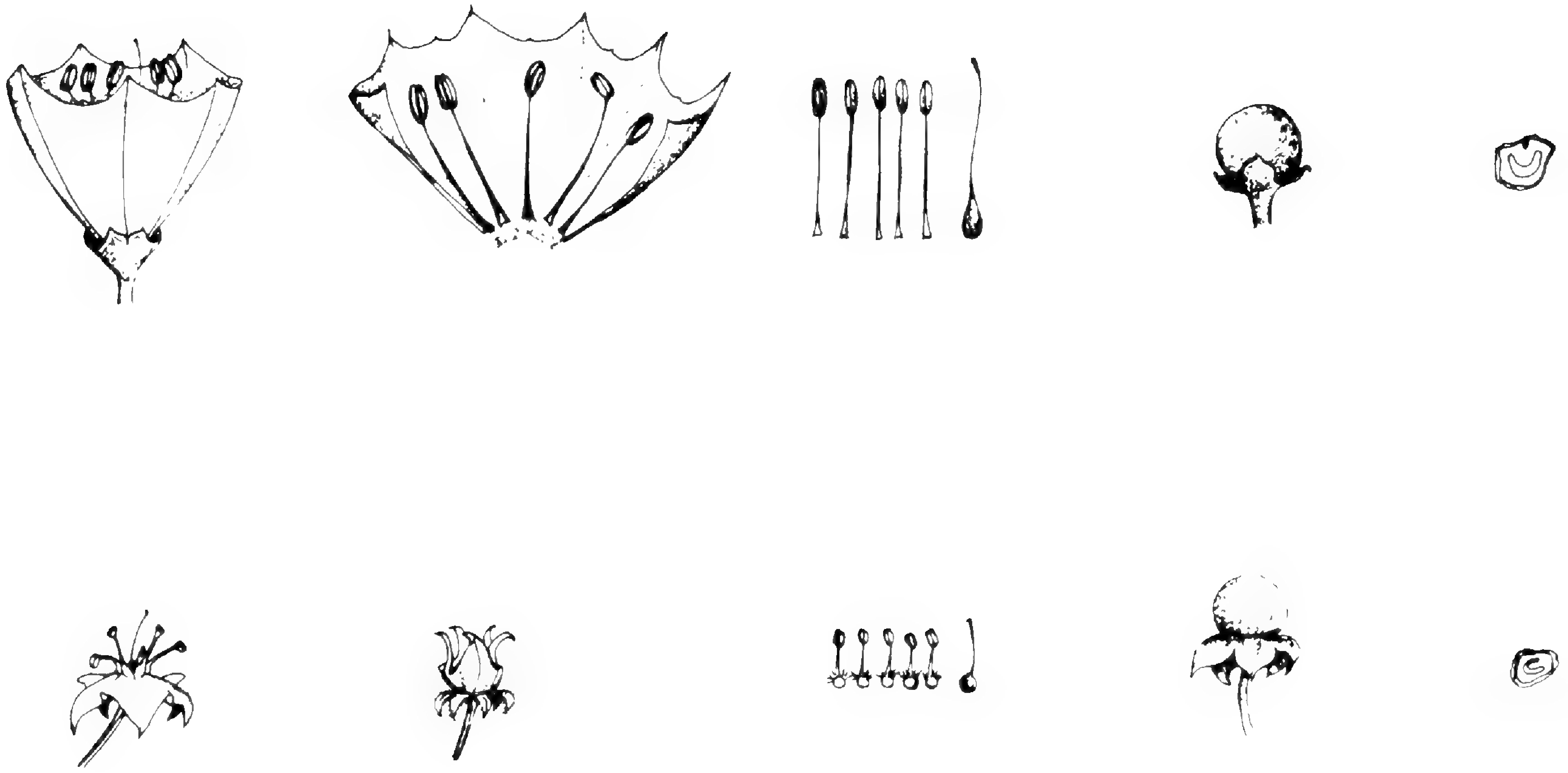

Figure 2. Comparative floral and fruiting calyx morphology. Top: *Saracha;* Bottom; *Jaltomata.*

provide further clarification of the species, and already *J. viscosa* D'Arcy & Davis has been published.

## MORPHOLOGY

The delimitation of Solaneae genera based on floral and fruiting morphology has been well established (Miers, 1848; Macbride, 1930, 1962; Morton, 1938; Waterfall, 1958; Averett, 1973).

*Saracha* and *Jaltomata* are morphologically distinct (Figures 1 & 2). The former is a shrub or tree with thickened leaves, strongly campanulate flower and a berry that is subtended by an involute accrescent calyx. The latter is an herb with relatively thin membranous leaves and rotate corolla with strongly reflexed calyx that spreads beneath the flower and fruit.

A summary of the important morphological features which distinguish *Saracha* and *Jaltomata* and some related genera is presented in the key below.

## KEY TO SARACHA AND JALTOMATA AND SOME CLOSELY RELATED GENERA

Anthers dehiscing through terminal pore............................ *Solanum*
Anthers not dehiscing through terminal pore,
  Herb; inflorescence a single, axile, umbel; fruiting calyx strongly reflexed, rotate and spreading beneath the berry,
    Flowers rotate................................ *Jaltomata*
    Flowers tubular............................ *Hebecladus*
  Tree or shrub; inflorescence axile, not umbellate; fruiting calyx accrescent neither strongly reflexed nor spreading beneath the berry; flowers campanulate............................................ *Saracha*

## TAXONOMY

**Saracha** Ruiz & Pavon. Florae Peruvianae et Chilensis Prodromus, p. 31, t. 34. 1794. *Sarachea* (sic) Anal. Fam. **24.** 1829. *Sarracha* (sic) Bull. Acad. Brux **12:** 133. 1845. *Sarachaea* (sic) O. Kuntze. Rev. Gen. Pl. **2:** 452. 1891. TYPE SPECIES: *Saracha punctata* Ruiz & Pavon. Florae Peruvianae et Chilensis **2:** 42, t. 178b. 1799.

*Bellinia* Roemer & Schultes. R. & S. Systema. Veg. **IV**. 687–690; LVI. 1819.
*Diskion* Rafinesque. Sylva Tell. **55:** 1838.
*Poecilochroma* Miers. Lond. J. Bot. **7:** 353. 1848.

Tree or shrub, perennial; stems erect, ascending, suffruticose, round, glabrous; leaves simple, opposite, rarely alternate, ovate to oblong, glabrous, prominently veined, petiolate, upright, dusty; flowers 2–7, axillary, pedicels elongating, calyx campanulate, rounded at base, glabrous; corolla variably with punctate markings, large 2–3 cm., campanulate, lacinate, ovate, acute, slightly reflexed at margin; stamens inserted at the base of the corolla, erect, expanding at the base; filaments to 2 cm. long; anthers longitudinally dehiscent; styles filiform; stigma capitate, obtuse; fruit a globose berry, fleshy, bilocular with an involute calyx, seeds flattened, reniform; embryo peripheral, curved around endosperm.

*Saracha* is restricted to the northwestern part of South America: Venezuela, Colombia, Ecuador, Peru, and Bolivia, in montane regions from 2500 to 4300 meters. Although habitat associations with *Adiantum*, *Ambrosia* and some Malvaceae have been reported, very little is known about the biology of this genus. A thorough study needs to be done.

**Jaltomata** Schlechtendal. Index Seminum Hort. Hal. **1838:** 8. 1838.
TYPE SPECIES: *J. edulis* Schlechtendal.
*Jaltonia* Steudel. Nom. Bot. ed. 2. **1:** 796. 1840.
*Saracha* sensu auct., non Ruiz and Pavon. Fl Peru. et. Chil. Pro. **31.** t. 34. 1794.

Herb; stems erect, ascending or spreading, glabrous to pubescent, angled, usually hollow; leaves simple, often thin, membranous, petiolate, ovate to acuminate, entire or broadly lobed; inflorescence solitary, axillary, and umbellate, situated at a dichotomy of the stem; flowers pedicillate with the calyx enclosing the bud, later spreading, becoming reflexed, subtending but not enclosing the fruit; corolla rotate to broadly campanulate, shallow to deeply lobed, laciniate, the lobes usually broad to deltoid; filaments exserted, filiform, and inserted near the base of the corolla, basally swollen, glabrous, style thin, stigma small; fruit globose, a mucilaginous berry; seeds few to numerous, laterally compressed, reniform, wavy-thick testa cell walls, browning with age; embryo peripherally curved around endosperm.

*Jaltomata* is a group of mostly perennial herbs ranging from the southwestern border of the United States to Bolivia. Annual members of the genus have been collected in the West Indies and

Galapagos Islands. *Jaltomata* occurs at lower elevations than *Saracha,* generally from near sea level to 3200 meters throughout its range.

These herbs have been collected from pine-oak forests, cafetales, and more disturbed sites such as river banks, perimeters of agricultural fields, and along roadsides. *Jaltomata* occurs with *Solanum, Physalis, Margaranthus, Chenopodium, Mentha,* and *Amsinckia. Solanum americanum* Mill. is the most consistent association with *Jaltomata.* A biosystematic study of the genus is now underway.

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## LITERATURE CITED

AVERETT, J. E. 1973. Biosystematic study of *Chamaesaracha* (Solanaceae). Rhodora **75:** 325–365.

DE ROJAS, C. E. B. 1974. Los generos de las Solanaceae de Venezuela. Rev. Fac. Agron. (Maracay) **VII** (3): 25–108.

GENTRY, J. L. 1973. Restoration of the genus *Jaltomata* (Solanaceae). Phytologia **27**(4): 286–288.

———. 1974. The generic name *Saracha* Ruiz & Pavon (Solanaceae). Field Bot. **36**(8): 69–72.

HUMBOLT, F. A., A. BONPLAND, C. S. KUNTH. 1818. Nova Genera et Species Plantarum **3:** 55–56; **4:** 43–44.

MACBRIDE, J. F. 1930. Spermatophytes, mostly Peruvian-II. 3. Peruvian Solanaceae. Field Mus. Bot. **8:** 110.

———. 1962. Solanaceae. *In:* Flora of Peru. Field Mus. Bot. **13,** part V-B. No. 1: 27.

MIERS, J. 1845. Contributions to the botany of South America. Lond. J. Bot. **4:** 319–325.

———. 1848. Contributions to the botany of South America. Lond. J. Bot. **7:** 353–359.

———. 1853. Observations on the Solanaceae. Lond. J. Bot. **11:** 90–105.

———. 1857. Illustrations of South American plants. **2:** 1–22; 148–150; Appendix 41–69; pl. 35, 38 & 39.

MORTON, C. V. 1938. Notes on the genus *Saracha.* Proc. Biol. Soc. Wash. 51: 75–77.

ROEMER, J. J., AND J. A. SCHULTES. 1819. L. Syst. Veg. **4:** 56; Introd. 687–690.

Ruiz, H., and J. Pavon. 1794. Florae Peruvianae et Chilensis Prodromus 31, *tab. 34*. Facsimile edition. 1965.

______. 1799. Florae Peruvianae et Chilensis. 2: 42, *tab. 178b*.

Schlechtendal, D. F. L. 1838. Index seminum horto academico halensi. p. 8.

______. 1839. Index seminum horto academico halensi. p. 8.

Waterfall, U. T. 1958. A taxonomic study of the genus *Physalis* in North America and Mexico. Rhodora 60: 113 114.

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# NEW TAXA IN THE GENUS *DAHLIA* (ASTERACEAE, HELIANTHEAE—COREOPSIDINAE)

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When I formulated my view on the morphological limits of *Dahlia merckii* (see Sorensen, 1969a) my concept embraced a wide assortment of specimens collected from three allopatric regions of central and northern México. Most collections came from the main center of distribution of the species, which included the lectotype locality, in the humid mountains surrounding the Vallé de México and eastward to near Orizaba in Veracruz. A second group of specimens came from the state of San Luis Potosí to the north. To date I have seen no collections which would join these two centers nor any which would join either of these with the third and northernmost region of collecting activity in the very high and poorly traversed Sierra Madre Oriental in the state of Nuevo León and Tamaulipas. Since the time when my original understanding of *D. merckii* included populations of these three regions I have learned that those collections from Nuevo León and Tamaulipas belong to a different and distantly related species herein described as the new *Dahlia tubulata* as follows:

**Dahlia tubulata** Sørensen *sp. nov.* TYPE: Mexico, Nuevo León; at K-7.1 along road from Diez y Ocho de Marzo to Micro-wave relay station near summit of Cerro Potosí, about 2400 m, in a zone of scrub oak and *Arbutus* with scattered *Pseudotsuga,* soil rocky red clay. 13 September 1969, *Sørensen & Beaman 6724* (HOLOTYPE: F!, ISOTYPES: A!, DEK!).

Herba perennis 6–13(–19) dm alta. Caules foliosi usque ad ramos floriferos, 3.5–7 mm diametro, internodiis 5–9.5(–12) cm longis, fistulosis vel tubulatis. Folia media pinnata vel bipinnata, petiolo incluso 8–15 cm longa; foliolis (3–)5(–7), oppositis, pinnis basilaribus 4–7 cm longis, petiolulis 6–15 mm longis, segmentis ultimis oppositis, suboppositis, vel alternis secus rhachillam; stipellis saepe praesentibus, plerumque ad nodum basilrem rhachidis affixis; petioli 3.5–7(–9) cm longis, in sectione transversali lunaribus, supra sulcatis, longistrorsum cavis (raro farctis), orificio minus quam dimidio diametri exterioris. Capitula (1)2–6 in quoque ramo principali, 4.5–6 cm diametro ligulis inclusis; involucri squammae exteriores reflexae sub anthesi, (6.5–)8–11(–13) mm longae, 1–2.1(–3.8) mm latae. Flosculi ligulati lavanduli usque lilacini, 2–3 cm longi, 0.8–1.4 cm lati. Achenia ca. 6.5 mm longa, 1.8 mm lata. Chromosomatum numerus: $n = 16$.

Lightly wooded rocky slopes, forested ridges, and shaded ravines, sclerophyllous forest, zone of oaks, *Arbutus,* and scattered conifers, 1900-3100 m, in the Sierra Madre Oriental of Nuevo León and Tamaulipas. Flowering August-September.

EXSICCATAE. MEXICO. **Nuevo Leon:** 18 mi S of paved rd from Linares to Rte 57, along rd to Dr. Arroyo, 4 Jul 1968, *Anderson & Anderson 4630* (MICH); Cerro Potosí, near Micro-wave tower, 8 Jul 1963, *McGregor, Harms, Robinson, Rosario, & Segal 296* (MSC); 15 mi sw of Galeana, Sierra Infernillo, 16 Jun 1934, *Mueller & Mueller 837* (F, GH, MICH, TEX); trail from La Trinidad to Sierra de la Cebolla, Municipio de Montemorelos, 20 Aug 1939, *Mueller 2879* (GH, MICH, NA, UC); on Cerro Grande c. 3 mi SW of Ascensión, 18 Jul 1958, *Straw & Forman 1389* (MICH); Hacienda Pablillo, Galeana, 17 Aug 1936, *Taylor 183* (F, MO, TEX). **Tamaulipas:** just E of the border near Dulces Nombres, Nuevo León, 24° N, 99.5–100.5° W, on E side of Cerro Linadera, 9 Aug 1948, *Meyer & Rogers 1894* (F, GH, MICH, MO, US [2 sheets]); cañon 4 km W of Miquihuana, 4 Aug 1941, *Stanford, Retherford, & Northcroft 767* (F [3 photos], GH, MO, NY).

The early confusion which led to the consideration of *Dahlia merckii* and *D. tubulata* as conspecific reveals a problem which every systematist has faced at one time or another, namely, of relying too much on certain "favorite" technical characters. In the present case, *D. merckii* possessed two interesting foliar characters which I earlier considered unique among the taxa of Section *Dahlia* to which *D. merckii* belongs: 1) **hollow petioles,** otherwise typifying the "tree-dahlias" of Section *Pseudodendron;* and 2) **secondary leaflets** (pinnules) **alternate on their rachillae,** a prominent and diagnostic character among the recently established Section *Entemophyllon* (Sorensen, 1969a). The presence of these two characters among the specimens, cited above as representing *D. tubulata,* figured prominently in my former understanding of *D. merckii* as evident in the several references made by me (1969a, pp. 352–353) to exceptional material (leaf size, position of stipels, number of flowers, and the wide range in some measurements) from northern México.

The tubular characteristic of the petioles mentioned above shows up easily in dried material after soaking sections in warm water. The mature leaves of *Dahlia merckii* have a petiolar cavity which usually takes up more than one-half the outside diameter of the petiole and runs nearly its entire length from the point of attachment at the base distally to the basal rachis node. In *D. tubulata,* however, the cavity occupies a proportionately much smaller amount of the petiole diameter and occurs reliably only in the middle one-third of the axis and usually only on mature median leaves. Despite the small "bore" of the petiole this character shows up quite easily in most specimens following softening of the tissues. A very few specimens lack the character entirely.

As happens so often when one sees fresh, living materials under natural conditions versus seeing only herbarium specimens, one's perception and understanding can change remarkably. At last, when I had the opportunity to sample wild populations of *Dahlia tubulata* seeing its habit alone clearly marked it as distinct from *D. merckii.* The latter has a compact growth habit and bears its leaves low down on the stem with very short internodes. Its numerous flowering heads overtop the leafy portion of the plant on long, stiff branches devoid of true leaves. *Dahlia tubulata* bears its flowering heads on the summit of leafy stems having evenly and widely spaced nodes nearly throughout their length. Such a growth habit typifies most species of Section *Dahlia.*

In addition to the differences between these two taxa in the expression of the hollow petiole character, the character of the alternate pinnules, though shared by both, also differs between them in degree rather than in kind. Typically, *Dahlia merckii* has basal primary leaflets bearing more than two secondary leaflets (pinnules) invariably arranged alternately on their rachillae. The primary leaflets of *D. tubulata* produce only one or two (rarely three) pinnules alternately arranged and these usually not fully distinct but appearing merely as lobes. Individually the ultimate segments of each species' leaves differ in size, with those of *D. tubulata* usually having the greater amount of blade surface. Frequently the leaflets of the secondary and tertiary ranks of *D. merckii* give a rather "toothy" or lacerate appearance resulting from the differing sizes of the individual teeth. The blades of *D. tubulata,* on the other hand, have a much more rounded aspect owing to the more nearly equal size of the marginal teeth or the absence of them altogether.

Stipels (stipule-like leafy appendages attached at the base of the leaflets) occur on the leaves of many species of *Dahlia* and are often diagnostic. On *D. merckii* the conspicuous stipels may attain a size equal to or exceeding that of the secondary leaflets and are attached at *each* of the rachis nodes as well as sometimes also at the basal rachilla node. The stipels of *D. tubulata* occur only at the basal rachis node or not at all.

Finally, the chromosomal evidence argues in favor of recognizing two species. *Dahlia merckii* has a haploid number of $n = 18$ while in *D. tubulata* the number is $n = 16$. All of the species of Section *Dahlia* yield chromosome counts of $n = 16$ and/or 32 except *D. merckii*.

The morphological and cytological evidence described above amply supports the view that *Dahlia merckii* and *D. tubulata* are distinct species and, as suggested by the chromosomal evidence, that they may not even belong to the same evolutionary line. The evolutionary affinities of *D. tubulata* seem to lie with *D. sherffii*, a species which I first collected in the Sierra Madre Occidental at several locations along the well-known highway between Durango and Mazatlán (Map 1). I have based my alignment of *D. sherffii* with *D. tubulata* on the following: **1)** their general overall appearance as viewed in the field where they look more like each other than either of them resembles any other species of *Dahlia* described to date. They both grow erect with leafy stems to the flowering portions. **2)** The leaves of both species exhibit about the same degree of segmentation ranging from once to twice compound. **3)** Both species possess the character of the pinnules or pinnular segments arranged alternately on their pinnae. In *D. tubulata* this character is quite consistent and diagnostic whereas in *D. sherffii* it appears irregularly and could go unnoticed. **4)** After considering the morphological evidence the chromosomal condition in each taxon seems to suggest that *D. sherffii* represents a tetraploid ($n = 32$) race of the diploid ($n = 16$) *D. tubulata*. This attractive hypothesis awaits verification from more detailed studies than those carried out so far. Meanwhile, it is worthy to note that two other *Dahlia* species, both in Section *Dahlia*, are represented by both diploid and polyploid plants and populations: *D. australis* of southeastern México and adjacent Guatemala, and *D. coccinea*, a widespread and common roadside wildflower in México and Central America (see Sorensen, 1969b, pp. 378–387 & 397–409 respectively).

When working the keys to the species of Section *Dahlia* (Sorensen, 1969a, pp. 323–326), *Dahlia tubulata* could emerge under two different paired leads. If the specimen at hand lacked the tubular petiole, the condition of many uppermost leaves and a very few median leaves, the key would take one to *D. sherffii.* At this juncture the investigator could invoke geographic distribution (see Map 1) as a basis for separation of these taxa inasmuch as neither species has clear qualitative distinctions over the other. On the other hand, if the unknown specimen possessed the tubular petiole one would emerge from the key at *D. merckii.* At this point the growth habit would be most useful in distinguishing between *D. tubulata* and *D. merckii.* Geographic distribution figures here as well since their respective ranges do not overlap at all (See Figure 2).

The removal of *Dahlia tubulata* from *D. merckii* has resulted in the latter species now having a much narrower morphological circumscription and a greatly reduced geographic distribution. *Dahlia merckii* more than ever seems to represent an anomalous and atypical taxon when compared to the other species in Section *Dahlia.* This has led me to consider removing it to a section of its own. I believe such action would lay greater emphasis on its representing an evolutionary line slightly apart from that within Section *Dahlia.* On the basis of chemical evidence pertaining to studies on the flavonoids of *Dahlia,* Giannasi (1975) has arrived at a similar conclusion. He proposed that *D. merckii* occupy a separate subsection with Section *Dahlia.* I have chosen to follow the suggestions of Giannasi as a conservative manner in which to deal with this question and offer a description of the proposed new Subsection Merckii, as follows:

**Subsection Merkii** Sørensen *subsectio nova.* TYPUS: *Dahlia Merkii* Lehm.

Herba perennis. Caules plures vel multi, e radicibus tuberosis, foliosi infra medium; nodis inferioribus confertis. Folia bipinnata vel bipinnato-pinnatisecta, pinnis oppositis, pinnulis alternis; stipellis ad omnem nodum rachidis affixis, aliquando ad nodum basilarem rhachillae; petiolis cavis. Chromosomatum numerus: n = 18.

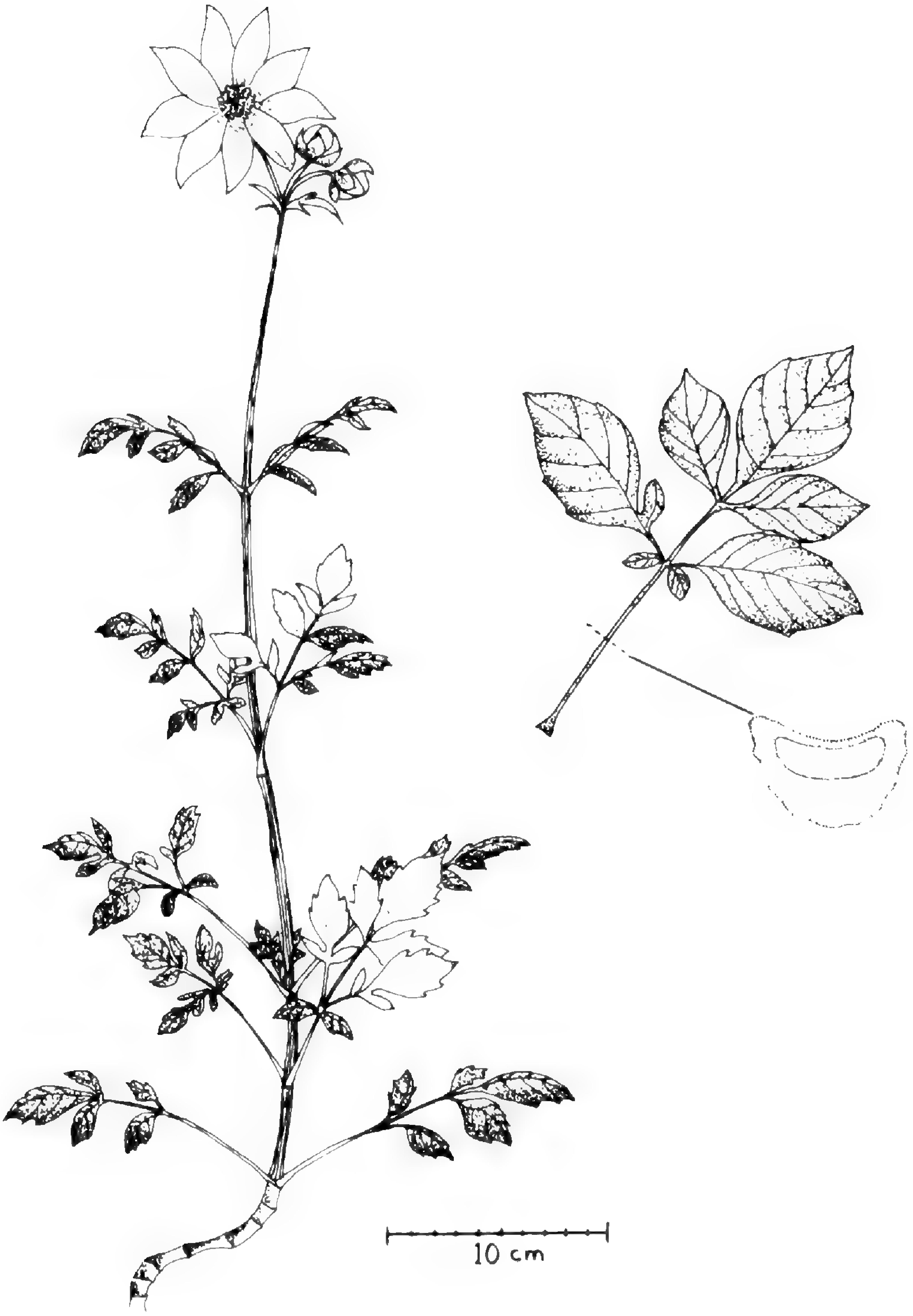

Figure 1. *Dahlia tubulata* drawn from *Sørensen & Beaman 6724*, the Holotype. On the right hand side is a leaf taken from a different plant in the same population to show the range of segmentation and the hollow petioles observed in this species.

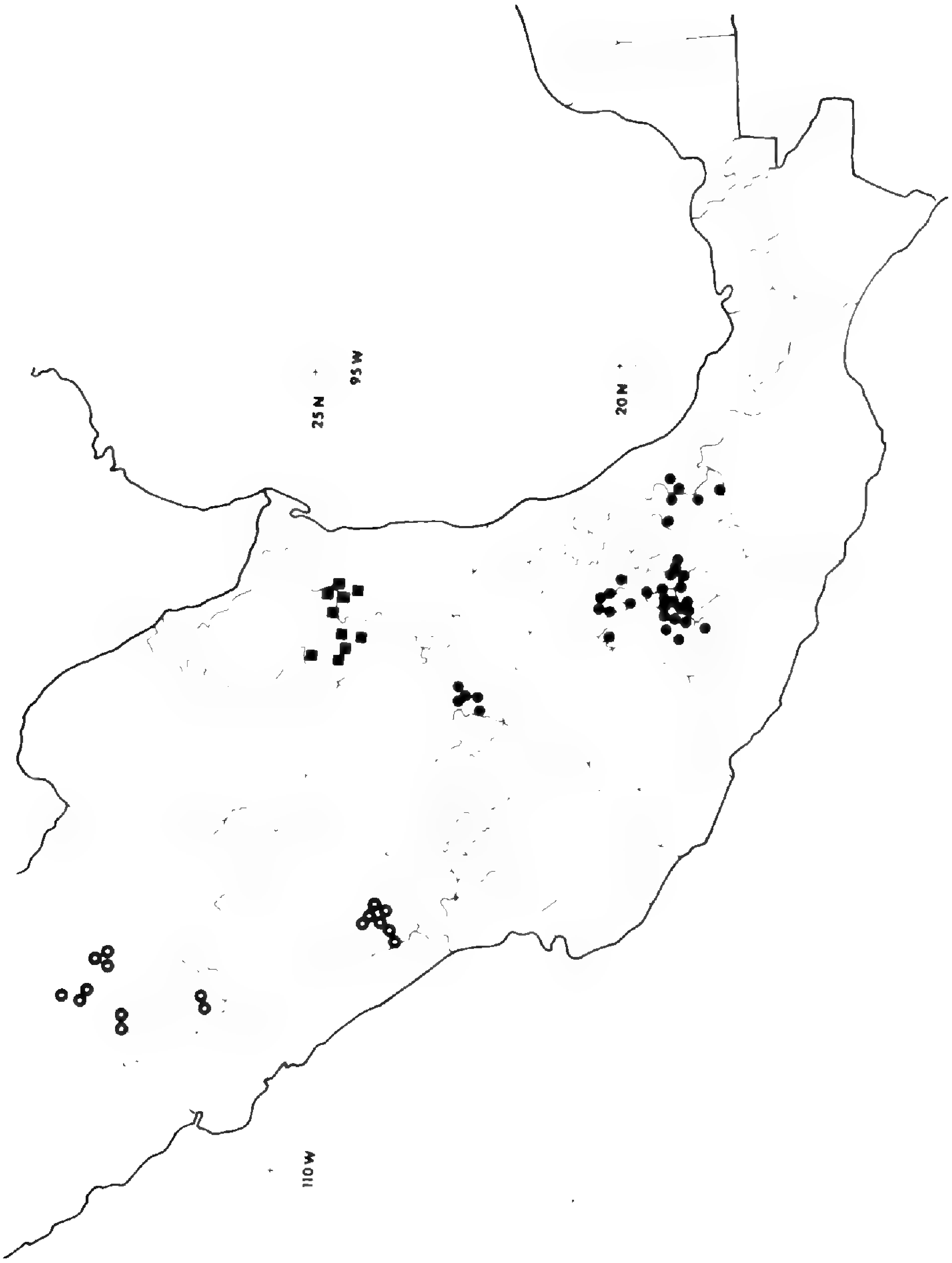

Figure 2. The geographic distribution of *Dahlia merckii* (dots), *D. sherffii* (circles), and *D. tubulata* (squares).

I wish to thank Dr. & Mrs. John Beaman who permitted me to travel with them and who guided me on the slopes of Cerro Potosí and in the vicinity of Galeana, Nuevo León, México, making it possible for me to visit wild populations of *Dahlia tubulata*. I am also grateful for the loan of specimens from herbaria signified in the list of exsiccatae. I am indebted to Mr. Lowell Brewick and Ms. Penny Matekaitis who drew portions of Figure 1.

## REFERENCES

GIANNASI, DAVID E. 1975. The flavonoid systematics of the genus *Dahlia* (Compositae). Mem. New York Bot. Gard. **26(2):** 1-125.

SORENSEN, PAUL D. 1969a. Revision of the genus *Dahlia* (Compositae, Heliantheae—Coreopsidinae), I. Rhodora **71:** 309-365.

______. 1969b. Revision of the genus *Dahlia* (Compositae, Heliantheae—Coreopsidinae), II. Rhodora **71:** 367-416.

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# CYTOGEOGRAPHY OF *ACHILLEA MILLEFOLIUM* IN OKLAHOMA AND ADJACENT STATES

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The circumboreal *Achillea millefolium* L. (Asteraceae: Anthemidae) is one of the most extensively studied polyploid complexes. Comprising diploids, tetraploids, hexaploids, and octoploids ($x=9$), the complex is cytologically most diverse in southeastern Europe and southwestern to central Asia. Investigations by Schneider (1958) and Ehrendorfer (1952b, 1953, 1959a-d) indicate that the complex in Eurasia is composed of isolated diploid cytotypes and extensive polyploids of hybrid origin. Species names have been applied to these ploidy levels; Ehrendorfer (1952b) recognized four diploid, one tetraploid, two hexaploid, and one octoploid species.

Studies of polyploidy and geographical distribution in North America west of the Sierra-Cascade crest have been extensive beginning with the now classical studies of Turesson (1939) and Clausen, Keck, & Hiesey (1938, 1940, 1948). These and other cytogeographical studies by Lawrence (1947), Ehrendorfer (1952b, 1973) and Tyrl (1969, 1975) revealed only tetraploids ($n = 18$), hexaploids ($n = 27$), and their pentaploid, septaploid, and octoploid hybrids. Hexaploid *Achillea* principally occupies coastal habitats from Alaska to Baja California, while the tetraploid occurs in the interior except for the coastal areas of northwestern Washington and southwestern Oregon -northwestern California where it replaces the hexaploid cytotype.

Although the distributions of *Achillea* cytotypes have been studied extensively in the Pacific Coast states, relatively few counts have been made of populations in central and eastern North America. Widely spaced counts by Turesson (1939), Ehrle (1958), Mulligan & Bassett (1959), Turner et al. (1961), DeJong & Longpre (1963), Löve & Solbrig (1964), Löve & Löve (1966), Löve & Ritchie (1966), Hedberg (1967), Smolinski et al. (1967), Jones (1968), Suda & Argus (1969), Ehrendorfer (1973), and Gervais (1977) indicate that tetraploids predominate but with hexaploids occasionally occurring such as those found in Illinois (Smolinski et al., 1967), Ontario (Mulligan & Bassett, 1959), and Quebec (Ehrendorfer, 1973).

The studies by Tyrl (1969, 1975) indicated that although broad generalization concerning cytotype distribution in *Achillea* may be made, the distribution of tetraploids and hexaploids is often much more complex at the population level. Frequently hexaploid plants or populations are found in areas containing primarily tetraploids and vice versa. Populations comprising both 4*x* and 6*x* plants occur. In addition, the discovery of tetraploid plants producing unreduced gametes suggests active formation of hexaploids in North America. The objective of this study was to determine the chromosome number of *Achillea* plants growing in Oklahoma and adjacent states in order to determine if similar, complex cytogeographic patterns occur in the interior.

## MATERIALS & METHODS

Chromosome counts were made of 218 populations in Oklahoma and adjacent states (Pireh, 1978). A population sample normally consisted of material from three or four plants growing in road right-of-ways and adjacent fields. Each locality was assigned an accession number and located by range, township, section as well as mileage from a permanent landmark.

Heads in various stages of flowering were fixed in chloroform, 95% ethanol, glacial acetic acid (6:3:1) for a minimum of 24 hours, then washed and stored in 70% ethanol. Heads were stained in bulk, using hydrochloric-alcoholic carmine stain for 24 hours at 60° C and then washed in 70% ethanol. Excised anthers were squashed and mounted in Hoyer's Medium and examined with phase-contrast optics. Metaphase chromosomes were counted, being easily observed in microspores undergoing the first post-meiotic mitosis. Counts were obtained from three or four microspores per plant.

Somatic cell counts were also made. Achenes were germinated on moist filter paper in petri dishes. The fresh root tips were pretreated with a saturated aqueous solution of paradichlorobenzene for 3 hours at about 60° C, fixed in 95% ethanol and glacial acetic acid (3:1), washed in 70% ethanol, and then stained, squashed, and mounted in 1% aqueous acetocarmine. The chromosomes of three or four cells per root tip were counted.

## RESULTS

The 293 chromosome counts obtained from 218 populations in this study are combined with those of earlier reports (cited above) in Figure 1. All plants examined by us, with one exception, were tetraploid ($2n = 36$). Meiotic divisions were regular, all microspores having 18 chromosomes and exhibiting uniform cytoplasmic staining and morphology. One plant from Caddo County in western Oklahoma was an aneuploid with a somatic chromosome number of 34. Meiosis was normal with spores having 17 chromosomes.

## DISCUSSION

Tetraploid *Achillea* appears to predominate in central and eastern North America; the additional chromosome counts reported here confirm the broad distributional pattern described by Ehrendorfer (1973). The hexaploids found in the St. Lawrence River Valley and along the Atlantic Coast are believed to be recent introductions from Europe, being found near seaports or closely resembling commonly imported cultivars. Additional information, however, is needed regarding the occasional hexaploid plants reported from the interior of the continent (Mulligan & Bassett, 1959; Smolinski et al., 1967; Ehrendorfer, 1973). Their status as native plants or escaped ornamentals is yet unresolved; verification of their chromosome numbers is needed, as well as extensive sampling of adjacent populations.

Further study of putative hexaploids along the Arctic coast is also warranted. Determining ploidy level by measuring pollen grain diameters, Mulligan & Bassett (1959) reported hexaploids as present only along the northern coasts of Alaska, the Yukon, the Northwest Territories, Ontario, Quebec, and Newfoundland. Gervais (1977), however, has discovered that known tetraploids from northern Quebec possess pollen grains with diameters equal to or greater than those of hexaploid plants.

The presence of only $4x$ plants from diverse climatic and edaphic regimes, and the absence of meiotic irregularities in the continental interior support the hypothesis advanced by Ehrendorfer (1952b, 1973) and Tyrl (1969, 1975) that evolutionary activity in the genus is centered in the Pacific Northwest, especially the Klamath and Olympic Mountains. In these areas, the occurrence of numerous tetraploid plants producing both reduced ($n = 18$) and unreduced ($n = 36$) microspores, the occurrence of solitary hexaploid plants among tetraploids having unreduced spores, and the occurrence of septaploids ($2n = 63$) and octoploids ($2n = 72$) among tetraploids and hexaploids producing unreduced spores suggest that functional unreduced gametes are responsible for increases in ploidy level in *Achillea*. For example, the union of 2x and 4x gametes results in the

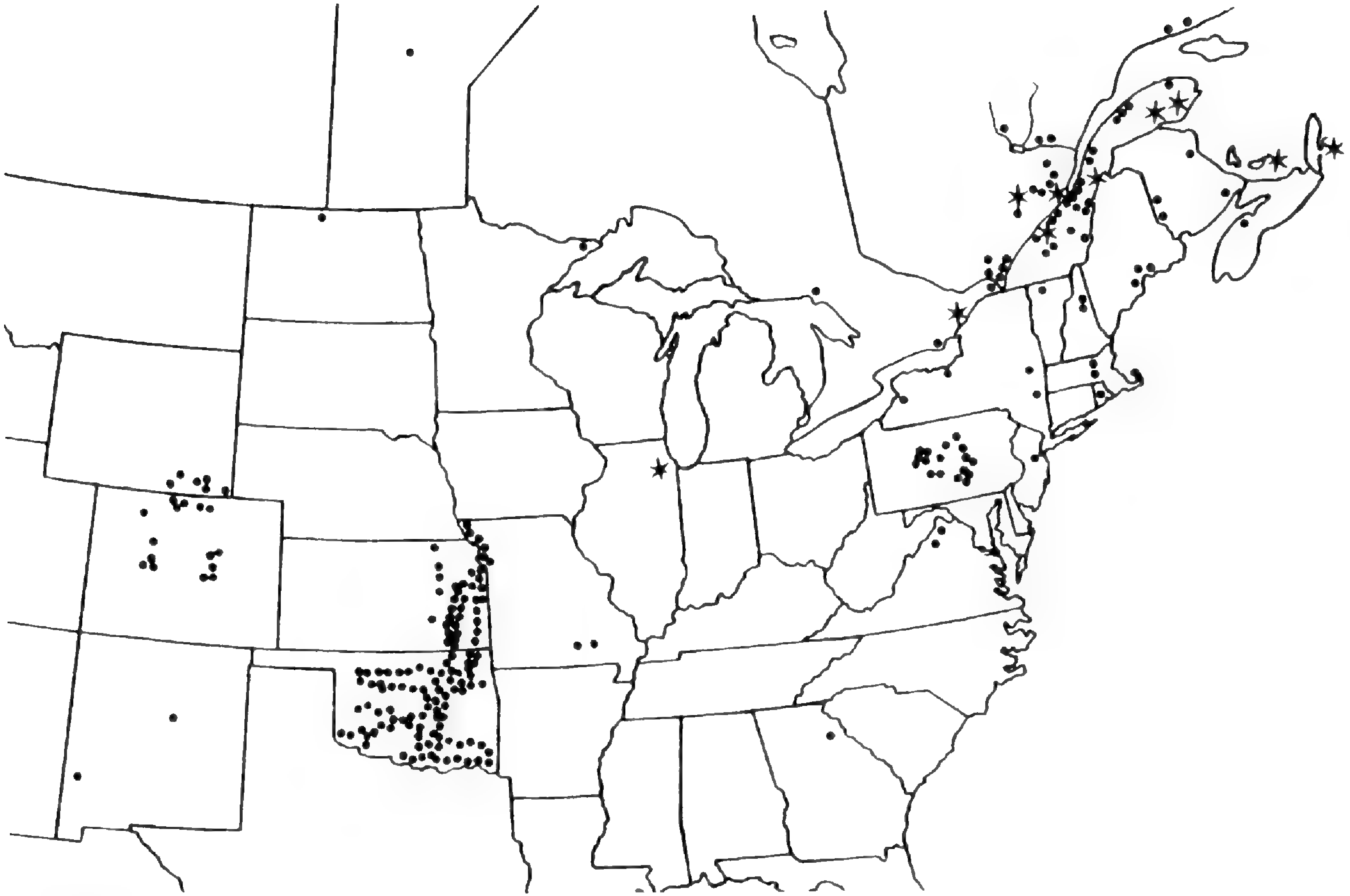

Figure 1. Distribution of *Achillea* cytotypes in the central and eastern United States and adjacent Canada. Solid circles, tetraploid populations ($n = 18$); solid stars, hexaploid populations ($n = 27$).

formation of a 6x zygote ($2n = 54$). The coastally restricted hexaploids appear to be indigenous to western North America and to arise from previously established tetraploid progenitors. The extensive observations of 4$x$–6$x$ intergradation in morphology, ecology, and environmental responses support this conclusion (Clausen et al., 1940, 1948; Hiesey, 1953; Hiesey & Nobs, 1952). In additiion, the limited success in crossing Eurasian and North American hexaploids indicates a distinct genetic relationship (Clausen et al., 1940; Ehrendorfer, 1952a; Hiesey & Nobs, 1970). In contrast, crosses between old and new world tetraploids are successful. Nondisjunction apparently is not a factor in south-central North America. Presumably as a consequence, the meiotic system of *A. millefolium* is evolutionally conservative in this region.

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## LITERATURE CITED

CLAUSEN, J., D. KECK & W. M. HIESEY. 1938. Chromosome number and environment. Carnegie Inst. Wash. Year Book. **37:**220–221.

———. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Publ. Carnegie Inst. Wash. **520:**1–452.

———. 1948. Experimental studies on the nature of species. III. Environmental responses of climatic races of *Achillea.* Publ. Carnegie Inst. Wash. **581:** 1–129.

DEJONG, D. C. D. & E. K. LONGPRE. 1963. Chromosome studies in Mexican compositae. Rhodora **65:**225–240.

EHRENDORFER, F. 1952a. Cytology of *Achillea* hybrids. Carnegie Inst. Wash. Year Book. **51:**124–125.

———. 1952b. Cytotaxonomic studies of *Achillea.* Carnegie Inst. Wash. Year Book. **51:**125–131.

———. 1953. Systematische und Zytogenetische Untersuchungen an Europasichen Rassen des *Achillea millefolium* Komplexes. Österr. Bot. Z. **100:** 583–592.

———. 1959a. *Achillea roseo-alba* Ehrendf., *spec. nov.*, eine hybridogene, di- und tetraploide Sippe des *Achillea millefolium* Komplexes. Österr. Bot. Z. **106:**363–368.

———. 1959b. Differentiation—hybridization cycles and polyploidy in *Achillea.* Cold Spring Harbor Symp. Quant. Biol. **24:**141 152.

———. 1959c. The results of comparative phylogenetic studies on *Galium, Knautia,* and *Achillea.* Congr. Internatl. Bot. 9th. **2:**102.

______. 1959d. Mechanisms of micro-evolution in diploid and polyploid races of *Achillea*. Ber. Deutsch. Bot. Ges. **72**:11–12.

______. 1973. New chromosome numbers and remarks on the *Achillea millefolium* polyploid complex in North America. Österr. Bot. Z. **122**:133–143.

EHRLE, E. B. 1958. A cytotaxonomic study of the genus *Achillea* in Pennsylvania. Rhodora **60**:7–9.

GERVAIS, C. 1977. Cytological investigation of the *Achillea millefolium* complex (Compositae) in Quebec. Canad. J. Bot. **55**:796–808.

HEDBERG, O. 1967. Chromosome numbers of vascular plants from arctic and subarctic North America. Ark. Bot., Ser 2. **6**:309–326.

HIESEY, W. M. 1953. Comparative growth between and within climatic races of *Achillea* under controlled conditions. Evolution **7**:297–316.

______. & M. A. NOBS. 1952. Genetic structure of climatic races and species of *Achillea*. Carnegie Inst. Wash. Year Book. **51**:122–125.

______ & ______ 1970. Genetic and transplant studies on contrasting species and ecological races of the *Achillea millefolium* complex. Bot. Gaz. **131**:245–259.

JONES, S. B. 1968. Chromosome numbers in southeastern United States Compositae. II. Bull. Torrey Bot. Club **95**:488–494.

LAWRENCE, W. E. 1947. Chromosome numbers in *Achillea* in relation to geographic distribution. Amer. J. Bot. **34**:538–545.

LÖVE, A. & O. T. SOLBRIG. 1964. IOPB chromosome number reports. I. Taxon **13**:99–110.

______ & D. LÖVE. 1966. Cytotaxonomy of the alpine vascular plants of Mt. Washington. Univ. Colo. Stud., Ser. Biol. **24**:1–74.

______ & J. C. RITCHIE. 1966. Chromosome numbers from central northern Canada. Canad. J. Bot. **44**:429–439.

MULLIGAN, G. A. & I. J. BASSETT. 1959. *Achillea millefolium* complex in Canada and portions of the United States. Canad. J. Bot. **37**:73–79.

PIREH, W. 1978. Cytogeography and reproductive biology of *Achillea millefolium* in Oklahoma and adjacent states. M.S. Thesis. Oklahoma State University, Stillwater, OK.

SCHNEIDER, I. 1958. Zytogenetische Untersuchungen an Sippen des Polyploid-Komplexes *Achillea millefolium* L. *s. lat.* (Zur Phylogenie der Gattung *Achillea* I.) Österr. Bot. Z. **105**:111–158.

SMOLINSKI, S. J., C. L. BELL, L. BELL & L. BAUER. 1967. The isolation of Achillin from *Achillea millefolium*. Lloydia **30**:144–149.

SUDA, Y. & G. W. ARGUS. 1969. IOPB chromosome number reports. Taxon **18**:221.

TURESSON, G. 1939. North American types of *Achillea millefolium*. Bot. Not. **1939**:813–816.

TURNER, B. L., J. H. BEAMAN & H. F. L. ROCK. 1961. Chromosome numbers in the Compositae. V. Mexican and Guatemalan species. Rhodora **63**: 121–129.

TYRL, R. J. 1969. Cytogeography of *Achillea millefolium* in Western Oregon. Brittonia **21**:215–223.

______. 1975. Origin and distribution of polyploid *Achillea* (Compositae) in Western North America. Brittonia **27**:187–196.

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# A NEW SPECIES OF CAREX § EXTENSAE

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During the Canadian Botanical Association's A.G.M. field tour of western Newfoundland (7–12 August 1978), a dwarf member of the genus *Carex* § *Extensae* was found on calcareous limestone barrens along the seashore at several locations from Bellburns to Pointe Riche on the Northern peninsula. A description of the species follows.

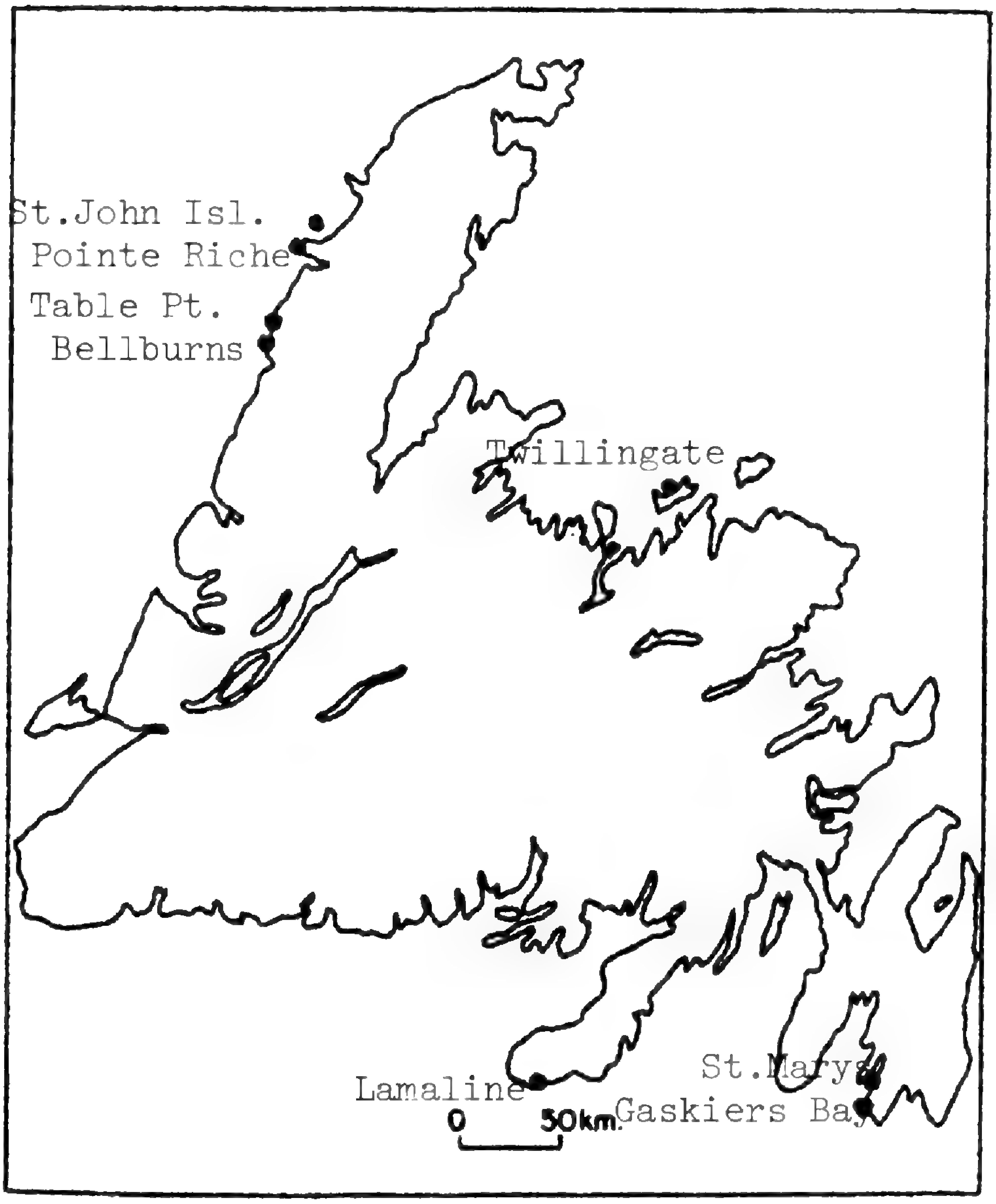

Figure 1. Distribution of *C. saxilittoralis* in Newfoundland.

**Carex saxilittoralis** Robertson, *spec. nov.*, (*Extensae*)

Perennis laxe cespitosa, alta vel 1–5 cm. Caudex emmittens stolones brevis, radix longa gracilis atrobrunneus. Vaginae fulvus ad brunneus, foliorum deciduorum marcescens obtecta basibus ; fasciatus interiora hyalinus, concavus et sinuolatus; ligula lates quam longus. Culmi phyllopodi, folio 3 vel 4 ad basim aggregata vaginis, ascendens-diffusus vel recurvatus, 3–8 cm longae, 1.5–5.0 latae, complanatus ad plicatus, inconspicuus septatus-nodulus, margine et costa scabrellus in supra 1/4–1/3. Culmi sterilis cespitosa. Culmi frondosa unus vel aliquot ascendens rigidus 0.5–8.0 cm alti plerumque valde quam folio laterum quadricostatus spiratum prope summum, angulo obtusus et laevis, transversus sectio cum amplus cavitas centralis et prominens fasciculus vascularis. Spici terminalis masculae, pedunculatus vel subsessilis, 1.5–2.0 cm longae, 2.0 mm latae, linearus-cylindraceus; spicis lateralis feminae, 1–2 (raro 3) contiguus-approximatae et sessile vel infimus interdum basibus et subsessilis 5.0–7.0 mm longae, 3.0–6.0 mm latae, globus-ovoideus; bractae infimus (spici basibus) foliaceus ascendens aequano inflorescentia longivaginans, bractae summum brevior plus minusve exedens inflorentia divaricatus vel defluxus spathiformis vel subterminalis squamatis et inconspicuus. Squama feminae vinaceus ad brunneus aequans et angustata quam corpus perigynium ovatus-lanceolatus summa obtusus et erose costa viridi pallens trinervis quasi summum. Squama masculae pallens brevior lanceolatus. Perigynia squarrosus fulvus ad brunneus 2.0–3.0 mm longae, 1.0–1.5 mm latae, obovoideus biconvexus manifeste bicostatus et decinervis basi-truncatus, rostrum 0.5 mm latae abruptus et tennis stricto vel ventraliter obliquus emerginatus. Achenium perigynium laxe complens atrobrunneus obovoideus trigonus subapiculatus; stylus contortus basibus brunneus 0.3 mm longae tristigmata 2.0mm longae a intra rostrum.

A loosely cespitose perennial, 1–5 cm tall. Leaves clustered toward base, generally diffuse and recurved; 3–8 cm long, 1.5–5mm wide. Fertile culms 1-few, exceeding leaves; terminal spikes solitary, staminate, peduncled-subsessile; lateral spike 1–2(3), contiguous-approximate and sessile, or the lowermost basal and peduncled. Perigynia squarrose, yellowish-green or brown, beak 1/4 as long as body. Achene dark brown; style contorted at base; stigmas 3.

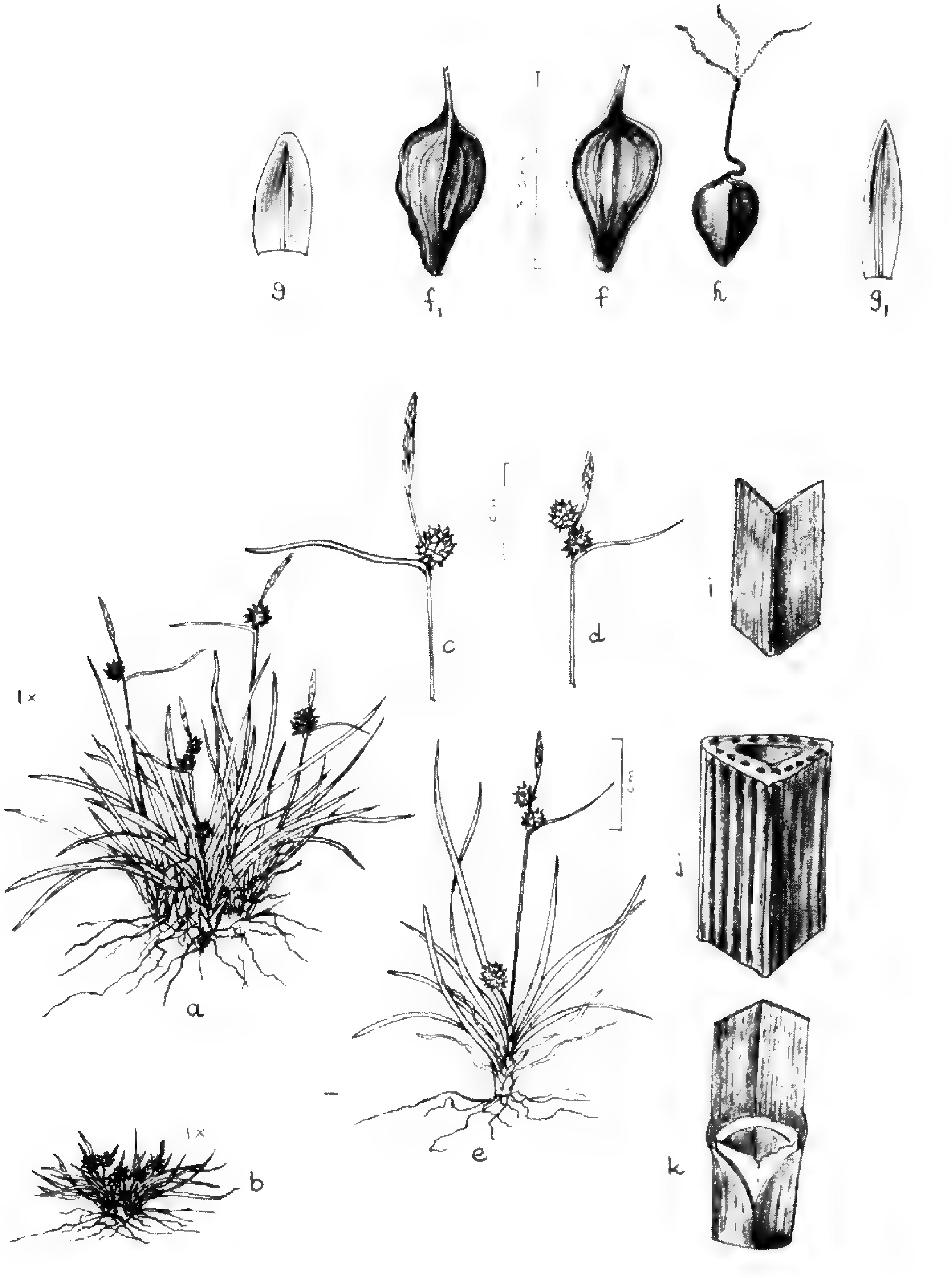

Figure 2. Illustration of C. saxilittoralis. **a & b**, habit; **c–e**, variations of fructifications; **f**, dorsal view of perigynium; **f$_1$**, lateral view of perigynium; g, pistillate scale; g$_1$, staminate scale; h, achene; i, midsection of leaf; j, midsection of culm; k, ligule.

Figure 3. Photographs of *C. saxilittoralis* at type locality.

Photos by E. D. Wells, NFRC

Habitat: Clay soils mixed with limestone gravel on exposed calcareous barrens near seashore and on gravelly beaches in transitional zone between high tide and small brooks.

SPECIMENS EXAMINED. CANADA. NEWFOUNDLAND. **St. Barbe South District.** Bellburns, *A. Robertson 3,430* (NH CAN), TYPE, duplicate in NFRC; Bellburns, Table Point, *A. Robertson 3,431* (NFRC); Pointe Riche, *Fernald & Weigand 2,912* (GH), *A. Robertson 3,432* (NFRC); St. John's Island, *Fernald, Weigand, Long, Gilbert, & Hotchkiss 27,733* (GH). **Twillingate District.** Twillingate, *D. Weber 16,738* (MUN). **Placentia West District.** Lamaline, *E. Rouleau 5,891* (MT). **St. Mary's District.** Gaskier's Bay, *A. Robertson 3,614* (NFRC); St. Mary's, *A. W. H. Damman 1,081* (MUN) (as *C. demissa*).

*Carex saxilittoralis* is one of two species in the EXTENSAE group which frequently have one lateral spike; the other is *C. lepidocarpa* Tausch. In fact this feature, plus the peduncled terminal staminate spike common to both species, suggests that they are closely allied.

Specimens of *Carex saxilittoralis* were first collected by Weigand on Pointe Riche in 1910 and later by Fernald and his colleagues on St. John's Island (Fernald, 1926). Fernald identified these as *C. Oederi* Retz. var. *subglobosa* (Meilich.) Richter. Harold St. John (1922) also collected a dwarf *Carex* which he identified as *C. Oederi* Retz. var. *pumila* (Coss. & Germ.) Fernald. Both these names are synonymous with an European species of the *C. flava* aggregates, namely *C. scandinavica* E. W. Davies (= *C. Oederi* Retz. subspecies *pulchella* (Lonnr.) van Ooststr.) which is taxonomically and phytogeographically distinct from *C. saxilittoralis*. Close examination of specimens in the field and in herbaria shows that this taxon is morphologically distinct and ecologically isolated from other members of the EXTENSAE group. Since existing classifications fail to incorporate this knowledge it is proposed to describe this taxon as a new species.

I wish to thank my friend Dr. Dwight Kincaid of the Gray Herbarium for his encouragement and assistance.

## REFERENCES

DAVIES, ELIZABETH W. 1953. Notes on *Carex flava* and its allies: I. A sedge new to the British Isles. Watsonia **3:** 66–69.

FERNALD, M. L. 1926. Two summers botanizing in Newfoundland. Rhodora **28** (328–336): 49–241.

ST. JOHN, HAROLD. 1922. A botanical exploration of the north shore of the Gulf of St. Lawrence, including an annotated list of the species of vascular plants. Canada Dept. of Mines, Victoria Memorial Museum, Ottawa, Memoir **126:** No. 4 Biological Series.

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# NEW ENGLAND NOTE: CHANGE IN STATUS FOR *PRUNUS GRAVESII*

GREGORY J. ANDERSON

One of the results of a recently completed study of *Prunus Gravesii* was the recognition that this species would best be treated as a variety of *P. maritima.*

**Prunus maritima** Marshall var. **Gravesii** (Small) Anderson, *stat. nov.* BASIONYM: *Prunus Gravesii* Small, Bull. Torrey Bot. Club **24:** 44. 1897.

Small did not designate a type specimen. In an effort to select one, Graves' specimens collected before 1897 were examined from the following herbaria: A, GH, CONN, Connecticut College, NCBS, NEBC, NY, US, and YU. Four specimens from NY have both Graves' and Small's handwriting on the label. Two of these bear only, or primarily, vegetative material ("Aug. 8. 1894", "Aug. 15. 1895"), the other two flowering material. Both of the latter bear the date "May. 29. 1895". I have selected the one with the best preserved flowers as the lectotype (it has a number 2 written in pencil in the upper right hand corner of the label). In addition, filed with the sheets at NY, there are two letters from Graves (one to N. L. Britton, the other to Small) that contain the data Small used in the description of *P. Gravesii.*

This variety is easily distinguished by its orbiculate leaves from the typical variety *maritima* which is characterized by lanceolate leaves. Other distinguishing characteristics of this variety are given in Anderson (1980).

## ACKNOWLEDGEMENTS

I thank the curators of the herbaria given above for the loan of specimens, Dr. R. Barneby for identification of Small's handwriting, Dr. B. Tiffney for examination of the specimens in the Yale and Connecticut Botanical Society collections, and Dr. C. B. Heiser, Jr., for comments.

## LITERATURE CITED

ANDERSON, GREGORY J. 1980. The status of the very rare *Prunus Gravesii.* Rhodora 82: 113–129.

SMALL, J. K. 1897. An apparently undescribed species of *Prunus* from Connecticut. Bull Torrey Bot. Club **24:** 44–45.

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*Geum Peckii* Pursh

This rare species is a Northeastern endemic, known from the White Mountains of New Hampshire and from three sites in Nova Scotia.

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Vol. 82 July, 1980 No. 831

# CHROMOSOMES OF MEXICAN *SEDUM* III. SECTIONS CENTRIPETALIA, FRUTICISEDUM, AND OTHER WOODY SPECIES

Charles H. Uhl

This is the third paper in a series reporting the chromosomes of 100 or so species of Mexican *Sedum*. A general introduction, materials and methods, and acknowledgements are included in the first paper, which dealt with 10 annual and biennial species (Uhl, 1976). A second paper reported the chromosomes of 19 more or less woody species having lateral inflorescences, considered to represent Section *Pachysedum*, plus three of their hybrids that have been named as species (Uhl, 1978).

This paper reports the chromosomes of 24 or possibly 25 additional more or less woody Mexican species that differ from Section *Pachysedum* in having terminal inflorescences. In part through the generosity of several collaborators, plants have been available from the type collections of ten species (two of them reduced to synonymy) and from at or very near the type localities of five others (including one that is reduced to synonymy). Most of the species reported here were classified by Berger (1930) in his sections *Dendrosedum, Fruticisedum,* and *Leptosedum,* along with several species having lateral inflorescences that appear to belong in section *Pachysedum,* reported in the preceding paper (Uhl, 1978). Clausen (1943) designated these four woody sections, plus his new section *Craigia,* as subgenus *Pachysedum*. Extensive experiments with hybridization in cultivation show that the distinction between those woody species having lateral inflorescences (Section *Pachysedum*) and those having terminal inflorescences appears to correspond to an important genetic discontinuity in the genus. In general, species of section *Pachysedum* are more easily hybridized with other species of section *Pachysedum* than they are with most or all of the woody species reported here, all of which have terminal inflorescences (Uhl, 1978, and unpub.). Hybrids between species with terminal inflorescences and species of section *Pachysedum,* once obtained, are likely to be much slower to flower than are hybrids between two species of section *Pachysedum,* and several such hybrids more than ten years old have never flowered. In particular, chromosome pairing is nearly always much more nearly normal in hybrids between two species of section *Pachysedum* than it is in hybrids between species of *Pachysedum* and species with terminal inflorescences.

The woody species reported in this paper represent a much more diverse group cytologically and genetically than do the species of section *Pachysedum* (Uhl, 1978). Choice of species to be reported here (or not) in some cases has necessarily been arbitrary, and it is likely that some of them are more closely related to some of the smaller, more "typical" species of *Sedum,* to be reported later, than they are to each other.

Among these species are several groups that are morphologically similar and that have the same or similar basic chromosome numbers. These species have been grouped here accordingly, but no new names for species or sections are introduced, since such groupings require more extensive morphological studies. This paper makes available the cytological evidence (the chromosome numbers and some information on hybrids and chromosome pairing) which is necessary to any new classification.

During these studies of the Mexican Crassulaceae several thousand crosses have been attempted, in part to establish the species that can be hybridized with each other and to note the form of their hybrids, and in particular to note the extent and manner of pairing among the chromosomes at meiosis in the hybrids. These features can be valuable indicators of the homologies among the chromosomes and of their changes during evolution. Many hybrids have been produced between species that are very different and that are widely separated taxonomically—some hybrids even have parents that, by the conventional taxonomy, are classified in different subfamilies. Many thousands of additional hybrids also might have been attempted, given enough time and space. (Some readers may be skeptical regarding certain hybrids because their parents differ so greatly and have been separated so widely in classification. However, most of the hybrids cited here have flowered, and pairing of their chromosomes has been analyzed; color photographs of many have been made; and herbarium vouchers have been prepared. I can only invite any skeptics to inquire further.)

In discussing each species here it seems useful to mention its hybrids, even though for some species only a few crosses have been attempted. However, some caution must be exercised before drawing sweeping conclusions about relationships based upon the ability of two species to produce hybrids. Several cases are noted below of unsuccessful attempts to cross two similar, presumably closely related, species. Failure to hybridize can result from many causes, ranging from massive incompatibility because of too distant relationships to individual genes that regulate cross compatibilities, from choice of pollen or stigmas at unfavorable times or stages to unfavorable temperatures or other environmental conditions. In some cases two plants that failed to hybridize in earlier attempts may later have been successfully crossed. On the other hand, some very wide crosses might have succeeded because of plain good luck, and many efforts to duplicate them might fail.

The extent of pairing between the parental chromosomes should be a better indicator of the degree of relationship between the parents, but even this can sometimes be misleading. In several cases preparations made at different times from the same plant have shown significant differences in the amount of pairing among the chromosomes. This is probably caused by factors such as temperature or the general vigor of the plant, which seem able sometimes to affect the degree of homology that chromosomes must have in order to pair. In some hybrids, especially in those resulting from wide crosses, a wide range of pairing configurations is noted in different cells that are side by side. The natural tendency in such cases is to analyze those cells that are clearest and easiest to study, i.e., those which show the most nearly normal meiosis. Nevertheless, in spite of these hazards and reservations, it seems worth presenting here some of the information regarding hybrids and the pairing of their chromosomes.

## SECTION CENTRIPETALIA ALEXANDER

This section consists of two closely related species that are interfertile in cultivation, *Sedum allantoides* Rose and *S. platyphyllum* Alexander. Both species have thick leaves and they have terminal inflorescences of a type—compound pleiochasium—that is very unusual in the Crassulaceae (Moran, 1966). The flowers are nearly identical in the two species, with separate, whitish petals that are usually marked distally (sometimes faintly) with patches of reddish brown. Somewhat similar markings occur on the petals in the genus *Graptopetalum* of Subfamily Echeverioideae, which has lateral inflorescences and sympetalous corollas. The two species of section *Centripetalia* appear to represent extremes of a morphological and genetic gradient or continuum in leaf shape, with more or less terete-leaved forms (*S. allantoides*) to the north and west, near the Puebla-Oaxaca border, flat-leaved forms up to 5 times as wide as thick (*S. platyphyllum*) 200–300 km. to the southeast, and intermediate forms (e.g., *U2383*) in between. Most collections, including plants of the type collections of both species, have $n = 29$ (Fig. 1,3). One collection of *S. allantoides* obtained from cultivation in Mexico (*M6358*, Fig. 2) and one plant of an otherwise diploid collection of *S. platyphyllum* (*M7737*, Fig. 4) were tetraploids, with $n = 58$.

A plant of the type collection of *Graptopetalum goldii* Matuda also has $n = 29$ (Fig. 5). This name was given to a plant with inflorescences and flowers similar to those of *Sedum allantoides* and *S. platyphyllum*, but intermediate in leaf shape, said to have been collected by Dudley Gold near Ixmiquilpan, Hidalgo. However, the locality is far removed from the ranges of the latter two species; Gold denies having collected any such plant there (Moran, 1966); and other collectors have been unable to find it there. Nevertheless, the true affinities of *G. goldii* appear to be beyond question, and Moran (1966) reduced the species to synonymy under *S. allantoides*, since that is the more variable of the two related species. In fact, *U2383* appears to be a good match for *G. goldii*, which may well have come from the same locality, only a few meters from the main highway from Mexico City to Oaxaca.

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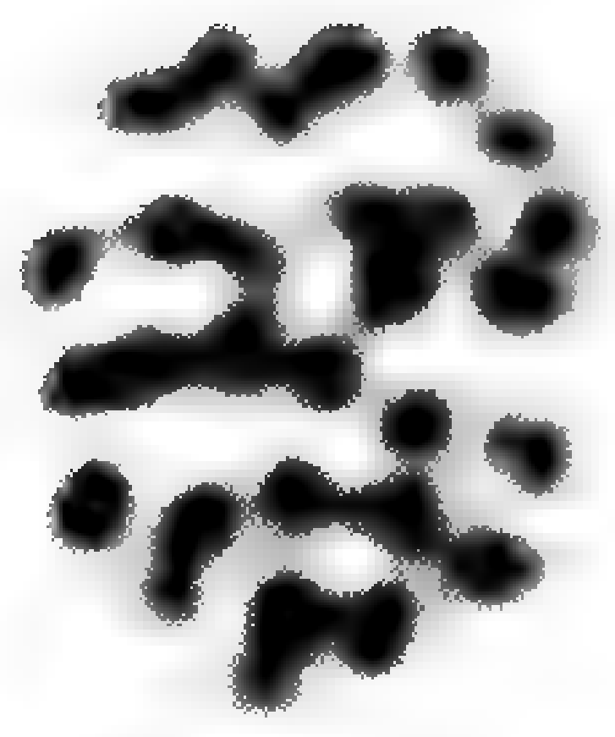
Figures **1–20**. Chromosomes of *Sedum* at metaphase I in pollen mother cells, ×2000, except as indicated. **1–2,** *S. allantoides:* 1, M7724, $n = 29$; 2, M6358, $n = 58$; **3–4,** *S. platyphyllum,* M7737; 3, $n = 29$; 4, $n = 58$; **5,** *"Graptopetalum goldii"*, M8431, $n = 29$; **6,** *S. platyphyllum* × *S. allantoides*, M7737 × M7724, $n = 29$; **7,** *S. bourgaei*, M10155, $n = 29$; **8,** *S. chloropetalum,* M10096, $n = 29$ (metaphase II); **9,** *S. frutescens,* M6400, $n = 30$; **10–11,** *S. griseum;* 10, C44-112, $n = 26$; 11, MVR-SL10, $n = 30$; **12,** *S. guadalajaranum,* U2322, $n = 29$; **13,** *S.* cf. *guatemalense,* U1653, $n = 27$; **14,** *S. oxycoccoides,* U2330, $n = 29$; **15,** *S. oxypetalum,* M7786, $n = 29$; **16–17,** *S. retusum;* 16, U1642, $n = 27$; 17, U1872, $n = 29$; **18,** *S. obcordatum,* U1583, $n = 34$; **19–20,** *S. palmeri;* 19, U1367, $n = 34$; 20, U1836, $n = 68$.



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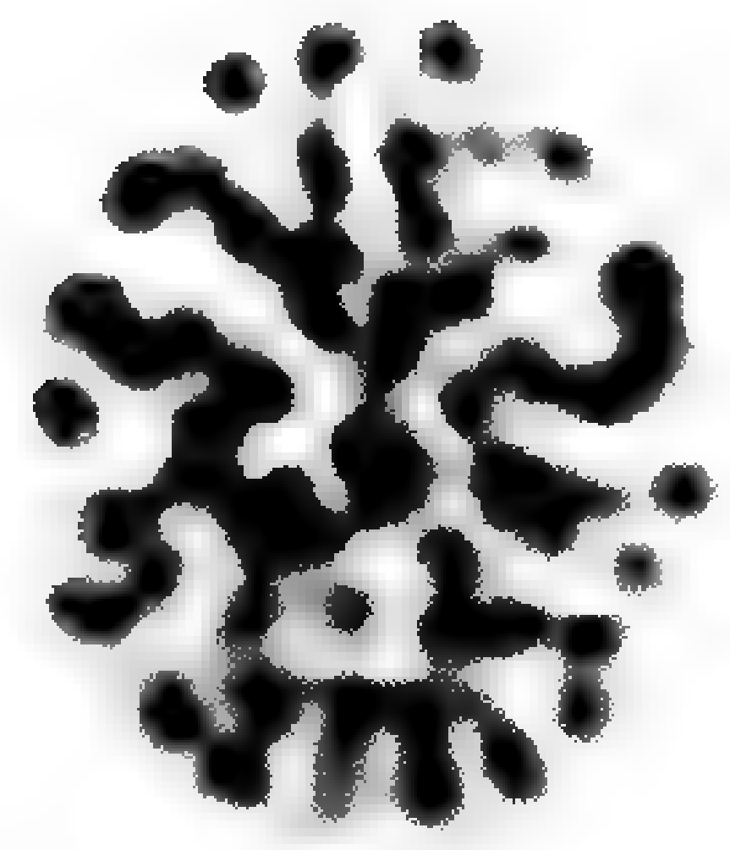

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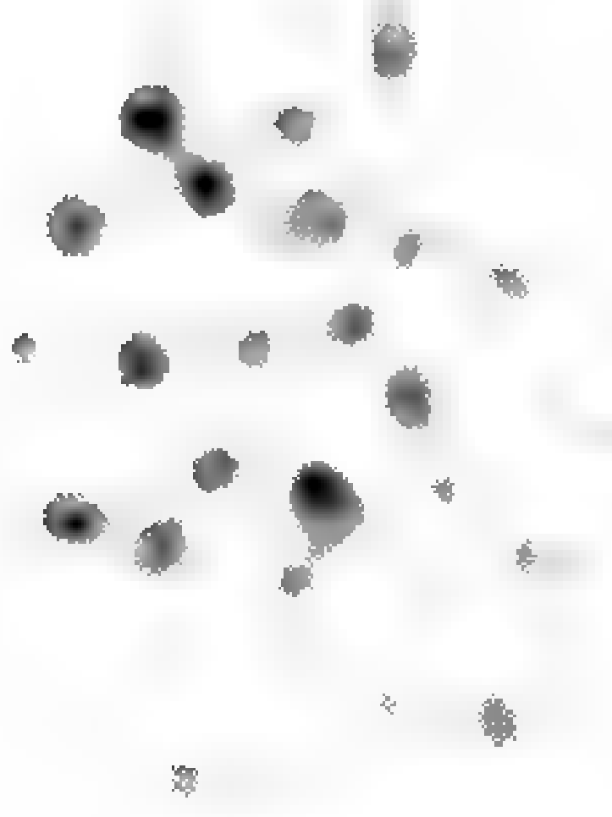

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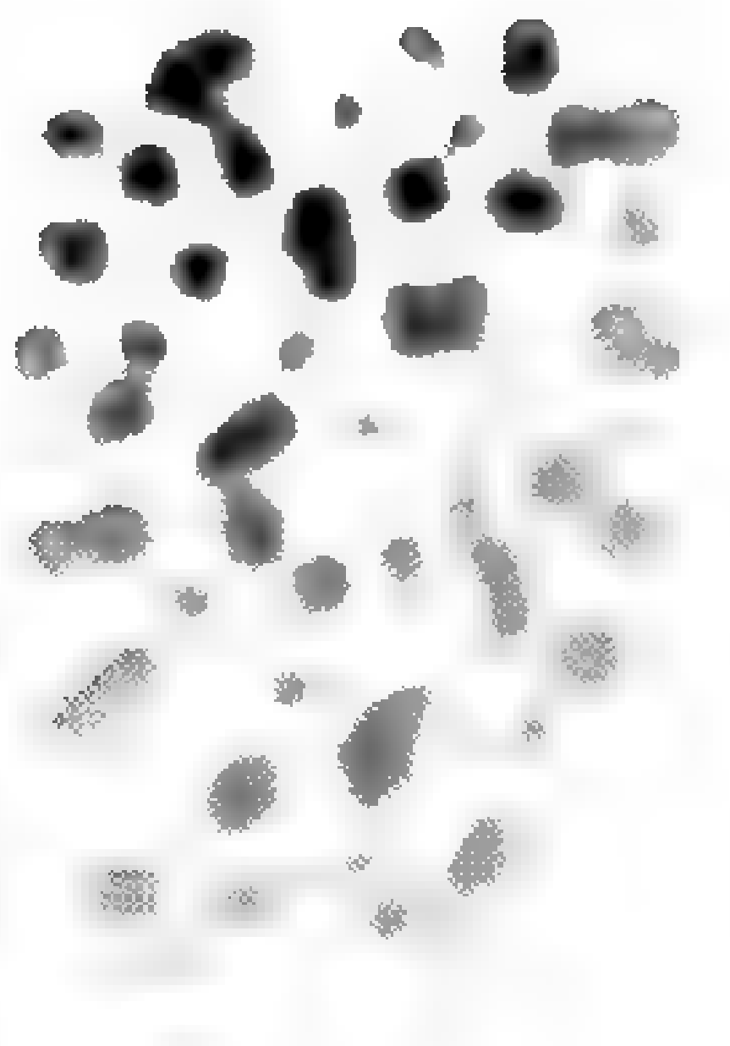

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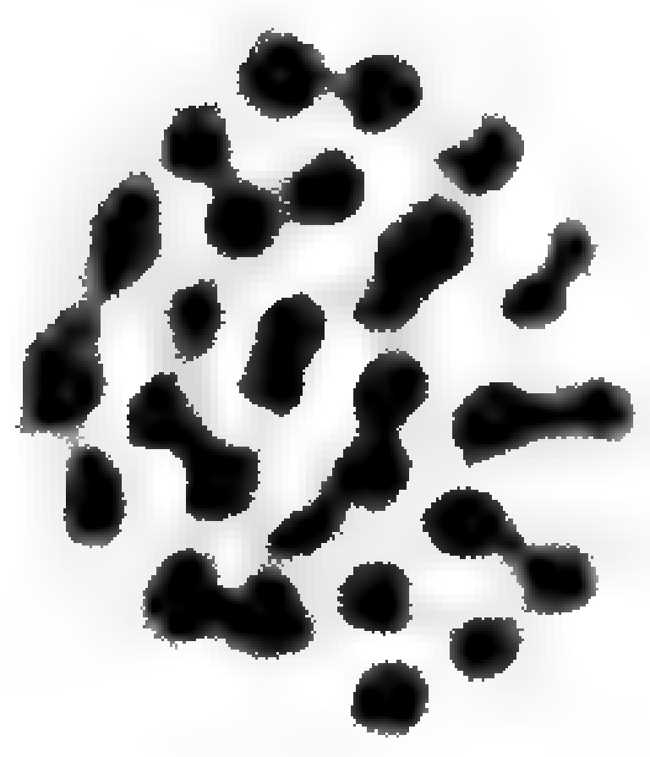

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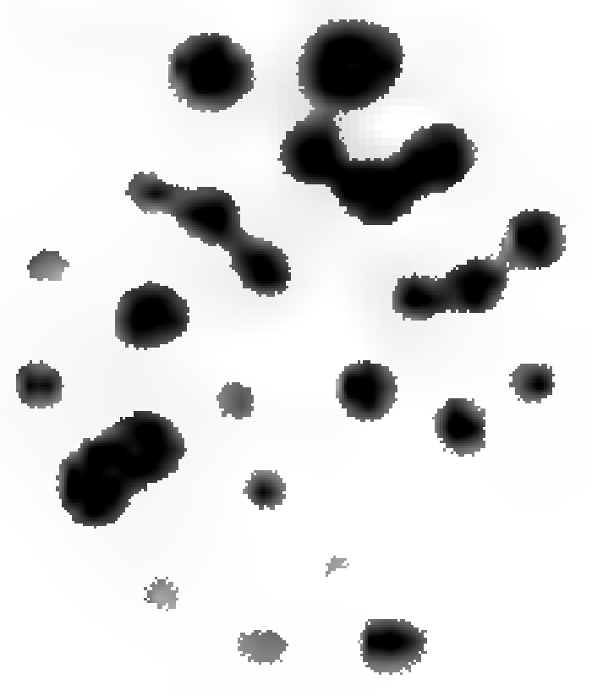

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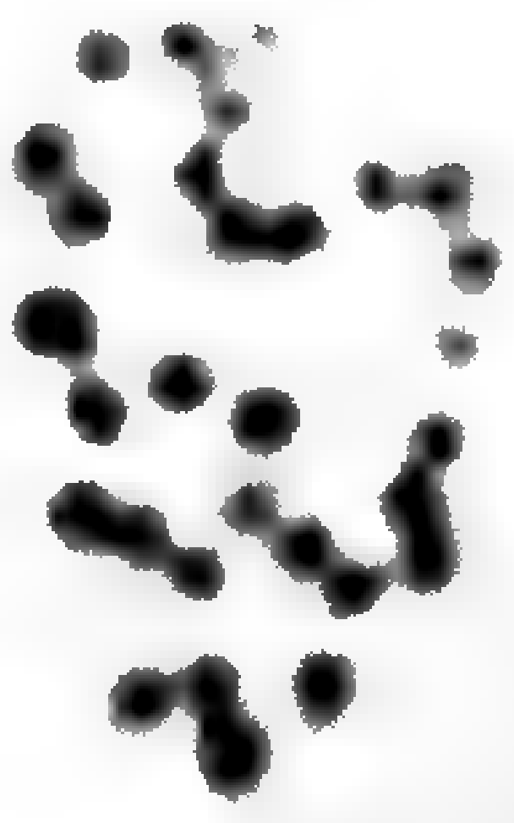

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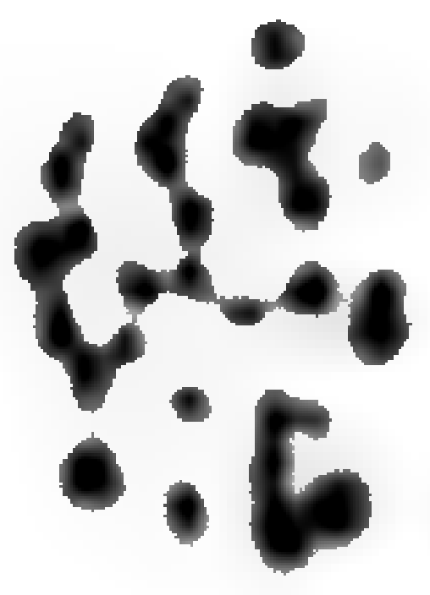

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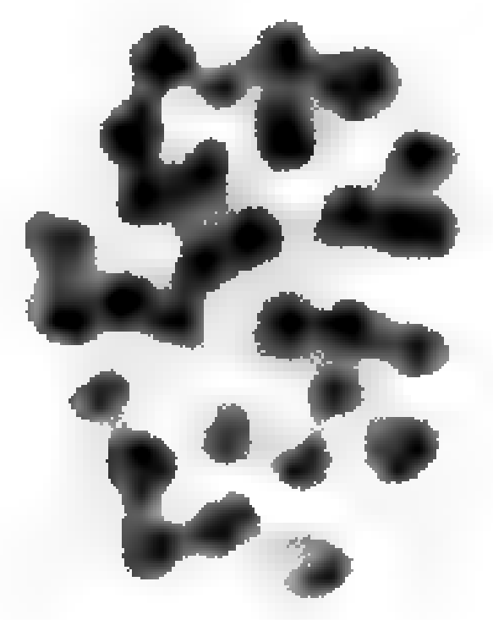

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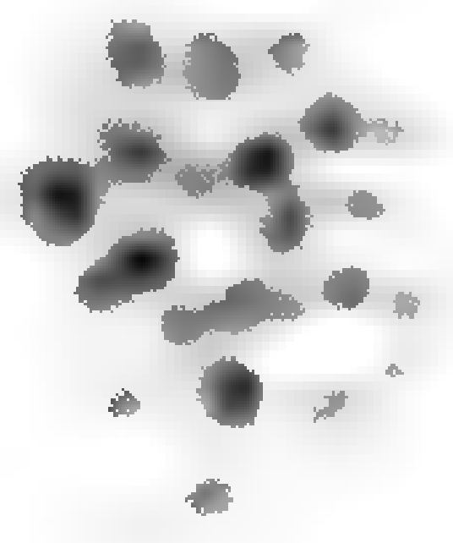

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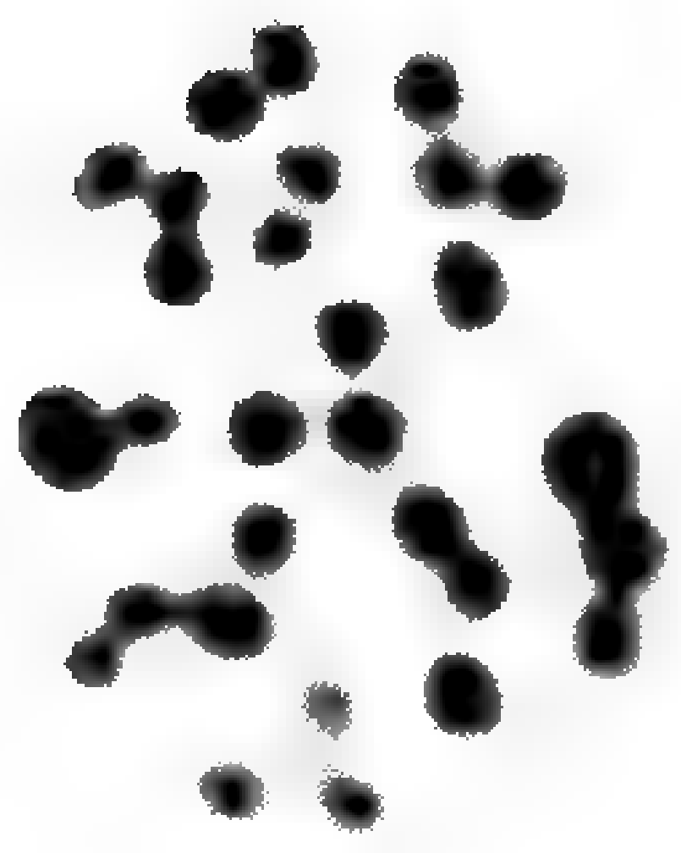

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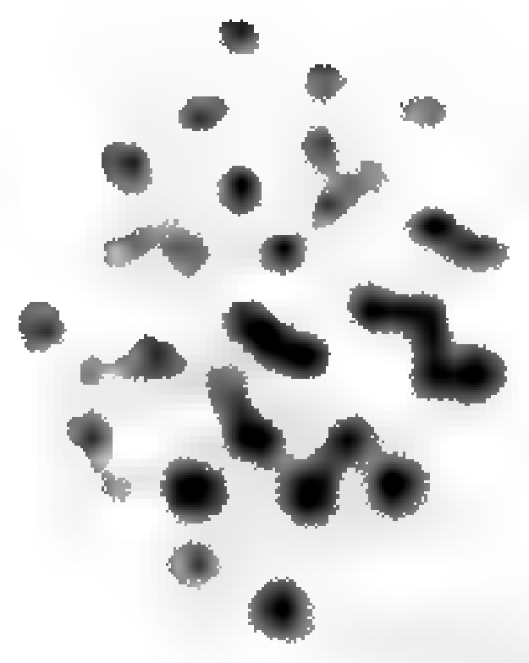

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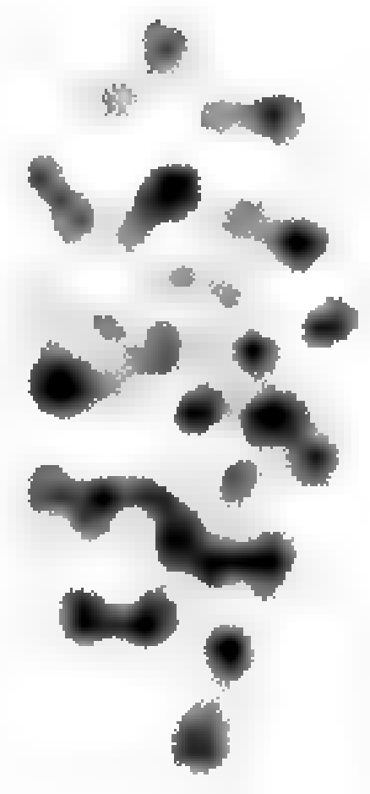

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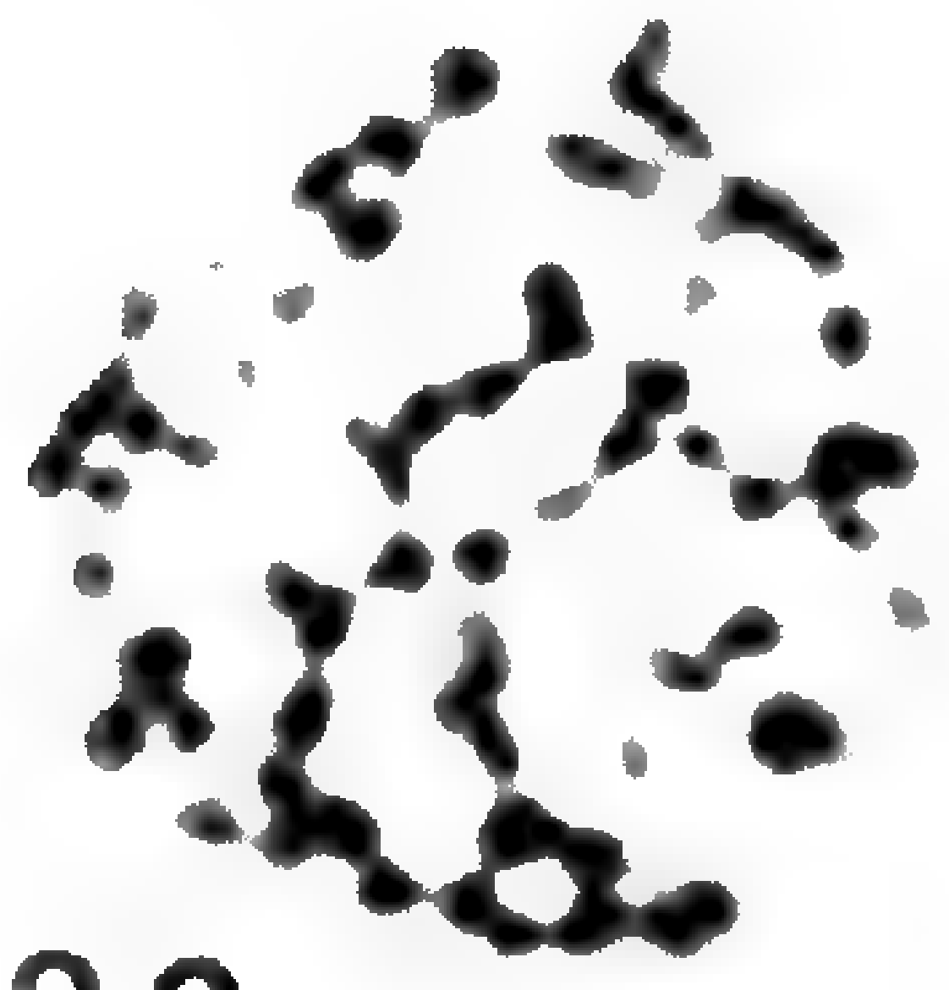

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Artificial hybrids between *Sedum platyphyllum* and *S. allantoides* (*M7737* × *M7724*) also are a good match for *Graptopetalum goldii*, show normal chromosome pairing and distribution at meiosis (Fig. 6), and are fertile. One second-generation plant, the only one studied cytologically among 65 obtained after selfing the $F_1$ hybrid, also shows mostly normal meiosis, with $n = 29$.

The similarities between Section *Centripetalia* and *Graptopetalum* in the fetid odor and in the markings of their petals are probably the result of convergence, possibly adaptations to pollination by carrion flies or the like. The terminal inflorescences of Section *Centripetalia* (vs. lateral inflorescences in *Graptopetalum*), the separate petals spreading from the base (vs. petals that are connate and erect at the base), the erect (vs. reflexed) stamens after anthesis, and probably the basic chromosome number ($n = 29$ vs. $x = 30$–$35$, Uhl, 1970) argue against a close relationship between these two species and *Graptopetalum* (Moran, 1966).

Furthermore, most diploid species of *Graptopetalum* are relatively easily hybridized with each other and also with other genera of subfamily Echeverioideae, as well as with species of section *Pachysedum* of *Sedum*; and a very substantial amount of chromosome pairing occurs in nearly all such hybrids. By contrast, diploid *Sedum allantoides* and *S. platyphyllum* seem more difficult to cross with species of *Graptopetalum* (only two definite hybrids obtained in nine such attempts) and with other genera of Echeverioideae (four definite hybrids in 18 attempts) and also with species of *Sedum* section *Pachysedum* (one hybrid in nine attempts). Six of the hybrids resulting from these crosses have been studied cytologically, and their meiosis was very irregular, with analysis of chromosome pairing very difficult and usually with more univalents than paired elements at metaphase I. For example, in *S. allantoides* (*M6368*, $n = 29$) × *Graptopetalum fruticosum* (*U1078*, $n = 31$) only three cells could be analyzed at metaphase I; these had 16–19 bi- and multi-valents and 22-28 univalents. *Sedum platyphyllum* (*M7737*, $n = 29$) × *S. cremnophila* of section *Pachysedum* (*M10174*, $n = 33$) showed 16–26 bi- and multi-valents and 7–27 univalents in 12 cells analyzed at metaphase I (Uhl, 1976a), with numerous laggards and 3 or more bridges at anaphase I and mostly abnormal-appearing microspores. Hybrids of *Sedum allantoides* with *Echeveria nodulosa* ($n = 16$) and of *S. platyphyllum* with *E. ciliata* ($n = 25$) and with *Pachyphytum hookeri* ($n = 32$) are about as irregular at meiosis. Thus the genomes of the two species of Section *Centripetalia* appear to be organized very similarly to each other but very differently from those of *Graptopetalum* and other genera of subfamily Echeverioideae and also from those of *Sedum*, section *Pachysedum*. Relatively little chromosome pairing was seen also in three other hybrids between *S. platyphyllum* ($n = 29$) and two additional species belonging to other groups of *Sedum* (*S. stahlii* and *S. greggii*).

The best chromosome pairing noted in any hybrid of either species of Section *Centripetalia* with any outside species occurred in *Sedum platyphyllum* ($n = 29$) × *S. obcordatum* ($n = 34$) (*M7737* × *U1583*), where 27–29 bi- and multi-valents and 0–4 univalents were noted in 15 cells analyzed, and mostly normal-looking microspore quartets were seen. This was unexpected, because the parental species are quite different both morphologically and in their chromosome numbers and seem not closely related.

The relatively poor chromosome pairing seen in most of the hybrids cited above means that the chromosomes of *Sedum allantoides* and *S. platyphyllum* probably have relatively little homology for those of most other species of *Sedum* and the other genera; this provides genetic support for Moran's (1966) conclusion that the two species of section *Centripetalia* are morphologically distinct from other species and should be maintained as a separate group. (*Sedum platyphyllum* × *S. obcordatum* is the lone exception to the rule of poor pairing in these hybrids, but, as noted, the latter species otherwise seems not closely related.)

The very limited chromosome pairing in most of these hybrids also means that few or none of the 29 chromosomes contributed to a hybrid by *Sedum allantoides* or by *S. platyphyllum* have enough homology with any of the 28 other chromosomes from the same parent that they can pair with each other. Thus, in spite of their relatively high basic chromosome numbers ($n = 29$), *S. allantoides* and *S. platyphyllum* are regarded here as effectively diploid now, regardless of how they may have originated. The same kind of evidence has argued for relatively high basic chromosome numbers in other groups of Mexican Crassulaceae: $x = 30–34$ in *Sedum* section *Pachysedum* (Uhl, 1978) and also in *Graptopetalum* (Uhl, 1970), $x = 31–33$ in *Pachyphytum* (Uhl & Moran, 1973), $x = 33$ in *Sedum cremnophila* and its relatives (Uhl, 1976a).

Fertile hybrids have been produced in the Mexican Crassulaceae from crosses between a number of very different pairs of tetraploid parents, some belonging to different genera (Uhl, unpublished). These hybrids show normal, or nearly normal, pairing of their chromosomes at meiosis, apparently because the two sets of chromosomes that the hybrid received from each parent regularly pair with other other (autosyndesis). This allows a balanced distribution of the chromosomes to the reproductive cells, some of which are functional even in some intergeneric hybrids. The extensive, often apparently complete, autosyndesis means that the parents are autotetraploid.

One collection of *Sedum allantoides* appears to be such an autotetraploid (*M6358*, $n = 58$). A hybrid of this with the diminutive *S. compactum* ($n = 60$, probably) has nearly normal meiosis, with 59 bivalents in many cells, and it produces quartets and microspores that appear normal and 10.2% pollen that is stainable in aniline blue-lactophenol. Ten second-generation hybrids were grown from seed produced spontaneously by the $F_1$ hybrid. The presumed formation of 29 bivalents by autosyndesis among the 58 chromosomes that this hybrid received from tetraploid *S. allantoides* (*M6358*) contrasts sharply with the apparent inability of any of the 29 chromosomes contributed to other hybrids by other collections of the same species to pair with each other, and it strongly reinforces the conclusion above that the plants of *S. allantoides* with $n = 29$ are effectively diploid. Tetraploid *S. allantoides* has also been crossed with tetraploid collections of *Graptopetalum macdougallii* ($n = 66$), *G. saxifragoides* ($n = 64$), and *Echeveria secunda* ($n = 30\pm$).

## SECTION FRUTICISEDUM BERGER

A second probably natural group is listed here as section *Fruticisedum* Berger. Ten shrubby and subshrubby species of this section, as it is interpreted here, have been studied. The leaves are linear or thin and mostly narrow, and the flowers mostly white or pale pinkish. All of these species have $n = 26$ to $n = 31$ or a multiple, and six of them have $n = 29$. Five of these species (*Sedum chloropetalum, S. frutescens, S. oxypetalum, S. pulvinatum,* and *S. retusum*) were listed under section "*Frutisedum*" by Jacobsen (1974); three others (*S. bourgaei, S. griseum,* and *S. guadalajaranum*) were under section *Leptosedum* (which is here merged); one (*S. guatemalense*) was listed under section *Pachysedum*, and one (*S. oxycoccoides*) as a "true" *Sedum*. Of additional species listed in

*Frutisedum* by Jacobsen, *S. amecamecanum* is a natural hybrid of *S. praealtum* with *Villadia batesii* (Clausen, 1959; Uhl, 1978), *S. conzattii* was not available, *S. cuspidatum* ($n = 34$) and *S. hultenii* ($n = 26$) have lateral inflorescences and belong to section *Pachysedum* (Uhl, 1978), and *S. quevae* ($n = 20$ and 21), *S.* tortuosum ($n = 15$ and 16) and *S. tuberculatum* ($n = 16$) differ cytologically from the others and probably are not closely related to them.

Six species of this section have the same chromosome number ($n = 29$) as the two species of section *Centripetalia*, but only two crosses between the two groups have been attempted, both unsuccessful, and nothing is known of homologies between their chromosomes.

Some species of *Villadia* subgenus *Altamiranoa* (e.g., *V. batesii, n* = 25, and *V. elongata, n* = 23) are very similar in general habit and in other characters to some species of section *Fruticisedum* (e.g., *Sedum bourgaei*), differing chiefly in their basally erect and connate corollas, which are approached by several species of this section. It seems likely that *Villadia,* or at least its subgenus *Altamiranoa*, may have been derived from a common ancestor with section *Fruticisedum.*

*Sedum bourgaei* Hemsley ($n = 29$ in eight collections from seven localities, Fig. 7) is a subshrub with reddish brown stems, linear leaves, and white flowers. It occurs from near Mexico City west into central Michoacan and north to southern Queretaro (Clausen, 1959). Although Berger (1930) and Jacobsen (1974) classified it in a different section, in many respects the species seems both morphologically and geographically to occupy a central position in section *Fruticisedum*, and some of the other species are easily characterized by how they differ from it: *S. chloropetalum* by its lanky stems and green flowers, *S. frutescens* by its large size and massive stems, *S. griseum* by its somewhat thicker, grayish stems with peeling bark, *S. guadalajaranum* by its tubers and more delicate leaves, *S. oxycoccoides* by its deep red flowers, *S. oxypetalum* by its massive stems and broader leaves, and *S. retusum* by its broader leaves with retuse tips. A hybrid between *S. bourgaei* and the diminutive *S. greggii* ($n = 26$) (U1535 × M10155) showed very little chromosome pairing at meiosis. Attempted crosses with *S. palmeri, S. platyphyllum,* and *S. quevae* were unsuccessful.

*Sedum chloropetalum* Clausen ($n = 29$ in two collections, including the type, from two localities, Fig. 8) resembles *S. retusum* but grows taller and differs conspicuously in its rounded leaf apices and yellowish green petals. The species is native in the Sierra Madre del Sur of southeastern Oaxaca. No hybrids have been produced in two attempts.

*Sedum frutescens* Rose ($n = 30$ in five collections from three localities, Fig. 9) resembles *S. oxypetalum* in its large size (up to a meter or more in height), thick stems (up to 10 cm. or more in diameter at the base), and exfoliating bark. It differs from the latter in its white (vs. pinkish) flowers and longer, narrower leaves and in its time of flowering (dry season—winter and spring—often when leafless or nearly so, vs. wet season—summer—for *S. oxypetalum*). The chromosome number ($n = 30$) also differs consistently from that in *S. oxypetalum* ($n = 29$). *Sedum frutescens* has been crossed with two species of subfamily Echeverioideae, *Graptopetalum fruticosum* ($n = 31$) and *Pachyphytum hookeri* ($n = 32$). The latter hybrid has flowered and shows very irregular meiosis, as expected, with relatively poor chromosome pairing. Attempted crosses with *S. cremnophila* and *S. torulosum* were unsuccessful.

*Sedum griseum* Praeger, as here reported, consists of two morphological and cytological forms. Populations from Guanajuato, and possibly also from Queretaro, have grayish, glaucous leaves and $n = 26$ (in nine collections from five localities, Fig. 10). Plants from farther south, in Jalisco and Michoacan, are greener and differ in other characters and all have $n = 30$ (seven collections from five localities, Fig. 11). The type collection originated in Mexico without further information as to locality, but Clausen (1959) considered that a cultivated plant like those reported here from Guanajuato with $n = 26$ was a closer match for the type than those from farther south. However, he concluded from his morphological studies that both forms should be kept in the same species, possibly as separate subspecies. The consistent difference in chromosome numbers, with no intermediate numbers known, and also the disjunct distributions indicate that a significant separation into at least incipient species has occurred between these two. Possibly a reexamination of their morphological differences might justify their recognition as separate species. *Sedum griseum* is most likely to be confused with *S. bourgaei* (Clausen, 1959), but the latter species consistently has $n = 29$. *Sedum griseum* has been crossed with the diminutive *S. greggii* ($n = 26$), but 11 other crosses (five of them with species of *Villadia*) yielded nothing.

## Table 1. **Chromosome numbers.**

### Section *Centripetalia* Alexander

**Sedum allantoides** Rose ($n = 29$)

*U1200* Type collection. Puebla: Hills near San Luis Atolotitlan, 2000–2100 m. (J. N. Rose 07/471 via Univ. Mich. Bot. Garden 9369).

*M7724* (Figure 1) Topotype (R. Moran).

*U1456, M6368* Oaxaca: Rocks above Mex. 125 at S. edge of Miltepec, 1900 m. (C. H. Uhl, R. Moran).

*U2383* Oaxaca: Small cliffs along Mex. 190 at Km. 32.3 SE of Huajuapan, ca. 6 km. N. of Tamazulapan, 1900 m.

*U1207, M3209, C47-11* All cultivated.

*M8431* (Figure 5) Type collection of *Graptopetalum goldii* Matuda. Cultivated.

**Sedum allantoides** Rose ($n = 58$)

*M6358* (Figure 2) Cultivated: San Antonio Texcala, Puebla (R. Moran).

**Sedum platyphyllum** Alexander ($n = 29$)

*M7737* Oaxaca: 6 km. NW of Totolapan, 1300 m., shaded cliff (R. Moran) (One plant had $n = 29$, Figure 3, another $n = 58$, Figure 4)

*M10143* Oaxaca: El Convento, near Portillo Nejapa, ca. 1500 m. (T. MacDougall, via R. Moran).

*M11808* Oaxaca: Cerro San Pedro, Tehuantepec, 1150 m. (T. MacDougall, via R. Moran).

*C42-7, C47-40* Type collection. Oaxaca: Cerro Guiengola, near Tehuantepec (T. MacDougall, via R. T. Clausen).

### Section *Fruticisedum* Berger

**Sedum bourgaei** Hemsley ($n = 29$)

*C48-39* Michoacan: pine-oak woods 8 km. S. of Patzcuaro, 2300 m. (R. T. Clausen).

*U2261* Michoacan: Cliffs along Mex. 15 at Km 190.8 (W. of Toluca), 2.4 km. W. of Puerto Garnica (summit of Sierra de Ozumatlan), 2850 m.

*U1414, Z-Z3* Michoacan: Rocks along Mex. 15, 20 km. E. of Zitacuaro, 2600 m. (C. H. Uhl, R. T. Clausen).

*M10149* State of Mexico: Amanalco, 2300 m. (R. Moran).

*M10155* (Figure 7) State of Mexico: 11 km. E. of Temascaltepec, 2150 m. (R. Moran).

*U2515* State of Mexico: 14 km. NE of Temascaltepec, 2320 m.

*U2512* State of Mexico: 5 km. NE of Meson Viejo, 3200 m.

**Sedum chloropetalum** Clausen ($n = 29$)

*M10096* (Figure 8) Oaxaca: Portillo de Zeta (R. Moran).

*C45-50* Type collection. Oaxaca: Santo Tomas Teipa, SW of Tehuantepec (ca. 16° 20′N, 95° 35′W) (T. MacDougall, via R. T. Clausen).

**Sedum frutescens** Rose ($n = 30$)

*U2022, U2067* State of Mexico: Above Santo Tomas hydroelectric plant, W. of Valle de Bravo (Jay Dodson 471).

*U1431, M6400* (Figure 9) Near topotypes. Morelos: Pedregal above Cuernavaca (C. H. Uhl, R. Moran).

*U1446* Guerrero: 1 km. E. of east entrance to Taxco, Mex. 95.

**Sedum griseum** Praeger ($n = 26$)

*U2475* Guanajuato: Near San Felipe, 1800 m. (F. Otero).

*U2116, M14729* Guanajuato: Pichachos de la Bufa, on NE side of Guanajuato, 2300 m. (C. H. Uhl, R. Moran).

*U2272, M10193* Guanajuato: Sierra de Guanajuato, 3.3 km. SW of Mesa San Jose & 32 km. SW of Dolores Hidalgo, 2350 m. (C. H. Uhl, R. Moran).

*C49-3* Guanajuato: E. of San Luis de la Paz (C. L. Gilly 131, via R. T. Clausen).

*C44-111* Queretaro: San Juan del Rio (J. N. Rose #05/120, N.Y. Bot Garden 24066, via R. T. Clausen).

*C44-112* (Figure 10), *C47-32* Cultivated (R. T. Clausen).

**Sedum griseum** Praeger ($n = 30$)

*U2061* Jalisco: Below La Joya, N. slope of Nevado de Colima, 2300 m. (F. C. Boutin & F. K. Brandt 2375).

*U1403, MVR-SL* (2 plants, Figure 11) Michoacan: SW of San Lorenzo on lava, ca. 20 km. N. of Uruapan. (C. H. Uhl, R. T. Clausen).

*U837, MVR-SO* (3 plants) Michoacan: Sierra de Ozumatlan, near Las Trojes, 35 km. E. of Morelia, 2320 m. (H. E. Moore, Jr., R. T. Clausen).

*U1413* Michoacan: E. side of Puente Rio Turundeo, Mex., 15, 8.4 km. N. of Tuxpan, 1825 m.

*U1425* State of Mexico: W. side of Lake Valle de Bravo.

**Sedum guadalajaranum** Watson ssp. **viridifolium** Clausen ($n = 29$)

*U2322* (Figure 12) Zacatecas: 24 km. SW of Valparaiso, 2275 m. (M. Kimnach & H. Sanchez-Mejorada).

**Sedum** cf. **guatemalense** Hemsley ($n = 27$)

*U1653* (Figure 13) Oaxaca: Epiphytic on oak in cloud forest near Cerro Pelón, N. of Oaxaca at Km. 129 on Mex. 175, 2820 m. (W. Handlos 370A).

**Sedum oxycoccoides** Rose ($n = 29$)

*U2330* (Figure 14) Nayarit: 24 km. SW of San Juan Capistrano, Zac., on road to Jesus Maria, Nay., 2675 m. (M. Kimnach & H. Sanchez-Mejorada 1892).

**Sedum oxypetalum** H.B.K. ($n = 29$)

*M7786* (Figure 15) Hidalgo: above Velasco (escaped?). (R. Moran.)

*U1417* State of Mexico: summit of hill on N. side of Toluca, 2700 m.

*U1287*, M6402 Morelos: on lava flow 3 km. S. of summit of highway N. of Cuernavaca. (M. Kimnach, R. Moran).

*M3281* Cultivated.

**Sedum pulvinatum** Clausen ($n =$ ca. $54$)

*C45-46* Type collection. Oaxaca: mountains E. of Ayutla. (W. H. Camp 2835, via R. T. Clausen).

**Sedum retusum** (Hemsley ($n = 27$)

*C7452, U1642* (Figure 16) San Luis Potosi: Sierra de Alvarez, ca. 36 km. E. of San Luis Potosi & 2 km. W. of Puerto Altamira summit, 2250 m. (R. T.

Clausenn, W. Handlos 301).

*M10005, M13374* Near topotypes. San Luis Potosi: Sierra de Alvarez, S. and above Puerto Altamira summit, 2600 m. (Both $n = 27 + 1$) (R. Moran & C. H. Uhl).

*U486, C43-74* Cultivated.

**Sedum retusum** Hemsley ($n = 28$–$31$)

*C7416* Tamaulipas: Ca. 9 km. NW of Gomez Farias (R. T. Clausen). ($n = 28+1$).

*U1872* (Figure 17) Hidalgo: on limestone 19 km. S. of Jacala & 1 km. S. of MInas Viejas, at Km. 79 on Mex. 85, 2050 m. ($n = 29$).

*M7811* (Figure 35) Hidalgo: 21 km. S. of Jacala at El Salto ($n = 31+1+1B$). (R. Moran).

### *Sedum palmeri* Group.

**Sedum obcordatum** Clausen ($n = 34$)

U1583 (Figure 18) Veracruz: Barranca de Mala Cara, on SE slope of Orizaba, 4200 m. (R. T. Clausen).

**Sedum palmeri** S. Watson ($n = 34$)

*C7596* Nuevo Leon: Villa de Garcia (R. T. Clausen).

*U1367* (Figure 19) Near topotype. Nuevo Leon: along road to Chipinque Mesa, SW of Monterrey, 600 m.

*C7568* Nuevo Leon: Saddle Mountain, SE of Monterrey (R. T. Clausen).

*C7545* Nuevo Leon: Near Villa Santiago (R. T. Clausen).

*U1940, U2084* Nuevo Leon: 24 km. W. of Mex. 85 on road to Rayones, 650 m. (M. Kimnach, C. Glass).

*U1918* Nuevo Leon: Santa Rosa Canyon, 7 km. E. of Iturbide, 1200 m.

*U2575* Tamaulipas: La Reforma (A. Lau #052).

*U120, C47-80* Cultivated.

**Sedum palmeri** S. Watson ($n = 35$)

U2075 Nuevo Leon: 1 km. S. of Grutas de Garcia, 850 m. (M. Kimnach 1383).

**Sedum palmeri** S. Wats. ($n = 68$) (= *S. compressum* Rose)

*U1836* (Figure 20), *C7375* Tamaulipas: Canyon 14–16 km. SW of Ciudad Victoria (C. H. Uhl, R. T. Clausen).

*C7371* Topotype of *S. compressum* Rose. Tamaulipas: Canyon SW of Ciudad Victoria (R. T. Clausen).

*C7389* Tamaulipas: Canyon W. of Ciudad Victoria (R. T. Clausen).

*U1837* Tamaulipas: Limestone along Mex. 101, 27 km. SW of Ciudad Victoria.

*U2030,* U2153, U2478 Cultivated.

*C47-79* Cultivated. N. Y. Botanical Garden (via R. T. Clausen). Believed to be from the type collection of *S. compressum* Rose.

**Sedum** sp. aff. **palmeri** ($n = 34$)

*M7658* (Figure 21) San Luis Potosi: Zaragoza, in the Sierra de Alvarez ($n = 34 + 3B$) (R. Moran).

*M14756* Guanajuato: 16 km. E. of San Luis de la Paz (R. Moran).

**Sedum torulosum** Clausen ($n = 34$)
UC54.234 (Figure 22) Same clone as the type collection. Cultivated (H. Rush, via Univ. of Calif. Bot. Garden, Berkeley).

Miscellaneous species.

**Sedum botteri** Hemsley ($n = 24$)
*6A* (Figure 23) Veracruz: Barranca de Cuautilla, 10 km. NW of Huatusco (R. T. Clausen).
*M10153½* Chiapas: El Triunfo (T. MacDougall, via R. Moran).
*UC58.832* Chiapas: El Rosario, Motozintla, 2100 m. Epiphytic. (T. MacDougall B-205).

**Sedum burrito** Moran ($n = 34+1$)
*U2446* Type collection. Cultivated: Coatepec, Veracruz, via P. C. Hutchison, Tropic World, Inc., 1328A.
*U2073* (Figure 24) Cultivated: Guadalajara, Jalisco (F. Boutin & M. Kimnach 3221).

**Sedum calcicola** Robinson & Greenman ($n = 32$)
*U1941, U2081* Nuevo Leon: Rayones Canyon, 20 km. W. of Mex. 85, 600 m. (C. Glass & R. Foster 3282, M. Kimnach 1393).
*U2079* Nuevo Leon: 9 km. E. of Rayones, 825 m. (M. Kimnach 1411).
*U832* Tamaulipas: 8 km. before Huisachol on road from Ciudad Victoria to Jaumave. (H. E. Moore, Jr. 8005).
*M13368* (Figure 25) San Luis Potosi: Rocky river bank at E. side of Ocampo (formerly Bagre), ca. 16 km. WNW of Cañada Verde (R. Moran & C. H. Uhl).
*U1646* Near Topotype. San Luis Potosi: S. of Las Canoas (W. Handlos 303A).

**Sedum calcicola** Robinson & Greenman ($n = 48$)
*U1839, M7816* (Figure 26) San Luis Potosi: 2 km. W. of Santo Domingo on Mex. 80, 18 km. E. of Mex 57 (C. H. Uhl, R. Moran).

**Sedum calcicola** Robinson & Greenman ($n = 64$)
*U1370* Near topotype of *S. lenophylloides* Rose. Nuevo Leon: Chipinque Mesa, SW of Monterrey.
*U1529* San Luis Potosi: S. side Rio Verde 3 km. WNW of Cañada Verde.
*M10046* (Figure 27) Hidalgo: Barranca de Toliman (R. Moran).
*C47-16, C47-56* Cultivated (R. T. Clausen).

**Sedum furfuraceum** Moran ($n = 34$)
*M7659* (Figure 28) Type collection. San Luis Potosi: 18 km. SE of Zaragoza, Sierra de Alvarez, 2100 m. 21° 59′N., 100° 42′W. (R. Moran).

**Sedum morganianum** Walther ($n = 35$)
*UC54.419* Probably from type collection. Cultivated: Dr. Meredith Morgan.
*U1270* (Figure 29), and *"unumbered"* (fixed buds only, no voucher). Cultivated.

**Sedum quevae** Hamet ($n = 20$)
*U1289* Morelos: km. 9 on road from Cuernavaca to Tepoztlan (M. Kimnach).
*SB1C* Tlaxcala: 1 km. SW of San Bernabé & 6 km. NE of Tlaxcala (R. T.

Clausen).

*SE3* (Figure 30) Tlaxcala: 2 km. NE of San Bernabé (R. T. Clausen).

*C7496* Tlaxcala: Santa Maria Atlihuitzia (R. T. Clausen).

**Sedum quevae** Hamet ($n = 21$)

*U2377* Oaxaca: ½ km. S. of El Estudiante & 12 km. N. of junction Mex. 190 at Oaxaca. Sierra de Juarez.

*M7767* (Figure 31) Oaxaca: Ixtepec. (R. Moran).

**Sedum stahlii** Solms ($n = 29$)

*U1460* Puebla: 2½ km. S. of Cumbres de Acultzingo, Ver.

*M7774* Veracruz: El Paraje (R. Moran).

*M2129* (Figure 32), *M3250, UC54.169* Cultivated.

**Sedum tortuosum** Hemsley ($n = 15$)

*M7759* Oaxaca: Portillo San Andres (R. Moran).

*M10127* Oaxaca: Cerro San Felipe (R. Moran).

*UC58.830* (Figure 33) Oaxaca: Cerro Madreña, Santo Tomas Quieri, 2100 m. (T. MacDougall B-203).

**Sedum tortuosum** Hemsley ($n = 16$)

M7620 (Figure 34) Durango: Los Angeles, 5½ km. E. of Revolcaderos (R. Moran).

*U2063* Jalisco: Sierra de Minatitlan, above Haceradero, 1800 m. (F. C. Boutin & F. K. Brandt 2496).

**Sedum tuberculatum** Rose ($n = 16$)

*C47-54* Oaxaca: Sierra de Miahuatlan (from R. T. Clausen).

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*Sedum guadalajaranum* Watson ($n = 29$, one collection, Fig. 12) appears like a more delicate version of *S. bourgaei* ($n = 29$), with generally smaller leaves and tuberous roots. The plant studied belongs to the recently described subspecies *viridifolium* Clausen (1978). Tuberous roots also occur in some populations of *S. bourgaei. Sedum guadalajaranum* occurs at several localities from Guadalajara north almost to Aguascalientes (Clausen, 1978), all localities well to the northwest of the range of *S. bourgaei.* A recent cross with *S. oxycoccoides* yielded five seedlings which died before their hybrid nature could be established. An attempted cross with *S. oxypetalum* was unsuccessful.

The plant listed here as *Sedum* cf. *guatemalense* Hemsl. ($n = 27$, one collection, Fig. 13) was a short subshrub, epiphytic on oak in a cloud forest in northern Oaxaca. The leaves were shiny green, 1 mm. thick, 3 mm. wide, and up to 12 mm. long, with a longitudinal groove above leading to a slightly retuse tip. The corolla was yellowish, with numerous small reddish streaks, especially toward the base. If this plant is not *S. guatemalense* it is probably an unnamed species. Authentic *S. guatemalense* (*U2491*), recently collected in Guatemala, is vegetatively rather similar to this, but it has not yet flowered. Of the other species, this plant seems perhaps closest to *S. retusum*, several collections of which also have $n = 27$. The plants later named as *S. rubrotinctum* Clausen were earlier thought to be *S. guatemalense*, an error that still persists in some collections, but they differ in many characters (Clausen, 1948b).

*Sedum oxycoccoides* Rose ($n = 29$ in one collection, Fig. 14) also resembles *S. bourgaei* but has flowers that are deep red in color. It occurs in the Sierra Madre Occidental in the state of Nayarit and probably also in Zacatecas. Seedlings have resulted from recent crosses with *S. griseum* ($n = 26$), *S. guadalajaranum*, *S. quevae* ($n = 21$), and *Pachyphytum hookeri*, but an attempted cross with *S. oxypetalum* was unsuccessful.

*Sedum oxypetalum* H.B.K. ($n = 29$ in five collections from three localities, Fig. 15) is a large species with deciduous leaves, massive stems up to 12 cm. in diameter at the base, and peeling bark. It closely resembles *S. frutescens* ($n = 30$) with which it sometimes occurs, but its leaves are broader and it flowers during the wet season (summer). *Sedum frutescens* flowers during the dry season (winter), often when leafless. The difference in chromosome number appears consistent. *Sedum oxypetalum* occurs from the eastern part of the state of Mexico to central Michoacan (Clausen, 1959), often on lava. Recently a single seedling has resulted from a cross with *S. griseum* ($n = 26$), but attempted crosses with *S. guadalajaranum*, *S. oxycoccoides*, *S. retusum*, and *Pachyphytum hookeri* have been unsuccessful.

*Sedum pulvinatum* Clausen ($n =$ ca. 54 in the type collection) of central Oaxaca has solitary white flowers. Clausen (1948a) classified it in Section *Fruticisedum*, which he redefined to include also Section *Dendrosedum*. He thought it closest to the yellow-flowered *S. luteoviride*, but that species appears to be a natural hybrid, *S. praealtum* × *S. greggii* (Uhl, 1978). In terms of the chromosome numbers in the other species of this section, *S. pulvinatum* appears to be a tetraploid.

*Sedum retusum* Hemsley has relatively broad leaves (up to 6 mm.) that are often subspatulate and retuse, white petals that are often pink at the base, and pink carpels. It resembles *S. oxypetalum*, to which Fröderström (1935) considered it closely allied, but it never develops the massive stems of the latter species. Four collections from near the type locality (Alvarez, San Luis Potosi) had $n = 27$ (Fig. 16) (two of them trisomic), as did two other plants from cultivation. However, three other collections from farther east, in the Sierra Madre Oriental of southern Tamaulipas and Hidalgo, had $n = 28 + 1$, $n = 29$ (Fig. 17), and $n = 31$ plus an extra chromosome of standard size and also a small B-chromosome (Fig. 35). An attempted cross with *S. oxypetalum* was unsuccessful, as were also crosses with 14 other species. However, unlikely at it seems, *S. retusum* has been hybridized with *Pachyphytum hookeri* of subfamily Echeverioideae, but the hybrid shows very little chromosome pairing.

## SEDUM PALMERI GROUP

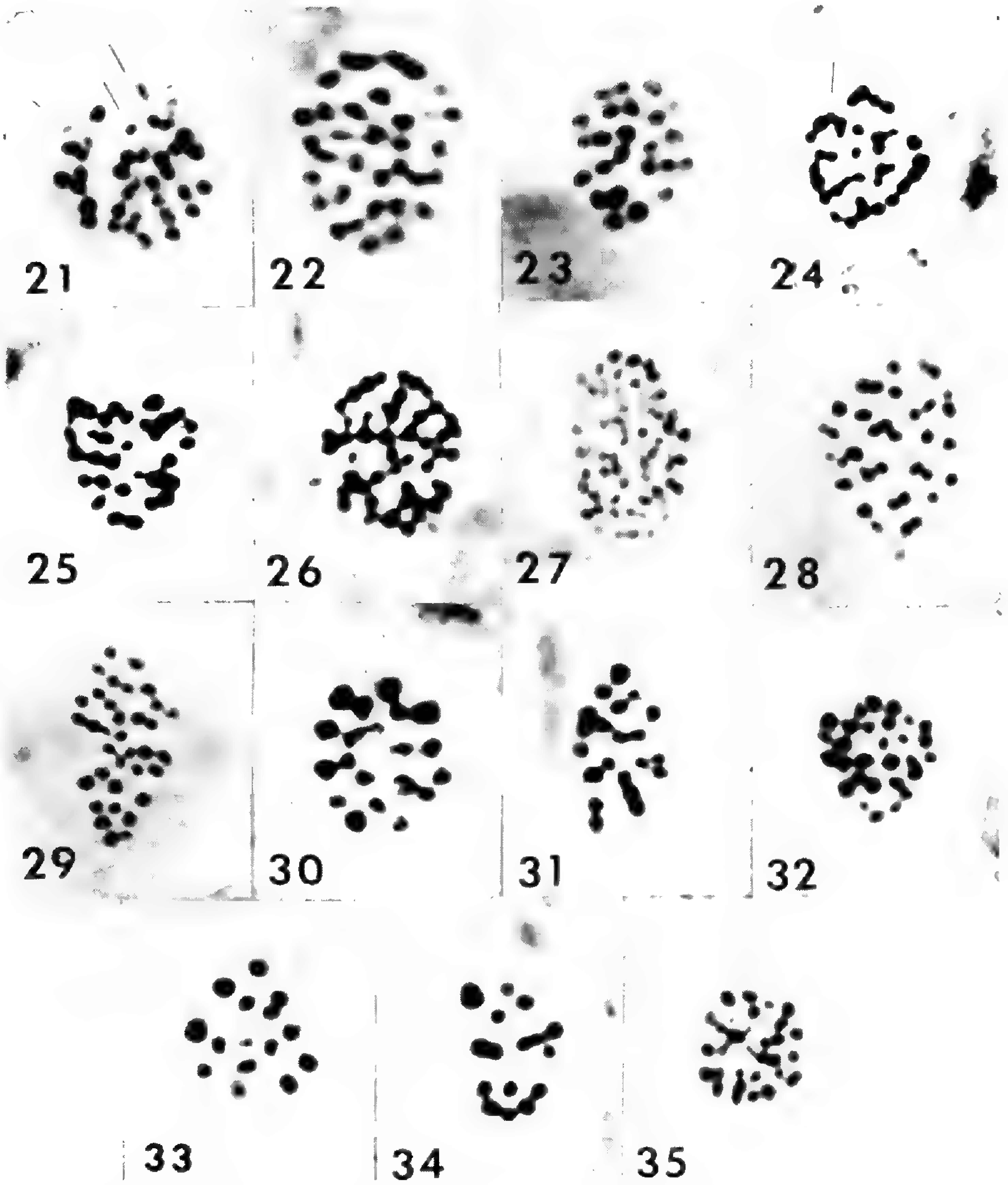
A third possibly natural group is referred to here as the *Sedum palmeri* group. It consists of at least three, and possibly four, subshrubby species with rather broad, glaucous leaves and yellow flowers, all with $n = 34$ (or $n = 68$). Jacobsen (1974) listed *S. palmeri, S. compressum* (here considered to be no more than a tetraploid subspecies of *S. palmeri*), and *S. torulosum* in his section *Dendrosedum,* and he classified *S. obcordatum* as a "true" *Sedum.* From their vegetative appearance and chromosome numbers these species might be classified in section *Pachysedum,* but they all have terminal inflorescences.

The chromosome numbers in 11 of 19 species of section *Pachysedum* are also $n = 34$, and it is likely that the evolutionary connection between *Pachysedum* and other species of *Sedum* lies somewhere among the immediate ancestors of the *Sedum palmeri* group. Most genera of subfamily Echeverioideae also have the same or similar basic chromosome numbers (Uhl, 1970, 1976a, Uhl & Moran, 1973), and they may have originated from the ancestral genus *Sedum* as a further development from ancestors that would have been classified in Section *Pachysedum* (Uhl, 1978).

Vegetative axes in species of the *Sedum palmeri* group are continued beyond the terminal inflorescences by branches which develop from the axils of leaves a few nodes below the inflorescence. Sometimes, after flowering, growth of the axillary vegetative axis pushes aside the terminal inflorescence so that the latter superficially appears to be lateral. In some members of section *Pachysedum* (e.g., *S. praealtum, S. cremnophila*) the lateral vegetative and inflorescence axes are not all distinguishable when young, and commitment of a branch to remain vegetative or to become an inflorescence is not immediately apparent. From ancestors similar to the *S. palmeri* group evolution of lateral inflorescences characteristic of section *Pachysedum* (and also of subfamily Echeverioideae) could be accomplished by maintaining only vegetative growth in the meristem of the main axis while only certain lateral axes (probably determined by seasonal factors) become committed to produce inflorescences.

*Sedum obcordatum* Clausen ($n = 34$, one collection, Fig. 18) is readily distinguished from *S. palmeri* by its decussate leaves and erect petals, but the chromosome numbers are the same. It occurs at high elevations on Cofre de Perote and Citlaltepetl (Orizaba) on the boundary between the states of Puebla and Veracruz (Clausen, 1959). A hybrid with *S. cremnophila* ($n = 33$) of section *Pachysedum* (=*Cremnophila nutans*) (*U1583* × *M10174*) shows the greatest proportion of chromosome pairing seen in any hybrid between species with terminal and with lateral inflorescences——30–33 bi- and multi- valents and 0–6 univalents in 12 cells analyzed—but it produces no stainable pollen (Uhl, 1976a). Surprisingly, a hybrid with *S. platyphyllum* ($n = 29$) of section *Centripetalia* (q.v.) (*M7737* × *U1583*) also shows mostly bivalent pairing at metaphase I. *Sedum obcordatum* has also been crossed with the cytologically variable *S. greggii* ($n = 33$) and with *Graptopetalum fruticosum* ($n = 31$), *Villadia grandisepala* ($n = 44$), *S. craigii* ($n = 30$), and *Pachyphytum hookeri* ($n = 32$)—the two last have not yet flowered. Forty-nine other attempts have yielded no hybrids. Three of the unsuccessful attempts were with *S. palmeri,* and these two species may not really be as closely related as their grouping together here implies.

*Sedum palmeri* S. Watson occurs on the eastern slopes of the Sierra Madre Oriental from the vicinity of Monterrey southeast beyond Ciudad Victoria, Tamaulipas. Plants from the northern part of the range, including a near topotype (*U1367*), are all diploids, with $n = 34$ (ten collections, Fig. 19) or $n = 35$ (one collection), but most plants from southwestern Tamaulipas, including a topotype of *S. compressum* Rose, are tetraploids ($n = 68$, 9 collections, Fig. 20). Most tetraploids are a bit smaller than most diploids, but the differences seem not sufficient to warrant status as a separate species.



Figures **21–35.** Chromosomes of *Sedum* at metaphase I in pollen mother cells, ×2000. Thin lines point to univalents or B-chromocomes. **21,** *S.* cf. *palmeri,* M7658, $n = 34 + 3B$; **22,** *S. torulosum,* UC54.234, $n = 34$; **23,** *S. botteri,* 6A, $n = 24$; **24,** *S. burrito,* U2073, $n = 34 + 1$; **25–27,** *S. calcicola;* 25, M13368, $n = 32$; 26, M7816, $n = 48$; 27, M10046, $n = 64$; **28,** *S. furfuraceum,* M7659, $n = 34$; **29,** *S. morganianum,* U1270, $n = 35$; **30–31,** *S. quevae;* 30, SE3, $n = 20$; 31, M7767, $n = 21$; **32,** *S. stahlii,* M2129, $n = 29$; **33–34,** *S. tortuosum*; 33, UC58.830, $n = 15$; 34, M7620, $n = 16$; **35,** *S. retusum,* M7811, $n = 31 + 1 + 1B$.

On the other hand, two plants from still farther south, in eastern San Luis Potosi and eastern Guanajuato, on the western ranges and slopes of the Sierra Madre Oriental system, have thicker, whiter leaves borne in much looser rosettes than the others. These plants also have $n = 34$ (one of them with B-chromosomes, Fig. 21), but are worth consideration as a new species.

Diploid *Sedum palmeri* has been crossed with three species of section *Pachysedum, S. craigii* ($n = 30$), *S. cremnophila* ($n = 33$), and *S.* sp. nov. (*UC58.858,* $n = 34 + 1$), and with two species of subfamily Echeverioideae, *Echeveria derenbergii* ($n = 27$) and *Pachyphytum hookeri* ($n = 32$), and also with *Villadia nelsonii* ($n = 20$). Thirty-eight other attempted crosses involving 28 other species gave no progeny. Tetraploid *S. palmeri* (= *S. compressum*) has given no progeny after attempted crosses with three other species. The anomalous diploid from San Luis Potosi and Guanajuato has been crossed with *Graptopetalum fruticosum* ($n = 31$), but attempts with five other species were unsuccessful.

*Sedum torulosum* Clausen ($n = 34$ in a clonotype, Fig. 22) forms plants up to a meter tall, with knobby stems up to 10 cm. or more in diameter at the base. Originally described from cultivated material of uncertain origin, it is now known to occur in northwestern Oaxaca. In many years of cultivation at Ithaca it has never flowered, although it does so profusely outdoors in California. Using flowering material brought from California, *S. torulosum* has been crossed with two species of section *Pachysedum, S. clavatum* and *S. cuspidatum,* and with two members of subfamily Echeverioideae, *Graptopetalum fruticosum* and *Pachyphytum hookeri.* None of these has yet flowered. Attempted crosses with *S. frutescens* and *S. lucidum* yielded no progeny.

## MISCELLANEOUS SPECIES.

Some other more or less shrubby species are listed here alphabetically. However, their affinities with each other and with the species and groups listed previously are not clear, either on cytological or on morphological grounds, or both. Probably at least some of them are more closely related to one or another of the more herbaceous species of *Sedum* than they are to other shrubby or subshrubby species.

*Sedum botteri* Hemsley ($n = 24$, three collections, Fig. 23) is usually epiphytic, with rather large, obovate or oblanceolate leaves and greenish flowers, speckled with reddish. It ranges from Veracruz to Chiapas. Clausen (1959) considered it most closely related to *S. tortuosum* ($n = 15$ and 16) and to be relatively unspecialized, possibly "most like the ancestral stock from which various other groups of species have evolved." However, its chromosome number is unique among all the woody Mexican species of *Sedum,* and this suggests that it may not be closely related to any of them.

The recently described *Sedum burrito* Moran (1977) has pendent stems like the very similar *S. morganianum,* but its floral parts and leaves are shorter and blunter, and the leaves are more spreading. No definite locality is yet known for it in the wild, but, like *S. morganianum,* it is suspected that it may be native somewhere on the eastern slopes of Mount Orizaba or nearby (Moran, 1977). Two plants obtained from cultivation at widely separated places in Mexico both have 35 chromosomal elements at metaphase I (Fig. 24), as does *S. morganianum,* but in both collections of *S. burrito* one element consistently is a univalent, and at anaphase I a laggard is usually seen. It is not clear whether these plants are monosomics ($2n$-1) based on $n = 35$ or trisomics ($2n+1$) based on $n = 34$. Study of field-collected plants may be necessary to determine whether the normal chromosome numbers of *S. burrito* and *S. morganianum* are the same, but no such plants are yet known for either species. Most (all?) inflorescences of *S. burrito* are definitely lateral, and the species perhaps should be assigned to section *Pachysedum.* Its chromosome number is compatible with this.

Hybrids of *Sedum burrito* have been produced with *S. morganianum,* with *S. lucidum* of Section *Pachysedum* and with two species of subfamily Echeverioideae, *Graptopetalum fruticosum* and *Pachyphytum hookeri.* Crosses with three other species were unsuccessful.

*Sedum calcicola* Robinson and Greenman is an older name for the species better known as *S. lenophylloides* Rose (Clausen, 1978). It occurs in the Sierra Madre Oriental from the vicinity of Monterrey south to the state of Hidalgo. The 13 collections studied represent three levels of ploidy, with a presumed basic chromosome number, not yet found, of $x = 16$, but the relationship, if any, between polyploidy and distribution is not clear. The northernmost collection (*U1370*), which is a near topotype of *S. lenophylloides,* and also the southernmost (*M10046*) and three others were all octoploid ($n = 64$, Fig. 27). Tetraploids ($n = 32$, Fig. 25), including a near topotype of *S. calcicola* (*U1646*), were widely distributed in the interior of the range (six collections, four localities), and two hexaploids ($n = 48$, Fig. 26) came from probably the same population in north central San Luis Potosi.

*Sedum furfuraceum* Moran ($n = 34$ in a plant of the type collection, Fig. 28) forms mats with thick, fleshy, creeping stems and small, egg-shaped leaves with a scaly cuticle. Its type (and only) locality is near Zaragoza, San Luis Potosi (Moran, 1961). A cross with *S. greggii* ($n = 33$) yielded a single hybrid (*M7807* × *M7659),* but 12 other attempted crosses produced nothing. Its chromosome number is common in Mexican *Sedum,* but the species seems not closely related to any others.

*Sedum morganianum* Walther, the "donkey's tail", has $n = 35$ (Fig. 29) in three collections, all from cultivation and possibly all the same clone, but including one traceable back to the type collection. The species is popular and very widely cultivated in Mexico and elsewhere, but no definite locality is known for it in the wild. Rumors of possible wild populations near the eastern slopes of the peak of Orizaba have not yet been confirmed (Moran, 1977).

This species has pendent stems with blue-glaucous leaves and deep pink, erect petals. Its woody stems and thickened, subterete leaves and its erect petals resemble those of some species of section *Pachysedum* (e.g., *Sedum corynephyllum,* $n = 34$), and its chromosome number is similar. The inflorescences are terminal on the pendent shoots, which arise laterally from a crowded basal branching system, and which rarely or never branch before flowering. *Sedum morganianum,* along with the very similar *S. burrito,* should perhaps be assigned to section *Pachysedum.*

Attempts to cross *Sedum morganianum* with three species of section *Pachysedum* have been unsuccessful, but the species has been crossed with *S. burrito* and *S. platyphyllum* and with nine species of subfamily Echeverioideae (in 25 attempts): *Echeveria ciliata, E. cuspidata, E. walpoleana, Graptopetalum amethystinum, G. fruticosum, Pachyphytum compactum, P. hookeri, P. kimnachii,* and *P. viride.* Chromosome pairing in some of these hybrids is not so nearly complete as it is in most hybrids within or between section *Pachysedum* and subfamily Echeverioideae, but it is more extensive than in most other hybrids. *Sedum morganianum* and *S. burrito* may have evolved from the same ancestral stocks in parallel with section *Pachysedum* and perhaps also with the *S. palmeri* group.

*Sedum quevae* Hamet has oblanceolate leaves and tuberous roots. It occurs from Morelos and Tlaxcala to Oaxaca. Collections from four northern localities all had $n = 20$ (Fig. 30), but plants from two localities in Oaxaca had $n = 21$ (Fig. 31). *Sedum quevae* has the morphological characters of section *Fruticisedum*, to which Jacobsen (1974) assigned it, but its very different chromosome numbers raise doubt that it truly belongs there. Tuberous roots also occur in most species of *Villadia*, and Clausen (1959) reported two natural hybrids between *S. quevae* and *V. scopulina*. Recent crosses with *S. oxycoccoides* resulted in three seedlings and with *S. bourgaei* in ten seedlings. Parentage of these seedlings has not yet been confirmed. A cross with *S. palmeri* was unsuccessful.

*Sedum stahlii* Solms has leaves that are terete, puberulent, decussate and usually strongly flushed with red, and it has bright yellow petals each with a subapical mucro. It occurs mostly in the area between Tehuacan, Puebla, and Orizaba, Veracruz. Although its chromosome number ($n = 29$, five collections, Fig. 32) is the same as in many other woody Mexican sedums, its affinities are not clear. Perhaps it is closest to *S. allantoides* of section *Centripetalia*, which also has $n = 29$, thickened, subterete leaves, and petals with a subapical mucro. An attempt to cross these two was unsuccessful, but a hybrid was obtained of *S. stahlii* with *S. platyphyllum* ($n = 29$), which is very closely related to *S. allantoides* (*M7737* × *U1460*). This hybrid showed very irregular meiosis that defied precise analysis, with more univalents than paired elements in most cells at metaphase I, indicating that the chromosomes of the parental species have only relatively scant and weak homology for each other.

Hybrids of *Sedum stahlii* with *S. cuspidatum* ($n = 34$) and with *S. cremnophila* ($n = 33$), both members of section *Pachysedum*, and also with *Graptopetalum fruticosum* ($n = 31$) of subfamily Echeverioideae also show more univalents than paired elements at metaphase I. Attempted crosses with eight other species were unsuccessful.

The subapical mucro on the petals of *Sedum stahlii* appears in reduced form in its hybrids. It also is seen on petals of *S.* × *rubrotinctum*, which appears to be a garden hybrid having *S. stahlii* as one parent and probably *S. pachyphyllum* ($n = 34$) of section

*Pachysedum* as the other (Uhl, 1978). A single seedling resulted from a cross between these two species but died without flowering.

*Sedum tortuosum* Hemsley is usually epiphytic, with winged seeds attached to nearly basal placentas (Clausen, 1959). Plants from two localities in Durango and Jalisco had $n = 16$ (Fig. 34). These may correspond to *S. lignicaule* Fröderström, but Clausen (1959) reduced that species to *S. tortuosum*. Plants from three localities in Oaxaca all had $n = 15$ (Fig. 33), one of them usually with univalents (precociously separated bivalents?) at metaphase I. Clausen thought *S. tortuosum* most closely related to *S. botteri* ($n = 24$) and to *S. guatemalense* ($n = 27$), but the chromosomes are very different. *Sedum tortuosum* was listed in section "*Frutisedum*" by Jacobsen (1974), but its chromosomes differ significantly from those of other species in that section, as it is delimited here. Six attempts at hybridizing *S. tortuosum* (*U2063*, $n = 16$), involving four other species of *Sedum*, were unsuccessful.

*Sedum tuberculatum* Rose of southern Oaxaca has $n = 16$ (one collection). Jacobsen (1974) classed this species in his section "*Frutisedum*", but the chromosome number suggests that it may not be closely related to the species of that section, as it is conceived here, which have $n = 29$, more or less.

## Summary

Chromosome numbers are reported for 127 collections representing at least 24 more or less woody species of Mexican *Sedum* having terminal inflorescences. Nine species have $n = 29$, six have $n = 34$, and the others have from $n = 15$ to $n = 68$. One species is tetraploid and four others include polyploid races. Five other species have dysploid chromosome races, and some plants of three species have unpaired and/or B-chromosomes. Cytologically and morphologically these species fall into at least three groups, plus a number of miscellaneous species, some of which may be more closely related to various non-woody species: (1) Section *Centripetalia*, with two closely related species, both $n = 29$; (2) Section *Fruticisedum*, with ten species, $n = 26$ to 31 or a multiple, including six species with $n = 29$; (3) the "*Sedum palmeri* group", with three or four species, all with $n = 34$ or 68, and (4) a miscellaneous group of nine species, several of which are quite different cytologically from all the others, with $n = 15$, 16, 20, 21, 24, 29, 32, 34, 35, 48 and 64.

Although these species resemble section *Pachysedum* in their woody habit, with several possible exceptions they seem to be not closely related to that section. This conclusion is based on the contrast between the relative difficulty of hybridizing almost any one of these species with a species of section *Pachysedum* and especially on the more limited chromosome pairing observed in most hybrids so obtained, compared with a usually much greater ease of hybridizing two species of *Pachysedum* with each other and a much more extensive pairing among the chromosomes in such hybrids. The same kind of evidence also suggests that, among the species reported here, *Sedum palmeri* and *S. obcordatum* (both $n = 34$), and also *S. morganianum* ($n = 35$) and *S. burrito* ($n = 34+1$), are probably the ones that are most closely related to section *Pachysedum* and to the common ancestral stocks.

## LITERATURE CITED

BERGER, A. 1930. Crassulaceae. *In:* A. Engler, Die natürlichen Pflanzenfamilien 2nd ed. **18a:** 352–485.

CLAUSEN, R. T. 1943. A new species and section of *Sedum* from Chihuahua. J. Cactus Succ. Soc. Amer. **15:** 167–169.

______. 1948a. A new shrubby species of *Sedum* from the Sierra Madre del Sur. J. Cactus Succ. Soc. Amer. **20:** 36–37.

______. 1948b. A name for *Sedum guatemalense* of horticulturists. J. Cactus Succ. Soc. Amer. **20:** 79 83.

______. 1959. *Sedum* of the Trans-Mexican Volcanic Belt. Cornell Univ. Press, Ithaca, N.Y.

______. 1978. *Sedum*—seven Mexican perennial species. Bull. Torrey Bot. Club **105:** 214–223.

FRÖDERSTRÖM, H. 1935. The Genus *Sedum* L., part IV. Acta Horti Gotoburgensis **10:** Appendix.

JACOBSEN, H. 1974. Lexicon of Succulent Plants. Blandford Press, London.

MORAN, R. 1961. *Sedum furfuraceum*. J. Cactus Succ. Soc. Amer. **33:** 103 105.

______. 1966. The Section *Centripetalia* of *Sedum*. J. Cactus Succ. Soc. Amer. **38** 75–81.

______. 1977. *Sedum burrito* a new species from eastern Mexico. J. Cactus Succ. Soc. Amer. **49:** 266–268.

UHL, C. H. 1970. Chromosomes of *Graptopetalum* and *Thompsonella* (Crassulaceae). Amer. J. Bot. **57:** 1115–1121.

______. 1976a. Chromosomes, hybrids, and ploidy of *Sedum cremnophila* and *Echeveria linguifolia* (Crassulaceae). Amer. J. Bot. **63:** 806–820.

———. 1976b. Chromosomes of Mexican *Sedum* I. Annual and biennial species. Rhodora **78:** 629–640.

———. 1978. Chromosomes of Mexican *Sedum* II. Section *Pachysedum*. Rhodora **80:** 491–512.

———, and R. Moran. 1973. Chromosomes of *Pachyphytum* (Crassulaceae). Amer. J. Bot. **60:** 648–656.

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# ECOLOGY OF *RUPPIA MARITIMA* L. IN NEW HAMPSHIRE (U.S.A) TIDAL MARSHES[1]

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*Ruppia maritima* L. is a submersed aquatic angiosperm of saline environments. The taxonomy of this nearly cosmopolitan genus has been the subject of numerous studies although no definitive classification of the various taxa has been established. *Ruppia* has been placed in the monogeneric family, Ruppiaceae, by Hutchinson (1934, 1959). It has also been included in the Potamogetonaceae, Zosteraceae, and Najadaceae. Davis and Tomlinson (1974) reviewed the systematic position of *Ruppia*. Similarities between *Ruppia* and *Potamogeton* in vegetative morphology, anatomy, and especially floral morphology (Uhl, 1947; Posluszny & Sattler, 1974) appear to outweigh dissimilarities, hereby substantiating its inclusion in the Potamogetonaceae. A number of varieties of *R. maritima* based on morphological criteria have been described for Eastern North America by Fernald and Wiegand (1914).

*Ruppia* grows in a wide diversity of coastal and estuarine habitats in New Hampshire. It is commonly found in the relatively still water of shallow pannes or in deeper pools, but may also occur in drainage ditches and occasionally in creeks which ebb and flow with each tide. *Ruppia* is highly variable in growth form, apparently due to changes in environmental conditions at different locations. Factors such as depth of water, temperature, salinity, and structural characteristics of the habitat, together with biotic and physicochemical parameters, significantly influence its growth, development, and reproductive biology. Under certain conditions *Ruppia* may exist as a perennial by means of vegetative reproduction and overwintering rhizomes, or it may employ an annual reproductive strategy producing abundant seed.

A number of investigators have reported on environmental conditions and growth of *Ruppia*, but the relationship between environmental parameters and clinal variation in *Ruppia* populations has not been established. Setchell (1924, 1946) studied *Ruppia maritima*

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L. and *R. spiralis* Dumort. and their environmental factors in California. Many of my findings on seasonal periodicity and temperature and salinity optima concur with his. Setchell's treatment, unfortunately, embodies no graphical presentation of his data with which quantitative comparisons can be made. Joanen (1964) studied factors influencing the establishment of natural and artificial stands of *Ruppia maritima* L. in Louisiana. Gore (1965) studied the effects of small salt marsh impoundments on *Ruppia* sp. in Maine. Bourn (1935) conducted greenhouse experiments on *Ruppia maritima* L. which originated on Martha's Vineyard, Massachusetts, to determine sea-water tolerance. McKay (1935) investigated lakes of high magnesium sulfate content in Washington and British Columbia to assess the salt tolerance of *Ruppia maritima* L. Mayer (1967, 1969) studied the effect of salinity on growth, reproduction, and fruit size in *Ruppia maritima* L. Verhoeven (1975) and Verhoeven and van Vierssen (1978) have examined the distribution and structure of communities consisting of three taxa of *Ruppia* [*R. cirrhosa* (Petag.) Grande, *R. maritima* L., and *R. maritima* var. *brachypus* (Gay) Marsson] in relation to salinity and salinity fluctuations in the Camargue, France, and at "De Bol", Texel, The Netherlands. Verhoeven (1978) found that natural regulation of plant biomass in *Ruppia*-dominated communities is a seasonal phenomenon involving biotic and abiotic factors. Davis and Tomlinson (1974) reported a new species of *Ruppia* (*R. tuberosa* Davis & Tomlinson) growing in very high salinity (92 132 0/00) in Western Australia. Gutierrez (1977) investigated the asynchronous development of *Ruppia maritima* L. beds in a coastal lagoon in Mexico and found that changes in turbidity, currents, soil pH and texture, as well as fluctuations in temperature and salinity, differentially affect growth and vegetative propagation. Graves (1908) presented information on salinity tolerances and halophytic adaptations in a detailed study of the morphology of *Ruppia maritima* L.

This paper reports on selected environmental parameters and salient features of the habitats of *Ruppia* in an effort to contribute to an understanding of the dynamics of these habitats as integral parts of the tidal marsh ecosystem. These data, when correlated with information on the growth and development of the *Ruppia* populations indigenous to various habitats, provide insight to the morphological variability and the reproductive strategies observed in this species as a function of its environment.

## MATERIALS AND METHODS

### Selection of Sites

A reconnaissance of various *Ruppia* habitats was conducted during the summer and fall of 1973 while making a soil survey of New Hampshire tidal marshes (Breeding et al., 1974). Approximately thirty sites were observed for: (1) type of habitat; (2) water depth, temperature, and salinity; (3) composition of the substrate; (4) characteristics of the *Ruppia* population; (5) surrounding vegetation. Ultimately, ten sites were selected as representing a range of ecologically distinct habitats of *Ruppia maritima* (Fig. 1). Plants at these sites exhibited variation in growth habit conforming to three varieties (vars. *rostrata* Agardh, *longipes* Hagstr., and *subcapitata* Fern. & Wieg.) described by Fernald and Wiegand (1914). The sites were monitored during the growing season of *Ruppia* (mid-April to early September) in 1974 and 1975. Seven of the ten sites in 1974 and five in 1975 were visited every week to ten days, the others less frequently. A comparison of five representative sites is presented in this paper. For more detailed information see Richardson (1976a). All sites were visited between 10:00 a.m. and 3:00 p.m. on the same day, each within a specified time. At each site all measurements were made at a place designated by a marker. Collections of *Ruppia* were made at each of the regularly sampled sites throughout the study period.

### **Seasonal Studies** (April–September 1974 and 1975)

*Water Depth:* Fluctuations in water depth as an expression of the effects of flooding tides, precipitation, and evaporation were measured with a meter stick alongside the permanent marker at each site.

*Temperature:* Air and water temperatures were measured with an adjustable boom apparatus which could be lowered to the required depth. Copper vs. constantan thermocouple wires were attached to a vertical probe by rubber bands so that they could be adjusted to divide the depth of the water column into equal increments no more than 10 cm apart. The thermocouple wires were joined to a multiple switch which was connected to a Leeds and Northrup millivolt potentiometer via an Omega-CJ cold junction compensator. Temperature stratification in the water column could be measured accurately with this apparatus.

*Salinity:* A Yellow Springs Inst. model 33 S-C-T meter was used to measure salinity at the same series of depths at which temperature readings were taken. The instrument was periodically standardized against a silver nitrate titration of sea water (Strickland & Parsons, 1968).

*Oxygen content:* Dissolved oxygen (D.O.) values were determined by the Winkler method (A.P.H.A., 1971; Strickland & Parsons, 1968) using Hach dry chemical pillows for the three fixation reagents. Water was collected just below the surface, therefore the D.O. values expressed in this paper do not represent an average for the entire water column but, nevertheless, do give an approximation of the seasonal patterns at different sites.

Precipitation data were obtained from the Durham, New Hampshire weather station. Information on tidal periodicity and photoperiod was taken from U.S.D.C., N.O.A.A. tide tables (Anon., 1974, 1975). Estimates of percent cover by algal mats, epibiota, turbidity, and conditions of the substrate (e.g., color as an indication of the degree of reducing conditions) were made on a comparative basis on each visit to a site.

**Ten Day Study** (Vols Island, July 22–31, 1974)

To determine what sort of changes occurred between sampling days and to obtain data on diel fluctuations of the physicochemical parameters a ten day study was conducted. Vols Island was selected as a representative site which was easily accessible for thrice daily visits. The study began shortly after flood tides had filled the pool to near maximum so that the effects of evaporation during the following neap tide period could be observed. For nine days the site was visited at 6:00 am, 12:00 am and 6:00 pm; on the tenth day hourly measurements were taken over a twelve hour period to record diurnal fluctuations.

In addition to the parameters recorded in the seasonal studies, during the ten day study, pH values were measured with a VWR Scientific solid state pH meter standardized before each reading with a buffer solution. Two replicates of three readings (open water, moderate plant cover, and dense plant cover) were taken to record a pH range. All readings were taken at 5 cm below the water surface. Incident radiation was recorded with an Argomet—Lintronic dome solarimeter connected to the millivolt potentiometer. Radiation values represent an average of readings over a ten minute period.

## DESCRIPTION OF STUDY AREAS

### 1. Johnson Creek

Location: Durham, New Hampshire (43° 9′N, 70° 54′W)

Habitat type: A vertically sided pool with undercut banks, measuring 24 m × 7 m, situated on the inner bend of a creek meander in proximity to upland drainage.

Substrate: The bottom of this pool is extremely soft, deep organic muck. Black color indicated reducing conditions. The plants were deeply rooted but could be easily pulled up without damage to the roots.

Characteristics of the *Ruppia* population: A dense growth of plants conforming to var. *rostrata* was found at this site (Fig. 9,A). Most flowers appeared to be pollinated underwater. The plants fruited abundantly during the 1974 and 1975 seasons and produced large quantities of seed. An annual reproductive strategy appeared most successful at this site. Lower portions of the plants supported a growth of epiphytes (diatoms, blue-green algae, and other epibiota) by mid-summer. Phenological data are given in Tables 3 and 4.

Surrounding vegetation: The pool is bordered with a 1–2 m wide band of *Scirpus paludosus* Nels. on a *Spartina patens* (Ait.) Muhl. high marsh. Dense mats of filamentous algae (*Cladophora* sp. most abundant) covered nearly 90% of the water surface by late summer of 1974 and 1975.

### 2. Lubberland Creek

Location: Newmarket, New Hampshire (43° 5′N, 70° 55′W)

Habitat type: Extensive shallow pannes have formed in the areas between drainage ditches which have become impounded by slumping of the banks or by siltation. This site receives some upland drainage in the spring, but probably little or none in the summer.

Substrate: Standing surface water has caused differential decay of the underlying peat so that some areas have a relatively firm bottom while others are soft and highly decomposed. The plants became firmly rooted in the peat sod early in the season and could not easily be removed without damage to the roots.

Characteristics of the *Ruppia* population: A dense growth of plants at this site appeared to be intermediate between var. *rostrata* and var. *subcapitata* (Fig. 9,B). The entire population appeared to be pollinated underwater and formed abundant fruit. The reproductive strategy was primarily annual. The plants flowered and fruited early in the season, produced abundant seed and died off completely by late summer. Relatively few epiphytes were noticed until the plants were senescent. Phenological data are given in Tables 3 and 4.

Surrounding vegetation: Large areas of these pannes are covered with *Scirpus paludosus* growing in standing water. Narrow bands of *Spartina patens* persist along the edges of the ditches on levees where fine sediments are trapped during flood tides. 50–80% of the surface area of the pannes was covered with filamentous algal mats by mid-summer.

3. **Vols Island**

Location: Newmarket, New Hampshire (43° 5′N, 70° 54′W)

Habitat type: A pool with nearly vertical sides, measuring 10 m × 2 m, was determined to be a relict of a former creek meander from interpretation of aerial photographs and sounding the marsh soil. Situated on the high marsh, the site receives some upland drainage in the spring.

Substrate: The plants were loosely rooted in very soft deep organic ooze containing fractions of silt and clay. Black color was indicative of reducing conditions in the mud.

Characteristics of the *Ruppia* population: A fairly dense growth of plants conforming to var. *rostrata,* but with highly variable fruit shape, was present at this site (Fig. 9,C). Underwater pollination was dominant. An annual reproductive stategy was evident here as the pool contained only seed in early spring. The plants were nearly free of epiphytes throughout the season. Phenological data are given in Table 3 and 4.

Surrounding vegetation: A vigorous stand of *Spartina patens* surrounds the pool. A very dense mat of filamentous algae covered nearly 100% of the surface area by mid to late summer during both seasons.

4. **Awcomin Marsh** (deep pool)

Location: Rye, New Hampshire (43° 1′N, 70° 44′W)

Habitat type: A large, deep pool measuring 30 m × 6 m, with vertical sides, may have been formed, with others in the vicinity, as a primary panne on the intertidal marsh (see Redfield, 1972). Situated on a large flat expanse of tidal marsh, the pool receives virtually no upland runoff and is isolated from large creeks.

Substrate: One end of the pool has a firm sandy bottom with few plants. The remaining portion consists of a deposit of soft mud and organic matter overlying sand which provided a rooting medium for the large population of plants growing there in 1974. The mud was grey-brown, apparently not highly reduced.

Characteristics of the *Ruppia* population: In 1974 a dense growth of *Ruppia* with long flexuous to straight peduncles conforming to var. *longipes* was observed (Fig. 9,D). The plants in early spring of 1974 were well developed and covered with epiphytes, indicating that they had persisted from the previous season. Renewal growth was observed in the axils of leaves and from rhizomes producing new shoots and inflorescenses. Pollination occurred almost exclusively at the water surface. Few fruits were formed, however, and the plants became senescent in late summer. In early spring of 1975 the pool was nearly devoid of living *Ruppia*. There was no reestablishment of growth from either seed or vegetative propagation during the 1975 season. Phenological data are given in Tables 3 and 4.

Surrounding vegetation: The dwarf form of *Spartina alterniflora* borders the pool. In 1974 filamentous algal mats covered about 30% of the surface. In 1975 there was almost no growth of filamentous algae.

5. **Awcomin Marsh** (shallow panne)

Location: Rye, New Hampshire (43° 1′N, 70° 44′W) about 100 m west of the deep pool.

Habitat type: Unlike the deep pool, this large, shallow panne appears to be a secondary formation on the marsh surface (see Redfield, 1972) as the standing water is gradually decomposing the underlying peat.

Substrate: Approximately 10–15 cm of decomposing peat and sticky organic mud overlies coarse intertidal peat. Beneath a thin surface layer of detritus the mud was black, indicating reducing conditions.

Characteristics of the *Ruppia* population: In 1974 the vegetative portions of the plants were very similar to those in the deep pool; however, the peduncle lengths were highly variable and many more fruits were produced (Fig. 9,E). Pollination appeared to be entirely at the surface and, on occasion, masses of floating pollen were seen. The lower portions of the plants were covered with epiphytes in early spring, again giving evidence of persistence of a previous season's growth. As in the deep pool, this panne was entirely devoid of

*Ruppia* plants in 1975. Although fruits were produced in 1974, no seedlings were found in 1975. Phenological data are given in Tables 3 and 4.

Surrounding vegetation: The dwarf form of *Spartina alterniflora* borders the panne. Very scant growth of filamentous algae was noted during both seasons.

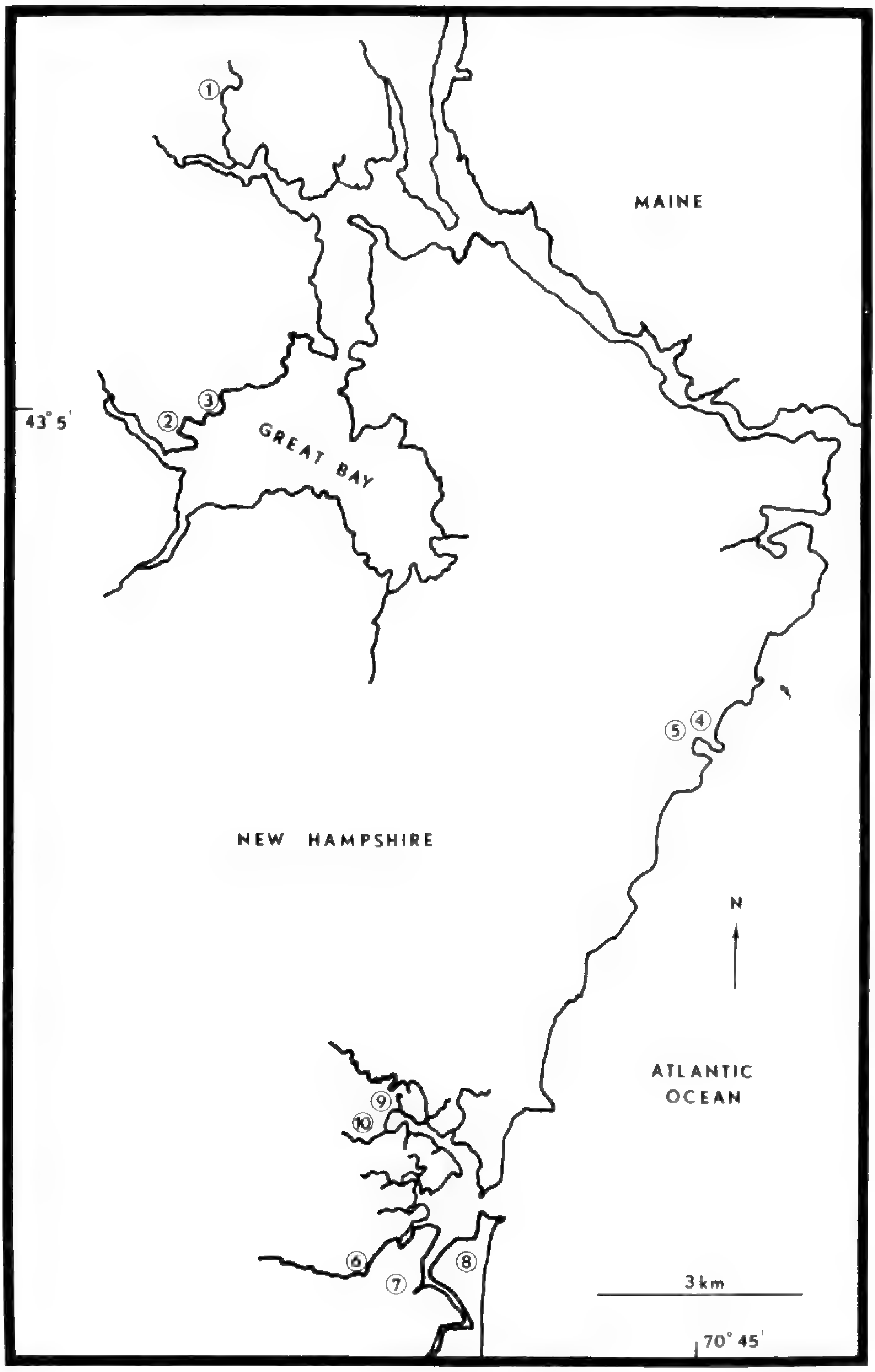
## RESULTS AND DISCUSSION

### Seasonal Studies

*Water Depth:* Verhoeven (1975) stressed the importance of evaporation to the aquatic environment since it results in lowering the water level, increasing the salinity, and subsequently increasing the chance of desiccation. Large shallow pannes such as those at Lubberland Creek had more rapid fluctuations in depth than deeper pools due to higher rates of evaporation from a large surface area with relatively small volume. Portions of the pannes at Lubberland Creek were frequently exposed with the mud surface drying, although a small amount of water usually remained under the mats of filamentous algae. This water protects the underlying *Ruppia* from desiccation. Rainfall and tidal flooding allowed for continued growth and development of the plants early in the season when the drying period was not prolonged. Maturation of fruits was observed to be rapid after reflooding.

Drying conditions in late summer, however, caused complete desiccation in the shallow pannes, but only after seeds had formed and become buried in the sediments or entangled in the algal mats. Seeds were very seldom found to be completely dried as there was moisture under the encrusted surface layer of mud and algae. *Ruppia* seeds, like those of most submersed aquatics, lose viability with prolonged drying (see Crocker, 1907; Guppy, 1897; Joanen, 1964; McLaughlin, 1974; Muenscher, 1936). McLaughlin reports that differential drying or non-drying requirements for three species of *Callitriche* are dependent on temperature, salinity, and seasonal phenomena at various habitats. Guppy inicates that drying requirements are characteristic of aquatic species in habitats subject to

Figure 1. Location map of study areas on New Hampshire tidal marshes: 1, Johnson Creek site, 2, Lubberland Creek site, 3, Vols Island site, 4, Awcomin Marsh sites, 5, Taylor River sites, 6, Cains Creek site, 7, Waltons Landing site, 8, Seabrook Dunes site, 9 & 10 Taylor River sites.


①
MAINE
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43° 5'
GREAT BAY
④
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periodic drying, but not characteristic of species indigenous to continuously wet habitats. An annual reproductive strategy is imperative to insure survival of *Ruppia* populations in areas where drying conditions are prevalent in late summer. The fragile, herbaceous portions of the plants, subject to complete desiccation, will persist only in a perpetually wet environment. Perennating rhizomes were found only in deeper pools and continuously wet habitats.

In deeper, vertically sided pools which do not receive frequent tidal inundation, some water loss may occur by transference into the surrounding peat soil as the interstitial water level drops during neap tide periods (see Chapman, 1938, 1940, 1960; Redfield, 1959, 1965). Surface algal mats tend to keep the underlying water cool and diminish the effect of wind on evaporation. On hot dry days, dense algal mats may have a wick effect, causing considerable water loss. The effects of evaporation were more apparent in 1974 than in 1975, due largely to differences in precipitation. Rainfall was 21.9 cm during the 1974 study period and 45.6 cm during the 1975 period.

The growth habit of *Ruppia* on New Hampshire tidal marshes is markedly influenced by water depth. Plants growing in shallow pannes exhibit a procumbent spreading habit with distinctly forking stems (Fig. 9,C) while those growing in deeper water are more ascending (Fig. 9,A). Internodal lengths are shorter on shallow water plants than on those growing in deeper areas. Inflorescences usually develop at the second or third node above the rhizome on shallow water plants while those of deeper water plants appear at the fifth or sixth nodes. As plants in deeper pools grow up through the water towards the surface the internodes become progressively shorter. In plants pollinated underwater, peduncle length varies little regardless of depth except for plants in very shallow pannes (which conform to var. *subcapitata*). Plants in which pollination occurs at the surface exhibit highly variable peduncle length. This variability is, presumably, a function of the distance between the point of origin of the inflorescence and the surface of the water.

*Temperature:* Seasonal temperature patterns at the various sites were similar, and the seasonal mean water temperature for all sites fell within a range of 5° C in 1974 and 1975. However, the thermal regime for each site varied according to its structural characteristics and the distribution of vegetation (Figs. 2 and 3). Temperature statification occurred at some sites while others remained nearly isothermal. Sites exhibiting temperature stratification frequently showed salinity stratification as well, whereas those with isothermal conditions were usually isohaline.

Thermal optima for germination, vegetative growth, flowering and fruiting of *Ruppia* were similar at all sites. Seed germination occurred over a range of 11–18° C. Seedling development and vegetative growth appeared to be most vigorous at 20–25° C. Flowering and pollination occurred at 24–30° C. Fruit development, maturation and seed production were observed to occur over a range of 26–32° C. These data compare with those of other workers.

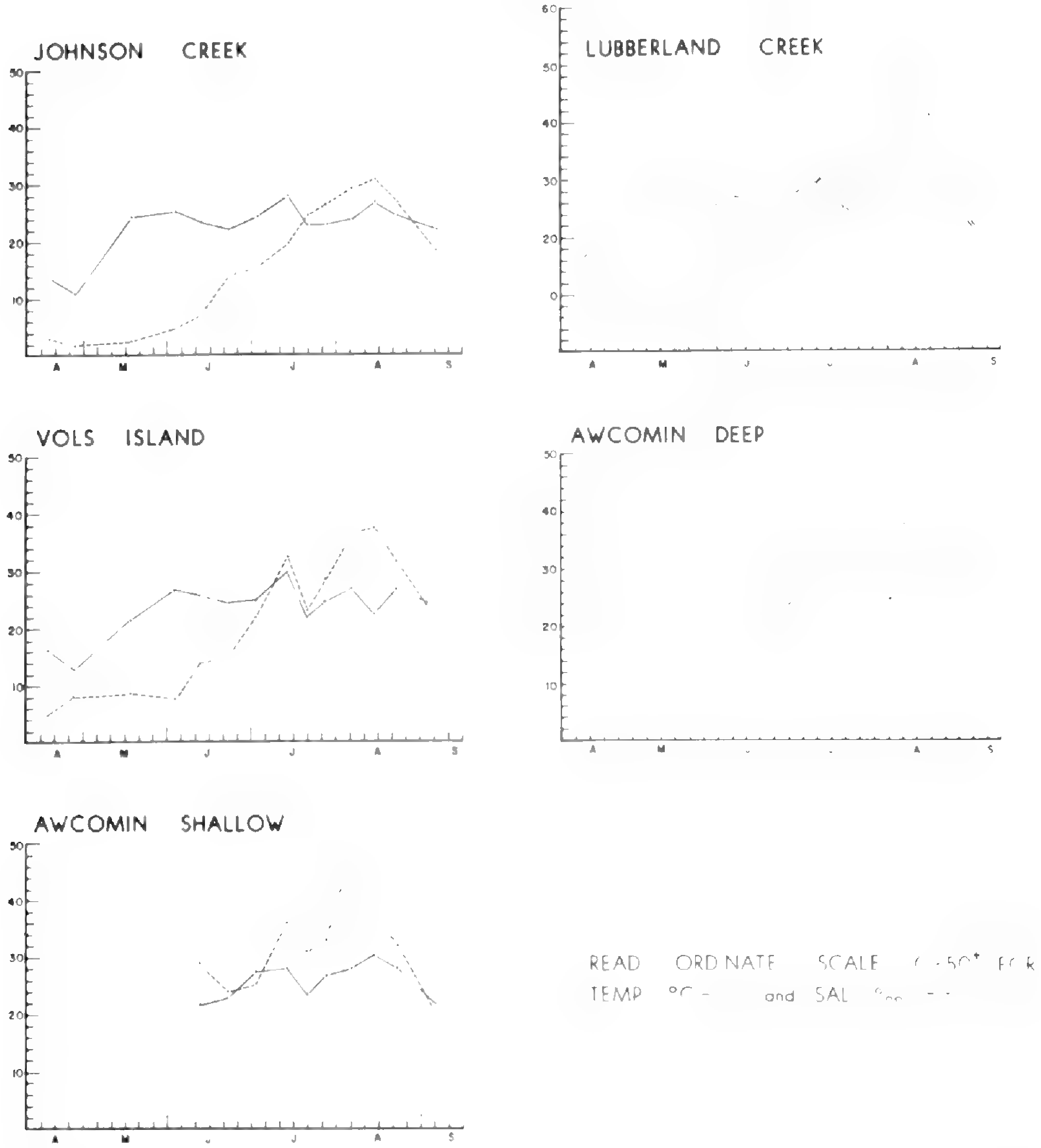


Figure 2. Seasonal water temperature and salinity patterns at five sites April September 1974.

Table 1. **Seasonal ranges and means of water depth, temperature, and salinity for five sites April-September 1974 and 1975**

| | 1974 | | | | | | 1975 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Depth**(cm) | | **Temp.**(°C) | | **Sal.**(0/00) | | **Depth**(cm) | | **Temp.**(°C) | | **Sal.**(0/00) | |
| | R | $\bar{X}$ | R | $\bar{X}$ | R | $\bar{X}$ | R | $\bar{X}$ | R | $\bar{X}$ | R | $\bar{X}$ |
| JOHNSON CREEK | 20–32 | 27.5 | 11–28 | 22.0 | 2–31 | 15.0 | 26–34 | 30.5 | 13–34 | 24.5 | 2–26 | 15.9 |
| LUBBERLAND CREEK | 5–18 | 11.8 | 16–30 | 27.2 | 5–58 | 22.2 | 14–22 | 17.4 | 11–37 | 26.7 | 13–37 | 23.0 |
| VOLS ISLAND | 10–30 | 23.1 | 11–30 | 23.2 | 3–39 | 21.9 | 18–32 | 26.2 | 12–32 | 24.5 | 7–33 | 20.0 |
| AWCOMIN (DEEP) | 28–56* | 46.5 | 19–29* | 24.9 | 23–38* | 32.9 | 38–60 | 52.8 | 12–34 | 24.1 | 22–35 | 30.0 |
| AWCOMIN (SHALLOW) | 9–28* | 20.4 | 22–30* | 26.0 | 20–49* | 31.7 | 11–26 | 20.8 | 15–38 | 26.6 | 23–35 | 29.5 |

*Measurements at the Awcomin site commenced four weeks later than the other sites in 1974.

Joanen (1964) reported 18–19° C as the thermal optimum for seedling development with temperatures up to 30° C being conducive to vegetative growth. He observed that flowering and fruiting began at 28–30° C and continued under a higher temperature than did vegetative growth.

Setchell (1924) reported that the progression from germination to anthesis and fruiting proceeds with a general rise in temperature, and that cessation of activity coincides with the advent of cold weather. He reported that seeds germinated at 10–18° C, but that development beyond the vegetative stage did not take place until the temperature reached 22–24° C and then development proceeded to

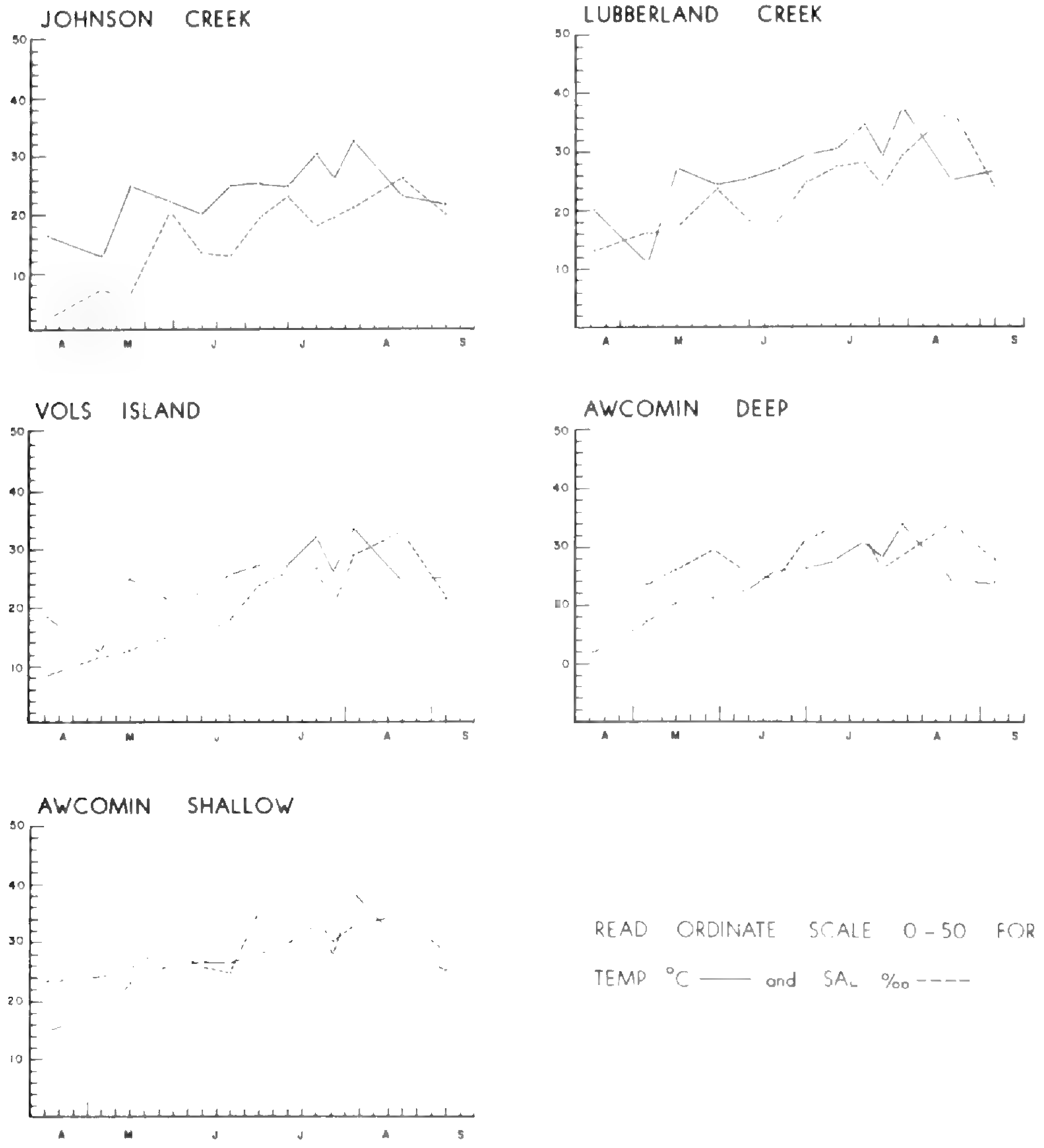


Figure 3. Seasonal water temperature and salinity patterns at five sites April–September 1975.

Table 2. **Dissolved oxygen values (mg•L$^{-1}$) and percent oxygen saturation (% Sat.) for five sites May-September 1975**

| | JOHNSON CREEK | | LUBBERLAND CREEK | | VOLS ISLAND | | AWCOMIN (DEEP) | | AWCOMIN (SHALLOW) | |
|---|---|---|---|---|---|---|---|---|---|---|
| Date | mg•L$^{-1}$ | %Sat | mg•L$^{-1}$ | %Sat | mg•L$^{-1}$ | %Sat | mg•L$^{-1}$ | %Sat | mg•L$^{-1}$ | %Sat |
| 5- 5 | 4.2 | 40.4 | 11.2 | 112.1 | 7.8 | 75.8 | – | – | – | – |
| 5-15 | 7.9 | 97.4 | 20.1 | 271.9 | 12.4 | 157.5 | 8.6 | 104.4 | 8.2 | 106.9 |
| 5-28 | 7.9 | 102.1 | 19.4 | 272.7 | 17.8 | 236.8 | 9.4 | 127.9 | 9.4 | 152.9 |
| 6-10 | 11.5 | 142.4 | 15.8 | 223.8 | 15.9 | 217.1 | 9.4 | 130.9 | 10.5 | 152.9 |
| 6-20 | 10.5 | 138.9 | 14.4 | 199.9 | 14.2 | 198.3 | 7.5 | 106.5 | 9.4 | 135.0 |
| 6-30 | 13.8 | 195.9 | 17.2 | 256.8 | 20.7 | 307.4 | 10.7 | 158.3 | 9.7 | 151.0 |
| 7- 9 | 11.8 | 171.2 | 15.1 | 238.6 | 11.5 | 182.7 | 3.2 | 49.8 | 6.5 | 102.3 |
| 7-19 | 16.7 | 256.8 | 10.0 | 166.5 | 3.6 | 60.3 | 8.5 | 131.8 | 8.6 | 144.9 |
| 7 26 | 15.7 | 222.4 | 13.3 | 201.3 | 6.6 | 97.2 | 6.5 | 93.5 | 8.9 | 133.0 |
| 8- 2 | 5.6 | 88.9 | 10.1 | 178.9 | 0.0 | 0.0 | 9.0 | 148.7 | 10.3 | 188.2 |
| 8-20 | 5.4 | 76.8 | 10.0 | 149.8 | 11.0 | 162.3 | 9.1 | 132.9 | 9.9 | 156.2 |
| 9- 4 | 9.0 | 118.9 | 6.9 | 97.4 | 8.4 | 119.0 | 7.1 | 100.5 | 7.7 | 109.0 |

anthesis and fruiting. Setchell recorded optimal ranges of 15–20° C for germination and seedling development and 20–25° C for vegetative growth and reproductive activity; anthesis was slow and eventually ceased after prolonged periods above 25° C. He concluded that temperature was the environmental parameter which most affected growth and development of *Ruppia.*

In a study of the benthic plant composition of a salt pond in Rhode Island, Conover (1966) reported a thermal range of 12–18° C to be optimal for rapid vegetative growth, while 18–22° C was conducive to reproduction. Conover also states that senescence of the *Ruppia* populations is coincident with the seasonal thermal maximum and suggests that since growth of the older tissues and organs begins to diminish in vigor during this time period, temperature had a kinetic effect upon growth.

Anderson (1969) examined the effects of heated water effluent from an electrical generating station of the Patuxent River, Maryland, as a factor related to the disappearance of a large population of *Ruppia maritima.* He found that *R. maritima* and *Potamogeton pectinatus* L. were capable of physiological adjustment to higher temperatures as the leaves matured, and that *Potamogeton* replaced *Ruppia* at 30–35° C.

Conover (1958) found the maximum growth rate of benthic marine plants (including *Ruppia*) in Cape Cod estuaries to occur during the thermal maximum in July and August rather than during the solar maximum. Such is not the case with the *Ruppia* populations in New Hampshire. The growth rate is at a maximum in mid-to late June during the solar maximum, gradually decreasing in July with the plants becoming senescent in late August. Increasing temperature, salinity, growth and attrition of epiphytes, and algal mats all have a limiting effect on growth of the *Ruppia* populations following the late June to mid-July flowering and fruiting maxima. High water temperatures may increase respiration rates, thereby reducing net growth (Conover, 1964).

Temperature stratification in the water column was observed to be more a result of the shading effects of surface algal mats and vegetation density than of depth alone. In the deepest pool at the Awcomin Marsh, with sparse surface cover and submersed vegetation, the water column remained nearly isothermal and isohaline throughout the season. The algal mats probably interfere with convection currents that would otherwise equalize the temperature

(Young & Zimmerman, 1956). Inverse temperature stratification was noted in early spring before algal mats and seedlings developed. This was apparently due to heating of the dark colored bottom sediments by direct insolation.

Boyd (1975) noted that in unshaded pools 51 cm deep the change in temperature from top to bottom seldom exceeded 2.8° C, while in shaded pools (covered with duckweeds) the temperature differential ranged from 5–10° C during the day. Butler (1963) noted that temperature stratification was more pronounced in turbid than in clear ponds of similar size and morphology.

Dale and Gillespie (1977, 1978) found temperature gradients in shallow water bodies to be influenced by submersed aquatic plants as a function of leaf area index and arrangement of leaves, and by the ratio of solar radiation to wind speed. Steep temperature gradients indicate interception of light energy near the surface of the water column by the plants. Sparse vegetation allows a more even distribution of the energy, with the system tending toward isothermy.

My observations suggest that temperature stratification may influence significantly the seed production and germination capacity of *Ruppia* populations. Flowering, fruiting, and seed production in *Ruppia* take place over a longer period in pools where surface algal mats and dense vegetation cause stratification and microthermoclines, than in those pools with isothermal conditions. There is evidence that seeds produced early in the season develop thicker seed coats than those produced later in the season (Mayer, 1969). A seed crop with a range of seed coat thicknesses would surely germinate over a longer period and under a wider range of conditions than would a crop with seed coats of uniform thickness. This may be an adaptation through which populations of an annual reproductive strategy are perpetuated successfully.

*Salinity:* The salinity characteristics of the *Ruppia* habitats are a function of : (1) tidal flooding; (2) precipitation; (3) evaporation: (4) interchange of water between the substrate and the overlying water; (5) upland runoff.

Many factors interact to determine the frequency of tidal flooding at various sites. Among these are: (1) proximity to drainage ditches or creeks; (2) isolation by levees along water courses; (3) the elevation and micro-relief of the marsh; (4) surface vegetation.

Fluctuations of salinity and temperature in the water column were larger at the estuarine sites than at the coastal sites. Tidal waters entering a panne or pool after a period of wet weather will increase the salinity. Tidal waters entering a panne or pool after a period of drying may appreciably decrease the salinity (Fig. 4). During periods of drying in 1974 the water in many shallow pannes completely evaporated (e.g., Lubberland Creek). Residual water trapped in depressions under algal mats had extremely high salinity (50–70 0/00). Twenty-four hours after tidal flooding the bottom salinity in a panne at Lubberland Creek dropped to 36 0/00 and the surface water was 28 0/00 in 15 cm of water. When heavy rainfall and flooding occur simultaneously after prolonged drying the layering may be even more pronounced provided winds have not accelerated the mixing.

At Johnson Creek and Vols Island, where salinity fluctuations in the water column were substantial, the proximity of the pools to an upland slope suggests that drainage or runoff may be influential in the salinity regime. Nicol (1935) reported that upland drainage of rainfall has an indirect effect on the salinity of salt marsh pools. Many of my observations concur with hers. Fresh water runoff and transference through the peat may be affected by silt-clay or sandy lenses in much the same way that subterranean drainage through upland soils is affected by hard-pans. These lenses are deposits of material from the embayment or creek bottom which were washed up over the marsh surface during violent storms coincident with flooding tides. As subsequent vertical accretion of the peat takes place these lenses become buried in the marsh strata (see Breeding, et al., 1974). Upland runoff may follow the course of these lenses and when they are continuous across the marsh, they may feed directly into the pools.

*Ruppia* will tolerate a wide range of salinities. Hypertonic death experiments with benthic plants conducted by Conover (1964) indicate that, in general, plant populations found in environments subject to salinity extremes are capable of adapting by some physiological mechanism. He reported *Ruppia* growing in a salinity range of 0–60 0/00. Graves (1908) classified *Ruppia* as a brackish water plant liable to plasmolysis in salinities above 30 0/00. Davis and Tomlinson (1974) described a species of *Ruppia* in Western Australia growing in a salinity range of 92–132 0/00. Mayer (1967, 1969)

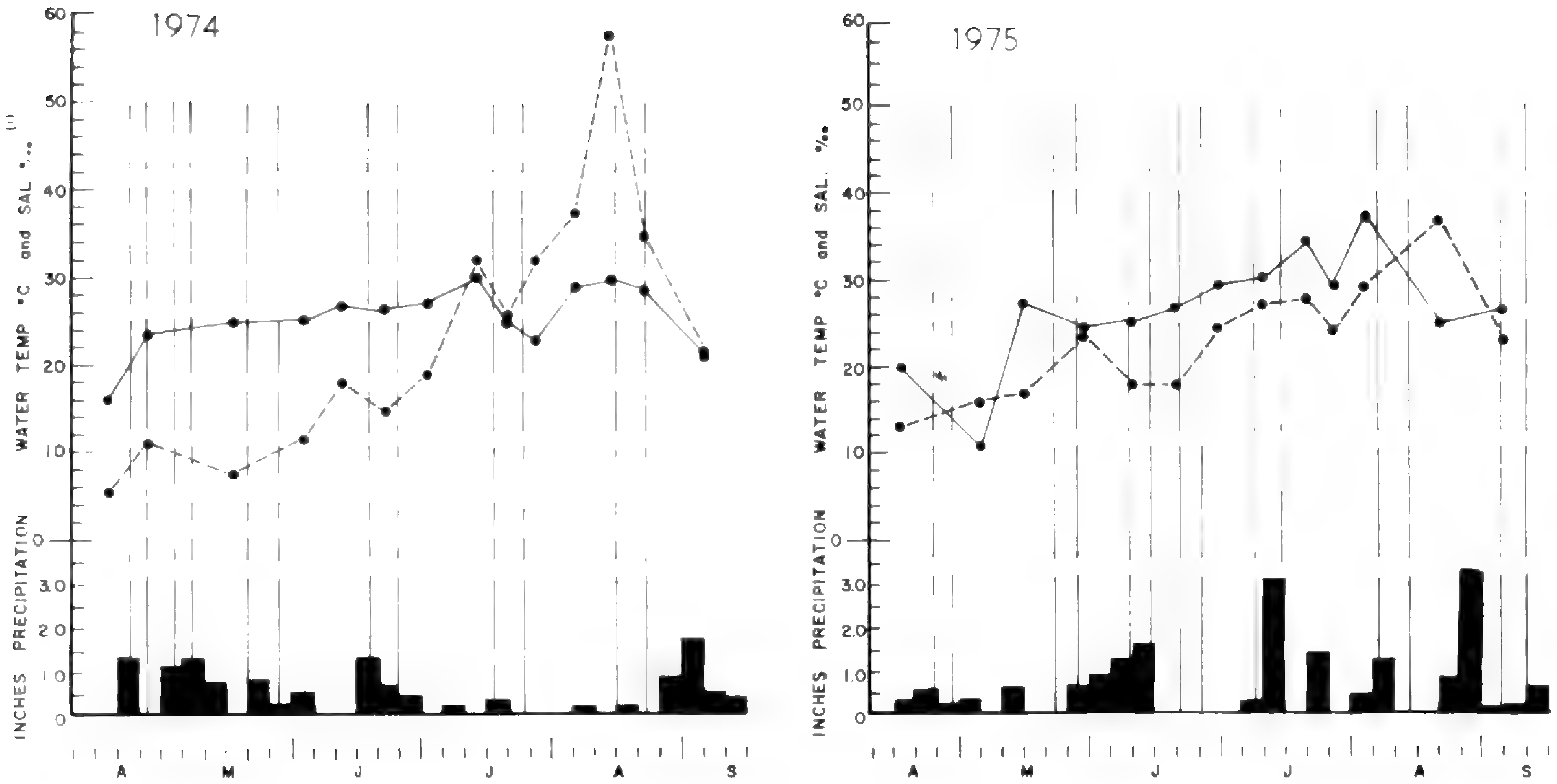


Figure 4. The effect of precipitation and tidal flooding on water temperature and salinity at the Lubberland Creek site 1974 and 1975.

described *Ruppia* as an obligate halophyte, dependent on salinity for growth and development, but requiring low salinity for maximum germination. He found the germination rate to be highest in fresh water with inhibition at 18 0/00 salinity.

Mayer noted that different salinities affected fruit size and shape. In his experiment, seeds produced by plants grown in salinities up to 12 0/00 correspond to var. *obliqua* and have a relatively thick seed coat, while those plants grown at 24–27 0/00 produced seeds corresponding to var. *rostrata* with relatively thin seed coats. I observed a wide range in seed morphology within the same population and often on the same plant throughout the periods of fruit development and seed production. McKay (1935) reported that total salt concentration may influence flowering and fruiting in *Ruppia* more than other parameters.

I found a gradient of salinity regimes in the *Ruppia* habitats. The Johnson Creek site, furthest from direct tidal influence, had a seasonal mean salinity of 15 0/00. The site receives upland runoff from a nearby wooded slope which probably decreases the salinity, especially in early spring when only 2 0/00 salinity was recorded. Lubberland Creek and Vols Island, both of which are in proximity to Great Bay and subject to flooding by more saline waters, had seasonal mean salinities of 22 0/00. At the coastal Awcomin marsh sites salinities averaged 31 0/00 with virtually no influence from fresh water sources.

*Ruppia* populations distributed along a salinity gradient exhibited clinal variation and adaptation in reproductive strategy. Annual populations are best suited for areas where low salinities in early spring facilitate rapid germination and seedling establishment. Annual populations undergo vigorous vegetative growth, flower, fruit and produce abundant seed before the seasonal salinity maximum occurs. A perennial reproductive strategy has evidently evolved in more saline environments where conditions are not conducive to germination and seedling development. The results of the present study show, however, that for large populations of *Ruppia* in the coastal habitats of New Hampshire, a perennial strategy does not assure continued seasonal growth. The recent disappearance of these populations is more likely the result of a complex of factors of which salinity may be only one. Setchell (1946) observed that the appearance and disappearance of *Ruppia* populations on California coastal marshes corresponds to variations in conditions of the habitat, and probably are affected most significantly by changes in temperature and salinity.

*Oxygen content:* During the 1975 season, dissolved oxygen content was recorded at each visit to the five regularly sampled sites. Because each site was sampled at approximately the same time of day throughout the season, the dissolved oxygen patterns indicate the trend in community metabolism at each site (Fig. 5). The values expressed for D.O. and percent oxygen saturation (Table 2) indicate the presence of oxygen including and in excess of that produced by *Ruppia*. Evolution of oxygen by surface mats of filamentous algae, epiphytic, planktonic, and benthic algae are also included in these values.

An oxygen profile is affected by a number of factors including: (1) shading by the algal mats and *Ruppia;* (2) temperature and salinity differences; (3) community respiration and microbial decomposition of senescent vegetation; (4) metabolism at the mud-water interface and in the sediments; (5) gains and losses at the air-water interface (see Sculthorpe, 1967). At sites with limited light penetration due to a dense algal mat or a canopy of *Ruppia,* maximum rates of photosynthesis will occur at or near the surface, whereas in areas with a more uniform distribution and lower density of vegetation in the water column this effect is diminished. It has been shown that in dense stands of aquatic plants in which little mixing of the water takes place, D.O. concentrations may fall sharply with depth and become stratified (Boyd, 1975; Buscemi, 1958).

In the ecocline of *Ruppia* populations on New Hampshire tidal marshes, sites having comparable salinity regimes exhibit similar seasonal oxygen patterns (Fig. 5). The pattern for Johnson Creek is unique in that a series of increases and decreases took place until maximum oxygen concentrations were reached in mid-July (16.7 $mg.L^{-1}$ $0_2$; 256.8% $0_2$ saturation). At this time the pool had maximum algal mat cover and the *Ruppia* population was flowering and fruiting. Senescence of *Ruppia* and the algal mats followed shortly and with subsequent drying conditions the oxygen values dropped sharply. The Lubberland Creek and Vols Island sites, both in proximity to Great Bay, had very similar oxygen patterns. At both sites oxygen concentration initially increased and then decreased in mid-June. This mid-June minimum occurred at all sites and is related to a period of cloudiness and intermittent sun. Oxygen content at Vols

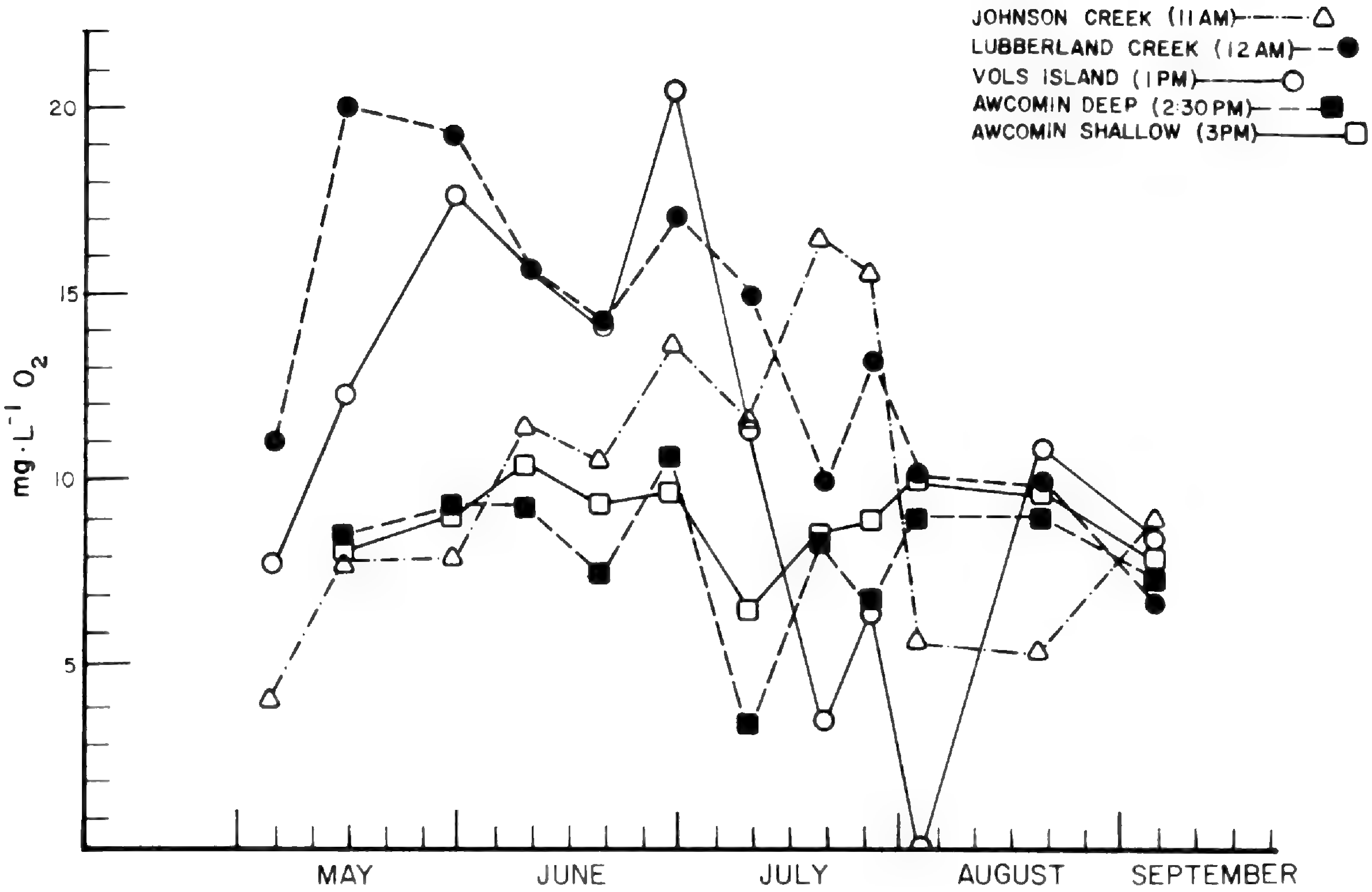


Figure 5. Seasonal dissolved oxygen patterns at five sites May–September 1975.

Table 3. **Phenological data for *Ruppia* at five sites April–September 1974**

| DATE | PHOTO PERIOD | JOHNSON CREEK | LUBBERLAND CREEK | VOLS ISLAND | AWCOMIN (DEEP) | AWCOMIN (SHALLOW) |
|---|---|---|---|---|---|---|
| 4–18 | 13hr 37min | Perennating rhizomes<br>Germination begins | Germination begins | | Perennating rhizomes | Perennating rhizomes |
| 4–27 | | | All growth from seed | Germination begins | | Scattered seedlings |
| 5–18 | 14hr 52min | 10% algal mat cover<br>Seedlings developing inflorescences | 40% algal mat cover | All growth from seed | Scattered seedlings | |
| 6–3 | | Perennating plants in flower<br>Underwater pollination | Seedlings developing inflorescences | Seedlings developing inflorescences | | Perennating plants developing inflorescences<br>Flowering |
| 6–12 | 15hr 27min | Perennating plants in fruit<br>Seedlings in flower | Flowering<br>Underwater pollination | 40% algal mat cover<br>Flowering, underwater pollination | Perennating plants developing inflorescences<br>Flowering | Surface pollination |
| 6–22 | | 50% algal mat cover | 80% algal mat cover | | 30% algal mat cover | Fruit development<br>Dense growth of epiphytes |
| 7–2 | 15hr 25min | Seedlings underwater pollination and fruit development | Abundant fruit development | Abundant fruit development | Perennating plants<br>Surface pollination | |

Table 3 (continued)

| | | | | | | |
|---|---|---|---|---|---|---|
| 7–13 | | | Drying conditions in shallow areas | 80–90% algal mat cover | Surface pollination<br>Very little fruit development | Period of drying evaporation of shallow areas |
| 7–20 | 15hr 02min | | Abundant mature fruit | | | |
| 7–27 | | Abundant fruit development for entire population | Plants becoming senescent<br>Seed production | Abundant Mature fruit | Plants becoming senescent<br>Dense growth of epiphytes | Plants becoming senescent |
| 8–6 | 14hr 23min | Abundant mature fruit<br>Algal mats decomposing | Algal mats decomposing<br>Very abundant sulfur bacteria | Pool nearly evaporated | Many inflorescences<br>No fruit development | Period of drying<br>Very abundant sulfur bacteria |
| 8–14 | | Plants becoming senescent<br>Very abundant sulfur bacteria | Abundant seed<br>All plants dead<br>Extreme drying | Plants becoming senescent<br>Seed production | No seed production | All plants dead<br>No seed production |
| 8–22 | 13hr 49min | Seed production | | All plants dead | Algal mats decomposing | |
| 9–6 | | All plants senescent<br>Further increase in sulfur bacteria growth | | Very abundant sulfur bacteria and chalky-white precipitate | All plants senescent | |

Island reached a maximum in late June when the highest value for any site was recorded (20.7 $mg.L^{-1}$ $0_2$; 307.4% $0_2$ saturation), then decreased markedly in July, and the pool became anoxic in early August. The two Awcomin marsh sites had nearly identical oxygen concentration patterns which were the lowest average value of all sites, due, no doubt, to the paucity of submersed and floating vegetation.

*Ruppia,* like most submersed vascular hydrophytes, retains a percentage of the oxygen produced in photosynthesis within the lacunar system for utilization in respiration (Hartman & Brown, 1967; Sculthorpe, 1967). The gas in the lacunar system of *Ruppia* functions in anther dehiscence and pollination, especially in those plants having underwater pollination (Richardson, 1976b). I have demonstrated, through time-lapse cinemicroscopy and extensive anatomical observations, the nature of an underwater pollination mechanism in *Ruppia*. Anatomical, morphological, and physiological variation in the floral biology of underwater and surface pollinating plants reveal adaptations which are no doubt of evolutionary significance in the genus *Ruppia*. A detailed report of these phenomena will be the subject of another publication

*Turbidity, epiphytes, and algal mats:* These three components of the *Ruppia* habitat were found to influence significantly growth, development, and seasonal periodicity of the *Ruppia* populations. Turbidity, which often appeared as a yellow to brownish coloration of the water, was attributed to: (1) dissolved organic matter derived from the substrate; (2) the concentration of organic and inorganic particulate matter in suspension due to roiling of the sediments by wind, tidal action, and fauna (e.g., crabs, fish, and worms); (3) the concentration of phyto- and zooplankton (see Sculthorpe, 1967). Sites with dense populations of *Ruppia* were occasionally turbid due largely to climatic effects and tidal flooding. Sites with sparse vegetation were frequently to consistently turbid due to a combination of the factors enumerated above and the lack of a substrate (submersed vegetation) for epiphytic attachment and settling of particulate matter.

At some sites (e.g., the Awcomin Marsh in 1975) masses of detrital material were observed to float up from the bottom and disperse over the surface of the pool. This may be attributed to the release of gases produced in the sediments and subsequent buoyancy of superficial sediments (Edwards, 1957). Anderson (1970) found *Ruppia* to be sensitive to turbidity and reported that large populations disappeared as a result of a rapid increase in turbidity. Boyd (1975) noted that turbidity attributed to plankton and suspended particulate matter can significantly lower the light available for photosynthesis and inhibit the daytime production of photosynthate. Joanen (1964) reported that turbidity caused by wave action, fish, and crabs could inhibit or prevent the growth of *Ruppia*. Phillips (1960) also reported that the disappearance of large populations of *Ruppia* was due to an increase in turbididy. Conover (1966) found that seasonal winds roiling the bottom sediments, which were thereby put into suspension, was more influential than living planktonic bodies in causing turbidity in shallow lagoons. Gutierrez (1977) found that turbidity influenced the competitive capacity of *Ruppia* in a given area, with high turbidity causing mortality or limiting growth to rhizomes, while clearer water was conducive to vigorous growth and flowering.

At sites where dense mats of filamentous algae developed during the growing season the water underlying the algal mats and canopy of *Ruppia* was usually clear. The surface vegetation no doubt diminished the effect of the wind in roiling the sediments, while shading limited the growth of plankton (see Boyd, 1975). Growth of epiphytes and the total accumulation of epibiota were reduced significantly in areas with surface algal mats and *Ruppia* canopies. At Lubberland Creek and similar habitats numerous small snails of the genus *Hydrobia* were seen grazing the epibiota present on *Ruppia* plants under the algal mats to the extent that the plants were nearly free of epibiota throughout most of the season.

Graves (1908), Johnson and York (1915), and Sculthorpe (1967) have shown that the anatomical leaf structure of *Ruppia* is similar to that of shade tolerant plants (e.g., absence of a cuticle; concentration of chloroplasts in epidermal layers). My observations show that the growth of *Ruppia* is more vigorous, and that fruit production is greatly increased, in areas where the plants are partially shaded by surface mats of algae and free of epibiota. At sites where algal mats were scant, epibiota accumulated on the stems and leaves. I found that if the epibiotic layer was stripped off early in the growing season the plants were green, but later in the season they became chlorotic, eventually taking on a pallid, yellow appearance. Sullivan (1976) has examined an epiphytic diatom community on *Ruppia* and found that the marsh sediments were the major source of colonizing cells.

Table 4. **Phenological data for *Ruppia* at five sites April–September 1975**

| DATE | PHOTO PERIOD | JOHNSON CREEK | LUBBERLAND CREEK | VOLS ISLAND | AWCOMIN (DEEP) | AWCOMIN (SHALLOW) |
|---|---|---|---|---|---|---|
| 4–16 | 13hr 28min | Germination begins<br>No rhizomatous growth | Germination began 3–28<br>Perennating rhizomes along ditches | Germination begins | Fragments of rhizomatous growth | No sign of restablishment |
| 5–5 |  | All growth from seed | Very abundant seedlings | All growth from seed |  |  |
| 5–15 | 14hr 46min | Seedlings developing inflorescences | Perennating plants developing inflorescences | 50% algal mat cover |  |  |
| 5–28 |  | 30% algal mat cover | 50% algal mat cover<br>Seedlings developing inflorescences | Scattered seedlings developing inflorescences | No seedlings<br>Very scant vegetative growth | No seedlings |
| 6–10 | 15hr 25min | Flowering<br>Underwater pollination/fruit development | All plants in flower<br>Underwater pollination/fruit development | Flowering<br>Underwater pollination/fruit development |  |  |
| 6–20 |  |  | 70% dense algal mat cover<br>Sulfur bacteria | 95% algal mat cover | 10% algal mat cover along edges<br>High turbidity | No sign of vegetative growth<br>Very high turbidity |

Table 4 (continued)

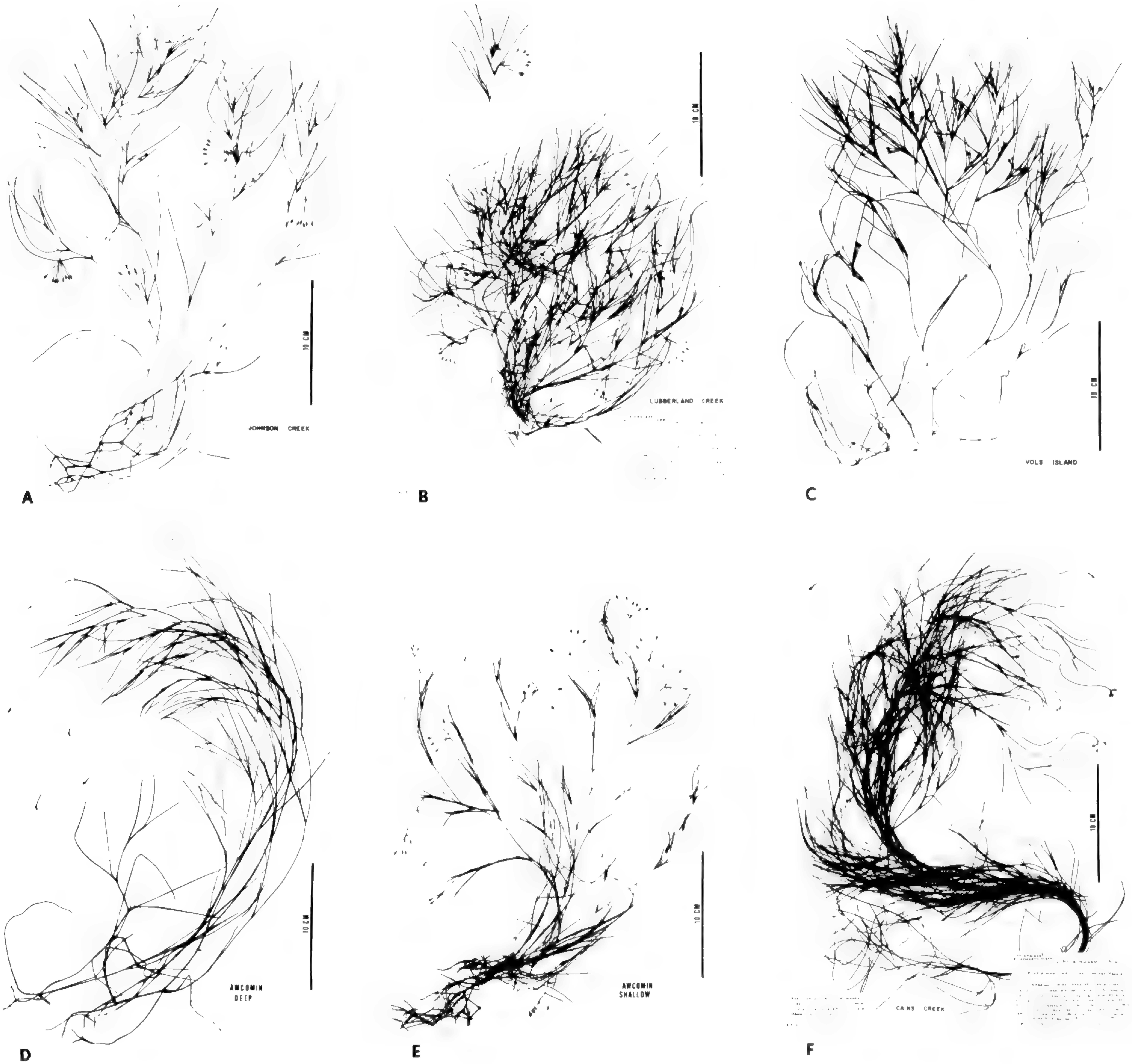
| | | | | | | |
|---|---|---|---|---|---|---|
| 6-30 | 15hr 27min | 90% algal mat cover | Very dense growth abundantly fruiting plants | Drying conditions<br>Maturing fruit<br>Abundant sulfur bacteria | | |
| 7-9 | | | Drying conditions<br>Reduction of algal mat cover | | No growth<br>High turbidity<br>Abundant sulfur bacteria | No growth<br>High turbidity<br>Abundant sulfur bacteria |
| 7-19 | 15hr 03min | Abundant mature fruit | Abundnt mature fruit<br>Abundant sulfur bacteria | Sparse mature fruit | | |
| 7 26 | | Initial signs of senescence | | Drying conditions<br>Plants becoming senescent | | Extremely abundant sulfur bacteria |
| 8-2 | 14hr 36min | Drying conditions | Seed prouction<br>Algal mats decomposing | Limited seed production | | |
| 8-20 | | Seed production<br>Abundant sulfur bacteria | Plants senescent<br>Very abundant sulfur bacteria | Plants senescent | | |
| 9-4 | 13hr 09min | Very thick algal mat decomposing<br>Very abundant sulfur bacteria<br>Plants senescent | | 100% cover algal mat decomposing<br>Very abundant sulfur bacteria | | |

The effects of epibiota on the growth, development, and reproductive capacity of *Ruppia* may be quite significant. Sand-Jensen (1977) reported that epiphytes reduce the photosynthetic rate of *Zostera marina* L. leaves by acting as a barrier to carbon uptake and by reducing light intensity. The dense growth and accumulation of epiphytic material on *Ruppia* plants may inhibit photosynthesis to the extent that (1) not enough oxygen would be produced and stored in the lacunar system to allow for night-time respiration in an environment where the oxygen demand is very high, and (2) production of photosynthate might be limited to the extent that sufficient storage products would not be available to maintain perennating rhizomes or that seed produced might be non-viable. *Ruppia* plants of either annual or perennial reproductive strategy are susceptible to the adverse effects of epibiota.

Epibiota may also limit nutrient availability to the vascular hydrophyte. *Ruppia* is more dependent upon hydrological than edaphic properties of the environment for nutrient assimilation (Conover, 1958, 1964, 1966; Conover & Gough, 1966; Graves, 1908; Sculthorpe, 1967). The rate of transfer of required gases and dissolved nutrients from the water into the plant is a function of the rate of movement of water over the leaf and stem surfaces (Conover, 1966). My observations support these findings. The most vigorous growth of *Ruppia* found during this study was that at Cains Creek (a coastal site, see Fig. 1) where the velocity of the water current is considerable as the tide rises and falls daily. These plants were almost free of epibiota and had a very dark-green robust appearance (Fig. 9,F). Conover and Gough reported that nutrient uptake by the leaves of *Ruppia* and *Zostera marina* L. will vary with the season because epiphyte growth apparently reduces the assimilation efficiency of the epidermis.

Conover and Gough found root growth and development in *Ruppia* and *Zostera* to be directly related to the type of sedimentary environment. In the highly reducing sedimentary environments characteristic of most *Ruppia* habitats, oxygen supply to the roots is essential. Dense epibiota, in limiting photosynthesis, would limit the amount of oxygen available for diffusion through the lacunar system to the roots. The effect was apparent at a number of sites where

Figure 9. Growth habit of mature *Ruppia maritima* L. plants from six sites: A, Johnson Creek; B, Lubberland Creek; C, Vols Island; D, Awcomin Marsh (deep pool); E, Awcomin Marsh (shallow pool); F, Cains Creek


A
10 CM
JOHNSON CREEK
B
10 CM
LUBBERLAND CREEK
C
10 CM
VOLS ISLAND
D
10 CM
AWCOMIN DEEP
E
10 CM
AWCOMIN SHALLOW
F
10 CM
CAINS CREEK

roots became flaccid, chalky white and rotted in appearance. Verhoeven (1978) reports that after four months of growth, the basal parts of *Ruppia cirrhosa* stems start to decay, the dense vegetation above the substrate gradually loses contact with the rooting parts, with senescence and complete detachment rapidly following. This process occurred at most sites in the New Hampshire marshes and was coincident with a marked increase on the plants and substrate of bacteria which produce or utilize hydrogen sulfide.

During the summers of 1977 and 1978 while collecting information on adaptation and variation in *Ruppia* populations, I noted that plants were again well established at sites where they had been absent for from one to three years (i.e., Awcomin Marsh). The reestablishment of these populations was from seed, indicating the presence of a seed bank in which dormancy has persisted for up to three years. Presently, core samples are being taken in an effort to determine the structure of the seed bank, while further research is necessary to understand the factors controlling seed dormancy and germination in these environments.

*Ruppia* habitats act as catchment basins for autochthonous and allochthonous organic matter. Pannes and pools are especially well suited for this. Fragments of vegetation from the adjacent marsh are carried into these areas by flood tides, and eventually settle out. This material provides additional substrate for microbial decomposition and the attachment of epibiota. Senescent *Ruppia* plants, epibiota, and the algal mats which decompose in later summer contribute to a detrital reservoir. The material entrained in these areas provides an important source of nutrients (see Nixon & Oviatt, 1973).

## Ten Day Study

The Vols Island site was visited for ten consectutive days to record diel and diurnal fluctuations of various parameters (Figs. 6, 7 & 8). The effect of the daily solar radiation load on photosynthesis is directly reflected in fluctuations of dissolved oxygen and percent oxygen saturation (Fig. 6). The degree of eccentricity in the pH envelope, as described by the upper and lower range of the daily measurements, illustrates an effect of photosynthetic depletion of carbon dioxide. Air and water temperatures are directly affected by insolation. The mean water temperature increased daily as evaporation and transference of water into the surrounding peat decreased

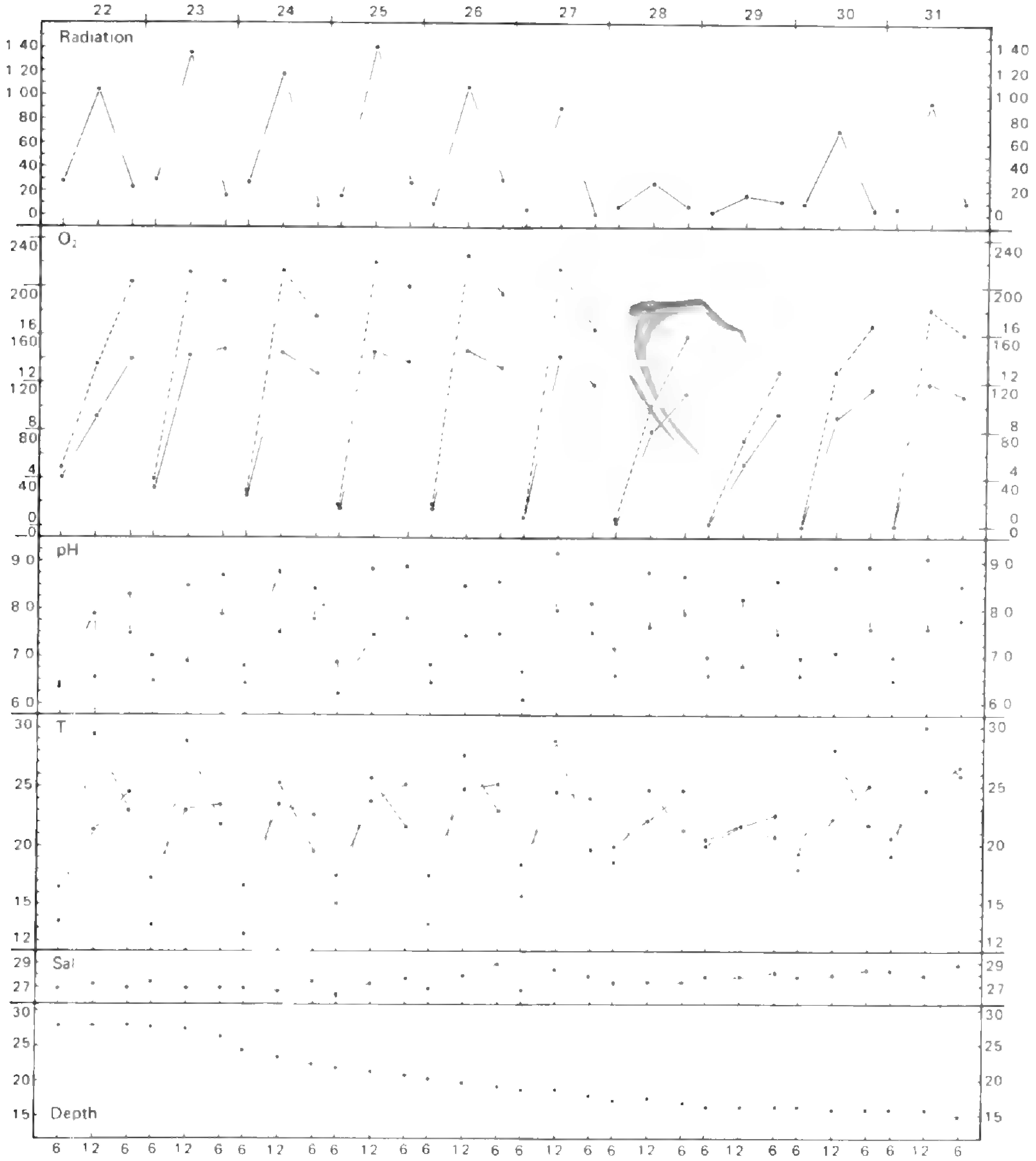


Figure 6. Diurnal fluctuations (6:00 am, noon, and 6 pm) in incident radiation, (readings averaged over 10 minutes), oxygen content (mg•L$^{-1}$) $O_2$, (solid line, 0–16; % $O_2$ saturation, broken line, 0–240), hydrogen ion concentration, temperature (air, broken line; mean of water column, solid line), salinity, and depth over ten days (July 22–31, 1974) at the Vols Island site.

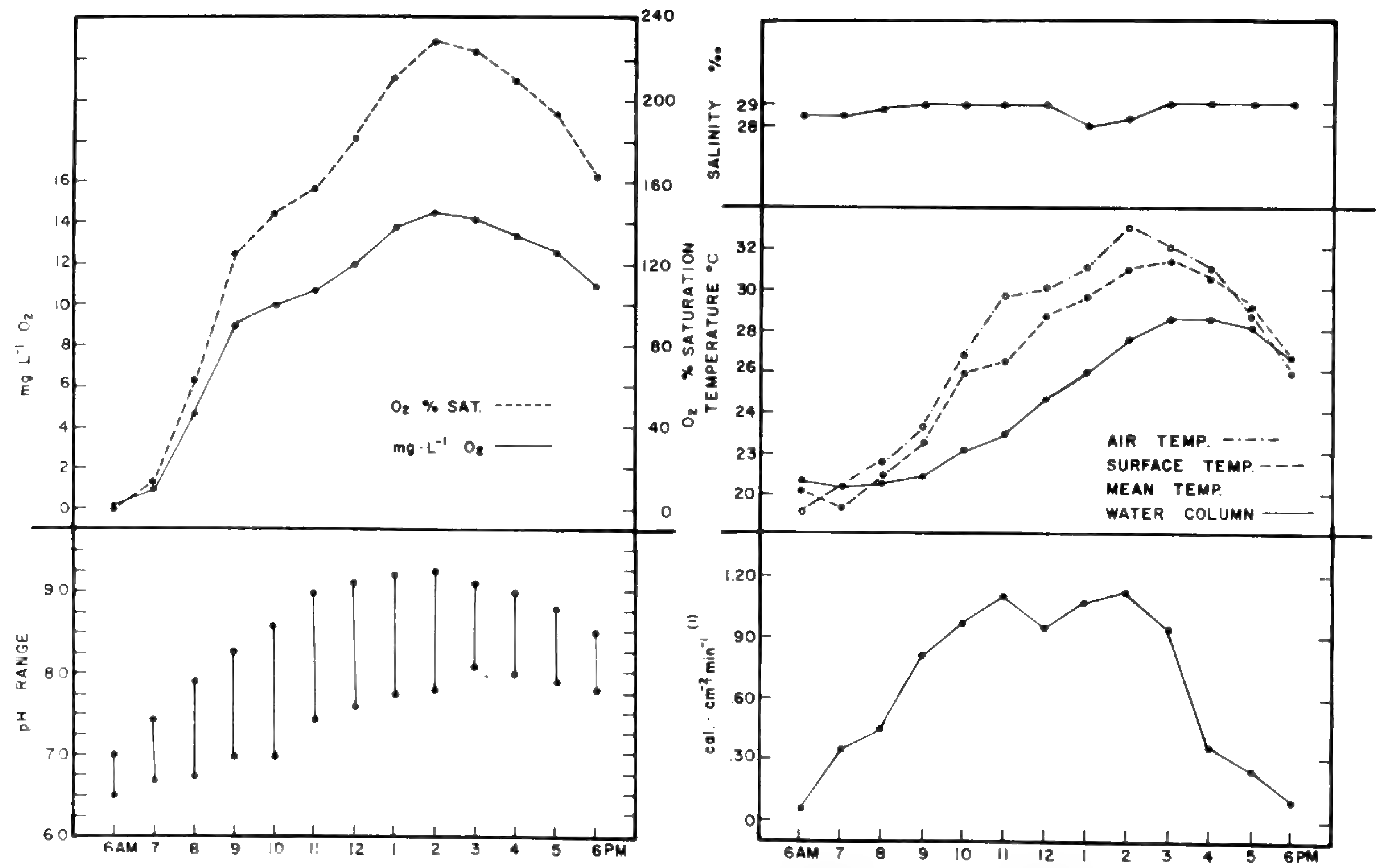
the depth. Only trace amounts of precipitation occurred throughout the study period so that the full effect of drying conditions during a neap tide period was apparent. A marked drop in the water level was noted with only about one-half the initial volume present after ten days. Salinity rose from 27 0/00 to 29 0/00 in a slightly erratic fashion. The most significant feature of the diel changes in the parameters was oxygen depletion, which occurred as the water level dropped and mean water temperature rose. Morning D.O. gradually dropped until the system became anoxic on the ninth and tenth days. Nighttime community respiration and chemical redox reactions apparently depleted the oxygen produced during the day. Because the sky was overcast on the seventh and eighth days, oxygen production was limited.

The curves for both pH and oxygen content coincide with the rise and fall of incident radiation (Fig. 7). There is an apparent time lag between oxygen values and solar radiation. Nixon and Oviatt (1973) reported that throughout the year oxygen curves tended to lag behind solar radiation by about one hour. Nicol (1935) described similar diurnal oxygen curves.

A temperature inversion occurred diurnally in the water column (Fig. 8). In early morning, inverse stratification was noted due to a time lag in heat dissipation within the water column so that the bottom temperature was warmer than the surface. The temperature profile changed as insolation increased, with the greatest fluctuation occurring at the surface and the least at the bottom. The temperature differential from surface to bottom in 15 cm of water was 1.5° C in early morning and 7.5° C by mid-day as the system became highly stratified. As insolation decreased in late afternoon the system tended toward isothermy as the pattern again began to reverse.

## CONCLUSIONS

*Ruppia maritima* L. is a plant of broad ecological amplitude. Persistence of a population in a particular habitat is due to a continuation of conditions favorable to growth and development. Seasonal periodicity and reestablishment of annual or perennial populations are related to ecological succession of the habitats as well as specific environmental parameters. Clinal variation in vegetative morphology and reproductive behavior are apparently expressions of adaptation by *Ruppia* to a diversity of habitats.



(1) INCIDENT RADIATION REPRESENTS AVERAGE OF READINGS OVER TEN MINUTE PERIOD

Figure 7. Diurnal fluctuations (hourly) in incident radiation, oxygen content, hydrogen ion concentration, temperature, salinity and depth over twelve hours (July 31, 1974) at the Vols Island site.

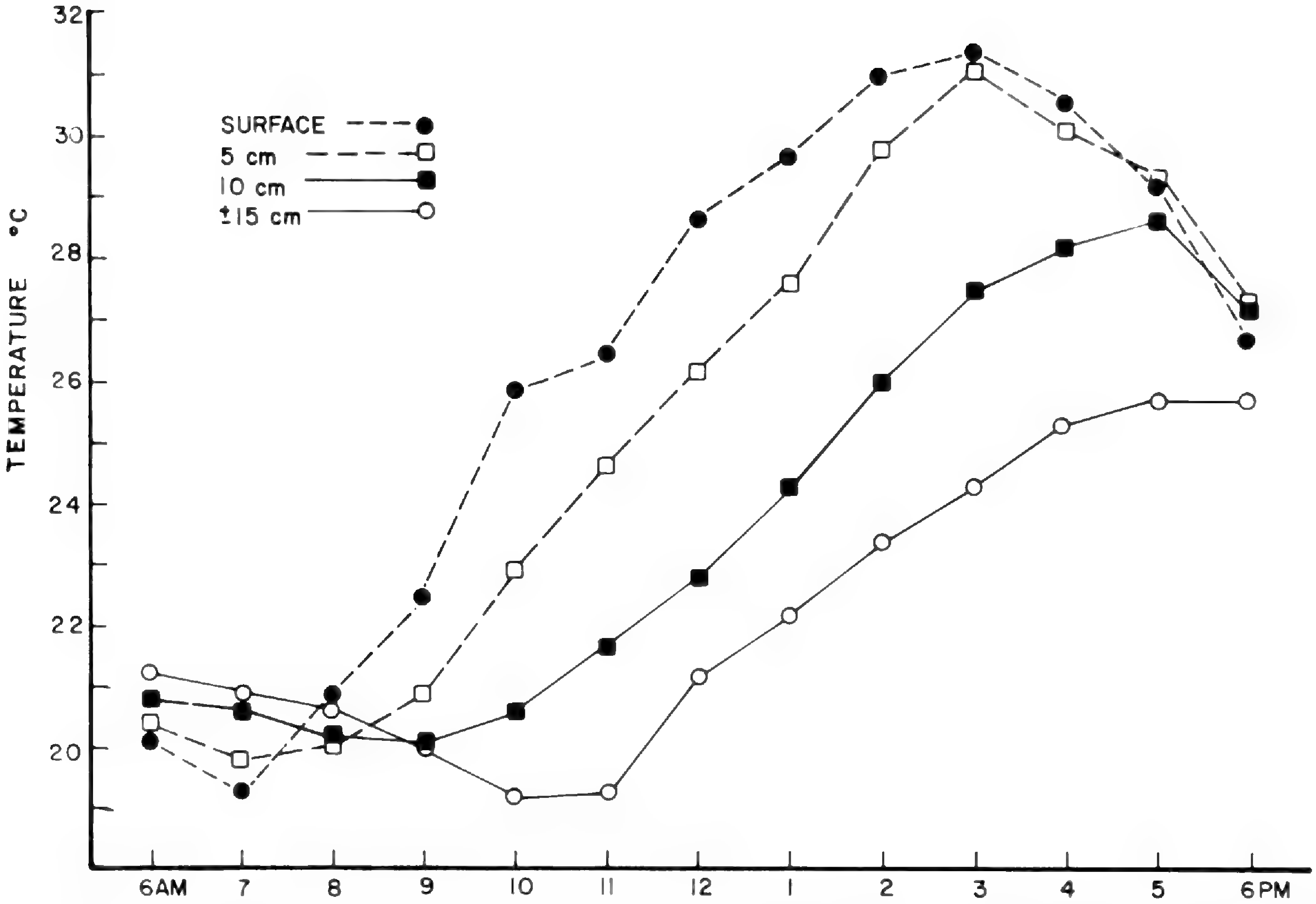


Figure 8. Diurnal fluctuations (hourly) in temperature of the water column (surface, 5 cm, 10 cm, bottom) over twelve hours (July 31, 1974) at the Vols Island site.

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## LITERATURE CITED

ANDERSON, R. R. 1969. Temperature and rooted aquatic plants. Ches. Sci. **10:** 157–164.

———. 1970. The submerged vegetation of Chincoteague Bay. p. 136–155 *In:* Assateague Ecological Studies, part 1. Environmental Information. Nat. Res. Inst. U. Maryland, Contrib. No. **446.**

ANON. 1974 & 1975. Tide tables high and low water predictions 1974 & 1975 East coast of North America including Greenland. U.S.D.C., N.O.A.A., Nat. Ocean Surv. Washington D.C. 288p.

A. P. H. A. 1971. Standard methods for the examination of water and wastewater. 13th ed., Amer. Publ. Health Assoc., New York. 874 p.

BREEDING, C. H. J., F. D. RICHARDSON, & S. A. L. PILGRIM. 1974. Soil survey of New Hampshire tidal marshes. N.H. Agr. Exp. Sta. Res. Rept. No. **40.** 94 p. and maps.

BOURN, W. S. 1935. Sea-water tolerance of *Ruppia maritima* L. Boyce Thompson Inst. Contrib. **7:** 249–255.

BOYD, C. E. 1975. Competition for light by aquatic plants in fish ponds. Auburn Univ. Agr. Exp. Sta. Circ. **215.** 19 p.

BUSCEMI, R. W. 1958. Littoral oxygen depletion produced by a cover of *Elodea canadensis* Oikos **9:** 239–245.

BUTLER, J. L. 1963. Temperature relations in shallow turbid ponds. Proc. Okla. Acad. Sci. **43:** 90 95.

CHAPMAN, V. J. 1938. Coastal movement and development of some New England marshes. Proc. Geologists' Assoc. **49:** 373–384.

———. 1940. Succession on the New England salt marshes. Ecology **21:** 279–282.

———. 1960. Salt marshes and salt deserts of the world. L. Hill, London. 392 p.

CONOVER, J. T. 1958. Seasonal growth of benthic marine plants as related to environmental factors in an estuary. Texas Univ. Inst. Mar. Sci. Pub. **5:** 97–147.

———. 1964. The ecology, seasonal periodicity, and distribution of benthic plants in some Texas lagoons. Bot. Mar. **7:** 4–41.

———. 1966. The importance of natural diffusion gradients and transport of substances related to benthic marine plant metabolism. p. 5: 1 5:13. *In:* Tech. Rept. No. **3** Environmental relationships of benthos in salt ponds. Grad. Sch. Oceanography. Univ. R.I.

———. & E. GOUGH. 1966. The importance of stem and leaf vs. root assimilation in *Ruppia maritima* L. and *Zostera marina* L. related to seasonal growth. p. 6:1–6:19. *In:* Tech. Rept. No. **3** Environmental relationships of benthos in salt ponds. Grad. Sch. Oceanography. Univ. R. I.

CROCKER, W. 1907. The germination of seeds of water plants. Bot. Gaz. **44:** 375–380.

DALE, H. M. & T. J. GILLESPIE. 1977. The influence of submersed aquatic plants on temperature gradients in shallow water bodies. Can. J. Bot. **55:** 2216–2225.

———. 1978. Diurnal temperature gradients in shallow water produced by populations of artificial aquatic macrophytes. Can. J. Bot. **56:** 1099–1106.

DAVIS, J. S., & P. B. TOMLINSON. 1974. A new species of *Ruppia* in high salinity in Western Australia. J. Arnold Arb. **55:** 59–65.

EDWARDS, R. W. 1957. Vernal sloughing of sludge deposits in a sewage effluent channel. Nature (London) **180:** 100.

FERNALD, M. L., & K. M. WIEGAND. 1914. The genus *Ruppia* in Eastern North America. Rhodora **16:** 119–127.

GORE, L. F. 1965. Effects of small salt marsh impoundments upon *Ruppia* and macroinvertebrates. M.S. Thesis. U. of Maine, Orono. 111 p.

GRAVES, A. H. 1908. The morphology of *Ruppia maritima*. Trans. Conn. Acad. Arts Sci. **14:** 150–170.

GUPPY, H. B. 1897. On the postponement of the germination of the seeds of aquatic plants. Proc. R. Soc. Edinb. **13:** 344–359.

GUTIERREZ, M. G. 1977. Observaciones sobre un comportamiento atipico de *Ruppia maritima* L. en una laguna costera tropical. Bol. Soc. Bot. Mex. **37:** 53–68.

HARTMAN, R. T. & D. L. BROWN. 1967. Changes in internal atmosphere of submersed vascular hydrophytes in relation to photosynthesis. Ecol. **48:** 252–258.

HUTCHINSON, J. 1934. The families of flowering plants. II. Monocotyledons. Macmillan and Co. Ltd., London. 243 p.

———. 1959. The families of flowering plants. 2nd ed. Clarendon Press, Oxford. 792 p.

JOANEN, J. T. 1964. A study of factors that influence the establishment of natural and artificial stands of wigeon-grass, *Ruppia maritima* L., on Rockefeller Refuge, Cameron Parish, Louisiana. M.S. Thesis. Lousiana State Univ., Baton Rouge. 63 p.

JOHNSON, D. S., & H. H. YORK. 1915. The relation of plants to tide levels. Carnegie Inst. Wash. Publ. **206**. 162 p.

MAYER, F. L. JR. 1967. The effect of salinity on growth and reproduction of *Ruppia maritima* L. M.S. Thesis. Utah State Univ. 66 p.

———. 1969. Influence of salinity on fruit size in *Ruppia maritima* L. Proc. Utah Acad. Sci. Arts and Letters. **46:** 140–143.

MCKAY, E. 1935. Salt tolerance of *Ruppia maritima* in lakes of high magnesium sulphate content. Plant Phys. **10:** 425–446.

MCLAUGHLIN, E. G. 1974. Autecological studies of three species of *Calitriche* native in California. Ecol. Monogr. **44:** 1–16.

MUENSCHER, E. C. 1936. The germination of the seeds of *Potamogeton*. Ann. Bot. **50:** 805–821.

NICOL, E. A. T. 1935. The ecology of a salt-marsh. Mar. Biol. Assoc. U.K. **20:** 203–261.

NIXON, S. W., & C. A. OVIATT. 1973. Ecology of a New England salt marsh. Ecol. Monogr. **43:** 463–498.

Phillips, R. C. 1960. The ecology of marine plants of Crystal bay Florida. Quart. J. Florida Acad. Sci. **23:** 328–337.

Posluszny, U., & R. Sattler. 1974. Floral development of *Ruppia maritima* L. var. *maritima*. Can. J. Bot. **52:** 1607–1612.

Redfield, A. C. 1959. The Barnstable marsh. p. 37–39. *In:* Proc. Salt Marsh conference, Marine Institute, Univ. Georgia, Athens.

———. 1965. The thermal regime in salt marsh peat at Barnstable, Massachusetts. Tellus **17:** 246–258.

———. 1972. Development of a New England salt marsh. Ecol. Monogr. **42:** 201–237.

Richardson, F. D. 1976a. Environmental parameters of *Ruppia maritima* L. populations on New Hampshire tidal marshes. M.S. Thesis. University of New Hampshire. 98 p.

———. 1976b. Pollination mechanism in *Ruppia*. Helobiae Newsletter. Melbourne. **1:** 12–15.

Sand-Jensen, K. 1977. Effects of epiphytes on eelgrass photosynthesis. Aquat. Bot. **3:** 55–63.

Sculthorpe, C. D. 1967. The biology of aquatic vascular plants. Edward Arnold Ltd. London. 610 p.

Setchell, W. A. 1924. *Ruppia* and its environmental factors. Proc. Nat. Acad. Sci. **10:** 286–288.

———. 1946. The genus *Ruppia*. Proc. Calif. Acad. Sci. **25:** 469–478.

Strickland, J. D. H., & T. R. Parsons. 1968. A practical handbook of sea water analysis. Fish Res. Bd. of Canada. Ottawa. 311 p.

Sullivan, M. J. 1976. Structural characteristics of a diatom community epiphytic on *Ruppia maritima* L. Phycol. Soc. Amer. Ann. meeting. Tulane Univ., New Orleans. (Abstr.)

Uhl, N. W. 1947. Studies in the floral morphology and anatomy of certain members of the Helobiae. Ph.D. Thesis. Cornell University. 107 p. and plates.

Verhoeven, J. T. A. 1975. *Ruppia*—communities in the Camargue, France. Distribution and structure in relation to salinity and salinity fluctuations. Aquat. Bot., **1:** 217–241.

———. 1978. Natural regulation of plant biomass in a *Ruppia*-dominated system. Proc. EWRS 5th Symp. on Aquatic Weeds. 53–61.

———. & W. van Vierssen. 1978. Distribution and structure of communities dominated by *Ruppia, Zostera* and *Potamogeton* species in the inland waters of "De Bol", Texal, The Netherlands. Estuarine and Coastal Marine Science. **6:** 417–428.

Young, N. F. & J. R. Zimmerman. 1956. Variation in temperature in small aquatic situations. Ecol. **37:** 609–611.

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# THE FLORA, VEGETATION, AND PHYTOGEOGRAPHIC RELATIONSHIPS OF WHALEBOAT ISLAND, CASCO BAY, MAINE

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Despite the numerous relatively undisturbed islands in the Gulf of Maine and the increasing interest in island biogeography, few Maine island floras have been adequately studied. The flora of Mount Desert Island is probably the best known, from the descriptions of Rand and Redfield (1894), Moore and Taylor (1927), and Wherry (1928). Other investigations include those of Matinicus Island (McAtee, 1916), Matinicus Rock, Machias Seal Island, and Gull Rock (Hodgdon & Pike, 1969), Isle au Haut (Wise, 1970), and the Kent Islands in the Bay of Fundy (McCain et al., 1973; McCain, 1975). Studies of the Penobscot Bay area (Hill, 1919; 1923) and coastal spruce-fir forests (Davis, 1961) provide additional data for the region. During 1975 and 1976, I inventoried the vascular plant flora of Whaleboat Island, Casco Bay, Maine, and carried out phytosociological investigations of the island's spruce forests. This paper is a compilation of the Whaleboat Island flora and a discussion of the island's vegetation and biogeographic relationships.

Whaleboat Island lies at 43° 45′N latitude and 70° 03′W longitude, among the middle tier of the 222 offshore islands in Casco Bay. The 47-hectare island is approximately 2.7 km long, and varies in width from 100–400 m. It is protected from full marine exposure by a series of outer islands, and lies 1.3 km west of Harpswell Neck, a narrow promontory that extends some 22.5 km into the middle of the bay. Elevated, heavily wooded sections at each end are connected by a low, grassy swale, producing the physiographic configuration which inspired the island's name.

Whaleboat Island lies in an area of transition between a more southern coastline, dominated by long beaches with sand produced by the erosion of glacial deposits, and a rocky northern coastline which has no large glacial deposits and has experienced relatively little erosion (Leavitt, 1935). A few small, poorly developed silt and sand beaches and a salt marsh occur on the island's protected east side. Elsewhere the island is bounded by steep cliffs, rock, and shingle beaches. A large erratic is poised on the rocky edge of the southern tip.

Whaleboat Island and many of the other islands in Casco Bay are underlain by Cambro-Ordovician schists of the Cushing Formation (Hussey & Pankiwskyj, 1975), characterized by varying muscovite and biotite content in vertical laminae. Eighty percent of the island is covered by strongly acid, very well drained coarse-textured soils that were formed in glacial till. Depth to bedrock in these soils is 30–45 cm, and outcrops are common. A deeper, less well drained soil occupies a strip of the island near its center (U.S.D.A. Soil Conservation Service, 1974).

A vegetational transition also occurs in this area between coastal and boreal spruce-fir forests to the north and east and hardwoods-white pine-hemlock forests in the southwest and central interior (Westveld et al., 1956; Davis, 1961). Whaleboat Island supports two spruce forests, located on the hills at either end of the island. The low area between the forests is dominated by grasses with coarse shrubs and small trees on slightly higher ground. The southern tip of the island is covered largely by shrubs.

The climate of the area is strongly affected by offshore currents. The confluence of the cold Labrador Current and the warmer Gulf Stream some miles offshore results in frequent heavy fog. Coastal storms or "northeasters", bringing high winds and heavy precipitation, are often accompanied by high wind-driven tides and ice storms. Because of the moderating influence of the sea, coastal Maine experiences the coolest summers, warmest winters, longest growing season, and narrowest range between temperature extremes of any region of the state (Lautzenheiser, 1972).

Whaleboat Island, presently uninhabited, supported a small human population as late as 1905 (Etnier, 1974). An Indian shell mound on the northwest side of the island suggests a long history of human visitation. Other evidence of occupation are stone walls, an old dug well, and, near the southern end, the remains of a small shed that was used intermittently by rum traders in the 1920's. Present human disturbance is usually limited to the immediate shoreline. Turkeys, sheep, and cattle were formerly kept on the island, the latter until the 1950's. The island's southern half is now protected under a conservation easement granted to the Maine Department of Parks and Recreation. Whaleboat Island is listed as one of Maine's "Natural Areas."

## VEGETATION

The island forests are dominated by red spruce, *Picea rubens*. Minor elements in the canopy are *Abies balsamea* and *Betula papyrifera*. The understory, where not occupied solely by windthrown trees and litter, is dominated by *Dryopteris spinulosa, Cornus canadensis*, and *Trientalis borealis*. Shrubs are rare. Areas adjacent to freshwater springs support heavy growths of *Scirpus cyperinus, Hypericum virginicum*, and *Sphagnum* spp. Larger openings in the forest tend to be populated exclusively by *Dennstaedtia punctilobula*, while smaller openings are dominated by *Dryopteris spinulosa* and *Pteridium aquilinum*.

The spruce forests appear to be fairly mature. This vegetation type on Whaleboat Island exhibits substantially lower species diversity than most others on the island and contains exclusively native species. *Populus tremuloides, Betula lenta, Quercus rubra*, and *Prunus pensylvanica*, common in nearby mainland forests, are restricted to the edges of the Whaleboat Island forests.

The forest edge supports an assemblage of high species diversity. Many species, including *Salix discolor, Dirca palustris*, and *Viburnum recognitum*, are represented here by single individuals. *Juniperus communis, Myrica pensylvanica, Rubus idaeus*, and *Vaccinium angustifolium* are particularly successful shrubs. *Rumex acetosella, Fragaria virginiana, Ligusticum scothicum*, and *Achillea millefolium* are prominent herbs. Throughout much of the island this assemblage occurs as a narrow band on the cliffs between the shoreline and the forest.

Most of the central part of the island between the forests, as well as the southern tip, supports a dense growth of shrubs, particularly *Rosa rugosa, Rubus idaeus*, and *Myrica pensylvanica*, interrupted by a few small, isolated individuals of white pine, *Pinus strobus*, alder, *Alnus rugosa*, and red maple, *Acer rubrum*. Colonies of *Urtica dioica* and *Solidago rugosa* and other coarse herbs are scattered throughout the area.

Comparison of an aerial photograph taken in 1956 (USGS-VLE 1-4) just after the cessation of grazing, with a similar photograph taken in 1970 (USGS-VLCK-C 1-17) shows that the thick shrub cover has encroached upon the adjacent grasslands to some extent. When the central part of the island was forested, it probably supported a mixed white pine-hardwoods forest similar to the forests present on most of the other islands and peninsulas in the bay. It is likely that this area was cleared by the settlers, and, following abandonment, was quickly colonized by shrubs. Although several stunted red maples, white pines, and a red spruce now rise above the thick shrub cover, no seedling or sapling reproduction of these or other tree species is apparently occurring on the site. The adjacent edge of the forest is marked by a fringe of juniper (*Juniperus communis*) and dewberry (*Rubus flagellaris*) on exposed bedrock ledges.

This shrub community appears to have been relatively stable for at least the last 20 years, in the sense that the development of a tree-dominated community on the site does not appear to be imminent. Tree species may be largely excluded by the density of the shrubs, the smothering effect of their litter upon tree seedlings, and the ability of shrubs such as *Rubus idaeus* to spread quickly by suckering. Similar situations have been documented elsewhere (Pound & Egler, 1953; Niering & Egler, 1955; Niering & Goodwin, 1974). The competitive advantage possessed by spruce and fir on shallow, well drained upland soils elsewhere on the island apparently is not maintained in the deeper, moister soil at the center, and it is possible that this area may remain dominated by shrubs for an indefinite period of time.

A narrow strip of grassland on low ground at the island's center and another on the extreme southern tip are dominated by *Agrostis tenuis, Danthonia spicata,* and *Poa pratensis,* with *Ribes glandulosum, Rubus hispidus,* and *Cirsium arvense* also common.

The precise effects of grazing upon the plant species composition in the grasslands is difficult to determine. Some species such as the highly palatable *Trifolium repens* may have been markedly reduced in abundance. Only one individual of *T. repens* was observed on the island, although it is common elsewhere along the coast (Hill, 1923). Species representing genera which are less palatable and possess spines or prickles, including *Ribes, Rosa, Rubus, Urtica,* and *Cirsium,* are now prominent in the vegetation. The abundance of *Ribes* spp. has been used as an approximate measure of grazing pressure, since they are able to withstand prolonged grazing (Auclair & Cottam, 1971). Other species such as *Phleum pratense* still present in the vegetation may have been planted for pasturage.

The two meadows, sites of past human and animal activity, are slowly being invaded by shrubs, particularly bayberry, *Myrica pensylvanica,* wild rose, *Rosa rugosa,* and raspberry, *Rubus idaeus.*

Spruce does not appear to be colonizing the central grasslands, although the seed supply is sufficient. With increased colonization by raspberry and bayberry, conditions for the establishment of the conifers on the abandoned land may become more favorable. However, if storm tide overwash occurs on this low section, development of any woody vegetation besides bayberry and a few others is unlikely.

The shoreline communities on the island include a totally distinct group of species. Above the drift line, rock beaches are dominated by *Plantago juncoides* and *Solidago sempervirens,* pebble beaches by *Raphanus raphanistrum,* and beaches of finer substrate by *Elymus virginicus.* The drift line itself supports sporadic growths of *Chenopodium album* and *Sonchus asper.* The salt marsh on the eastern side of the island is dominated by *Spartina alterniflora, S. patens,* and *Salicornia europaea.*

## PHYTOGEOGRAPHY

Islands often show different assemblages of species from similar mainland sites (MacArthur & Wilson, 1967; Power, 1972). The Whaleboat Island flora is somewhat depauperate in comparison with two Casco Bay mainland spruce forests studied by Davis (1961). Many species which are important on the mainland are completely absent from the island. These include *Pinus resinosa, Thuja occidentalis, Medeola virginiana, Cypripedium acaule, Betula populifolia, Coptis groenlandica, Nemopanthus mucronata, Acer pensylvanicum, Kalmia angustifolia,* and *Epigaea repens,* as well as others. *Dryopteris spinulosa,* the dominant species in the island forest understory, is either not present or is only a minor element in nearby mainland forests. (Davis, 1961).

MacArthur and Wilson (1967) suggest that species may occupy wider niches on species-depauperate islands because of the absence of competitors. On Whaleboat Island, many aggressive mainland competitors are present, yet their importance on the island appears to be restricted by the comparative success of a different group of species. For example, only one individual of *Taraxacum officinale* was observed on the island in 1976. It was growing not in the grassland, but just above the drift line. Other introduced species, including *Verbascum thapsus* and *Rumex crispus,* and locally abundant natives such as *Rhus radicans* tend to be largely restricted to this area as well. They are replaced on the island by *Myrica pensylvanica,* a species highly adapted to succeed on nitrogen impoverished soils by nitrogen-fixing bacteria in its root nodules (Morris et al., 1974), and other species, including *Raphanus raphanistrum, Fragaria virginiana, Rosa rugosa,* and *Rubus idaeus.*

The depauperate nature of the island flora is also demonstrated by the large proportion of taxa which are represented by only one species. This characteristic was noted by McCain (1975) in his study of the Kent Island group. Table 1 shows the generic coefficient (total genera/total species × 100) of Whaleboat Island and seven other islands from the New England coast.

The reduced species diversity of these island floras is evident when they are compared to a mainland flora. The generic coefficient of the Penobscot Bay area flora (Hill, 1919) is 50, compared to a range of 60–91 among the island floras. This lower diversity reflects reduced ecological diversity of island habitats. This is readily apparent from the generic coefficient of 91 for Gull Rock, a very small island of only several hectares. The results of this study and comparison to those of similar islands tend to corroborate the findings of MacArthur and Wilson (1967), who attribute higher genus/species ratios in island faunas as well as floras to competitive replacement in the more restrictive island habitats.

The species diversity of these island floras shows a strong relationship to area. The number of species increases rapidly with increasing island area until islands as large as Kent and Cuttyhunk are reached. The relative difficulty of colonization of more distant islands is also apparent. Matinicus Island, although more than four times the size of either Kent Island or Cuttyhunk, lies at least 5 km farther from the mainland and supports fewer species. Matinicus Rock is approximately the same size as Machias Seal Island but is 13 km farther out to sea and supports 13 fewer species.

The archipelago effect, or the influence of nearby islands acting as stepping stones for mainland colonists, is also demonstrated in Table 1. Cuttyhunk, a member of the Elizabeth Islands chain in Buzzards Bay, Massachusetts, and Kent Island, part of the Grand Manan archipelago of New Brunswick, support far more species than oceanic Matinicus Island. Similarly, Penikese, also in the Elizabeth chain, is much farther from the mainland and smaller in area than Whaleboat, but supports a flora of comparable size.

A distinctive attribute of the Whaleboat Island flora is the low complement of introduced species. Table 1 also shows the percentage of non-native species in the eight New England island floras. The largest value is 47%, reported for Penikese Island. Previous collections on this island have yielded even higher percentages of alien elements (Lauermann & Burk, 1976). These authors cite previous human habitation, and dispersal by herring gulls which forage in mainland dump sites, among reasons for the high value.

Other workers have noted the effects of disturbance by large colonies of nesting seabirds upon island floras. Hodgdon and Pike (1969) suggest that bird islands may become largely populated by introduced weeds or by locally abundant natives following the initial elimination of many species by the new bird colonies. However, the lowest percentage of non-native species in Table 1 is 17%, shown for Kent Island. In view of the large nesting herring gull population on Kent Island (McCain et al., 1973), this value is surprisingly low when compared to those of other bird islands, Gull Rock, Machias Seal Island, and Matinicus Rock. The major families constituting the flora of these three islands are the Compositae, Gramineae, Polygonaceae, Caryophyllaceae, and Leguminosae, which together comprise a little over 50% of the flora (Hodgdon & Pike, 1969). In comparison, these taxa comprise only 25% of the Whaleboat Island flora. Nesting birds do not appear to be important agents of disturbance on Whaleboat Island. Although eiders, osprey, and a number of smaller passerine species nest in moderate numbers on the island, only two nesting pairs of herring gulls were observed in 1976.

While the proportion of alien elements is not always directly related to disturbance from nesting birds, a slight trend of increasing proportion of introduced species with decreasing latitude appears. This trend may be related to increasing proximity to areas that have been populated for the longest period of time.

All of these islands have sustained some type of major disturbance. Matinicus, Whaleboat, Cuttyhunk, and Penikese have been or are currently inhabited, and all have probably been grazed to some extent. Kent Island, Gull Rock, Machias Seal, Matinicus Rock, and Penikese also support nesting bird colonies of significant size.

Table 1. Phytogeographic relationships of eight New England island floras

| Island | Area(ha) | Distance from mainland (km) | Latitude | Number of Species | Generic Coefficient | % Non-Native Species | Index of floristic resemblance to Whaleboat Island |
|---|---|---|---|---|---|---|---|
| [1]Matinicus Island | 291 | 29 | 43° 52′ | 217 | 75 | 34 | 50.0 |
| [2]Kent Island | 61 | 24 | 44° 35′ | 224 | 60 | 17 | 49.4 |
| [3]Cuttyhunk Island | 61 | 21 | 41° 27′ | 260 | 64 | 29 | 29.2 |
| Whaleboat Island | 47 | 1.3 | 43° 45′ | 168 | 60 | 20 | — |
| [4]Penikese Island | 34 | 19 | 41° 27′ | 163 | 73 | 47 | 32.5 |
| [5]Machias Seal Island | 4 | 18 | 44° 39′ | 77 | 68 | 35 | 32.5 |
| [5]Matinicus Rock | 4 | 31 | 43° 52′ | 64 | 75 | 34 | 40.6 |
| [5]Gull Rock | 2 | 13 | 44° 55′ | 34 | 91 | 24 | 32.4 |

Sources:
[1]McAtee, 1916
[2]McCain, Hodgdon, and Pike, 1969
[3]O'Neill, 1975
[4]Lauermann and Burk, 1976
[5]Hodgdon and Pike, 1969

The Simpson index of resemblance has been used to compare the taxonomic composition of the total floras of each island with that of Whaleboat Island, according to the formula 100 $C/n_1$, in which C is the number of taxonomic units common to two floras, and $n_1$ is the total number of units in the smaller of the two (Simpson, 1965). This index is most useful for comparison of floras of similar size. The resemblance indices are included in Table 1.

Whaleboat Island shows the greatest floristic resemblance to Matinicus Island and Kent Island. Both of these support spruce forests and shrub communities similar to those on Whaleboat, and both have similar percentages of introduced species. They are also the largest of the six islands located in the Gulf of Maine.

Although the families represented on Gull Rock, Machias Seal Island, and Matinicus Rock are essentially all represented on Whaleboat as well, resemblance at the species level is markedly lower. In spite of the fact that the islands lie within the same geographic and climax vegetation zones as Whaleboat Island, resemblance is no higher than that between Whaleboat and the two Elizabeth islands. Smaller size and reduced habitat diversity appear to be more important than geographic or vegetational proximity. The somewhat higher resemblance of Whaleboat to Matinicus Rock may reflect the physical proximity of that island to Matinicus Island.

The two Elizabeth islands lie within a different climax forest vegetation zone (Westveld et al., 1956). The floras of these islands and the other two bird islands in Maine show a degree of floristic resemblance to Whaleboat Island not unlike that found between Cape Cod and the Outer Banks of North Carolina by Burk (1968). Examination of the species lists reveals that the major points of similarity among the islands are the shoreline and shrub communities, as also found by Burk. Many drift line colonists, introduced species, and unpalatable forms are common to all of these islands. Despite differences in climax vegetation, these segments of the floras converge taxonomically because of the common influences of human habitation, grazing, and marine exposure.

## FLORA OF WHALEBOAT ISLAND

Sixteen days were spent on six separate visits to the island during the fall of 1975 and the spring and summer of 1976. Specimens of all vascular plant species were collected, and observations on the abundance of each species were recorded.

A total of 168 species of vascular plants, representing 110 genera and 51 families, were collected on Whaleboat Island. Of these, 136 are native and 32 are non-native, chiefly introduced from Europe.

All of the plants collected on the island had been previously reported in the area except *Dryopteris fragrans,* the fragrant wood fern, which was growing in three small clumps on a dry ledge on the northwest side. The nearest previously known station is some 97 km north and east of Whaleboat Island (Seymour, 1969).

Nomenclature follows Fernald (1950). All specimens collected in the course of this study have been deposited in the herbarium of Smith College. Species marked by asterisk in the checklist are alien.

## ANNOTATED CHECKLIST

### EQUISETACEAE

*Equisetum arvense* – uncommon at the spring on the southern tip
*E. sylvaticum* — rare in the central shrub thicket

### LYCOPODIACEAE

*Lycopodium obscurum* — rare on moist ground in the forests

### OSMUNDACEAE

*Osmunda cinnamomea* — common on moist ground in the southern forest

### POLYPODIACEAE

*Dennstaedtia punctilobula* — abundant in the larger forest openings
*Dryopteris fragrans* — rare; in three small clumps on a mossy ledge on the northwest margin of the northern forest
*D. noveboracensis* — uncommon in the central shrub thicket
*D. phegopteris* — locally common at the spring on the southern tip, in the central shrub thicket, and rare in the northern forest
*D. spinulosa* — the most abundant fern in the spruce forests
*D. thelypteris* — common in the central shrub thicket
*Onoclea sensibilis* — locally abundant in the central shrub thicket and near the spring on the southern tip
*Pteridium aquilinum* — locally abundant in openings in the forests

### PINACEAE

*Abies balsamea* — rare in the forests
*Juniperus communis* — abundant on bedrock outcrops at the forest margins

*Picea rubens* — abundant in the spruce forests
*Pinus strobus* — rare in the central shrub thicket

JUNCAGINACEAE

*Triglochin maritimum* — locally common in the salt marsh

GRAMINEAE

**Agrostis tenuis* — dominant grass in the central meadow
*Danthonia spicata* — common in moist soil on the western side in the shrub thicket and in the grassland
*Elymus arenarius* — uncommon in the drift line, east central side
*E. virginicus* — locally common in the drift line
**Phleum pratense* — common in the central meadow
*Poa pratensis* — common in the central meadow
*Spartina alterniflora* — common locally in the drift line on finer substrate
*S. patens* — locally common in wet soils on the western side above the drift line
*S. pectinata* — locally common in wet soils on the western side

CYPERACEAE

*Carex hystricina* — locally common at the spring on the southern tip
*C. scoparia* — uncommon above the drift line, central
*C. silicea* — locally common on the east central side
*Scirpus atrocinctus* — uncommon in the drift line, east side
*S. cyperinus* — abundant at springs in the forests
*S. maritimus* — locally common on the mud flat, eastern shore

JUNCACEAE

*Juncus balticus* — uncommon in the central meadow
*J. gerardi* — locally common in the drift line, east central
*J. tenuis* — locally common on the east central shore

LILIACEAE

*Erythronium americanum* — rare in the southern spruce forest
*Maianthemum canadense* — common in the forests

IRIDACEAE

*Iris versicolor* — rare on ledges on the northern forest margin and on the west side of the grassland

### SALICACEAE

*Populus tremuloides* — locally common in a restricted area southwest of the northern forest and uncommon elsewhere on the forest edges
*Salix discolor* — one individual at the campsite on the northwest side

### MYRICACEAE

*Myrica pensylvanica* — abundant in the central shrub thicket and on forest margins throughout

### CORYLACEAE

*Alnus rugosa* — several large individuals in the central shrub thicket
*Betula lenta* — rare on the northwest forest margin
*B. lutea* — rare in the northern forest
*B. papyrifera* — common in the northern forest, rare in the southern forest

### FAGACEAE

*Quercus rubra* — rare on the western edge of the northern forest

### URTICACEAE

**Urtica dioica* — common in the central shrub thicket

### POLYGONACEAE

*Polygonum hydropiper* — uncommon in wet soil, west central shrub margin
*P. punctatum* — locally abundant at the spring on the southern tip
*P. sagittatum* — uncommon on the western central shrub margin
**Rumex acetosella* — common on dry ledges
**R. crispus* — uncommon above the drift line, central area

### CHENOPODIACEAE

*Atriplex patula* — uncommon in the drift line, east central
**Chenopodium album* — common in the drift line, stony beaches
*Salicornia europaea* — locally common in the salt marsh and in finer substrate in the drift line, east side
*Suaeda maritima* — uncommon in the drift line, stony beaches

### CARYOPHYLLACEAE

*Arenaria lateriflora* — uncommon in the central meadow
**Cerastium vulgatum* — common in the central meadow
*Spergularia rubra* — uncommon on the southern end

RANUNCULACEAE

*Anemone quinquefolia* — rare in the spruce forests

CRUCIFERAE

**Brassica juncea* — rare just above the drift line, west side
**B. kaber* — rare just above the drift line
**B. nigra* — uncommon in the drift line on the northeast side
*Cakile edentula* — locally common in the drift line, east side
**Capsella bursa-pastoris* – rare in rocky crevices, northeast side
**Raphanus raphanistru;m* — dominant plant just above the drift line in most areas

SAXIFRAGACEAE

*Ribes glandulosum* common in shrubby areas throughout
*R. hirtellum* — locally abundant on the southern tip

ROSACEAE

*Amelanchier stolonifera* — rare in the central shrub thicket
*Fragaria virginiana* - abundant on dry ledges and meadows throughout
*Geum aleppicum* — uncommon on the forest margin, northeast side
*Potentilla anserina* — common above the drift line
**P. argentea* — common in the central meadow
*P. norvegica* — uncommon in the central meadow
*P. simplex* — rare above the drift line, east central
*P. tridentata* — common on dry ledges, near the central meadow
*Prunus pensylvanica* — locally common at the forest margin, northwest side
*Pyrus arbutifolia* — uncommon in the central shrub thicket
**P. malus* — a single large individual at the southern margin of the northern forest near the stone wall
*P. melanocarpa* — locally abundant in a small area on the western shrub margin
**Rosa rugosa* — abundant above the drift line and in shrubby areas throughout
*R. virginiana* — common above the drift line and in shrubby areas
*Rubus allegheniensis* — locally common except in the meadow
*R. flagellaris* — abundant in the central meadow, the central shrub thicket, and on the southern tip
*R. hispidus* — abundant in the central meadow and in shrubby areas

*R. idaeus* — dominant in the central shrub thicket, common on the southern tip

*R. semisetosus* — rare in openings in the spruce forests

*Spiraea latifolia* — locally common in the central shrub thicket

*S. tomentosa* — locally common in the central shrub thicket

### LEGUMINOSAE

*Lathyrus japonicus* — common in the drift line, east and west

**Trifolium arvense* — uncommon on dry ledges

**T. repens* — rare on the southern tip

### OXALIDACEAE

*Oxalis corniculata* — rare in the spruce forests and uncommon on dry ledges

### GERANIACEAE

*Geranium bicknellii* — rare on the west central side, shrub margin

### POLYGALACEAE

*Polygala sanguinea* — locally common on the west central shrub margin

### ANACARDIACEAE

*Rhus radicans* — locally abundant in one small area on the west central shrub margin

*R. typhina* — locally common in one area on the southeast margin of the northern forest, close to the shore

### AQUIFOLIACEAE

*Ilex verticillata* — common in the central shrub thicket in moist soil, rare on the western margin of the southern forest

### ACERACEAE

*Acer rubrum* — uncommon in the central shrub thicket and on ledges on the eastern cliffs by the southern forest

### BALSAMINACEAE

*Impatiens capensis* — locally common on the northeast forest margin and in wet soil on the west central shrub margin

### GUTTIFERAE

**Hypericum perforatum* — common above the drift line, central

*H. punctatum* — uncommon above the drift line, west central shrub margin

*H. virginicum* — locally abundant in moist depressions in the forests and in moist soil in the central shrub thicket

### VIOLACEAE

*Viola lanceolata* — rare on moss on the northwest side

*V. septentrionalis* — common on moss on the northwest side and on the west central shrub margin

### THYMELACEAE

*Dirca palustris* — a single individual on a rocky ledge on the northwest side

### ONAGRACEAE

*Circaea alpina* — common in the central shrub thicket

*Epilobium glandulosum* — common above the drift line, central

*E. leptophyllum* — uncommon in shrubby areas on the southern end

*Oenothera biennis* — uncommon above the drift line

*O. perennis* — rare in moist soil on the west central shrub margin

### ARALIACEAE

*Aralia nudicaulis* — rare in the northern forest

*Panax trifolius* — uncommon in openings in the southern forest

### UMBELLIFERAE

*Heracleum maximum* — single group of plants on the eastern margin of the northern forest

*Ligusticum scothicum* — abundant on dry rocky ledges throughout

### CORNACEAE

*Cornus canadensis* — common throughout the spruce forests

### ERICACEAE

*Vaccinium angustifolium* — abundant in the central shrub thicket, common along forest margins, uncommon in the forests

*V. corymbosum* — uncommon near the forest on the southern tip, rare in the southern forest

*V. macrocarpon* — locally abundant only on the spring on the southern tip

*V. vitis-idaea* — uncommon on dry ledges, southern end

### PRIMULACEAE

*Glaux maritima* — uncommon in finer substrate, drift line east side

*Lysimachia quadrifolia* — rare in the spruce forest

*L. terrestris* — common in the central shrub zone, uncommon on the southern tip

*Trientalis borealis* — abundant in the spruce forests

### PLUMBAGINACEAE

*Limonium nashii* — common in rock crevices on the shore and abundant in the rocky cove on the central west side

### ASCLEPIADACEAE

*Asclepias syriaca* — uncommon on the northeast forest margin and in the central grassland

### CONVOLVULACEAE

*Convolvulus sepium* — common above the drift line in moist soil

*Cuscuta gronovii* — locally abundant in a single location in wet soil on west central shrub margin

### VERBENACEAE

*Verbena hastata* — locally common in wet soil, on the west central shrub margin

### LABIATAE

**Galeopsis tetrahit* — uncommon above the drift line, east side

*Lycopus americanus* — uncommon in wet soil on the west central shrub margin

*L. uniflorus* — abundant on dry ledges throughout

**Nepeta cataria* — uncommon above the drift line, east central

*Scutellaria epilobiifolia* — locally abundant just above the drift line

*Teucrium canadense* — common above the drift line, east central

### SOLANACEAE

**Solanum dulcamara* — uncommon above the drift line, east central

### SCROPHULARIACEAE

*Linaria canadensis* — uncommon on the southeast side

*Rhinanthus crista-galli* — rare above the drift line, east central

**Verbascum thapsus* — rare above the drift line, east central

### PLANTAGINACEAE

*Plantago juncoides* — abundant in rock crevices on the shore

### RUBIACEAE

*Galium palustre* — uncommon above the drift line, east central

*Houstonia caerulea* — abundant only on a dry ledge by the campsite on the northwest side

### CAPRIFOLIACEAE

*Sambucus canadensis* — uncommon on the northeast forest margin

*S. pubens* — rare on the east side

*Viburnum cassinoides* — single individual on the southeast side

*V. recognitum* — single individual on the southeast margin of the northern forest

### COMPOSITAE

**Achillea millefolium* — abundant on dry ledges throughout

*Ambrosia artemisiifolia* — uncommon in the shrub margin

*Aster johannensis* — uncommon on the west side

*Bidens frondosa* — locally common in wet soil on the west central shrub margin

**Chrysanthemum leucanthemum* — rare, above the drift line

**Cirsium arvense* — abundant in the central meadow

**C. vulgare* — common above the drift line, east central

*Erigeron strigosus* — uncommon on dry ledges, west central

*Gnaphalium obtusifolium* — uncommon on dry ledges, west central side

**Hieracium aurantiacum* — rare above the drift line, east central

**Senecio vulgaris* — locally common in the drift line, south and east

*Solidago bicolor* — rare, confined to a dry ledge on the west central side

*S. juncea* — uncommon in the central meadow

*S. rugosa* — common, central shrub area

*S. sempervirens* — abundant in rock crevices throughout and common on rocky beaches

*S. sempervirens* × *rugosa* (*S.* × *asperula*) — common in large colonies south of the northern forest and above the drift line in central sections

**Sonchus arvensis* — common in the drift line on rocky beaches

**S. asper* — common in the drift line on rocky beaches

**Taraxacum officinale* — rare above the drift line, east central shore

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I am grateful for the guidance and interest of Dr. John Burk during the course of this study. Thomas Duffus, Edward Mulligan, A. F. R. Duffus, and Gail Farnsworth provided cheerful field assistance. Dr. Stephen Tilley and Dr. Marshall Schalk provided helpful comments on an earlier version of the manuscript. Harry Ahles kindly identified or verified several specimens. I am also indebted to Mr. and Mrs. Stephen Etnier of South Harpswell, Maine, for permission to study on Whaleboat Island.

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## LITERATURE CITED

Auclair, A. N. & G. Cottam. 1971. Dynamics of black cherry (*Prunus serotina* Ehrh.) in southern Wisconsin oak forests. Ecol. Mono. **41**(2): 153–177.

Burk, C. J. 1968. A floristic comparison of lower Cape Cod, Massachusetts, and the North Carolina Outer Banks. Rhodora **70**(782): 215–227.

Davis, R. B. 1961. The spruce-fir forests of the coast of Maine. PhD Thesis, Cornell University, Ithaca, New York. University Microfilms **61**–1088.

Etnier, S. 1974. Great Whaleboat Island. Unpublished paper, S. Harpswell, Maine.

Hill, A. F. 1919. The vascular flora of the Penobscot Bay region, Maine. Proc. Portland Soc. Nat. Hist. **3.**

———. 1923. The vegetation of the Penobscot Bay region, Maine. Proc. Portland Soc. Nat. Hist. **3.**

Hodgdon, A. R. & R. B. Pike. 1969. Floristic comparison of three bird islands in the Gulf of Maine. Rhodora **71:** 510–523.

Hussey, A. M. & K. A. Pankiwskyj. 1975. Preliminary geologic map of southwestern Maine. Maine Geological Survey.

Lauermann, S. D. & C. J. Burk. 1976. The flora of Penikese Island: the centennial collection and its biogeographic implications. Rhodora **78**(816): 707–725.

Lautzenheiser, R. E. 1972. Climates of the states: Maine. U. S. Department of Commerce, Silver Spring, Maryland.

Leavitt, H. W. 1935. A survey of road materials and glacial geology of Maine. Maine Univ. College of Technology Expt. Sta. Bull. No. **30,** Vol. II, Orono, Maine.

MacArthur, R. H., & E. O. Wilson. 1967. The theory of island biogeography. Princeton, New Jersey. Princeton University Press.

McAtee, W. 1916. Plants collected on Matinicus Island, Maine. Rhodora **18:** 29 45.

McCain, J. W. 1975. A vegetational survey of the vascular plants of the Kent Island group, Grand Manan, New Brunswick, Rhodora **77:** 196–210.

———, R. B. Pike, & A. R. Hodgdon. 1973. The vascular flora of Kent Island, Grand Manan, New Brunswick. Rhodora **73:** 311 322.

MOORE, B. & N. TAYLOR. 1927. Vegetation of Mount Desert Island, Maine, and its environment. Brooklyn Botanic Garden Mem. 3.

MORRIS, M., D. E. EVELEIGH, S. C. RIGGS, & W. N. TIFFNEY, JR. 1974. Nitrogen fixation in the bayberry (*Myrica pensylvanica*) and its role in coastal succession. Amer. J. Bot. **61:** 867–870.

NIERING, W. A. & F. E. EGLER. 1955. A shrub community of *Viburnum lentago,* stable for twenty-five years. Ecology **36:** 356–360.

______, & R. H. GOODWIN. 1974. Creation of relatively stable shrublands with herbicides: arresting "succession" on rights-of-way and pastureland. Ecology **55:** 784–795.

O'NEILL, S. D. 1975. The flora of Cuttyhunk Island: the 1974 collection with an analysis of vegetational changes over the past half century. Unpublished M. A. Thesis, Smith College, Northampton, Mass.

POUND, C. E. & F. E. EGLER. 1953. Brush control in southeastern New York: fifteen years of stable tree-less communities. Ecology **34:** 63–73.

POWER, D. M. 1972. Island bird species diversity. Evol. **26:** 451–463.

RAND, E. L. & J. H. REDFIELD. 1894. Flora of Mount Desert Island, Maine. University Press, Cambridge, Mass.

SEYMOUR, F. C. 1969. The flora of New England. Charles E. Tuttle, Co., Rutland, Vermont.

SIMPSON, G. C. 1965. The geography of evolution. Chilton Co., Philadelphia, Pa.

U. S. D. A. SOIL CONSERVATION SERVICE. 1974. Soil Survey, Cumberland County, Maine. In cooperation with the Maine Agr. Expt. Sta.

WESTVELD, M., R. I. ASHMAN, H. I. BALDWIN, R. P. HOLDSWORTH, R. S. JOHNSON, J. H. LAMBERT, H. J. LUTZ, L. SWAIN, & M. STANDISH. 1956. Natural forest vegetation zones of New England. J. Forestry **54:** 332–338.

WHERRY, E. T. 1928. Wild flowers of Mount Desert Island, Maine. Pub. by Garden Club of Mount Desert Island.

WISE, D. A. 1970. The flora of Isle au Haut. Rhodora **72:** 505–532.

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# CLASSIFICATION, SPORES, AND NOMENCLATURE OF THE MARSH FERN

ALICE F. TRYON, ROLLA TRYON, AND FRÉDÉRIC BADRÉ

The Marsh Fern, *Thelypteris palustris,* represent one of the few species complexes in the ferns that occur on all of the large continents, and although absent from Australia, it is known from North Island, New Zealand. Several different taxonomic treatments have been based on diverse patterns of venation, the kinds and abundance of indument, and dimorphism of the leaves. However the diversity of these features has not been adequately reviewed over the broad geographic range of the species. Evidence from the surface and structure of the spore wall, pertinent to the classification, is presented here along with a reassessment of the classification and review of the nomenclature.

## CLASSIFICATION

In the treatment of *Thelypteris palustris* by Fernald (1929), four varieties were proposed: var. *palustris* of Europe, the Caucasus, eastward to the Himalayas and southern China; var. *pubescens* of the northeastern United States and adjacent Canada and east Asia from Kamtchatka, Amur, and Manchuria; var. *Haleana* of the southeastern United States and Bermuda; and var. *squamigera* of southern India, Africa, and northern New Zealand. This last variety of the southern hemisphere has been treated as a species by Ching (1963) and Holttum et al. (1970). The varieties were assessed by A. Tryon (1971) with respect to morphological variation especially of the spores, and that study is extended here. Structural differences in the spore walls, especially the perispore, are evident in SEM studies, but the surface architecture is also apparent with the light microscope.

It is concluded that the Marsh Fern complex consists of two species, one largely of the southern hemisphere and the other, including two varieties, in the northern hemisphere.

## METHODS AND MATERIAL

Whole, abraded, and sectioned spores were examined with an AMR 1000 scanning electron microscope at 20 KV. Specimens were fixed to stubs with doublesided adhesive tape and coated with goldpalladium in a Hummer sputter coater for three minutes, depositing approximately 200 Å of metal. Spores were examined, with the light microscope, fixed in 85% lactic acid for an hour. In addition to the collections cited in the captions other specimens were studied with SEM or light microscope as listed under each of the taxa. Spores were obtained from collections in the Harvard University Herbaria or in the United States National Museum, cited as (US).

**Thelypteris confluens**

Spores of specimens from Africa, New Zealand and South America are echinate (Figs. 1, 3, 4, 5) and mostly larger than those of *T. palustris.* The African material has somewhat denser echinate elements but the irregularly granulate surface is similar to that of spores from Argentina (Figs. 3,4). A lower reticulate formation is not evident but may be obscured early in sporogenesis. The perispore is underlaid by a thick, dense exospore stratum (Fig. 2). In the work on spores of the South African ferns, Welman (1970) recognized *T. confluens* and described the spores as densely subechinate with spinules 1–2.5 $\mu$ long.

The costal scales of the lamina are a conspicuous feature of the leaves distinguishing *T. confluens* from *T. palustris.* In the latter species scales may occur, especially in young leaves, but they usually are caducous. The indusia have abundant trichomes or may be glandular.

*Thelypteris confluens* occurs in Africa, Madagascar, southern India, Burma, Sumatra, New Guinea, New Zealand, and South America. The American material, from northeastern Argentina, was described as *Dryopteris Cabrerae* Weatherby based on *Cabrera 10087.* Resemblance of this species to the Marsh Fern was noted in the original description, and echinate spores were indicated as an unexpected character distinguishing it from other species in the

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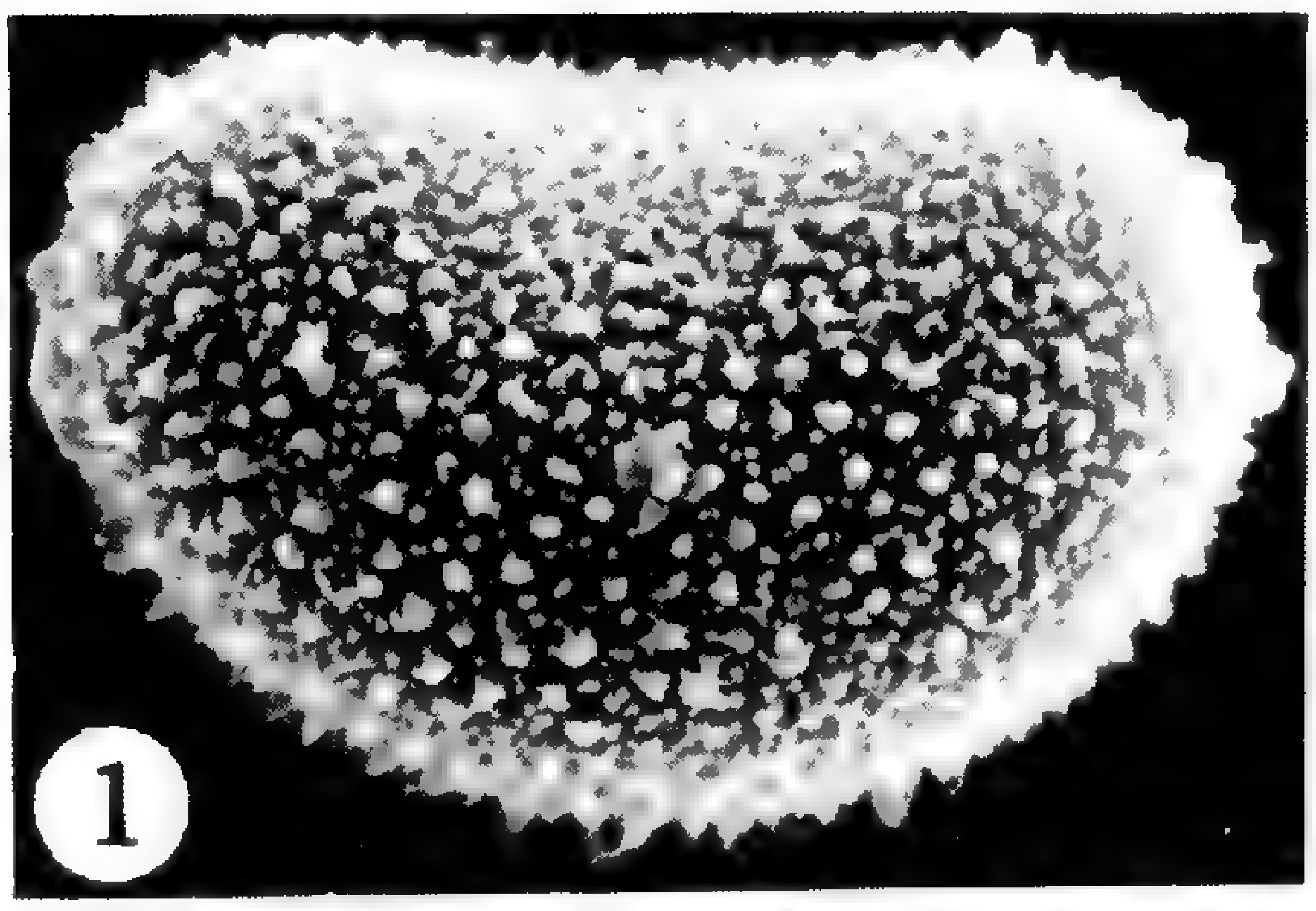
Figures 1–7. *Thelypteris* spores.

1–5. *T. confluens.* 1–3. *Abraham 11,* Natal, Africa. **1.** Densely echinate surface, × 1000. **2.** Wall profile, with eroded echinate perispore above thick exospore, × 10,000. **3.** Surface detail of echinate elements with granulate deposition, × 10,000. 4,5. *Schulz 831,* Chaco, Argentina. **4.** Spores with diffuse echinate elements, × 1000. **5.** Surface detail of echinate elements and granulate deposition, × 10,000.

6,7. *T. palustris* var. *palustris, Ivanova 4297,* Kurgan, West Russia. **6.** Proximal face with laesura at center, surface with projecting loops, × 1000. **7.** Wall profile (below) the spore interior with protoplast fragments at base, surface detail of reticulum (above), × 5000.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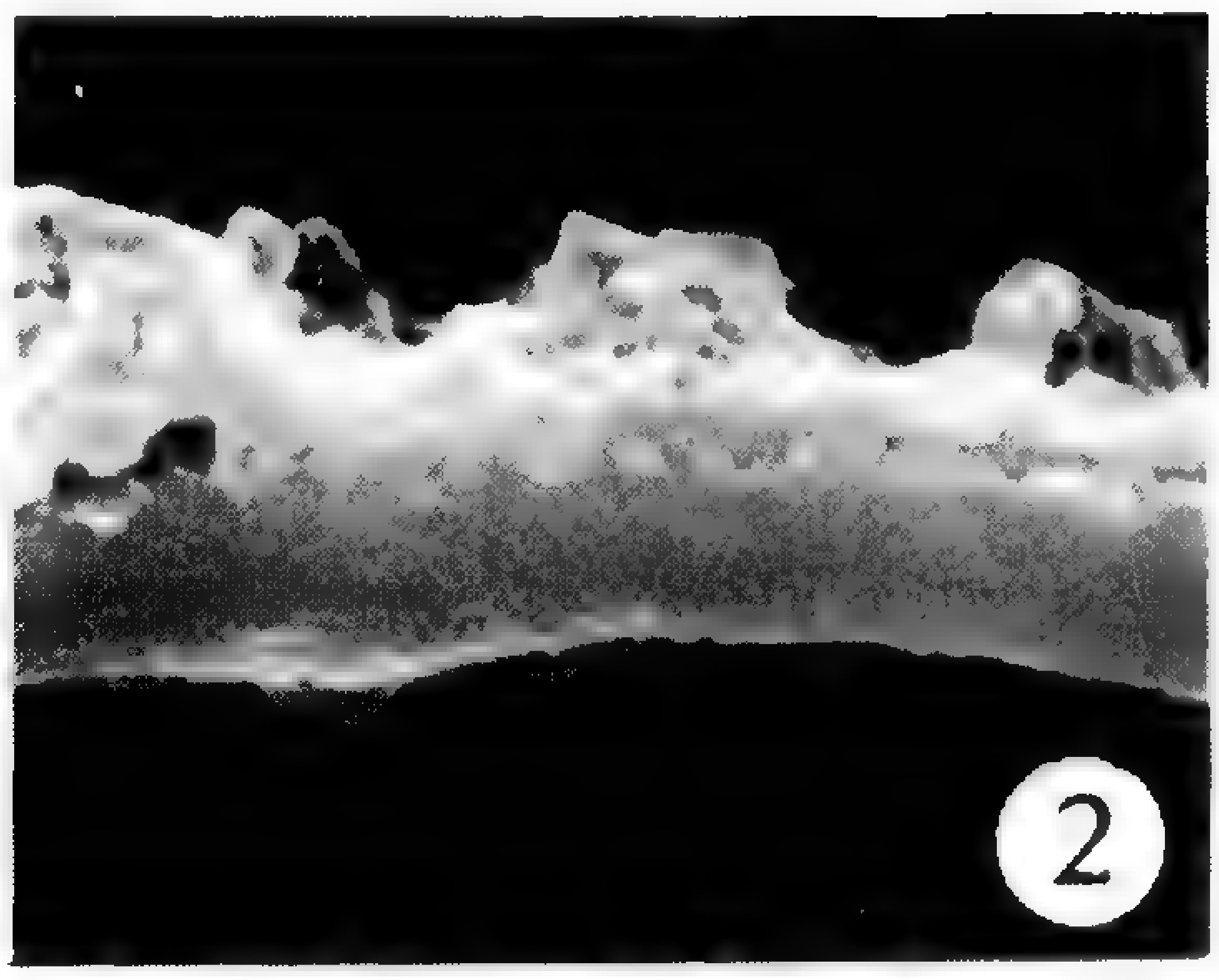
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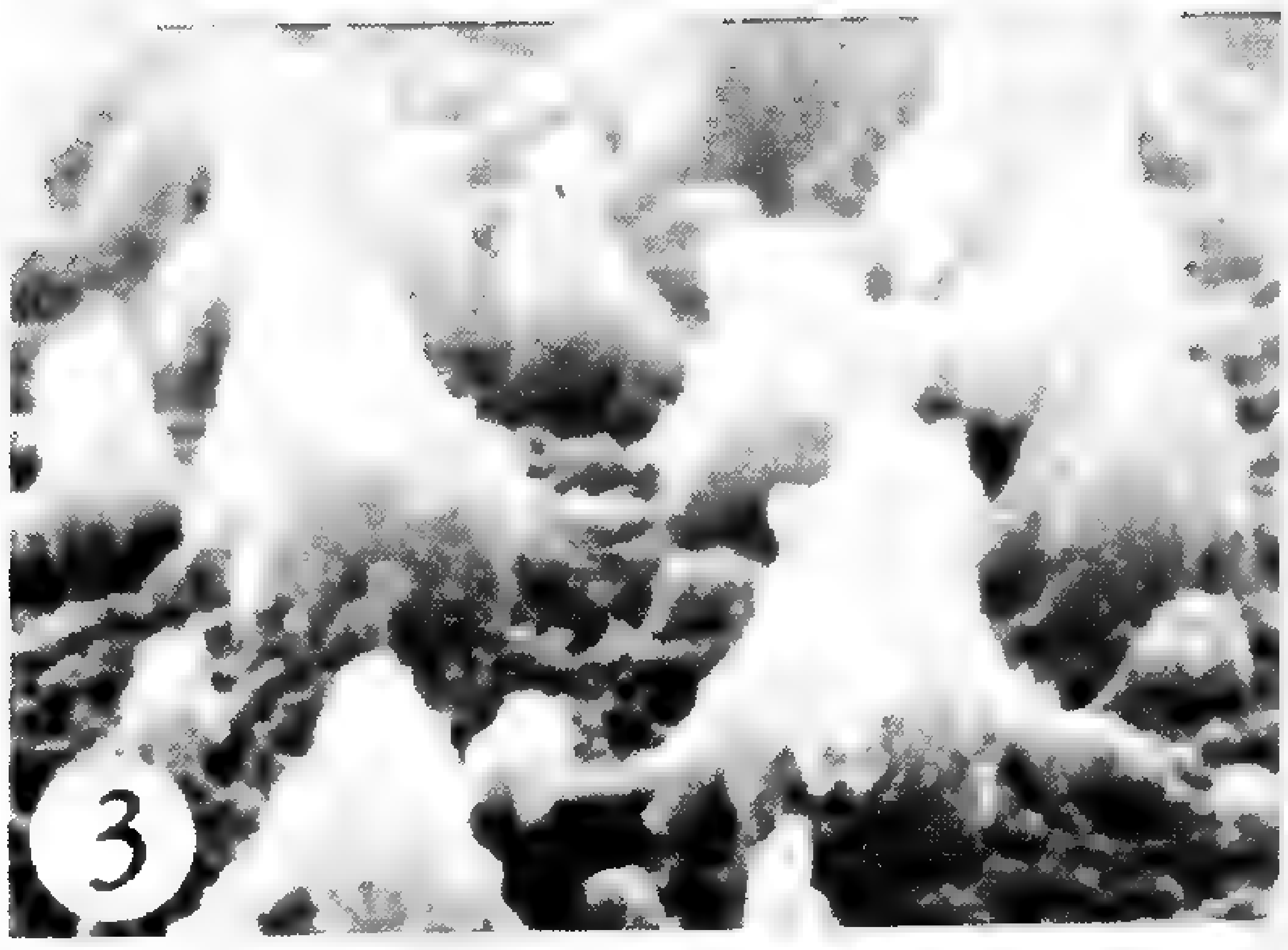
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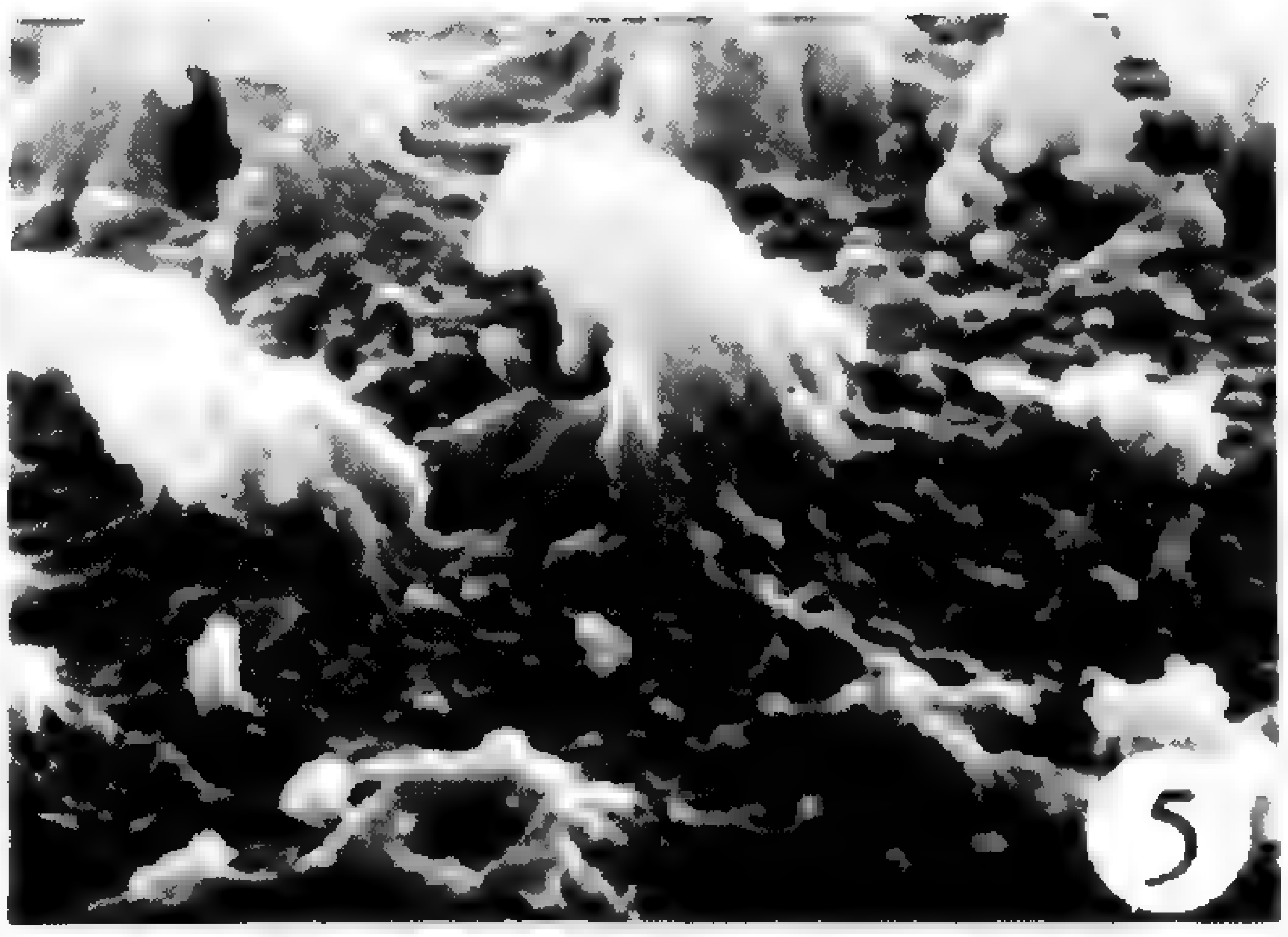
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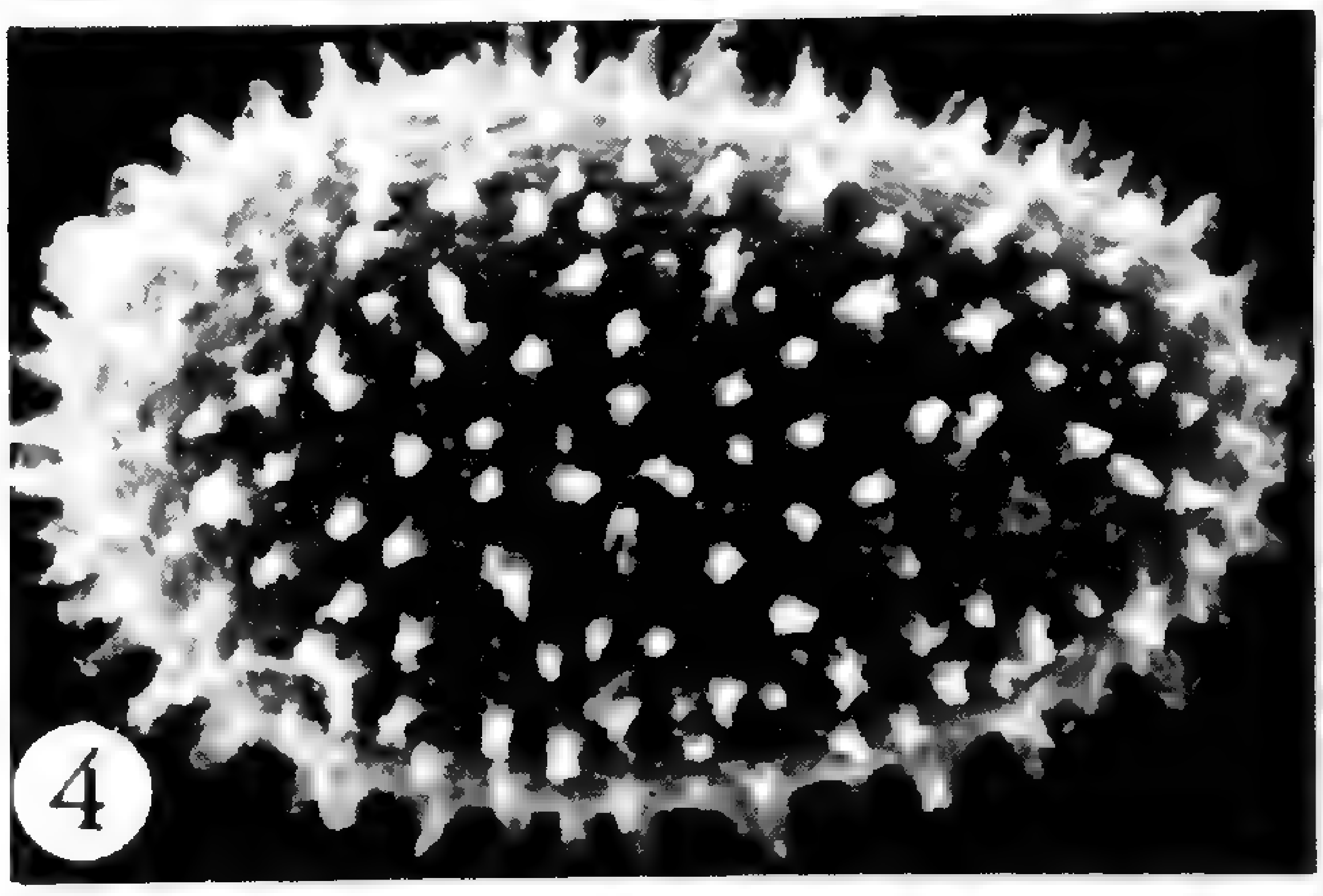
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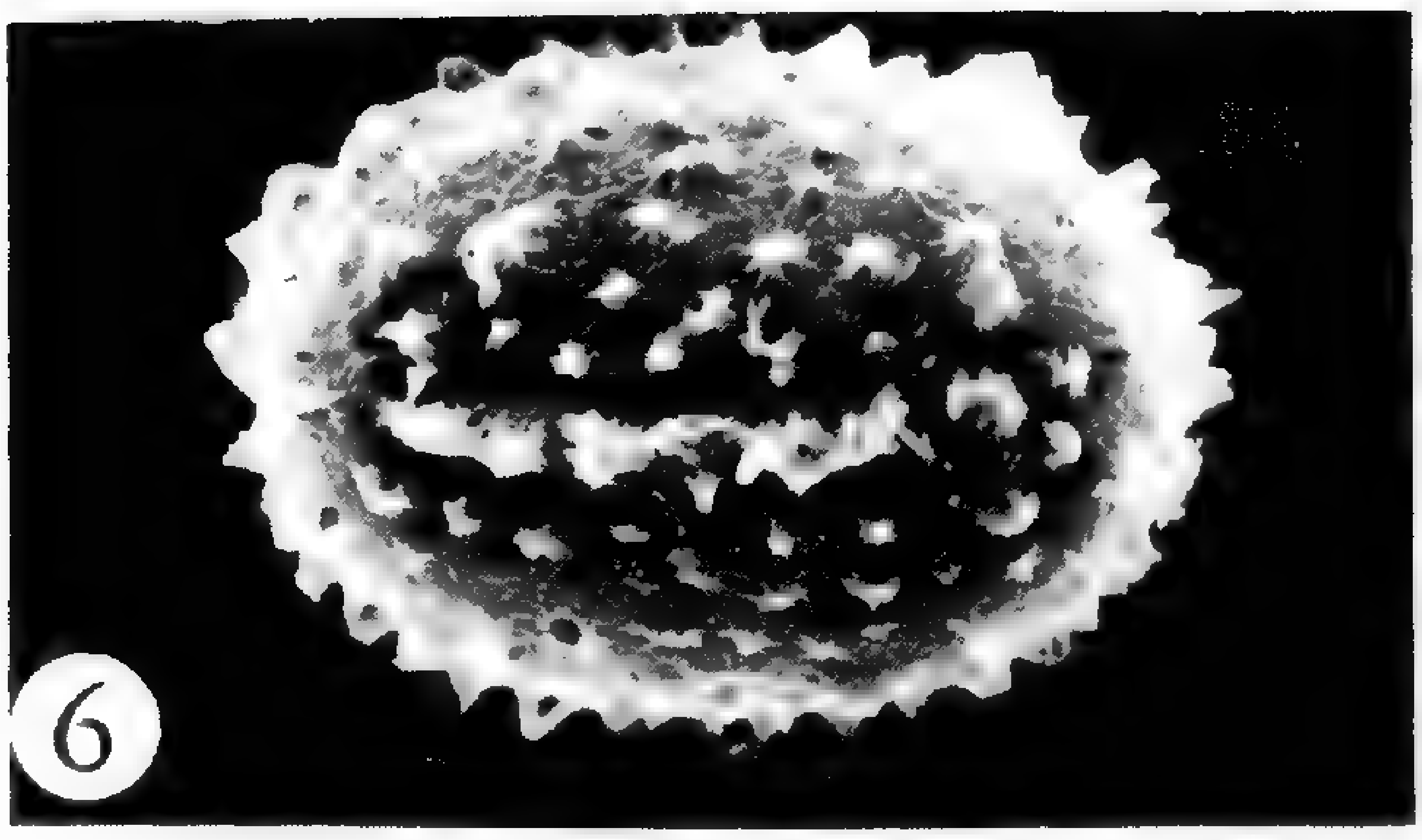
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group of *D. rivularioides.* Recognition of *T. confluens* as a species is reinforced by its austral geographical pattern known in other ferns as well as flowering plants.

Spores examined in additional collections are from: AFRICA. Uganda, *Longfield 65;* Tanganyika, *Drummond & Hemsley 2187;* South Africa, *Abraham 21, Buchanan* 554 (US), *Burchell* 4419, *Taylor 677.* INDIA. Berijam Lake, *Jarrett & Saldanha 17054* (US). ARGENTINA. Buenos Aires, *Cabrera 10087.* NEW ZEALAND. Bay of Plenty, *Kirk; Craig.*

**Thelypteris palustris** var. **palustris**

The spores have a coarsely reticulate perispore, with prominent projecting loops, overlaying a thick exospore (Figs. 6, 7). The reticulate perispore is relatively uniform throughout the range as shown in collections from Honan Province, China (Chang, et al., 1976) as well as those included here from Europe. The wall consists largely of thick exospore below the reticulate perispore as in the wall profile, in the lower part of Fig. 7. The spores from Kashmir were treated under var. *squamigera* (=*T. confluens*) by A. Tryon (1971) but the strongly projecting loops clearly indicate that this belongs with var. *palustris.* Muir & Grant (1971) reported that spores of *T. palustris* treated with ultrasonic probe or acetolysis retained the reticulum but lost the projecting loops. The source of the spores was not given but they doubtless represent var. *palustris.*

Variety *palustris* usually has nearly monomorphic leaves with the veins mostly forked in the fertile leaf and the indusia have glandular trichomes. Plants are most readily distinguished from var. *pubescens* by these characters.

Variety *palustris* occurs in Europe eastward to central Asia, extending to China and south to Kashmir.

Spores examined in additional collections are from: EUROPE. Denmark, *Nielsen & Pedersen 508;* Germany, *Vocke* in 1884; Austria, *Petrack Exsic. 702;* Estonia, *Walter-Calle Exsic. 42.* USSR, Turgai (Kirgiz steppes), *Dubyabskii 1522;* W. Siberia, Tobolsk, *Mameev 597.* ISRAEL. *Eig & Feinbrun 728* (US). INDIA. Kashmir, *Thompson.*

**Thelypteris palustris** var. **pubescens**

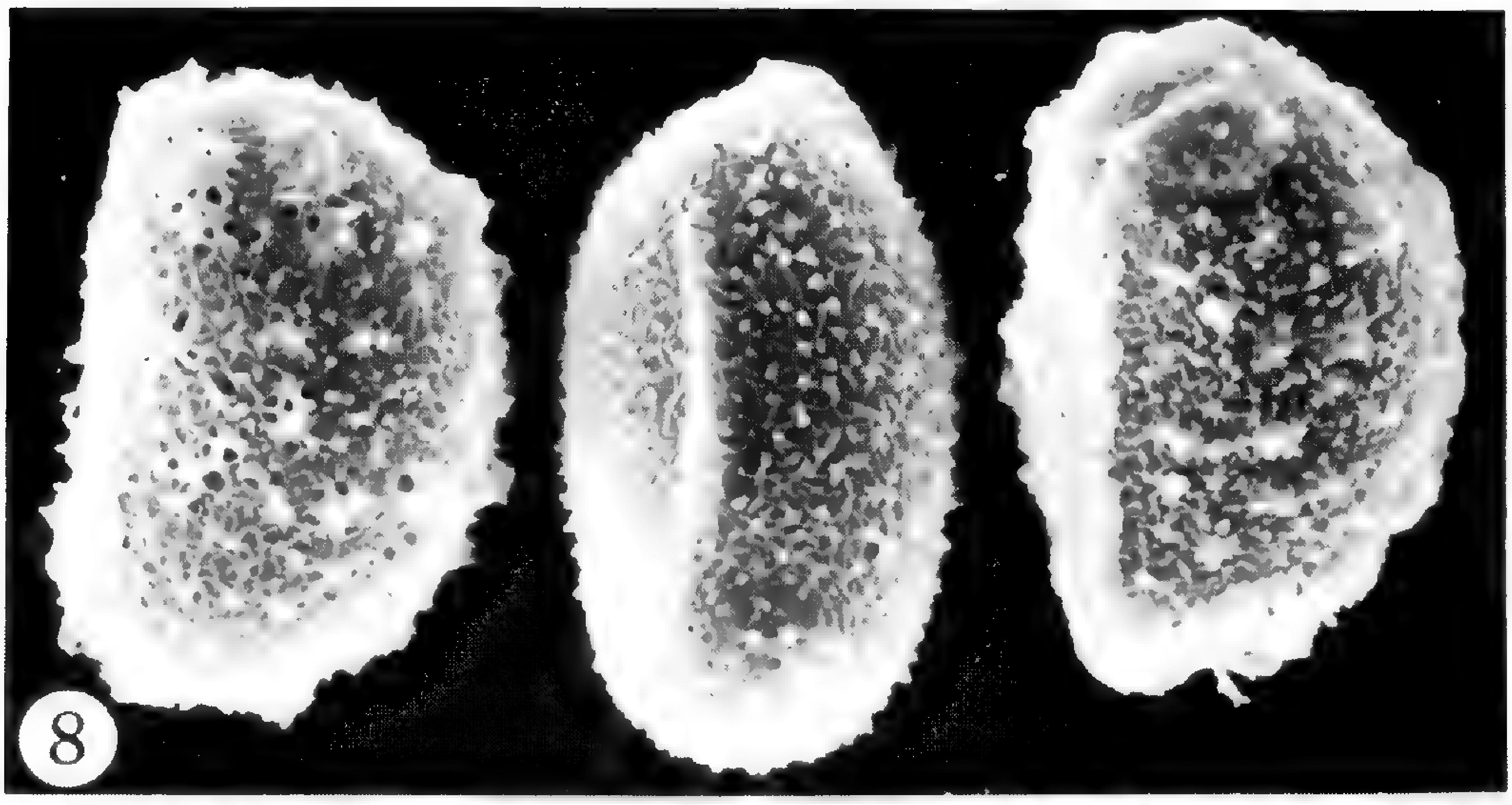
Spores of this variety have a granulate or papillate to irregularly tuberculate or reticulate perispore similar to that of var. *palustris* but without prominent loops. Variation in the surface formation appears to relate to additions in deposition of the perispore. The surface variation in spores of a collection from Iowa (Tryon 1971, Figs. 2–5) is similar to that in three spores shown here from a Massachusetts specimen (Fig. 8). Each spore appears mature but varies in complexity of the surface. The central spore has the thinnest perispore of slender more or less protruding rods that barely cover the laesura. A more complex reticulum has developed on the spore at left. The spore at the right has the most elaborate perispore of dense papillate structure. Spores from Japan have a dense papillate surface but the basal reticulate formation is usually evident (Figs. 10, 11). Spores of collections from the southern United States also have a compact, papillate surface with a somewhat reticulate base (Figs. 12, 13) and the exospore beneath is finely rugose. The profile of a portion of the perispore lifted above the exospore (Fig. 9) shows the relatively thin perispore in this variety.

The leaves of var. *pubescens* are rather dimorphic, mostly with simple veins in the fertile leaves and the indusia are not or rarely glandular. Costal scales are usually absent but may persist in some specimens from the western part of the range in the United States. Material formerly distinguished as var. *Haleana* of the southern United States and Bermuda is included in var. *pubescens*, for this seems to encompass the same kind of variability as that in other plants of the latter variety. Variety *pubescens* occurs in the eastern United States and adjacent Canada, Cuba, Bermuda, Japan, and northeastern Asia.

Spores examined in additional collections are from: UNITED STATES. Maine, *Robinson 723;* Massachusetts, West Cambridge, without collector, in 1894, *A. Tryon 70-18;* Indiana, *R. Tryon 4404;* Iowa, *Pammel 579*; Nebraska, *Clements 293b;* Virginia, *Fernald et al. 4731;* Florida, *Bloomfield & Correll 6163, Lakela et al. 26990*; Louisiana, *Correll & Correll 9177.* CUBA. Habana, *Acuna y Linero 20068* (US). JAPAN. Hondo, *Furse*, in 1957, Honsyo, *Uno 24129.* USSR. Amur, *Maximowicz*, in 1855, E. Siberia, Vladivostock, *Topping 4510.*

## COMENTS

The surface contour of these spores is formed by a relatively thin perispore overlaying a thick perispore. Spores of *Thelypteris confluens*, from widely disjunct areas of the southern hemisphere, are consistently echinate. A surface reticulum is not evident in mature



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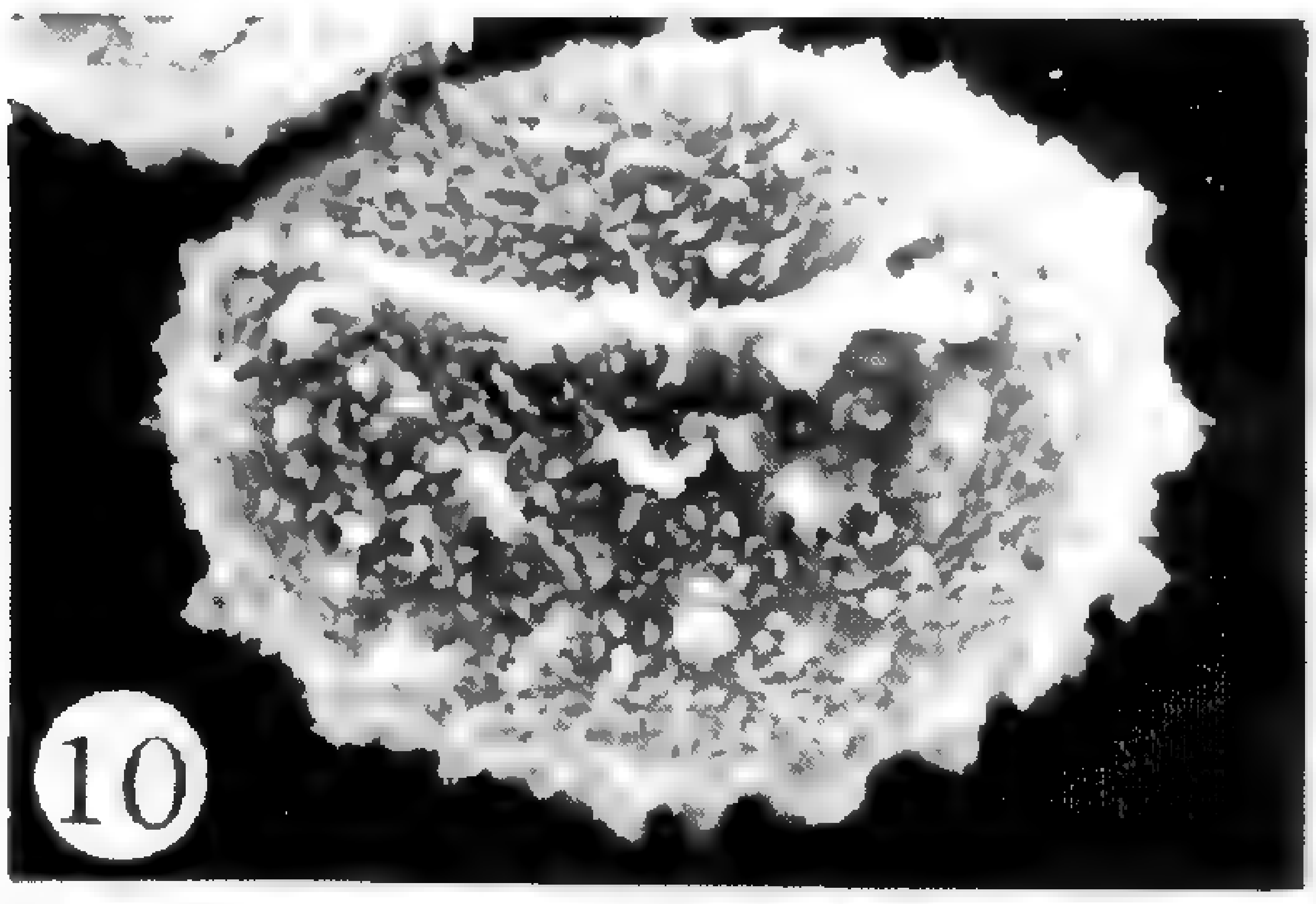

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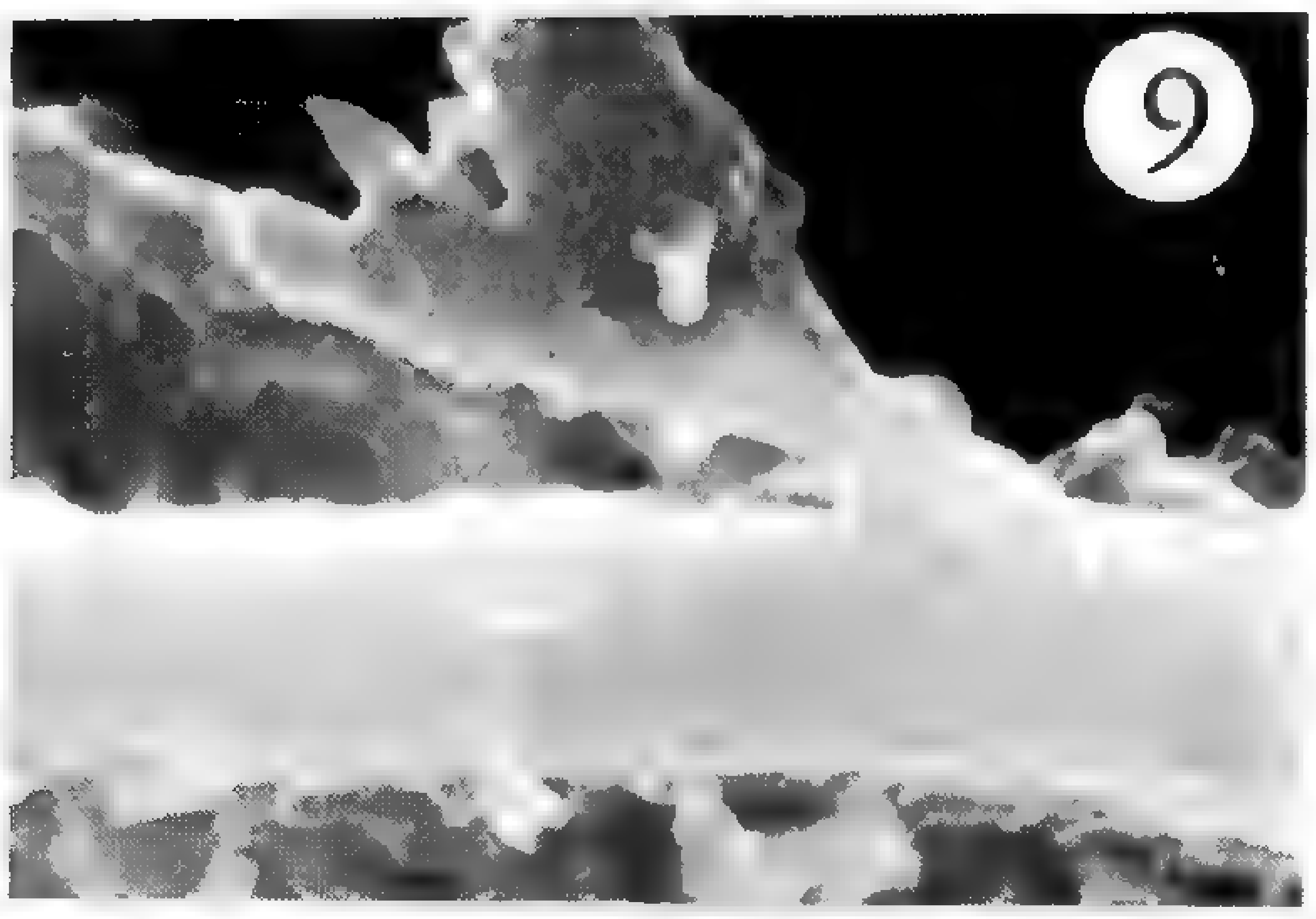

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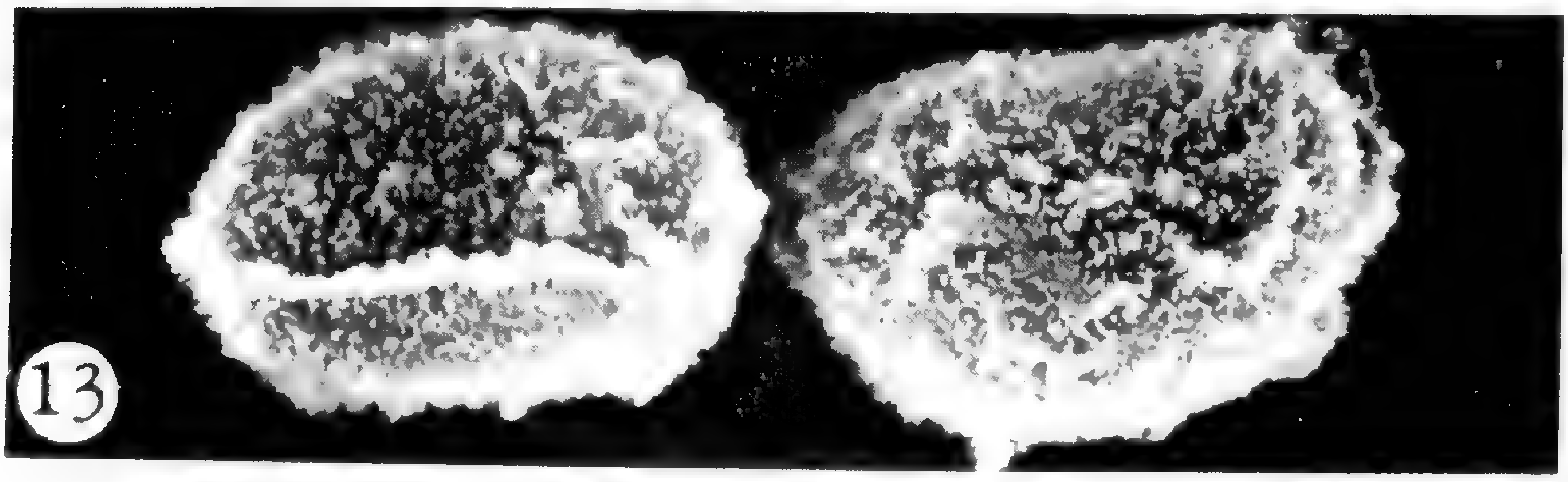

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spores and the echinate elements as well as the basal surface consist of granulate material. Spores of *T. palustris* of the northern hemisphere are characterized by a reticulate surface that may be more or less obscured by additional papillate or granulate deposits. Specimens sampled over the range of var. *palustris,* across Eurasia to northern India, are uniformly reticulate. The considerable variation in spores of var. *pubescens*, especially in North America, appears to relate to the density in granulate deposit on the basal reticulum. Variation in spores of single collections of var. *pubescens* is similar to that within the range of the variety. The larger spore size in *T. confluens* suggests a possible higher ploidy level in the southern hemisphere elements of the complex than in the diploid *T. palustris.* There are no reports of chromosome numbers for *T. confluens*, although *T. palustris* has been widely sampled and is consistently $n = 35$, in Europe, North America, and Japan.

## NOMENCLATURE

*Nephrodium thelypterioides* Michaux has long been cited as a synonym of the New York Fern (= *Thelypteris noveborancensis*), for example, by Eaton (1879) and Christensen (1905). This usage was changed by Morton (1967) in his paper on the ferns of the Michaux Herbarium by the designation of a specimen of the Marsh Fern (= *Thelypteris palustris*) as the holotype of Michaux's name. The typification of Morton was accepted by Holub who adopted the name *Thelypteris thelypterioides* (Michaux) Holub for the northern element of the Marsh Fern. Since D. C. Eaton examined the Michaux collection in 1866 and arrived at a different conclusion, the typification was reinvestigated during a visit to the Museum National d'Histoire Naturelle in 1979.

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Figures 8–13. *Thelypteris palustris* var. *pubescens* spores.

8,9. *Churchill,* in 1915, Berkshire Co., Mass. **8.** Three mature spores, the central one with more or less projecting strands or rods, the laesura vertical near center, the left spore with more complex reticulum, the right spore with papillate surface, the laesura at left, × 1000. **9.** Wall profile with part of perispore lifted above the thick exospore, part of the spore interior with protoplast fragments (below) × 10,000. 10,11. *Serizawa 11041,* Honshu, Japan. **10.** Spore slightly tilted with irregular papillate surface, the laesura horizontal, × 1000. **11.** Detail of papillate surface, × 10,000. 12,13. *Correll & Correll* 9177, Louisiana. **12.** Detail of abraded papillate surface raised above the exospore (at top), with a portion of the lower reticulate perispore structure at right, × 10,000. **13.** Spores with dense papillate surface, proximal face with laesura (left), lateral aspect (right), × 10,000.

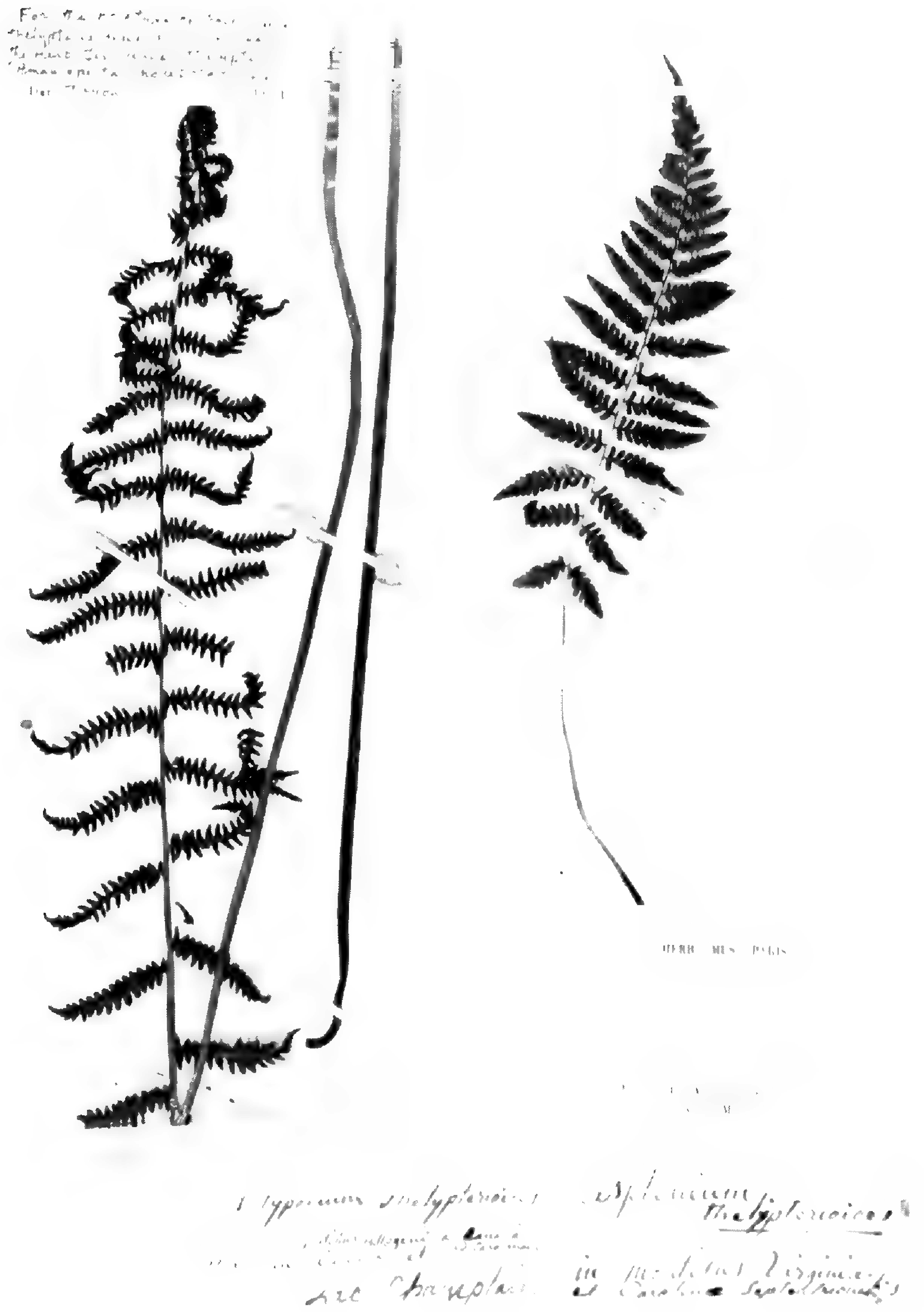

Figure 14. The specimen of "Polypodium thelypterioides Michaux" (left) in the Herbier Michaux (=*Thelypteris palustris*). At right is a sterile leaf of another collection labeled *Asplenium thelypterioides*.

There are three sheets that pertain to the typification of *Nephrodium thelypterioides* Michaux, one in the Herbier Michaux and two in the Herbier General. The specimen in the Herbier Michaux (Fig. 14), designated as the holotype by Morton, is named "Polypodium thelypterioides Michaux" and bears the data "Montibus Allegeni a Canada. Habitat in Canada et ad Carolinum. Lac Champlain." This specimen was annotated by D. C. Eaton in 1866 (Eaton, 1870) as *Aspidium thelypteris* Sw. and is clearly that species (=*Thelypteris palustris*). The locality data provided by Morton is incomplete, and he incorrectly indicated that the specimen is named *Nephrodium thelypterioides.*

In his *Ferns of North America,* D. C. Eaton (1879) cited *Nephrodium thelypterioides* as a synonym of *Aspidium noveboracense* (= *Thelypteris noveboracensis*), rather than of *Aspidium thelypteris.* This indicates that he did not accept the specimen of "Polypodium thelypterioides" that he had examined in the Herbier Michaux as the type of that name. A second sheet in the Herbier Richard and later in the Herbier Drake (Fig. 15) bears a typical Michaux label with the data "Polypodium thelypterioides Michaux. Canada et in montib. Allegenii adusque Carol. montibus." It includes two leaves clearly of different gatherings. The third sheet (Fig. 16) includes two collections; one, two leaves at the left "Amerique Septentrionale, venant de Mr Comte par Boisduval. 1828." and the other, two leaves, at the right, with a note in the handwriting of Bory de St. Vincent: "donne par Richard comme de L'herbier Michaux, des Monts. Alleghani sous le nom de *Nephrodium thelypteroides,* 1808." The Michaux specimens on this sheet are identical to the right leaf on the Herbier Richard sheet and are clearly of the same gathering. They are annotated, without date and in an unidentified script, as *Aspidium noveboracense.* All of these specimens are *Thelypteris noveboracensis.*

It is unfortunate that Morton overlooked these specimens in the general herbarium in his account of the Michaux material and did not recognize that Eaton had studied the specimen in the Herbier Michaux prior to his publication of the Ferns of North America.

The Michaux specimens in the Herbier Richard and the ones given to Bory are properly taken as the holotype of *Nephrodium thelypterioides* Michaux and they have been so annotated by Rolla Tryon. These specimens correspond to the Michaux protologue, especially to the contrast of the new species with the Marsh Fern

Figure 15. The Michaux holotype specimens of "Polypodium thelypterioides Michaux" in the Herbier Richard (=*Thelypteris noveboracensis*).

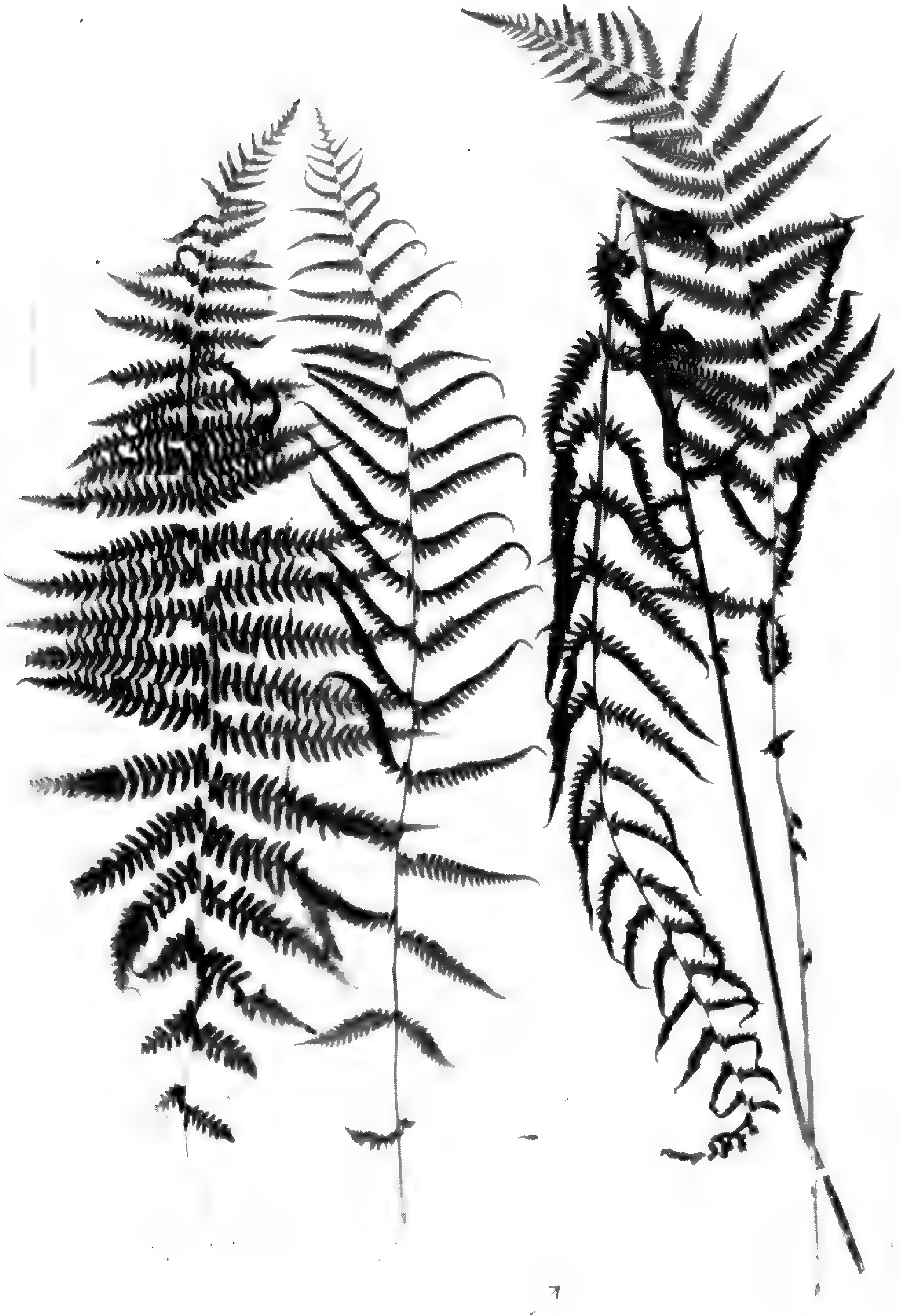

Figure 16. The Michaux holotype specimens of *Nephrodium thelypterioides* (right) given by Richard to Bory, in the Herbier Bory (=*Thelypteris noveboracensis*). At left are two leaves of a later, different collection of the same species.

which was given as "Strongly allied to *Polypodium Thelypteris;* with the sori even at maturity not running together in that way." One of them bears the published name (slightly altered); and they also agree with the identity of the name as established by D. C. Eaton. The role of Richard in the publication of Michaux's Flora Boreali—Americana especially implicates the Herbier Richard in the typification of Michaux names and supports the designation of holotype relating to his herbarium.

The essential nomenclature of the taxa discussed is as follows:

1. **Thelypteris confluens** (Thunb.) Morton, Contrib. U.S. Nat. Herb. **38:** 71. 1967.
   *Pteris confluens* Thunb., Prod. Fl. Cap. 171. 1800.
   *Aspidium thelypteris* var. *squamigerum* Schlect., Adumbr. **23.** 1825.
   *Nephrodium squamulosum* Hook. fil., Fl. N. Zeal. **2:** 39. 1855.
   *Thelypteris palustris* var. *squamigera* (Schlect.) Weath., Contrib Gray Herb. **73:** 40. 1924.
   *Thelypteris squamulosa* (Hook. fil.) Ching, Bull. Fan Mem. Instit. Biol. Bot. **6:** 329. 1936.
   *Dryopteris Cabrerae* Weath., Bol. Soc. Argent. Bot. **3:** 1949.
   *Thelypteris Cabrerae* (Weath.) Abbiatti, Rev. Mus. La Plata (Bot.) **9:** 19. 1958.

2. *Thelypteris palustris Schott,* Gen. Fil. adnot. t. 10. 1834, *nom. nov.* for *Acrostichum thelypteris* L. (*Aspidium thelypteris* (L.) Sw.)

2a. **Thelypteris palustris** var. **palustris**
   *Acrostichum thelypteris* L., Sp. Pl. 1071. 1753.
   *Polypodium pterioides* Lam., Fl. Franc. 1: Meth. Anal. **18.** 1778, *nom. superfl.* for *Acrostichum thelypteris* L.
   *Polypodium palustre* Salisb., Prod. 403. 1796, not Burm. 1768.
   *Aspidium palustre* S. F. Gray, Nat. Arr. Brit. Pl. **2:** 9. 1821, *nom. superfl.* for *Acrostichum thelypteris* L.
   *Thelypteris thelypterioides* ssp. *glabra* Holub, Taxon **21:** 332. 1972.

2b. **Thelypteris palustris** var. **pubescens** (Lawson) Fernald, Rhodora **31:** 34. 1929.

*Lastrea thelypteris* var. *pubescens* Lawson, Edinb. New Philos. Journ. n.s. **19:** 277. 1864, reprint as Syn. Canad. ferns filicoid plts. **21.** 1864; also Trans. Bot. Soc. Edinb. **8:** 38. 1864.

*Thelypteris palustris* var. *Haleana* Fernald, Rhodora **31:** 34. 1929.

*Thelypteris confluens* var. *pubescens* (Lawson) Pringle, Roy. Bot. Gard. (Ontario) Tech. Bull. **4:** 42. 1969.

3. **Thelypteris noveboracensis** (L.) Nieuwl., Amer. Midl. Nat. **1:** 226. 1910.

*Polypodium noveboracense* L., Sp. Pl. 1091. 1753.

*Nephrodium thelypterioides* Michaux, Fl. Bor. -Amer. 267. 1803.

*Thelypteris thelypterioides* (Michaux) Holub, Taxon **21:** 332. 1972.

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## LITERATURE CITED

CHANG Y. L., I. C. HSI, C. T. CHANG, K. C. KAO, N. C. TU, H. C. SUN, and C. C. KUNG. 1976. Sporae Pteridiphytorum Sinicorum. Botanical Institute Academia Sinica, Science Press. Peking. 451 pp., 89 plates.

CHING, R. C. 1963. A reclassification of the family Thelypteridaceae from the Mainland of Asia. Acta Phytotaxonomica Sinica **8:** 289–335.

CHRISTENSEN, C. 1905. Index filicum, p. 451. Hafniae, Hagerup.

EATON, D. C. 1870. Notes on some of the plants in the herbaria of Linné and Michaux. Canad. Nat. **13** (n.s. 5): 24–31.

______1879. Ferns of North America. Vol. 1. Cassino, Salem, Ma. 352 pp.

FERNALD, M. L. 1929. A study of *Thelypteris palustris.* Rhodora **31:** 27–40.

HOLTTUM, R. E., U. SEN, & D. MITRA. 1970. Studies in the family Thelypteridaceae 2. A comparative study of the type species of *Thelypteris* Schmidel, *Cyclosorus* Link, and *Ampelopsis* Kze. Blumea **18:** 195–215.

MORTON, C. V. 1967. The fern herbarium of André Michaux. Amer. Fern Jour. **57:** 166–182.

MUIR, M. D. & P. R. GRANT. 1971. Application of Scanning electron microscope techniques and optical microscopy to the study of sporopollenin, 422–439, *In:* J. Brooks, Ed., Sporopollenin, Proceedings of a Symposium, Geology Dept. Imperial College. Academic Press. London. 718 pp.

TRYON, A. F. 1971. Structure and variation in spores of *Thelypteris palustris.* Rhodora **73:** 443–460.

WELMAN, W. G. 1970. The South African fern spores, *In:* E. M. Van Zinderen Bakker, Ed. South African Pollen Grains and Spores 6. A. A. Balkema. Cape Town. 110 pp.

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# CHROMOSOME NUMBERS IN LEGUMINOSAE FROM THE STATE OF SÃO PAULO, BRAZIL

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Despite the large size of the family and its considerable economic and botanical importance, the Leguminosae continue to be poorly known cytologically. In 1974 Bandel indicated that less than 20% of the species had been studied cytologically, and it is doubtful that the current figure would attain 30%. Further, many of the taxa investigated are known from a single or few reports. Confirmation of these reports is clearly desirable, as are additional reports from different areas of geographical distribution. Although the Leguminosae are well represented in the Brazilian flora, the only significant investigations devoted exclusively to the cytology of Brazilian Legumes are those of Turner and Irwin (1961) who reported chromosome counts for 18 species in 10 genera and of Bandel (1974) who presented counts for 42 species in 25 genera and discussed the evolutionary significance of chromosome numbers in the family. The present paper has the objective of advancing the knowledge of the cytology of the Brazilian Leguminosae and reports chromosome counts for 53 species in 17 genera. Apparent first reports are presented for 19 species.

## MATERIALS AND METHODS

All the material studied during this investigation was collected within the state of São Paulo. The chromosome counts are all meiotic and were obtained through the study of microsporogenesis. Buds were fixed in a solution of 4 parts chloroform: 3 parts ethyl alcohol: 1 part propionic acid. Staining was done with acetocarmine. The chromosome numbers reported are the responsibility of the senior author. Voucher material was identified by the authors with the valuable collaboration of Dr. Graziella Maciel Barroso and Haroldo Cavalcante de Lima. The voucher of *Arachis prostrata* Benth. was identified by Dr. Arturo Burkart. A complete set of voucher material has been deposited in the herbarium of the Jardim Botânica do Rio de Janeiro (RB) and a nearly complete set in the herbarium of the Instituto de Botânica de São Paulo (SP). Darlington and Wylie (1955) and the annual Index to Plant Chromosome Numbers (Moore, 1974) were used as primary reference sources.

When possible, original publications were also consulted. Table 1 lists the species studied and summarizes the results. In all cases voucher numbers are those of the authors.

Table 1. List of material examined for chromosome number

| Species | $n=$ | Município of origin and voucher number |
|---|---|---|
| CAESALPINIODEAE | | |
| **Cassieae** | | |
| *Cassia bicapsularis* L. | 14 | São José do Rio Preto. 48. |
| | 14 | Jaboticabal. 56. |
| *Cassia flexuosa* L. | 8 | São José do Rio Preto. 1. |
| *Cassia javanica* L. | 14 | Piracicaba. Cultivated. 46. |
| *Cassia langsdorfii* Kunth. var. *parvifolia* Irwin | 7 | Botucatu. 29. |
| *Cassia latistipula* Benth. | 7 | São José do Rio Preto. Cultivated. 15. |
| *Cassia multijuga* Rich. | 12 | São José do Rio Preto. Cultivated. 42, 51. |
| | 12 | Amparo. Cultivated? 64. |
| *Cassia occidentalis* L. | 13 | São José do Rio Preto. 35. |
| *Cassia patellaria* DC. | 16 | São José do Rio Preto. 36. |
| *Cassia pilifera* Vog. | 11 | São José do Rio Preto. 53. |
| *Cassia rotundifolia* Pers. | 8 | São José do Rio Preto. 10. |
| *Cassia rugosa* G. Don. | 14 | Corumbataí. 40. |
| | 14 | São José do Rio Preto. 54. |
| *Cassia siamea* Lam. | 14 | Jaboticabal. Cultivated. 58. |
| *Cassia speciosa* Schrad. | 13 | São José do Rio Preto. Cultivated. 37. |
| | 13 | Piracicaba. Cultivated. 45. |
| *Cassia splendida* Vog. | 13 | Botucatu. 33. |
| *Cassia tetraphylla* Desv. var. *mollissima* (Benth.) Irwin | 7 | Corumbataí. 39. |
| *Cassia tetraphylla* Desv. var. *tetraphylla* | 7 | Botucatu. 17. |
| *Cassia tora* L. | 13 | São José do Rio Preto. 5. |
| *Cassia sp.* | 14 | São José do Rio Preto. Cultivated. 13. |
| PAPILIONOIDEAE | | |
| **Aeschynomemeae** | | |
| *Aeschynomene falcata* (Poir.) D.C. | 10 | Botucatu. 18. |
| *Aeschynomene racemosa* Vog. | 10 | São José do Rio Preto. 55. |
| **Crotalarieae** | | |
| *Crotalaria anagyroides* H. B. K. | 8 | São José do Rio Preto. 12. |

| | | |
|---|---|---|
| *Crotalaria depauperata* Mart. | 8 | Botucatu. 34. |
| *Crotalaria foliosa* Benth. | 16 | São José do Rio Preto. 62. |
| *Crotalaria incana* L. | 7 | Botucatu. 32. |
| | 7 | São José do Rio Preto. 49. |
| *Crotalaria laeta* Mart. | 8 | São José do Rio Preto. 11. |
| *Crotalaria maypurensis* H. B.K. | 8 | Botucatu. 25. |
| *Crotalaria spectabilis* Roth. | 8 | Botucatu. 47. |
| *Crotalaria stipularia* Desv. | 16 | São José do Rio Preto. 7. |
| | 16 | São Pedro. 43. |
| *Crotalaria velutina* Benth. | 16 | Botucatu. 30. |
| **Desmodieae** | | |
| *Desmodium platycarpum* Benth. | 11 | São José do Rio Preto. 70. |
| **Diocleae** | | |
| *Canavalia brasiliensis* Mart. ex Benth. | 11 | São José do Rio Preto. Cultivated. 59. |
| **Galactieae** | | |
| *Galactia decumbens* (Benth.) Chad. & Hassl. | 10 | Botucatu. 20. |
| *Galactia eriosematoides* Harms. | 10 | São José do Rio Preto. 74. |
| **Geoffroeeae** | | |
| *Pterodon pubescens* Benth. | 8 | São José do Rio Preto. 60. |
| **Glycineae** | | |
| *Centrosema bracteosum* Benth. | 10 | São José do Rio Preto. 61. |
| *Centrosema brasilianum* (L.) Benth. | 10 | São José do Rio Preto. 2. |
| **Indigofereae** | | |
| *Indigofera suffruticosa* Mill. | 8 | São José do Rio Preto. 8. |
| **Phaseoleae** | | |
| *Phaseolus bracteatus* Nees & Mart. | 11 | São José do Rio Preto. 4. |
| *Phaseolus lathyroides* L. | 11 | São José do Rio Preto. Cultivated. 44. |
| **Pterocarpeae** | | |
| *Machaerium aculeatum* Raddi | 10 | Botucatu. 23. |
| *Tipuana tipu* (Benth.) O.K. | 10 | São José do Rio Preto. Cultivated. 65. |
| **Robinieae** | | |
| *Gliricidia sepium* Steud. | 11 | São José do Rio Preto. Cultivated. 14. |
| **Stylosantheae** | | |
| *Arachis prostrata* Benth. | 20 | São José do Rio Preto. 3. |
| *Stylosanthes guianensis* Sw. | 10 | São José do Rio Preto. 9. |
| *Zornia diphylla* (L.) Pers. | 10 | Botucatu. 22. |
| *Zornia pardina* Mohl. | 10 | Botucatu. 27. |
| *Zornia sp.* | 10 | Corumbataí. 41. |
| *Zornia sp.* | 10 | Corumbataí. 38. |

Table 1 (*continued*)

MIMOSOIDEAE

**Mimoseae**

| | | |
|---|---|---|
| *Mimosa batucatuana* Hoehne | ca. 13 | Pardinho. 26. |
| *Mimosa capillipes* Benth. | 13 | Botucatu. 24. |
| *Mimosa daleoides* Benth. | ca. 52 | Botucatu. 19. |
| *Mimosa lasiocarpa* Benth. | 13 | São José do Rio Preto. 63. |
| *Mimosa macrostachya* (Benth.) Macbr. | 13 | São Pedro. 44. |
| *Mimosa rixosa* Mart. | 13 | Mirassol. 16. |
| | 13 | Botucatu. 31. |

## DISCUSSION

### CAESALPINIOIDEAE

**Cassieae**—The count of $n = 14$ for *Cassia rugosa* is evidently the first report for this species. The following species of *Cassia* are apparently invariable as to chromosome number and the numbers reported here confirm previous reports: *C. bicapsularis* ($n = 14$), *C. flexuosa* ($n = 8$), *C. javanica* ($n = 14$), *C. langsdorffii* ($n = 7$), *C. latistipula* ($n = 7$), *C. multijuga* ($n = 12$), *C. pilifera* ($n = 11$), *C. siamea* ($n = 14$), and *C. tetraphylla* ($n = 7$). *Cassia occidentalis* has been reported several times each as $n = 13$, or $2n = 26$, and $n = 14$, or $2n = 28$. Our material showed $n = 13$. Counts of $n = 16$ and $2n = 32$ and 64 have been reported for *C. patellaria*. We report $n = 16$. *Cassia rotundifolia* has been reported as $n = 8$ and $2n = 14$, 16, and 32. Our report is $n = 8$. *Cassia speciosa* has been reported as $n = 12$ and 13, and $2n = 24$. The present report is $n = 13$. *Cassia splendida*, which we determined as having $n = 13$, has also been reported as having $2n = 26$ and 52. A discussion of basic numbers in the genus *Cassia* is presented by Irwin and Turner (1960).

### PAPILIONOIDEAE

**Aeschynomeneae**—The counts of $n = 10$ for *Aeschynomene falcata* and *A. racemosa* are initial reports for these species. The genus has $x = 10$ with a low incidence of tetraploidy.

**Crotalarieae**—The counts for *Crotalaria depauperata* ($n = 8$), *C. foliosa* ($n = 16$), *C. laeta* ($n = 8$) and *C. velutina* ($n = 16$) constitute initial reports for these species. The counts presented for *C. anagyroides* ($n = 8$), *C. incana* ($n = 7$), *C. maypurensis* ($n = 8$), *C. specta-*

*bilis* ($n = 8$), and *C. stipularia* ($n = 16$) confirm previous reports. The great majority of the species of *Crotalaria* are based on $x = 8$ with tetraploidy being frequent in the genus.

**Desmodieae**—The count of $n = 11$ for *Desmodium platycarpum* is the first report for this species and agrees with the vast majority of previous reports in the genus.

**Diocleae**—The count of $n = 11$ for *Canavalia brasiliensis* is the first report for this species and is consistent with previous reports in the genus, all being based on $x = 11$.

**Galactieae**—The counts of $n = 10$ for *Galactia decumbens* and *G. eriosematoides* constitute the initial reports for these species. The genus has $x = 10$.

**Geoffroeeae**—The count of $n = 8$ for *Pterodon pubescens* is the second report for the species and confirms the first report (Bandel, 1974).

**Glycineae**—The count of $n = 10$ for *Centrosema brasilianum* is the first report for this species. The count for *C. bracteosum* ($n = 10$) confirms the initial report for that species (Bandel, 1974). Reports of $n = 9$, 10, and 11 have been made in the genus.

**Indigofereae**—The count of $n = 8$ for *Indigofera suffruticosa* concurs with several previous reports; however, Shibata (1962) has reported $2n = 32$ from Columbia.

**Phaseoleae**—The counts of $n = 11$ for *Phaseolus bracteatus* and *P. lathyroides* confirm previous reports for these species.

**Pterocarpeae**—A count of $n = 10$ is presented for *Machaerium aculeatum*. A previous count of $n = 8$ is available for this species (Bandel *in* Gurgel and Gurgel, 1969). The only other species reported in the genus, *M. acutifolium* Vog., also has $n = 10$ (Bandel, 1974). The count of $n = 10$ for *Tipuana tipu* confirms a previous report (Atchison, 1951) for this monotypic genus.

**Robinieae**—Previous reports of $2n = 20$ (Atchison, 1951) and $2n = 22$ (Simmonds, 1954; Tixier, 1965) have been published for *Gliricidia sepium* (= *G. maculatum* Benth.). Our count is $n = 11$.

**Stylosantheae**—The count of $n = 20$ for *Arachis prostrata* agrees with a previous report by Husted (1933). Mendes (1947), in reporting $n = 10$ for this species, left some question as to the exact identification of his material. The count of $n = 10$ for *Stylosanthes guianensis* confirms an earlier report for this species cited in Darlington & Wylie (1955) and is consistent with reports for other species of the genus. The count for *Zornia pardina* ($n = 10$) is the first report for this species. The genus has $n = 10$ with polyploidy apparently unreported.

### MIMOSOIDEAE

**Mimoseae**—First reports are made for six species of *Mimosa: M. batucatuana* ($n = c.\ 13$), *M. capillipes* ($n = 13$), *M. daleoides* ($n =$ ca. 52), *M. lasiocarpa* ($n = 13$), *M. macrostachya* ($n = 13$) and *M. rixosa* ($n = 13$). Meiotic chromosomes in *Mimosa* are difficult to study because of the small size of the microsporocytes and the tendency of members of bivalents to separate. The probable count of $n = 52$ for *M. daleoides* is the highest number yet reported in the genus. *Mimosa* has $x = 13$ as its most frequent basic number, and therefore *M. daleoides* is a probable octoploid.

## LITERATURE CITED

ATCHISON, E. 1951. Studies in the Leguminosae. VI. Chromosome numbers among the tropical woody species. Amer. J. Bot. **38:** 538–546.

BANDEL, G. 1974. Chromosome numbers and evolution in the Leguminosae. Caryologia **27:** 17–32.

DARLINGTON, C. D. & A. P. WYLIE. 1955. Chromosome atlas of flowering plants. George Allen and Unwin, London. 519 pp.

GURGEL, J. T. A. & O. A. GURGEL FILHO. 1969. Genética e melhoramento de essências florestais Brasileiras. *In:* Melhoramento e genética. Editora da Universidade de São Paulo, São Paulo. 301 pp.

HUSTED, L. 1933. Cytological studies on the peanut, *Arachis*. I. Chromosome number and morphology. Cytologia **5:** 109–117.

IRWIN, H. S. & B. L. TURNER. 1960. Chromosomal relationships and taxonomic considerations on the genus *Cassia*. Amer. J. Bot. **47:** 309–318.

MENDES, A. J. T. 1947. Estudos citológicos no gênero *Arachis*. Bragantia **7:** 257–267.

MOORE, R. J. (editor). 1974. Index to plant chromosome numbers, 1972. Regnum Veg. **91:** 1–108.

SHIBATA, K. 1962. Estudos citológicos de plantas columbianas silvestres y cultivadas. Jour. Agr. Sci. (Tokyo) **8:** 139–146.

SIMMONDS, N. W. 1954. Chromosome behavior in some tropical plants. Heredity **8:** 139–146.

TIXIER, P. 1965. Données cytologiques sur quelques Legumineuses cultivées ou spontanées du Vietnam et du Laos. Rev. Cytol. Biol. Veg. **28:** 135–155.

TURNER, B. L. & H. S. IRWIN. 1961. Chromosome numbers in some Brazilian Leguminosae. Rhodora **63:** 16–19.

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# EXPERIMENTAL TAXONOMY IN THE GENUS *AMELANCHIER*

## I: A NEW LOOK AT THE CHROMOSOME NUMBERS OF THE *AMELANCHIER* SPECIES GROWING IN THE NORTHEASTERN UNITED STATES

W. Ann Robinson[1] and Carl R. Partanen

Only a limited number of chromosome studies have included the *Amelanchier* species of the northeastern United States. These studies by Moffett (1931), Sax (1931), Cruise (1964), and Löve and Löve (1966) have resulted in conflicting conclusions that have yet to be resolved. Several factors may have contributed to this confusion. Changes in nomenclature and diverging taxonomic opinions could have led to errors in specimen identification. In addition, the formation of diploid gametes and autopolyploidy, not uncommon in the Maloideae, may also occur in *Amelanchier*. Finally the small size of the chromosomes and their multivalent chromosome associations make it difficult to discern with absolute accuracy the number of chromosomes.

The authors are aware of the efforts of our Canadian colleagues, McKay (1973) and Landry (1975), to simplify *Amelanchier* taxonomy by utilizing infraspecific categories. In this paper, however, the taxonomy of Fernald (1950) has been followed since it affords the greater number of species, and knowledge of their chromosome numbers may eventually contribute to a reevaluation of the validity of these species.

### MATERIAL AND METHODS

Chromosome counts were made from buds collected from native plants which had been transplanted to an experimental garden located in Monroeville, Allegheny County, Pennsylvania. The collecting of live material of *Amelanchier* for cultivation was guided by its growth habits. Both stoloniferous and fastigiate forms will tolerate the removal of a portion of the clone or base, with the segregate and parent plants continuing good growth.

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[1] This paper is based on a dissertation completed in the Department of Biological Sciences, University of Pittsburgh, Pa., in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Table I. **Chromosome Numbers of the *Amelanchier* Species of the Northeastern United States**

| Species | Gametic Chromosome Number | Possible Ploidy Level | Locality and Collection Numbers[c] | |
|---|---|---|---|---|
| *A. arborea* (Michx. f.) Fern. | 17[b] | 2*x* | Jefferson Co., W. Va. | R 93 |
| =*A. oblongifolia* (Torr. & Gray) Roemer | 17 | | Fayette Co., Pa. | R108 |
| *A. bartramiana* (Tausch) Roemer | 16[a] | 2*x* | McKean Co., Pa. | R168 |
| *Putative hybrid<br>=*A. bartramiana* × *A. laevis* | 25[a] | 3*x* | Forest Co., Pa. | R167 |
| *A. canadensis* (L.) Medic | 17 | 2*x* | Ocean Co., N.J. | R113 |
| | 17[b] | | Burlington Co., N.J. | R114 |
| | 17 | | Ocean Co., N.J. | R115a |
| | 17 | | Middlesex Co., N.J. | R116 |
| | 17[b] | | Norfolk Co., Mass. | R157 |
| | 17 | | Henrico Co., Virg. | R159 |
| Putative hybrid | 16[a] | 2*x* | Ocean No., N.J. | R115b |
| =*A. canadensis* × *A. laevis* | 17 | | Passaic Co., N.J. | R117 |
| *A. humilis* Wieg. | 33[b] | 4*x* | Monongalia Co., W. Va. | Davis=R132 |
| | 31[b] | 4*x* | Propagated specimen from R132 | R133 |
| | 34[b] | | Penobscot Co., Maine | R148 |

Table 1 (continued)

| | | | | |
|---|---|---|---|---|
| **A. *intermedia* Spach | 17 | 2*x* | Pike Co., Pa. | R119 |
| | 28[b] | 3*x* | Rutland Co., Vt. | R144 |
| *A. laevis* Wieg. | 15[a] | 2*x* | Washington Co., Md. | R109 |
| | 18[b] | 2*x* | Randolph Co., W. Va. | R161b |
| **A. nantucketensis* Bickn. | 34[a] | 4*x* | New London Co., Conn. | R156 |
| **A. obovalis* (Michx.) Ashe | 17 | 2*x* | Lackawanna Co., Pa. | R122a |
| | 24[b] | 3*x* | Lackawanna Co., Pa. | R122b |
| | 25[b] | 3*x* | Luzerne Co., Pa. | R123 |
| *A. sanguinea* (Pursch) D.C. | 20[a] | 3*x* | Pendleton Co., W. Va. | R128b |
| *A. stolonifera* Wieg. | 28[a] | 3*x* | Waldo Co., Maine | R149 |
| **A. wiegandii* Nielsen | 36 | 4*x* | Waldo Co., Maine | R150b |

*Indicates first chromosome report for taxon

[a] Chromosome number determined from a somatic count

[b] Univalents, bivalents, and multivalents observed in meiotic material

[c] Collection numbers preceded by R were made by Robinson

The following procedure for the preparation of the material for cytological examination partly resembles some work of Zielinski and Thompson (1967) with *Pyrus* but contains several modifications. As the time for microsporogenesis approached, from late February through April in southwestern Pennsylvania, daily squashes of fresh material in acetocarmine were made to judge the correct time for proper collection of buds. Collected buds were partially opened and transferred into 0.5% colchicine for approximately three hours. This technique had been noted by Namboodiri (1973) as an aid in the resolution of small chromosomes. The colchicine was washed out with several changes of water. The buds were then fixed in Carnoy's fluid (3 parts absolute ethyl alcohol to 1 part glacial acetic acid) for 24 hours and stored in 70% ethyl alcohol at −4° C. In the slide preparation the anthers were removed from the buds, macerated with a tissue grinder, washed with water, and placed in a 2.0% pectinase solution (Macerase: Calbiochem, San Diego, Calif.) pH 6.0 at 30° C. for two hours. The cells were washed free of pectinase with 50% ethyl alcohol and stained with an alcoholic hydrochloric acid-carmine solution (Snow, 1963). The cells could remain in this solution for a week with no harm, but five days seemed to be sufficient for a good stain. The slides were made semipermanent by squashing the cells in a small amount of 45% acetic acid and mounting in Hoyer's mounting medium (Cunningham, 1972). Camera lucida drawings and photographs were made utilizing an oil-immersion phase contrast system with a Wild M-20 Microscope. Voucher specimens and photographs were deposited in the herbarium of the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CM).

## RESULTS

Chromosome counts were obtained from 25 specimens representing 11 taxa and three putative hybrids. The results are detailed in Table I. With $n = 17$ considered to be the basic chromosome number in the Maloideae, the apparent ploidy level of the specimens is also indicated. To the authors' knowledge those counts preceded by an asterisk are being reported for the first time. Both recent literature and the following surveys of chromosome numbers have been reviewed: Darlington and Wylie (1956), Ornduff (1967–69), Moore (1970–72), and Federov (1969).

Photographic evidence is presented in figures 1–3 for three taxa: *Amelanchier arborea, A. humilis,* and the putative hybrid *A. canadensis* × *A. laevis.* The remaining counts can be substantiated from photographs in Robinson (1978) and photographs accompanying the voucher specimens.

As the specimens listed in Table I grew in the experimental garden, routine morphological observations were made. Except for *Amelanchier bartramiana* with its distinctive single or few flowered raceme, the specimens appeared to fall into two morphological complexes. The features of these complexes are detailed in Table II. This division, in part, resembles an earlier attempt by Blanchard (1907) to divide *Amelanchier* taxa into two classes.

If one accepts that a taxon does not have to fulfill every single criterion to be a member of a complex, those growing in the northeastern United States could be divided as follows:

Canadensis complex: *Amelanchier arborea, A. canadensis, A. intermedia, A. laevis,* putative hybrid *A. canadensis* × *A. laevis.*

Sanguinea complex: *A. humilis, A. nantucketensis, A. obovalis, A. sanguinea, A. stolonifera,* and *A. wiegandii.*

In our observations the morphological traits appeared to be correlated with a change in ploidy level, the Canadensis complex representing diploid taxa and the Sanguinea complex triploid and tetraploid taxa. The only taxa observed to be exceptions to this hypothesis were *A. intermedia* and *A. obovalis,* in which both diploid and triploid specimens have been identified. Both of these taxa have been noted for their marked variability (Wiegand, 1920; Fernald, 1941). Their origins may be the result of interspecific hybridizations between the two complexes. Additional breeding studies are presently being conducted to confirm this hypothesis.

It should be noted that only one specimen each of *Amelanchier sanguinea* and *A. stolonifera* has been cytologically examined in this study. Each has been identified as a triploid, but more specimens should be examined before the chromosome status of these taxa can be established.

Table II. **Morphological Features of the Sanguinea and Canadensis complexes**

| Characteristic | Sanguinea complex | Canadensis complex |
|---|---|---|
| winter bud color[a] | maroon | russet brown |
| flexion of sepals | sepals recurving from middle, giving calyx plus floral cup urceolate appearance | sepals not recurving from middle |
| flexion of flowering raceme | erect, resembling miniature candelabrum | flexion of raceme various |
| average $\frac{\text{length}}{\text{width}}$ mature leaves[b] | =or less than 1.5 | greater than 1.5 |
| top of ovary[b] | densely appressed pilosity | glabrous to varying amts. of pilosity |
| shape of fruit | pear shaped | round |
| anthesis | 3–4 days later than Canadensis complex | 3–4 days earlier than Sanguinea complex |

[a] Color observed was the darkest portion in the body of the bud scales. Color Harmony Manual, Container Corp. of Am., 1958.
Maroon: 7pi, 71/2pi, 71/2pg, 8pi
russet brown: 4pi, 4pg, 5pg, 5pi

[b] Additional data can be found in Robinson (1971).

Since the work of Sax (1931), there had been no substantiation of diploid specimens of *Amelanchier* from North America prior to this study, although Favarger and Correvon (1967) identified a diploid race of the common *Amelanchier* of Europe, *Amelanchier ovalis* Medikus. The evidence for diploid, triploid, and tetraploid specimens of *Amelanchier* helps to explain the variation in this genus. The amazing potential for variation and propagation in this genus makes the taxonomic confusion quite understandable. We feel that any revision of *Amelanchier* taxonomy would be premature until further chromosome and breeding studies have been conducted. The present studies will be extended beyond a regional basis and hopefully will include a fuller complement of *Amelanchier* species. In this regard the senior author (Dr. W. Ann Robinson, 4264 Northern Pike, Monroeville, Pa. 15146) would be most pleased to receive any semi-dried fruit from documented sources with the possibility of propagation of the taxa.

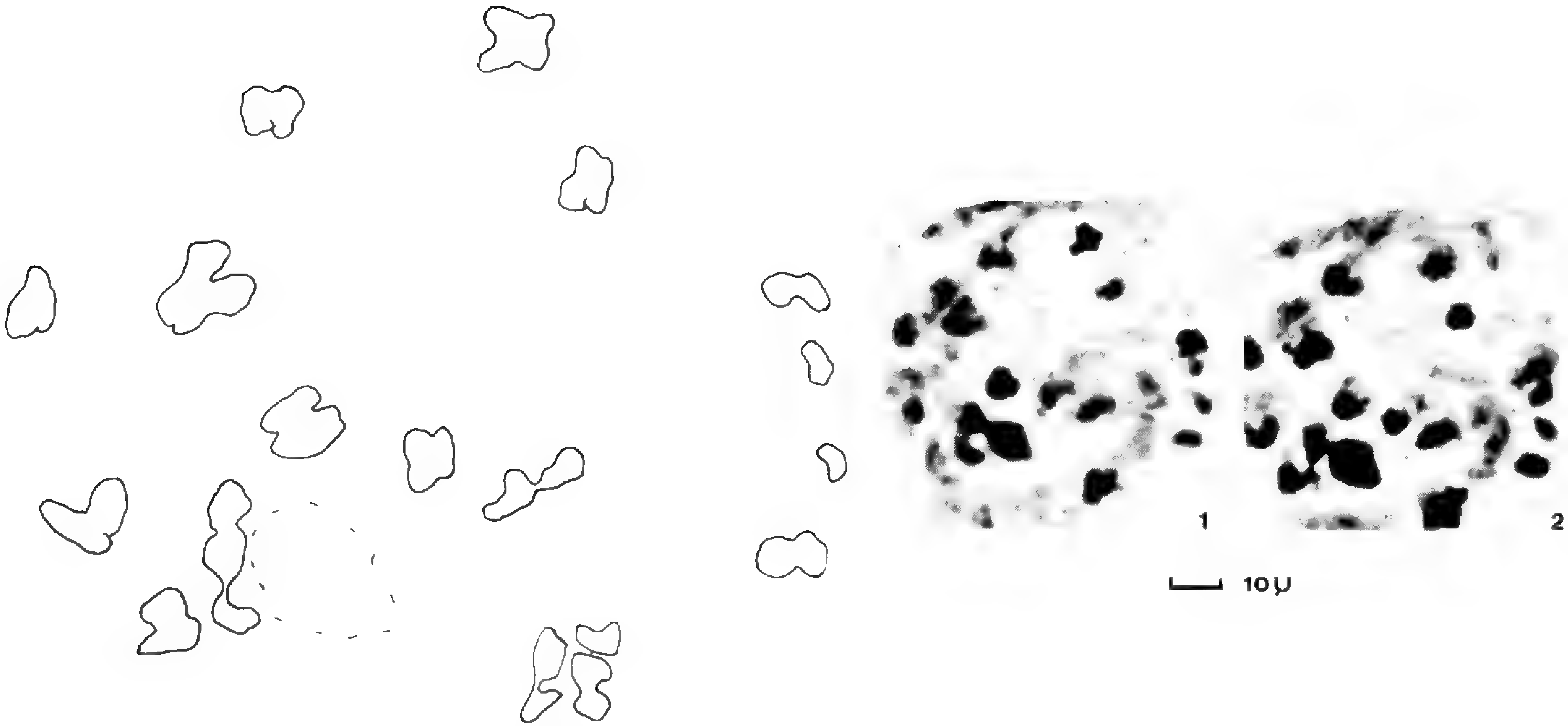

Figure 1. Camera lucida drawing (not to scale) and optical sections of diakinesis from microsporogenesis in *Amelanchier arborea*, specimen *R93*. Dashed line indicates nucleolus. $2_{I}$, $13_{II}$, $2_{III}$.

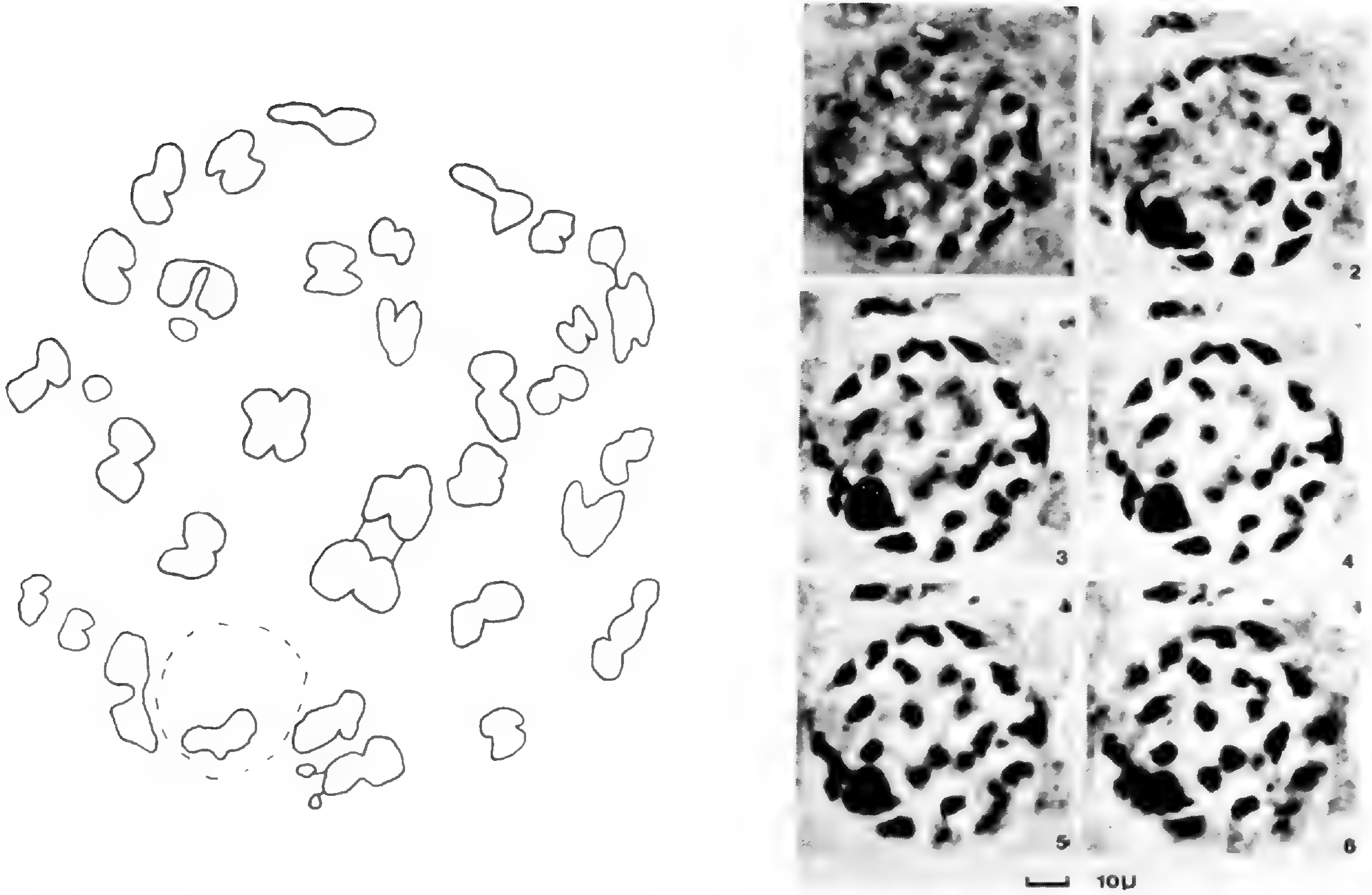

Figure 2. Camera lucida drawing (not to scale) and optical sections of diakinesis from microsporogenesis in *Amelanchier humilis*, specimen *R148*. Dashed line indicates nucleolus. $2_{I}$, $28_{II}$, $2_{III}$, $1_{IV}$.

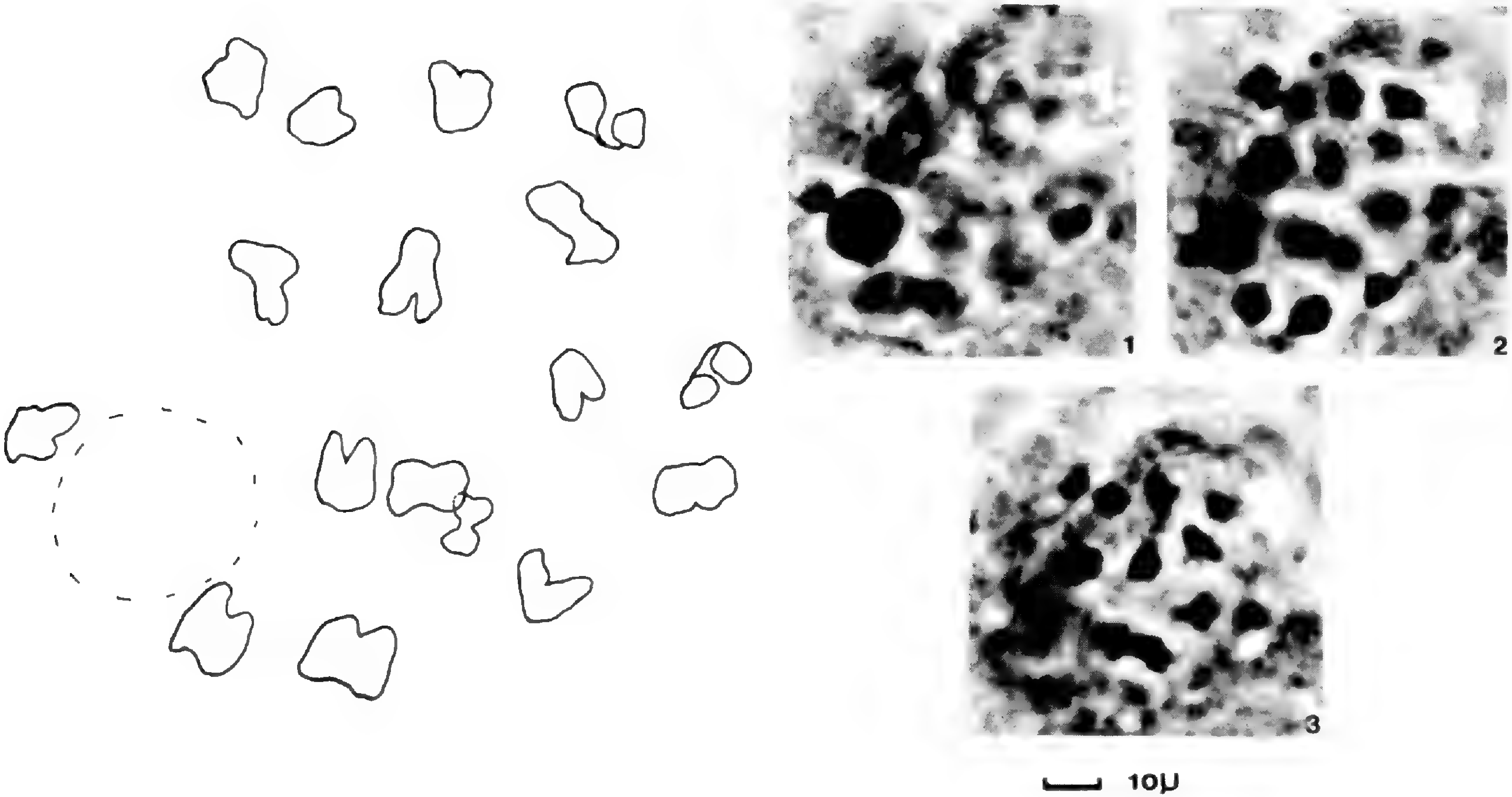

Figure 3. Camera lucida drawing (not to scale) and optical sections of diakinesis from microsporogenesis in the putative hybrid *Amelanchier canadensis* × *A. laevis*, specimen *R117*. Dashed line indicates nucleolus.

## BIBLIOGRAPHY

BLANCHARD, W. H. 1907. Our eastern shadwoods. Torreya **7:** 97–102.

CRUISE, J. E. 1964. Studies of natural hybrids in *Amelanchier.* Canad. J. Bot. **42:** 651–663.

CUNNINGHAM, J. H. 1972. A miracle mounting fluid for permanent whole-mounts of microfungi. Mycologia **64:** 906–911.

DARLINGTON, D. C. AND A. P. WYLIE. 1956. Chromosome atlas of flowering plants. George Allen and Unwin Ltd., London.

FAVARGER, C. AND CORREVON, P. 1967. Mise en évidence de "races chromosomiques" chez l'*Amélanchier.* Bull. Soc. Neuchâteloise Sci. Nat. **90:** 215–218.

FEDOROV, A. ed. 1969. Chromosome Numbers of Flowering Plants. Acad. of Science U.S.S.R., Komarov Bot. Inst., Leningrad, U.S.S.R.

FERNALD, M. L. 1941. Century of additions to flora of Virginia. Rhodora **43:** 559–630.

———. 1950. Gray's Manual of Botany. 8th ed. American Book Co., N.Y.

LANDRY, P. 1975. Le concept d'espèce et la taxinomie du genre *Amelanchier* (Rosacées). Bull. Soc. Bot. France **122:** 243–252.

LÖVE, A. AND LÖVE, D. 1966. Cytotaxonomy of the alpine vascular plants of Mt. Washington. Univ. Colorado Studies, Ser. Biol. **24:** 1–74.

MCKAY, S. M. 1973. A biosystematic study of the genus *Amelanchier* in Ontario. Master of Science thesis, University of Toronto, IV+255 pp.

MOFFETT, A. A. 1931. The chromosome constitution of the Pomoideae. Proc. Roy. Soc. London B. **108:** 426–446.

MOORE, R. J. ed. 1970. Index to plant chromosome numbers for 1968. Regnum Veg. **68:** 1–115.

———. 1971. Index to plant chromosome numbers for 1969. Regnum Veg. **77:** 1–112.

———. 1972. Index to plant chromosome numbers for 1970. Regnum Veg. **84:** 1–134.

NAMBOODIRI, A. N. 1973. Colchicine pretreatment and maceration for improved squashes of Dipterocarpaceae. Stain Technol. **48:** 98–100.

ORNDUFF, R. ed. 1967. Index to plant chromosome numbers for 1965. Regnum Veg. **50:** 1–128.

———. 1968. Index to plant chromosome numbers for 1966. Regnum Veg. **55:** 1–126.

———. 1969. Index to plant chromosome numbers for 1967. Regnum Veg. **59:** 1–129.

ROBINSON, W. A. 1971. The genus *Amelanchier* in the state of West Virginia. Master of Science thesis, West Virginia University, Morgantown.

———. 1978. Experimental taxonomy in the genus *Amelanchier.* Ph.D. dissertation, University of Pittsburgh, X+208 pp.

SAX, K. 1931. The origin and relationships of the Pomoideae. J. Arnold Arb. **12:** 3–22.

SNOW, R. 1963. Alcoholic hydrochloric acid-carmine as a stain for chromosomes in squash preparations. Stain Technol. **38:** 9–13.

WIEGAND, K. M. 1920. Additional notes on *Amelanchier.* Rhodora **22:** 146–151.

ZIELINSKI, Q. B. AND THOMPSON, M. M. 1967. Speciation in *Pyrus:* chromosome number and meiotic behavior. Bot. Gaz. (Crawfordsville) **128:** 109–112.

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# THE DELIMITATION OF ARENARIA (CARYOPHYLLACEAE) AND RELATED GENERA IN NORTH AMERICA, WITH 11 NEW COMBINATIONS IN MINUARTIA

J. McNeill

Throughout this century most North American botanists have followed Fernald (1919) in adopting a very broad circumscription of *Arenaria* L. (Caryophyllaceae), whereas botanists in other parts of the world have almost invariably recognised a number of genera of which five (*Arenaria, Moehringia* L., *Minuartia* L., *Honckenya*[1] Ehrh., and *Wilhelmsia* Reichenb.) are represented in North America. This narrower generic concept has been adopted not only by monographers of the genera (e.g. *Arenaria:* Williams 1898, *Minuartia:* Mattfeld 1922b, *Honckenya:* Pobedimova 1960) but also in the *Pflanzenfamilien* (Pax & Hoffman, 1934) and in the major Eurasian floristic works (Shishkin, 1936; Walters, 1964). The characters distinguishing the segregate genera are outlined in McNeill (1962), who also analyses the criteria for generic delimitation.

Two groups of genera exist. In one the capsule opens by as many valves as there are styles, whereas in the other capsule dehiscence is by twice as many valves or teeth as styles. The first group comprises the large genus *Minuartia* and the maritime and riparian genera *Honckenya* and *Wilhelmsia* each of which contains a single species or species complex. These genera are referred to the subtribe Sabulininae along with others that show similar capsule dehiscence such as *Sagina.* The other group resembles *Stellaria* and *Cerastium* in capsule dehiscence and is included with them in the subtribe Stellariinae. This group consists of *Arenaria* itself and the predominantly European *Moehringia* which is distinguished by its appendaged ('strophiolate') seeds.

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[1] Manitz (1975) and Rauschert (1977) have pointed out that in the long-overlooked original publication of this name Ehrhart (1783) used the spelling *Honckenya* although in 1778, in a republication of the name (hitherto considered the original publication), he altered the spelling to *Honkenya.* My examination of these publications confirms Rauschert's conclusions: Ehrhart in 1783 named *Honckenya* "in honorem nostri meritissimi Dom. *Honckeny,* Auctoris Florae Germanicae"; as this is the usual spelling of G. A. Honckeny, no typographic or orthographic error is involved and Ehrhart's change in the spelling five years later must be treated as an orthographic error. (Stafleu et al., 1978: Art 73.1).

An increasing number of taxonomic treatments of North American species are adopting some or all of these genera (e.g. Nannfeldt, 1954; Hultén, 1958, 1967, 1968, 1971 & 1973; Löve & Löve, 1965; Weber, 1967; Löve et al., 1971; McCormick et al., 1971; McNeill & Bassett, 1974; Shetler & Skoog, 1978; and Porsild & Cody, 1980). These include two important floristic works (Hultén's *Flora of Alaska* and Weber's *Rocky Mountain Flora*), and this has led to considerable confusion in uncritical compiling of species lists for North America. The purpose of this paper is to clarify generic delimitation so far as the North American species are concerned and to publish the new combinations required for forthcoming check-lists of the vascular plants of North America north of Mexico (Biota of North America Committee) and of the United States and its territories in the Carribean area (U.S. Soil Conservation Service).

Despite the confusion that exists, the problem is not one of generic circumscription but the much simpler matter of rank. It has been complicated, however, by the nomenclatural history of the genus that is correctly called *Minuartia*. Until the end of the nineteenth century this was generally known as *Alsine* L. (a name correctly typified by *Stellaria media* (L.) Vill.). Of those American botanists in the early part of this century who did recognise the genus, only Farwell (1919) and House (1921) used the name *Minuartia*. Small (1903, 1933) and Rydberg (1923, 1932) first called it *Alsinopsis* Small then *Sabulina* Reichenb., ignoring *Minuartia* and using *Alsine* for *Stellaria* (except Rydberg, 1932).

Fernald's (1919) analysis of the generic delimitation of *Arenaria* is somewhat superficial and in some places inaccurate. His claims that the capsule dehiscence character is both difficult to determine and separates closely related species are false. As Mattfeld (1922a) and McNeill (1962) note, the incipient lines of dehiscence are visible even in the immature ovary and no case of between species affinity running across generic boundaries drawn on the basis of this character is known in the Alsinoideae (unlike the Silenoideae, cf. McNeill, 1978). The one specific example given by Fernald, that of *A. paludicola* Robinson, is the result of erroneous observation of the capsule dehiscence in this species, a point already noted by Briquet (1911). Fernald's other criticisms are either of characters that are not in fact used to discriminate the genera or else represent assumptions of affinity based on superficial resemblance in habit, parallel-ing that between *Arenaria* and *Gypsophila* (Silenoideae) or even *Phlox* in the Polemoniaceae.

Maguire (1951) in his conspectus of the species of *Arenaria* (*sensu latissimo*) in America north of Mexico essentially follows Fernald, even to his mistake over *A. paludicola,* and admits to not having attempted detailed justification of his generic limits. Nevertheless because the disagreement is one of rank, four of the five genera are identifiable in the sectional classification that Maguire uses. The fifth, *Honckenya*, is excluded by Maguire, presumably because he did regard it as a distinct genus. *Arenaria* comprises his Sections *Euthalia* (= *Arenaria*), *Leiosperma* and *Pentadenaria* (species 1–19 & 36); *Moehringia* is Section *Moehringia* (species 20–21); *Wilhelmsia* is Section *Merckia* (species 22) and *Minuartia* is his "Section *Alsine*" (species 23–35 & 37–41) with *A. paludicola* (species number 36) transferred to *Arenaria* subgenus *Leiosperma* (see McNeill, 1962). Maguire's treatment of the species is in some need of revision (cf. Hickman, 1972; McNeill, in prep.) but it still serves as a useful synopsis of these genera in North America.

The desirability of discriminating *Minuartia* from *Arenaria* is not in doubt. The status of the other genera is, however, more debatable. *Honckenya* and *Wilhelmsia* are clearly related to *Minuartia* and although readily distinguishable are assigned generic rank largely because of their distinct habit and other features, such as large seeds, that are probably associated with their specialised maritime or riparian habitats. *Moehringia* is a small cohesive genus of about 25 species almost all in Europe. It has been traditionally kept separate from *Arenaria* but appears scarcely more distinct than some of the subgenera of *Arenaria* are from each other. Although the two North American species could well be included in *Arenaria,* from a world viewpoint it seems best to maintain the genus at least until its possible relationship with *Arenaria* Subgenus *Leiosperma* is clarified (cf. McNeill, 1962).

In recent years some subdivision of both *Arenaria* and *Minuartia* has been proposed. Ikonnikov (1973) has raised *Arenaria* Subgenus *Eremogone* (= Section *Pentadenaria* in Maguire, 1951) to generic rank (as *Eremogone* Fenzl) and Löve and Löve (1974, 1975a, 1975b and *in* Löve & Kjellqvist, 1974) adopt this genus and treat most of Mattfeld's (1922b) and McNeill's (1962) sections of *Minuartia* as genera as well as two of McNeill's sections of *Arenaria* subgenus

*Arenaria.* The latter are not represented in North America but five of the former are: *Alsinanthe* (Fenzl) Reichenb., *Porsildia* Löve et Löve, *Wierzbickia* Reichenb., *Lidia* Löve et Löve, and *Tryphane* (Fenzl) Reichenb. There is some argument on morphological grounds for the recognition of *Eremogone* but in segregating so many genera Löve and Löve seem to have been unduly influenced by differences in chromosome base number. The genera that they recognise are rather small groups of related species, better treated as sections either of the morphologically homogeneous *Minuartia* or of the equally homogeneous *Arenaria* subgenus *Arenaria.*

Because of the slow adoption in North America of the correct generic name *Minuartia* the following new combinations in that genus are required. Along with the usual convention of ≡ for homotypic synonyms and = for heterotypic ones, I am following Greuter (1973) in using — for misidentifications.

### NEW COMBINATIONS IN MINUARTIA

**Minuartia cumberlandensis** (Wofford et Kral) McNeill, *comb. nov.*
≡ *Arenaria cumberlandensis* Wofford et Kral, Brittonia **31:** 257 (1979).

**Minuartia douglasii** (Fenzl ex Torrey et A. Gray) Mattf. var. **emarginata** (H.K. Sharsm.) McNeill, *comb. nov.*
≡ *Arenaria douglasii* Fenzl ex Torrey et A. Gray var. *emarginata* H.K. Sharsm., Amer. Midl. Nat. **34:** 337 (1945).
≡ *Arenaria emarginata* (H.K. Sharsm.) Hoover, Leafl. W. Bot. **10:** 343 (1966).

**Minuartia filiorum** (Maguire) McNeill, *comb. nov.*
≡ *Arenaria filiorum* Maguire, Bull. Torrey Bot. Club **73:** 326 (1946).

**Minuartia godfreyi** (Shinners) McNeill, *comb. nov.*
≡ *Arenaria godfreyi* Shinners, Sida **1:** 51 (1962).
≡ *Stellaria paludicola* Fernald et Schubert, Rhodora **50:** 197 (1948), non *Arenaria paludicola* Robinson, nec *Minuartia paludicola* (Robinson) House
- *Minuartia uniflora* sensu Mattf., Repert. Spec. Nov. Regni Veg. Beih. **15:** 16–17 (1922), non (Walter) Mattf.
- *Sabulina uniflora* sensu Small, Man. S.E. Fl. 498–499 (1933), non (Walter) Small

**Minuartia muriculata** (Maguire) McNeill, *comb. nov.*
≡ *Arenaria muriculata* Maguire, Amer. Midl. Naturalist **46:** 507 (1951).

**Minuartia nuttallii** (Pax) Briq. subsp. **fragilis** (Maguire et A.H. Holmgren) McNeill, *comb. nov.*
≡ *Arenaria nuttallii* Pax subsp. *fragilis* Maguire et A.H. Holmgren, Madroño **8:** 260 (1946).

**Minuartia nuttallii** (Pax) Briq. subsp. **gracilis** (Robinson) McNeill, *comb. nov.*
≡ *Arenaria nuttallii* Pax var. *gracilis* Robinson, Proc. Amer. Acad. Arts **29:** 304 (1894).
≡ *Arenaria nuttallii* Pax subsp. *gracilis* (Robinson) Maguire, Madroño **8:** 461 (1946).

**Minuartia nuttallii** (Pax) Briq. subsp. **gregaria** (A.A. Heller) McNeill, *comb. nov.*
≡ *Arenaria gregaria* A.A. Heller, Bull. S. Calif. Acad. Sci. **2:** 67 (1903).
≡ *Arenaria nuttallii* Pax var. *gregaria* (A.A. Heller) Jepson, Fl. Calif. **1:** 492 (1914).
≡ *Arenaria nuttallii* Pax subsp. *gregaria* (A.A. Heller) Maguire, Madroño **8:** 261 (1946).

**Minuartia patula** (Michaux) Mattf. var. **robusta** (Steyerm.) McNeill, *comb. nov.*
≡ *Arenaria patula* Michaux forma *robusta* Steyerm., Rhodora **43:** 330 (1941).
≡ *Arenaria patula* Michaux var. *robusta* (Steyerm.) Maguire, Amer. Midl. Nat. **46:** 507 (1951).

**Minuartia pusilla** (S. Watson) Mattf. var. **diffusa** (Maguire) McNeill, *comb. nov.*
≡ *Arenaria pusilla* S. Watson var. *diffusa* Maguire, Amer. Midl. Nat. **46:** 508 (1951).

**Minuartia rosei** (Maguire et Barneby) McNeill, *comb. nov.*
≡ *Arenaria rosei* Maguire et Barneby, Leafl. W. Bot. **8:** 56 (1956).

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## LITERATURE CITED

Briquet, J. 1911. Decades plantarum novarum vel minus cogitarum. Annuaire Conserv. Jard. Bot. Genève **13–14:** 369–389.

Ehrhart, J. F. 1783. Botanische Zurechtweisungen und Beschreibung zweyer neuen Pflanzen, *Moenchia* und *Honckenya*. Neues Mag. Aerzte **5:** 193–208.

______. 1788. Honkenya, eine Pflanzengattung. *In:* Ehrhart, J. F., Beitrage zur Naturkunde **2:** 180–183. Hannover & Osnabrück.

Farwell, O. A. 1919. Notes on the Michigan flora. Annual Rep. Michigan Acad. Sci. **20:** 161–195.

Fernald, M. L. 1919. The unity of the genus *Arenaria*. Rhodora **21:** 1–7.

Greuter, W. 1973. Monographie der Gattung *Ptilostemon* (Compositae). Boissiera **22:** 1–215.

Hickman, J. C. 1972. *Arenaria*, section *Eremogone* (Caryophyllaceae) in the Pacific Northwest: a key and discussion. Madroño **21:** 201–207.

House, H. D. 1921. Nomenclatorial notes on certain American plants. I. Amer. Midl. Naturalist **7:** 126–135.

Hultén, E. 1958. The amphi-Atlantic plants and their phytogeographical connections. Kongl. Svenska Vetenskapsakad. Handl. ser. 4, **7(1):** 1–340.

______. 1967. Comments on the Flora of Alaska and Yukon. Ark. Bot. ser. 2, **7(1)** ; 1–147.

______. 1968. Flora of Alaska and neighboring territories. Stanford, California. 1008 pp.

______. 1971. The circumpolar plants. II. Dicotyledons. Kongl. Svenska Vetenskapsakad. Handl. ser. 4, **13(1):** 1–463.

______. 1973. Supplement to Flora of Alaska and neighboring territories. A study in the flora of Alaska and the transberingian connection. Bot. Not. **126:** 459–512.

Ikonnikov, S. S. 1973. Zametki o gvozdichnykh (Caryophyllaceae), 1. O rode *Eremogone* Fenzl. Novosti Sist. Vysshikh Rast. **10:** 136–143.

Löve, A. & Kjellqvist, E. 1974. Cytotaxonomy of Spanish plants: 3. Dicotyledons: Salicaceae-Rosaceae. Lagascalia **4:** 3–32.

Löve, A. & Löve, D. 1965. Taxonomic remarks on some American alpine plants. Univ. Colorado Stud. ser. Biol. **17:** 1–43.

______. 1974. Nomenclatural adjustments in the Yugoslavian flora. II. Pteridophytes and Dictotyledons. Preslia 46: 123–138.

______. 1975a. Cytotaxonomical atlas of the Arctic flora. Vaduz. 598 pp.

______. 1975b. Nomenclatural notes on arctic plants. Bot. Not. **128:** 497–523.

______, & Kapoor, B. M. 1971. Cytotaxonomy of a century of Rocky Mountain orophytes. Arctic Alpine Res. **3:** 139–165.

McCormick, J. F., Bozeman, J. R., & Spongberg, S. 1971. A taxonomic revision of granite outcrop species of *Minuartia* (*Arenaria*). Brittonia **23:** 149–160.

McNeill, J. 1962. Taxonomic studies in the Alsinoideae: I. Generic and infra-generic groups. Notes Roy. Bot. Gard. Edinburgh **24:** 79–155.

______. 1978. *Silene alba* and *S. dioica* in North America and the generic delimitation of *Lychnis, Melandrium,* and *Silene* (Caryophyllaceae). Can. J. Bot. **56:** 297–308.

______& Bassett, I. J. 1974. Pollen morphology and the infra-generic classification of *Minuartia* (Caryophyllaceae). Can. J. Bot. **52:** 1225–1231.

Maguire, B. 1951. Studies in the Caryophyllaceae – V. *Arenaria* in America north of Mexico. A conspectus. Amer. Midl. Naturalist **46:** 493–511.

Manitz, H. 1975. Friedrich Ehrhart's botanische Publikationen. Taxon **24:** 469–474.

Mattfeld, J. 1922a. Beitrag zur Kenntnis der systematischen Gliederung und geographischen Verbreitung der Gattung *Minuartia.* Bot. Jahrb. **57** Beibl. **127:** 13–63.

______. 1922b. Geographisch-genetische Untersuchungen über die Gattung *Minuartia* (L.) Hiern. Repert. Spec. Nov. Regni Veg. Beih. **15:** 1–228.

Nannfeldt, J. A. 1954. Some notes on *Minuartia stricta* (Sw.) Hiern and allied species. Nytt Mag. Bot. **3:** 159–170.

Pax, F. & Hoffman, K. 1934. Caryophyllaceae. *In:*Engler, A. & Harms, H. Die natürlichen Pflanzenflamilien, ed. 2, **16c,** pp. 275–364. Leipzig.

Pobedimova, E. G. 1960. Obzor roda *Honkenya* Ehrh. Bot. Mater. Gerb. Inst. Komarova Akad. Nauk. SSSR **20:** 142–162.

Porsild, A. E. & Cody, W. J. 1980. Vascular plants of the continental Northwest Territories. Ottawa.

Rauschert, S. 1977. Zur Nomenklatur der Farn- und Blutenpflanzen Deutschlands (V). Feddes Repert. **88:** 307–321.

Rydberg, P. A. 1923. Flora of the Rocky Mountains and adjacent plains. ed. 2. New York. 1144 pp.

______. 1932. Flora of the prairies and plains of central North America. New York. 969 pp.

Shetler, S. G. & Skoog, L. E. 1978. A provisional checklist of species for Flora North America. St. Louis, Missouri. 199 pp.

Shishkin, B. K. 1936. Gvozdichnye-Caryophyllaceae Juss. *In:* Komarov, V. L., Flora SSSR **6:** 386–870. Moskva & Leningrad.

Small, J. K. 1903. Flora of the southeastern United States, New York. 1370 pp.

______. 1933. Manual of the southeastern flora. Chapel Hill, North Carolina. 1554 pp.

Stafleu, F. A., et al. 1978. International code of botanical nomenclature, adopted by the Twelfth International Botanical Congress, Leningrad, July 1975. Bohn, Scheltema & Holkema, Utrecht. 457 pp.

WALTERS, S. M. 1964. LVII. Caryophyllaceae. *In:* T. G. Tutin et al. (eds.), Flora Europaea **1:** 115–204. Cambridge.

WEBER, W. A. 1967. Rocky Mountain Flora [ed. 3]. Boulder. 437 pp.

WILLIAMS, F. N. 1898. A revision of the genus *Arenaria* Linn. J. Linn. Soc. Bot. **33:** 326–437.

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# VACCINIUM SEMPERVIRENS (ERICACEAE), A NEW SPECIES FROM ATLANTIC WHITE-CEDAR BOGS IN THE SANDHILLS OF SOUTH CAROLINA

Douglas A. Rayner and James Henderson

In the course of routine field work for the South Carolina Heritage Trust Program (SCHTP), the senior author became interested in a small ericaceous plant growing in the Atlantic white-cedar community that has developed on the seepage slopes surrounding an old sandhills mill pond, Shealy's Pond, Lexington County, South Carolina. White-cedar bogs are scarce in South Carolina, and we at the SCHTP were particularly interested in this one because in addition to the 100–150 year old white-cedar, the area harbors three species of sundews (1 rare), three of the four species of pitcher plants found in South Carolina, a rare bulrush (*Scirpus subterminalis* Torrey), a rare spikerush *(Eleocharis robbinsii* Oakes), and the ericaceous plant in question.

The identity of this heath apparently has been in question for some time. Because it produces few flowers and even fewer fruits, most previous identifications have been based only on leaf characters and plant habit. The leaves of *Vaccinium sempervirens* superficially resemble those of both *Vaccinium crassifolium* Andrews and *Gaylussacia brachysera* (Michaux) Gray. Plants at the pond—white-cedar and white-cedar—sandhills ecotones tend to creep along the ground and produce few ascending branches (much like *V. crassifolium*); plants within the white-cedar community are almost inevitably erect or ascending (like *G. brachysera*). Therefore, it is not surprising that this species has been misidentified as either *V. crassifolium* or *G. brachysera* by a number of different botanists (Pers. comm. Dr. W. T. Batson, University of South Carolina, Columbia, and Dr. A. E. Radford, University of North Carolina, Chapel Hill).

After examining herbarium specimens and descriptions in local floras, it became evident that the leaves of this ericad were much too large for the plant to be either *V. crassifolium* or *G. brachysera.* In mid-June and late July, 1977, the senior author was able to find immature fruits and dried flowers. Since the fruits were 5-celled, many seeded berries, the plant obviously was a *Vaccinium.* But, it did not correspond to any species of *Vaccinium* described in Radford et al. (1964) or in Gleason (1968). A thorough search of the literature revealed no published description fitting this species. In the course of conversations and correspondence with Dr. Albert Radford (University of North Carolina) and Dr. Robert Godfrey (retired at The Florida State University), the senior author learned that several specimens determined as *Vaccinium sempervirens* Henderson, and identical to the ericad at Shealy's Pond, were on deposit in The Florida State University herbarium. Correspondence from Mr. Steven W. Leonard (a graduate student at The Florida State University and a former graduate student at the University of North Carolina) dated 12 Oct. 1977, revealed the following details: The first formal collection of the plant in question was made on July 14, 1968, by John Logue (now at the Sumter branch of the University of South Carolina) from, "Moist pocosin, Congaree girl scout camp. 4 1/2 miles SW of Edmund, Lexington County, S.C." Specimens from this collection were identified as *Gaylussacia brachysera* and sent out on exchange from the University of North Carolina to perhaps 100 institutions. In 1971, James Henderson, who was working on a revision of *Gaylussacia* at Vanderbilt University, annotated loans of Logue's *G. brachysera* as *Vaccinium sempervirens* Henderson.

Telephone conversations with Mr. Henderson revealed that he had not published a description of *V. sempervirens* because his tentative identification was based solely on fruiting material. Moreover, he had not visited the site. Since the senior author had seen flowering and fruiting material and had visited the site, we agreed to collaborate on the description of the species.

**Vaccinium sempervirens** Rayner and Henderson, *sp. nov.* (Figure 1)

Frutex erectus, ascendens aut repens, 1–4 dm altus, aut ad 1 m longus; ramunculis teretibus, puberulis usque glabris; laminis coriaceis sempervirentibus, obovatis usque ellipticus, 2.2–5.5 cm longis, 1.3–3.0 cm latis, margine leviter revolutis subtiliter mucronato-crenulatis, supra nitentibus, costa et nervis secondariis puberulis, infra subviridibus glabris, costa prominenti, nervis secondariis et venulis obscuris; petiolis 1–3 mm longis; inflorescentia axillari racemosa, floribus 3–9; rhacidi 6–18 mm longa; bracteis 1–2 mm longis persistentibus; calyce viridi, 2–2.5 mm longo, 5-lobato, lobis minu-

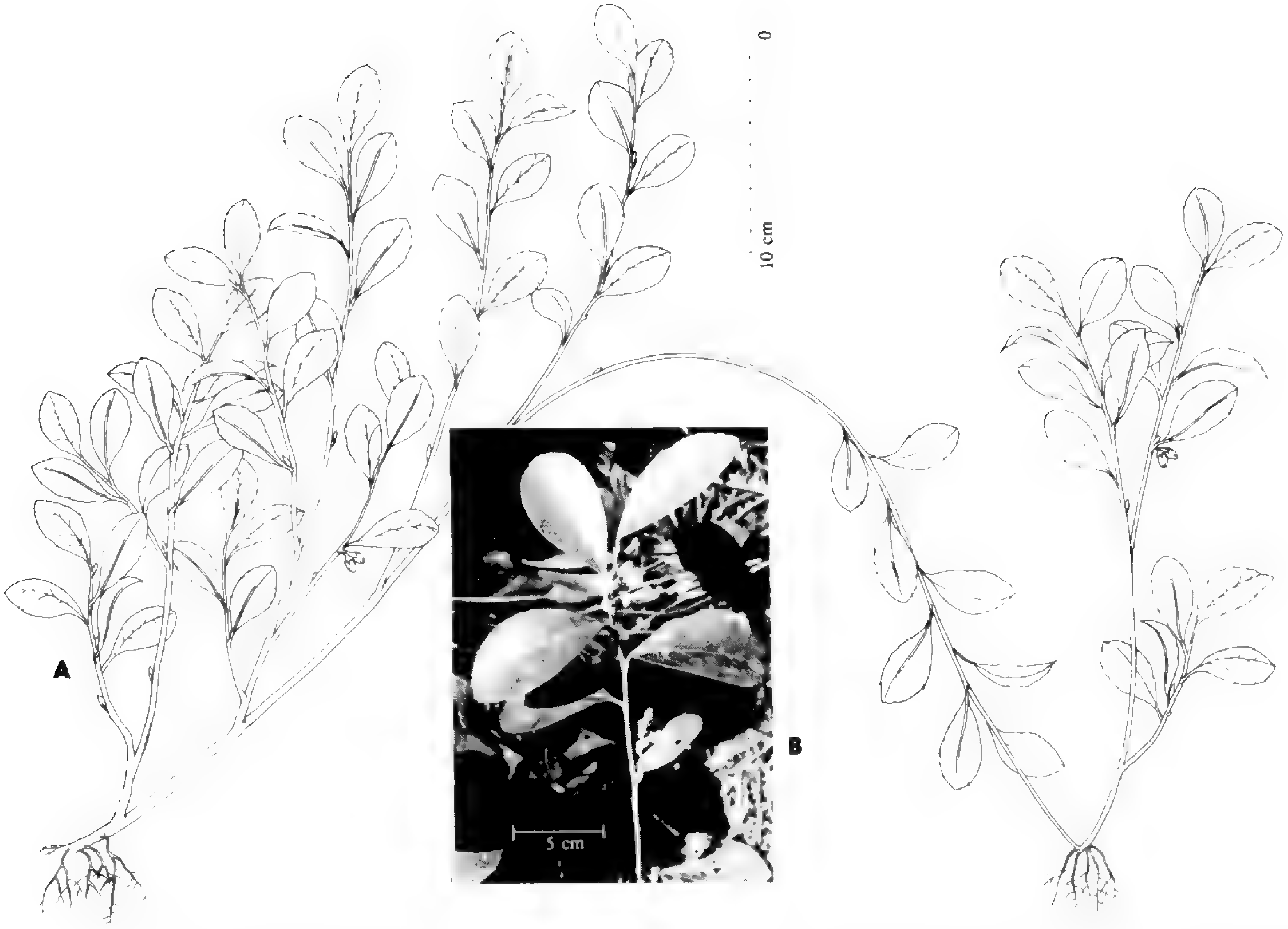

Figure 1. *Vaccinium sempervirens* Rayner and Henderson. **A.** Habit sketch showing vegetative reproduction by air layering **B.** Photo of flowering branch.

tis; corolla alba usque rubicunda sed diluta, globulari-urceolata, 3–5 mm longa, circiter 4 mm lata, tubo puberulo, lobis minutis acutis reflexis; bacca matura atra, 4–5 mm longa et 5–6 mm lata.

TYPE: UNITED STATES. **South Carolina.** Lexington Co.: within the Atlantic white-cedar stand that has developed on the sepage slopes surrounding an old sandhills millpond, Shealy's Pond, July 23, 1977, *D. A. Rayner 1000.* Holotype at USCH.

Habitat: Atlantic white-cedar communities on seepage slopes in the sandhills of South Carolina.

Flowering occurs in late April and early May, and fruits mature in late August and September. Asexual reproduction is by air layering and is the primary determinant of colony size.

*Ilex glabra* (L.) Gray, gallberry, is another species whose leaves superficially resemble those of *Vaccinium sempervirens.* The leaves of *I. glabra* are sparsely, but distinctly, crenate toward the apex; leaves of *V. sempervirens* are minutely crenate-serrate throughout, but most clearly toward the apex.

As far as is presently known, the species is restricted to Atlantic white-cedar communities that have developed on seepage slopes along the headwaters (about 6 miles) of Scouter Creek in the sandhills of Lexington Co., S. C. All other streams in the Lexington Co. area that are bounded by Atlantic white-cedar were examined during the summer of 1978; no *V. sempervirens* was found. An Atlantic white-cedar bog in Richland Co., S. C. also was examined, with negative results.

A comprehensive status report on this species was prepared by the senior author for the S. C. Wildlife and Marine Resources Department and was submitted on October 15, 1978 to the U. S. Fish and Wildlife Service, Office of Endangered Species, in support of formal listing of the species as Nationally Endangered.

## ACKNOWLEDGEMENTS

We extend our sincere appreciation to Mr. James Lipovsky, Classics Dept., University of South Carolina, Columbia, for assistance with the Latin translation. We, of course, assume responsibility for any errors or omissions.

We also wish to thank Mr. Joe Byrnn, S. C. Wildlife and Marine Resources Dept., Columbia, S. C., for the line drawing of *V. sempervirens*, (Figure 1A) and Mr. Phillip Jones, S. C. Wildlife & Marine Resources Dept., Columbia, S.C., for the photo of *V. sempervirens* (Figure 1B).

## LITERATURE CITED

RADFORD, A. E., H. E. AHLES & C. R. BELL. 1968. *Manual of the Vascular Flora of the Carolinas.* The University of North Carolina Press, Chapel Hill.

GLEASON, H. A. 1968. *The New Britton and Brown Illustrated Flora of the Northeastern United States and adjacent Canada.* (Fourth Printing) Hafner Publishing Company, Inc., New York and London.

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# ON THE PROCESS OF LECTOTYPIFICATION

REED C. ROLLINS

The frequency of the need for lectotypification of taxa of species rank and below is sufficiently great so that every active plant systematist should be thoroughly familiar with the process as set forth in the International Code of Botanical Nomenclature (1978). Section 2, typification, especially articles 7 and 8 together with the guide for the determination of types (p. 75 76) provide the basis for the procedure. A most important point often overlooked or ignored is the specification in paragraph 7.5 of Article 7 that a lectotype has to be selected from the original material used by the author of the taxon. This point is further emphasized in the guide by the statement (4a) "A lectotype must be chosen from elements that were definitely studied by the author up to the time the name of the taxon was published and included in the protologue." The sure way of finding elements that the author studied is to examine (a) the author's private herbarium, (b) material of the author's herbarium now housed in an institution, or (c) material in the institution where the author worked. In any one of these situations, the lectotype will assuredly fit the specifications of the Code. On the other hand, if a specimen not in the author's herbarium or the institution where he worked is designated as lectotype, even if it is of a collection cited by the author, there is always an element of doubt as to whether the author actually studied that particular specimen. I have previously emphasized the "need for care in choosing lectotypes" (Rollins, 1972).

One of the first questions to be answered when a researcher is seeking to lectotypify a particular taxon is, where is the author's herbarium or where did the author work? The answer will reveal where the material the author surely used in formulating the protologue is likely to be found. This procedure was not followed by McDonnell and Crow (1979) in a recent study published under the title, "The Typification and Taxonomic Status of *Spartina caespitosa* A. A. Eaton." Nowhere in the article do I find any indication that the authors were concerned as to where A. A. Eaton's herbarium is now located. But this should not have been a problem because on the Gray Herbarium Eaton specimen of *Spartina caespitosa* marked type, which they cited, there is a subsidiary label stating, "Herbarium of Alvah A. Eaton, purchased by the Gray Herbarium, 1909." Records of accessions to the Gray Herbarium (1977) show that indeed Eaton's herbarium was purchased in 1909 and on June 1, 1915, 1889 sheets were incorporated into the collections of the Gray Herbarium. At the same time 354 sheets were transferred to the New England Botanical club collections. Later the same year, 90 sheets were incorporated in GH and 66 transferred to NEBC. Some 712 specimens were sent in exchange to other institutions.

Evidently McDonnell and Crow (1979) felt they were not bound by the previous designation of the type of *Spartina caespitosa* as a specimen in the Gray Herbarium and sought to assemble as many Eaton-collected specimens of this taxon as they could find to provide the basis for a choice. From these they ultimately chose a specimen now present in the herbarium of the New England Botanical Club as lectotype. Their main reason for doing so was that the collection date Aug. 26, 1896, was the same as that mentioned by Eaton (1898) as being the date of his first encounter of the taxon. The specimen chosen, while agreeing with the date, does not agree with the locality given by Eaton. But in the protologue, Eaton gives more choices than one. He states, ". . . one tussock at Seabrook, N. H., Aug. 26, 1896, species subsequently traced on both sides of marsh from Hampton, N. H., on the north, to Ipswich, Mass., on the south, most abundant at the causeway, Salisbury, Mass." His description was obviously based on a number of different collections. Thus, the important point for lectotypification is not the one date mentioned but rather the selection of a specimen of Eaton's collecting that was certainly in his possession when he described the taxon. This certainty can only be achieved by choosing a specimen in the Gray Herbarium known to have previously been a part of Eaton's private herbarium. It is probable that the NEBC specimen chosen as lectotype by McDonnell and Crow was also a part of the Eaton herbarium but there is always the possibility that it was not. As indicated above, the Gray Herbarium specimens are labeled as being from the Eaton herbarium whereas the New England Botanical club specimen is not so labeled.

The words "type specimen" on the printed labels of several of the Eaton collections from different locations are not significant because it is obvious Eaton did not follow the same concept of "type specimen" that is a current part of the Code.

The conclusion to be drawn from the evidence now at hand is that the specimen of Alvah A. Eaton from Jim Brown's Pasture, Seabrook, New Hampshire, collected September 29, 1896 in the Gray Herbarium is and should be the lectotype of *Spartina caespitosa* as it was previously designated by a staff member of the Gray Herbarium. The different Eaton collection in the New England Botanical Club herbarium designated by McDonnell and Crow as the lectotype is not acceptable as such.

## LITERATURE CITED

Anonymous. 1977. Data related to collections added to the Gray Herbarium including lists of exchange sets distributed by the Gray; approximate dates 1890–1930. Typescript copy.

Eaton, A. A. 1898. Two new species. Bull. Torrey Bot. Club **XXV**: 338–341.

McDonnell, Mark J. & Garrett E. Crow. 1979. The typification and taxonomic status of *Spartina caespitosa* A. A. Eaton. Rhodora **81**: 123–129.

Rollins, Reed C. 1972. The need for care in choosing lectotypes. Taxon **21**: 635–637.

Stafleu, F. A. (Chairman). 1978. International Code of Botanical Nomenclature. 457 pp. Bohn, Scheltema & Holkema. Utrecht.

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# ON THE TYPIFICATION OF *SPARTINA CAESPITOSA* — A REPLY

MARK J. MCDONNELL AND GARRETT E. CROW

In an article "On the Process of Lectotypification" Rollins (this issue) rightly states that every active plant systematist should be thoroughly familiar with the process of lectotypification as set forth in the *International Code of Botanical Nomenclature* (1978). Contrary to Dr. Rollins' view, we very carefully followed the procedures outlined in the *Code* in the lectotypification of *Spartina caespitosa* A. A. Eaton (McDonnell & Crow, 1979), and remain assured we made the correct decision in selecting A. A. Eaton's specimen no. *501* (NEBC) to serve as the lectotype. Under Art. 8 of the Code, our choice cannot be superseded, since it was neither based on misinterpretation of the protologue nor made arbitrarily.

During our investigation of the taxonomic status of *Spartina caespitosa* we examined the Gray Herbarium collections, having been aware that the Herbarium of Alvah A. Eaton had been purchased by the Gray Herbarium. Included in the type collection was a specimen of *S. caespitosa* collected by A. A. Eaton and stamped TYPE. This was apparently stamped TYPE during the 1940's when staff, most likely under the direction of C. A. Weatherby or F. W. Hunnewell (Rollins, pers. comm), were searching for type specimens in the general collection.

Initially we did not question the appropriateness of this specimen to serve as the type. However, after we consulted the protologue (Eaton, 1898) a number of discrepancies arose. First, Eaton states that he made the original collection in Seabrook, N. H. on August 26, 1896, and then made an extended search on the 27th. The specimen in the Gray Herbarium stamped TYPE was collected on September 29, 1896, one month after the original collections. Furthermore, the only locality on the original label is "Jim Browns Pasture." There is no indication on the original label that this was collected in Seabrook, N. H., only a subsequent anonymous annotation, "Seabrook, N. H.," added above the label after it was purchased by the Gray Herbarium. A listing of Eaton's collecting localities compiled by his friend Raynold Dodge (in the Library of the Gray and Arnold Arboretum Herbaria) includes a "John Brown's, Hampton Falls, N. H." and the localities file in the New

England Botanical Club Herbarium adds a "Johnny Brown's meadow, Seabrook, N. H.," but we have been unable to confirm the location of a "Jim Browns Pasture." It is quite possible that this specimen was collected in one of the above localities. (Field studies revealed *Spartina caespitosa* growing at the upper edges of the salt marsh on *both* sides of Brown's Creek, which forms the boundary between Hampton Falls and Seabrook.) However, it is simply impossible to determine where the specimen was collected without the specific town originally included on the label.

Since the Gray Herbarium specimen stamped TYPE clearly is not the holotype nor was it ever formally designated as the lectotype, we carefully followed the recommendation of the *Code* and sought to locate all of Eaton's specimens of *Spartina caespitosa* in order to find the holotype, and then in the absence of one, to select from Eaton's original material a specimen to designate formally as the lectotype.

Rollins suggests that one "sure way" of finding elements studied by the author of a taxon is to consult material of the author's herbarium now housed in an institution, and therefore believes that the Eaton specimen in the Gray Herbarium stamped TYPE should be the lectotype primarily because it was part of Eaton's herbarium when it was purchased by the Gray Hebarium. However, the *Code* states that it must be selected from the author's original material and that "In choosing a lectotype, all aspects of the protologue should be considered as a basic guide" (p. 75). In addition to the lack of a specific locality on the label of the Gray Herbarium specimen, the spelling of the epithet on the label, "*cespitosa*" contrasts with Eaton's spelling, "*caespitosa*" in the protologue and adds an element of doubt as to whether this specimen was definitely studied by the author up to the time the name of his taxon was published.

In the protologue Eaton (1898) gives us additional choices, stating ". . . one tussock at Seabrook, N. H., Aug. 26, 1896, species subsequently traced on both sides of marsh from Hampton, N. H., on the north, to Ipswich, Mass., on the south, most abundant at the causeway, Salisbury, Mass." Three other of Eaton's specimens in the Gray Herbarium, dated August 29, 1896, are from Plum Island, Massachusetts (within the range included in the protologue), but these do not have A. A. Eaton's original label and thus there is always an element of doubt as the whether these specimens were actually studied by the author.

Of all the extant specimens of *Spartina caespitosa* collected by Eaton only one, *Eaton 501* (NEBC), can best serve as the lectotype. (A critical analysis of the morphology of all of Eaton's original material suggests his original description was based on a number of specimens.) The date on the label is August 26, 1896, coinciding with the date cited in the protologue. Additionally the specimen has a special printed label:

Ex. Herb. ALVAH A. EATON
Spartina caespitosa A. A. Eaton
TYPE SPECIMEN

and written on the label, *in Eaton's own hand*, is "First collection, one root in Hampton Falls, N. H." (see fig. 1, McDonnell & Crow, 1979). The presence of a special printed label with the inclusion of "TYPE SPECIMEN" on it strongly suggests that Eaton regarded this as particularly characteristic of his new taxon (even though Eaton's concept of a type specimen was not the same concept of the present *Code*). An examination of many Eaton specimens (including other taxa) revealed only very few labels with this designation. Everything about *Eaton 501* (NEBC)[1] agrees well with the protologue: its morphology, the spelling of the epithet on the label, the date cited, and the locality (Hampton Falls locality being included in ". . . both sides of the marsh . . ."). There is no doubt that this specimen was part of the original material Eaton used to describe *Spartina caespitosa* as a new species.

## LITERATURE CITED

EATON, A. A. 1898. Two new species. Bull. Torrey Bot. Club **25:** 338–341.

McDONNELL, M. J. and G. E. CROW. 1979. The typification and taxonomic status of *Spartina caespitosa* A. A. Eaton. Rhodora **81:** 123–129.

ROLLINS, R. C. 1980. On the process of lectotypification. Rhodora **82:** 509–511.

STAFLEU, F. A. (Chairman). 1978. International Code of Botanical Nomenclature. Bohn, Scheltema and Holkema. Utrecht. 457 pp.

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[1] It is quite possible that *Eaton 501* (NEBC) came to the New England Botanical Club Herbarium as a transfer from the Gray Herbarium. Rollins (this issue) notes that at the time Eaton's herbarium was incorporated into GH collections some 354 sheets were transferred to NEBC with an additional 66 sheets transferred later in the year.

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# HYDROCOTYLE UMBELLATA IN NOVA SCOTIA

A. E. ROLAND

During the summer of 1921 Professor M.L. Fernald found *Hydrocotyle umbellata* in Yarmouth County, southwestern Nova Scotia: "Wet sandy and gravelly margin of St. John (Wilson's) Lake; first time east of Massachusetts. Very rare and local and appearing like a waif washed down from some as yet undiscovered station farther up the valley of the Tusket".[1] This plant was not seen again in Nova Scotia for over fifty years. In 1975, while the author was carrying out a survey of the coastal plain plants in Kejimkujik National Park, situated in the center of the province south of Annapolis, this plant was found in four different locations up to five miles apart: twice on Jeremy Bay, a few scattered plants on the east side of Lake Kejimkujik, and in a cove on the north end of George Lake.

Most of the plants were growing in the water with the leaf-blades on long slender petioles and floating on the surface. Occasionally, small plants up to two inches high were found on the muddy shores where the water had receded. The water level became relatively low in 1975, and one plant exposed on the shore of George Lake showed a flower-stalk in bud on the first of September. Water levels during the next two years were normal or higher. No flowering material was seen and the plants sometimes grew in water 18 inches deep with petioles up to two feet long.

During August, 1978, lake-levels were exceptionally low. The *Hydrocotyle*, which had been barely visible in previous years, was exposed on the muddy flats and formed large open patches with tangled horizontal rootstocks and numerous erect leaves and flowering stalks.

Meanwhile, in 1977, the plant was rediscovered in Yarmouth County by Mr. Joseph Johnson — in the same lake but apparently at the opposite end from where Fernald had picked it up fifty-six years earlier. The location was difficult to find, for the name of the lake had changed and it appeared on more recent maps of the county as Bennet Lake.

This location was visited September 1, 1978, when the water was again abnormally low, much as in 1921 when Fernald stated that the

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[1] Fernald, 1922, p. 179.

summer was phenomenally dry, to the point of extreme drouth. Along a dry stream-bed leading south to the north end of the lake was a luxuriant growth of Skunk Cabbage, here at the extreme northeastern edge of its range. A meadow nearer the lake had scattered patches of *Sabatia Kennedyana* in flower, with mats of *Proserpinaca pectinata* in the lower areas. At the lake the silty and gravelly margin had hundreds of flowering plants and established seedlings of the *Sabatia* and of *Coreopsis rosea*; while along the cove at the northern tip of the lake, growing on the muddy exposed lake-bed, was half an acre of the *Hydrocotyle* with large numbers of the plants in flower.

As with some other coastal plain plants which range south to Mexico, *Hydrocotyle umbellata* is also found on the West Coast and has been reported, by Boivin, from British Columbia.

## REFERENCES

FERNALD, M.L. 1922. Notes on the Flora of Western Nova Scotia. Rhodora **24:** 157–164; 165–180; 201–208.

BOIVIN, BERNARD. 1966. Énumération des Plantes du Canada. Le Naturaliste Canadien **93:** 636.

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# CAREX CHORDORRHIZA IN GLACIER NATIONAL PARK, MONTANA

ALFRED E. SCHUYLER

While collecting sedges in Glacier National Park during the summer of 1978, I found plants of *Carex chordorrhiza* L. f. growing abundantly in a calcareous boggy meadow along Glacier Route 7 about 6.8 kilometers north northwest of Apgar, Flathead County, Montana. Other sedges growing in this meadow, most of which are rare in Montana, were *Carex buxbaumii, C. limosa, C. livida, Eleocharis elliptica, Eriophorum alpinum, E. viridi-carinatum,* and *Scirpus cespitosus*. Also present were *Drosera anglica, D. rotundifolia, Menyanthes trifoliata, Scheuchzeria palustris* and *Tofieldia glutinosa*.

*Carex chordorrhiza* is circumboreal and occurs across Canada (Scoggan, 1978). Although it is known as far south as Pennsylvania, Ohio, Indiana, Illinois, and Iowa farther east, it has not been previously reported from any of the northwestern United States (Hermann, 1970; Hitchcock & Cronquist, 1973). This report thus extends the western North American range of *Carex chordorrhiza* southward to northwestern Montana from Alberta and British Columbia.

My Montana specimens of *Carex chordorrhiza* have been deposited in the Glacier National Park Herbarium. I thank Robert L. Hall, Frederick J. Hermann, Patricia R. Schuyler, and Daniel E. Wujek for help in various ways.

## LITERATURE CITED

HERMANN, F. J. 1970. Manual of the Carices of the Rocky Mountains and Colorado Basin. Agricultural Handbook No. **374**, Forest Service, U. S. Department of Agriculture, Washington.

HITCHCOCK, C. L. & A. CRONQUIST. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

SCOGGAN, H. J. 1978. The Flora of Canada, Part 2, Pteridophyta, Gymnospermae, Monocotyledoneae. National Museums of Canada, Ottawa.

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# FIRST REPORT OF SPECULARIA BIFLORA (R. & P.) FISCH. & MEV. IN NEW YORK STATE

WILBUR J. SETTLE

On June 18, 1978 I noticed a few plants of *Specularia biflora* (R. & P.) Fisch. & Mev. (Campanulaceae) growing between large rocks forming a retaining wall on the campus of the State University College at Oneonta, New York. This wall is well drained, faces south, and provides a dry habitat for several "weedy" species of herbaceous plants. I had never noticed this species growing there previously, even though I frequently walk past this area during the summer.

*Gray's Manual of Botany* (Fernald, 1950) lists the northeastern limit of the range of this species as south-east Virginia, southern Kentucky, Missouri, and Kansas. The revised edition of *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada* (Gleason, 1963) sets the northeastern limit as southern Virginia to Kentucky and Missouri. *Plants of the Vicinity of New York* (Gleason, 1962) does not mention *Specularia biflora* (R. & P.)Fisch. & Mev., although it does include *Specularia perfoliata*(L.) A. DC.

Recently Dr. Charles J. Sheviak, Curator of Botany at the New York State Museum in Albany, was kind enough to check the records there for me. He said that there are no records of *Specularia biflora* (R. & P.) Fisch. & Mev. in the state herbarium or in their files on the New York flora. So, it appears that it has never been reported in New York state.

I collected and pressed one plant which has been deposited in the herbarium of the State University College at Oneonta, New York. The few remaining plants were still growing on the wall at the end of the summer, and seeds were released from fruits formed on the specimen that was collected. A few plants were growing in the same area of the wall in the summer of 1979.

## LITERATURE CITED

FERNALD, M. L. 1950. Gray's manual of botany. Edition eight. Corrected printing, 1970. American book Co. New York. 1632 pp.

GLEASON, H. A. 1962. Plants of the vicinity of New York. Hafner Press. New York. 307 pp.

GLEASON, H. A. 1953. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Revised edition. Volume 3. Hafner Press. New York. 595 pp.

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# NEW ENGLAND NOTE: A NATURALIZED POPULATION OF RHAMNUS CITRIFOLIA IN CONNECTICUT

Joe D. Pratt

In 1976, during a survey of the flora of Spicebush Swamp Preserve in West Hartford, Connecticut, numerous shrubs were encountered which did not fit *Rhamnus cathartica*, a common species in this area. Preliminary identification by Joseph J. Dowhan, then with the Connecticut Geological & Natural History Survey, suggested that the shrub was *Rhamnus davurica*. On August 6, 1978, a specimen of this shrub was collected and identified as *Rhamnus davurica* Pallas by Harry E. Ahles, curator of the herbarium at the University of Massachusetts and deposited in the University of Massachusetts herbarium (MASS). The species was renamed *Rhamnus citrifolia* (Weston) Hess & Stearn in November 1979 (Hess & Stearn, 1979).

This station represents the first known naturalized population of this species in the state. Seymour (1969) reports the species only at two localities in Massachusetts, Holden and Worcester. It is native to Siberia, northern China, and Korea.

The thirty-three acre Spicebush Swamp Preserve is characterized by red maple (*Acer rubrum*) swamp over two thirds of its area and rolling old field slopes on the remainder. The land has not been used as pasture since 1962 and the old field portion is now dominated by *Juniperus virginiana, Rosa multiflora, Cornus racemosa, C. amomum, Lonicera morrowii, Prunus serotina, Malus spp., Fraxinus americana, Rhamnus cathartica* and *R. citrifolia. Rhamnus citrifolia* is an integral and freely reproducing member of this community; specimens of the shrub can be found in every stage of maturity. The largest individual measures 3 3/4 inches d.b.h. and another plant is about 16 1/2 feet tall. During the three years I have observed this species there has been heavy fruiting each year.

In a 150 square foot area burned over in 1969 *Rhamnus citrifolia* is especially dense. It grows to the virtual exclusion of other woody and herbaceous plants in this small area.

I am grateful to Harry E. Ahles and Martha Capizzano who helped with this brief note.

## REFERENCES

Dowhan, J. J. 1979. A preliminary checklist of the vascular flora of Connecticut growing without cultivation. Connecticut Geological & Natural History Survey, Hartford, Connecticut.

Emery, J. L. 1971. A field guide to Spicebush Swamp. Conservation & Environment Commission, West Hartford, Connecticut.

Hess, William J., & William T. Stearn. 1979. The identity of *Cornus citrifolia* Weston. Taxon **28**(5/6): 553–556.

Seymour, F. C. 1969. The Flora of New England. Charles E. Tuttle Co., Inc., Rutland, Vermont.

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Cover illustration

*Geum Peckii* Pursh

This rare species is a Northeastern endemic, known from the White Mountains of New Hampshire and from three sites in Nova Scotia.

Original artwork by Lisa Bandazian

Rhodora

JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 82 October 1980 No. 832

# THE IDENTITY AND STATUS OF SPIRANTHES OCHROLEUCA (RYDBERG) RYDBERG[1]

C. J. SHEVIAK AND P. M. CATLING

*Spiranthes* is taxonomically the most complex orchid genus in the flora of eastern North America. Within the genus, some of the greatest problems center on *S. cernua* (L.) L. C. Rich., a very poorly understood species which has been the recurrent victim of both splitters and lumpers for over one hundred years. A number of segregates have been proposed; these subsequently have been accorded various taxonomic ranks, relegated to synonymy, or forgotten altogether. One such taxon, *Gyrostachys ochroleuca* Rydberg, was described in 1901 (Rydberg, *In:* Britton, 1901, p. 300) and has been the object of controversy ever since.

The original description of *Gyrostachys ochroleuca* provided few points of difference from the description of *G. cernua* in the same publication. Rydberg's species was reported to bear leaves on the lower portion of the stem similar to the basal leaves, and lanceolate to ovate-lanceolate acuminate floral bracts, the lower of which were longer than the flowers. The flowers were described as ochroleucous or greenish-yellow and strongly fragrant. In contrast, in *G. cernua* cauline leaves were reportedly merely bract-like and floral bracts were acute and generally not longer than the flowers. Flowers of *G. cernua* were reported to be white and fragrant. Additionally, the diameter of the spike was given as 15–20 mm for *G. ochroleuca* and 12–14 mm for *G. cernua.* The key preceding the description separated *G. ochroleuca* from *G. cernua* on the basis of yellow

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[1] Published by permission of the Director, New York State Museum, State Education Department, Journal Series No. 272.

flowers, acute spike, and lower floral bracts longer than the flowers. The description ended: "Otherwise as in *G. cernua*," and gave the distribution as "N.H. to N. Car., and Penn." Rydberg dismissed typification of *G. ochroleuca* with the phrase, "Type from Mt. Washington, Mass.," and a type specimen is unknown.

Ames (1905) early reduced *Gyrostachys ochroleuca* to varietal status under *Spiranthes cernua*. Later he (Ames, 1921) commented on the near impossibility of separating the two taxa and stated that the only reliable difference known to him was the presence of polyembryonic seeds in var. *cernua* and of monoembryonic seeds in var. *ochroleuca*. Since that time, authors of various manuals of the northeastern flora and regional studies of the Orchidaceae have treated it as a variety, a separate species, or have omitted it altogether, either considering it part of the variation of *S. cernua* and unworthy of recognition, or being unable to identify it with certainty in the area covered. Ames (1924), referring to *ochroleuca* as a variety, extended its range into Nova Scotia and included "Mo. (Palmer)." Rydberg (1932) retained its specific rank, transferring it to *Spiranthes*, and expanded its range to most of the eastern United States, from Maine to Georgia and west to South Dakota and Texas.

Swamy (1948), in a detailed study of the embryogenesis of the group, showed that polyembryony in *Spiranthes cernua* was a consequence of agamospermy. He recognized a strictly apomictic race marked by the production of polyembryonic seeds, a sexual race exhibiting solely monoembryonic seeds, and a facultatively apomictic "intermediate" race in which both sexually produced monoembryonic and apomictically derived polyembryonic seeds were characteristically developed in the same capsule. He failed to mention var. *ochroleuca*, but wrote, "unfortunately no reliable characters in gross morphology are known which would help to segregate the sexual and agamospermic races;" this suggests that he was influenced by Ames' (1921) statement concerning the seeds. Swamy indicated a very widespread eastern North American distribution for the polyembryonic, asexual race, a more limited and sporadic occurrence of the "intermediates", and a restricted northeastern range for the monoembryonic, sexual race. Much of the material upon which he based his initial work was obtained from Ames, and consequently it is reasonable to conclude that his agamospermic races correspond to *S. cernua* var. *cernua* and the

Figure 1. Type drawing of *Spiranthes ochroleuca* at NY labelled "*Gyrostachys ochroleuca* Rydb. *ined.* Britton's Manual 1901. Drawings by Mrs. Long, Mt. Washington, Mass. 1897."

strictly sexual race to *S. cernua* var. *ochroleuca,* as understood by Ames. If this conclusion is correct, the range reported by Swamy was certainly contrary to that reported by Rydberg (1932) who should have known the plant best; however, Swamy's map was based on 5,000 herbarium specimens representing 28 states!

Correll (1950) did not treat var. *ochroleuca* separately, but alluded to it briefly as an upland form with yellowish-tinged flowers and longer floral bracts in his treatment of *Spiranthes cernua* var. *odorata* (Nutt.) Correll. He also indicated that it was separated primarily on the basis of its monoembryonic seeds, and commented further: "to the average individual such ultratechnical characters are not readily useable."

Fernald (1950), according *ochroleuca* varietal status under *Spiranthes cernua,* characterized it similarly, but made the significant addition: "Its callosities longer." Longer basal calli in *S. ochroleuca* are shown in the plate provided by Correll (1950, Plate 70) which was earlier used by Ames (1921, Plate 127). Jennings (1906) cited the long calli of specimens from Presque Isle, Lake Erie, as the salient feature separating *Ibidium incurvum* Jennings from *I. cernuum.* He later (1953) reported these specimens to be merely vigorous *S. cernua,* and further indicated the occurrence of long calli in both typical *S. cernua* and *S. cernua* var. *ochroleuca.* Recent authors have overlooked the name *I. incurvum* altogether.

State floras have been equally variable in their treatments of *Spiranthes ochroleuca.* For example, Deam (1940) specifically excluded it from the Indiana flora, although Steyermark (1963) reported it from Missouri, and Barkley (1968) included it in the Kansas flora. Case (1964) reported it from Michigan, but Voss (1972) has not mentioned it from that state. Sheviak (1973) considered this disparity of treatments to be largely a result of the confusion of this taxon with other members of the *S. cernua* complex, and did not (Sheviak, 1974) report it from Illinois.

Most recently Luer (1975) has accorded *ochroleuca* specific rank. Here it was distinguished from *Spiranthes cernua* by its larger incurved basal calli, lesser dilation at the base of the lip, creamy flowers, flowers more widely spaced on the rachis, lip that expands more broadly into a crenulate margin, later flowering time, more restricted distribution, and drier habitat. This characterization of *S. ochroleuca* agrees well with the concept evolved earlier in this

Figure 2. The type of *Spiranthes cernua* (L.) L.C. Rich. (LINN *1056.9*).

century. The confusion which has surrounded the taxon, however, suggests that the actual situation is very complex. Luer's recognition of *S. ochroleuca* at the specific level, a decision based primarily on field experience and discussion with local botanists, has both drawn attention to the problem and generated additional questions. This is evident from the repeated requests the authors have received to clarify the matter. Without type material and additional supportive evidence, and considering the nature of the original description, it has been difficult to do so.

The confusion which has surrounded the application of Rydberg's name has not been limited to difficulties in the separation of *Spiranthes ochroleuca* from *S. cernua*. In the Midwest, *S. ochroleuca* has been confused with *S. magnicamporum* Sheviak (Sheviak, 1973). *Spiranthes ochroleuca* is also sometimes confused with *S. casei* Catling and Cruise (Catling & Cruise, 1974). Most recently, Luer (1975) has compared *S. ochroleuca* to *S. laciniata* (Small) Ames.

It is clear that both the taxonomic status and identity of *Spiranthes ochroleuca* have been problems, and indeed continue to be. The present authors independently came to recognize the same group of plants as *S. ochroleuca* and became convinced of its distinctness. A number of questions persist, however. What are the distinctions in both qualitative and quantitative terms? Can the species be discriminated on the basis of morphology alone, and to what extent can herbarium material be discriminated? Do the names presently in use correctly apply to the taxa they are taken to represent? What is the actual distribution? Is specific status justified?

## METHODS

### 1. General survey of natural populations

Notes were made on flower colour, flowering time, habitat, and distinctive features in colonies over a wide geographical area extending from New England to southwestern Ontario. Special attention was given to localities where *Spiranthes ochroleuca* and *S. cernua* grew in close proximity. One such area is the type locality of *S. ochroleuca:* Mt. Washington, Mass. Here populations referable to *S. ochroleuca* and *S. cernua* were studied in detail to allow for accurate redescription.

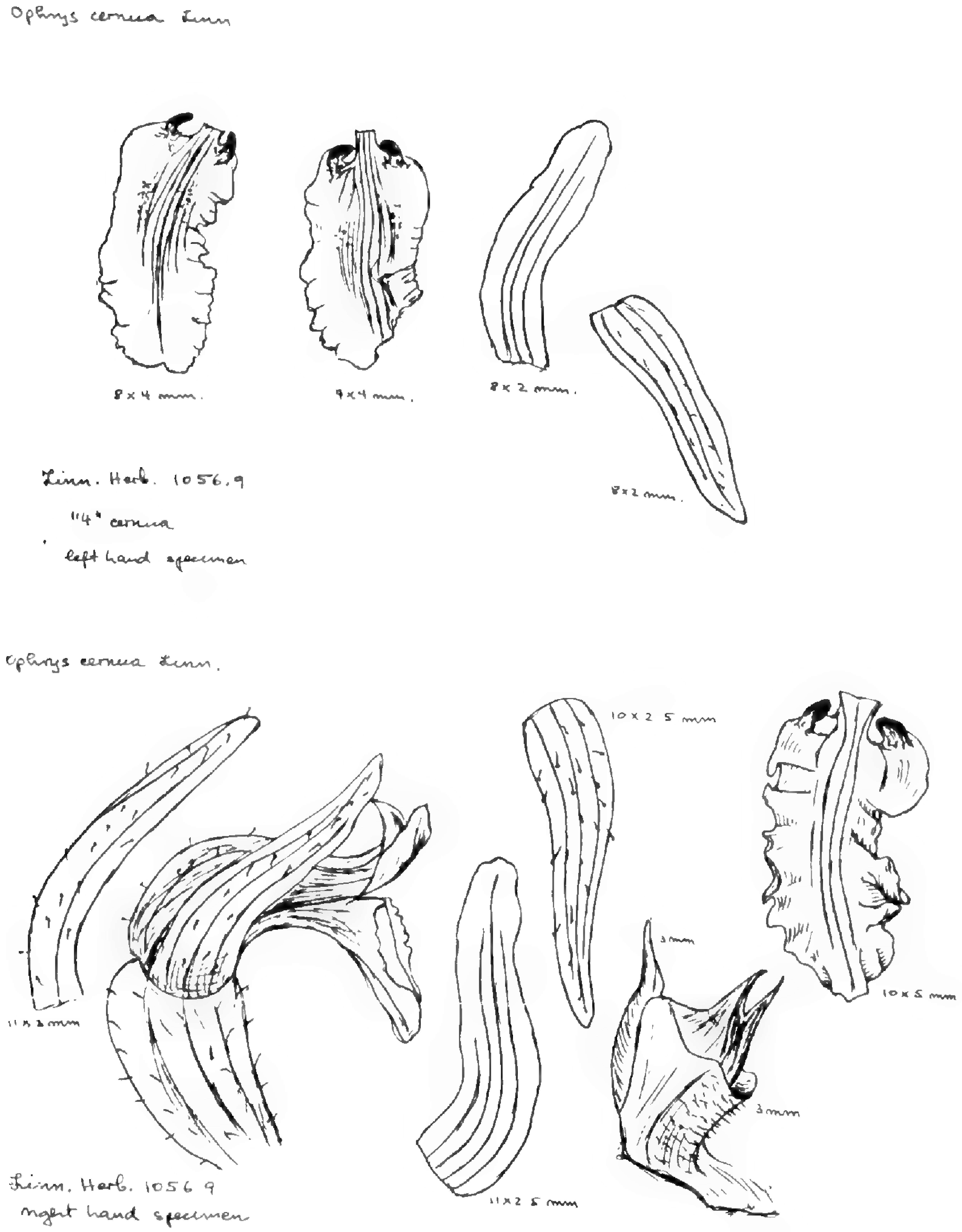


Figure 3. Camera lucida drawings of flowers from the type material of *S. cernua* (LINN *1056.9*) made by Dr. L. A. Garay. Above, left hand specimen, from left to right, lip 8 × 4 mm, lip 7 × 4 mm, petal 8 × 2 mm, lateral sepal 8 × 2 mm. Below, right hand specimen, from left to right, lateral sepal 11 × 3 mm, flower in lateral view, petal 11 × 2.5 mm, lateral sepal 10 × 2.5 mm, column 3 mm with anther sac 3 mm and lip 10 × 5 mm.

Plants photographed and/or measured in the wild were grown under uniform greenhouse conditions (soil, light, moisture, and temperature). This allowed for a test of the extent to which various presumably characteristic features are modified by the environment.

In order to evaluate the features of floral morphology that separate *Spiranthes ochroleuca* from *S. cernua*, and in an attempt to find additional features, 20 flowers of each taxon pickled in standard FAA fixative were examined closely. These had been collected by the authors throughout the northeast. Camera lucida drawings were made to illustrate the salient differences. As well as providing illustrations, this examination allowed the selection of characters to be used in the statistical analyses described below.

### 2. **Herbarium studies**

Since a large part of the difficulty in determining the application of the name *Spiranthes ochroleuca* results from the apparent absence of type material, extensive herbarium searches were conducted in an effort to locate a specimen seen by Rydberg. The collection of the New York Botanical Garden (NY), where many of Rydberg's types are located, was searched intensively. In addition, the collections of several other herbaria were examined; these included AMES, CAN, CM, DAO, F, ILL, KANU, MICH, MIL, MIN, NDA, NEBC, NYS, OKL, OKLA, PENN, PH, TRT, US, VDB, WIS, and others. These herbaria provided the specimens of *S. ochroleuca* which formed the basis of our range map.

### 3. **Cytological studies**

Chromosome counts were obtained from over sixty individuals collected throughout the range of the *Spiranthes cernua* complex. Chromosome number determinations were made primarily on somatic tissue. Complex pairing in some polyploids and small chromosome size precluded the general use of meiotic figures for counting. Tissues utilized included root tips from pot-grown plants and ovules from both cultivated and collected material. Root tips and ovaries were deeply incised and then placed in a saturated aqueous solution of monobromonaphthalene for four hours at 18–24° C. or overnight on ice. They were then fixed in Carnoy's solution for about 25 minutes before storage in 70% ethanol at ca. −15° C. or squashing. Root tips and ovaries were hydrolyzed in 1 N. HCl at 55–60° C. for 8 to 15 minutes and stained with acetolacmoid.

Chromosome numbers and seed characteristics, which have been found to correlate with ploidy level (Sheviak, unpubl.), were studied throughout the range of *Spiranthes cernua*. To a lesser extent, pollen characters were also examined. Attempts were made to correlate these features with other characters. Some of the material for which chromosome numbers had been determined was used in the statistical analysis (see below).

### 4. Statistical analysis of flower morphology

As mentioned previously, plants referable to *Spiranthes ochroleuca* and *S. cernua* were found in abundance at the type locality, Mt. Washington, Mass. Here 22 flowers of each species were collected for measurement. In addition three flowers were collected from plants that could not be readily assigned to either species, but appeared in the field more like *S. cernua*. These were labeled "intermediate". Each flower was collected from the basal portion of the inflorescence of a different plant, and all flowers were pickled in standard FAA. Twenty-four measurements made on each of these flowers are listed in Table 1.

Some of the measurements require explanation. The method of measurement of the separation of dorsal and lateral sepals (1), the angle of curvature of the lip from the basal stalk (8), and the angle of basal curvature of the lip (22) are illustrated in Figure 4. The aperture (5) refers to the aperture formed at the base of the lip by the lip, the basal lateral petal, and the top of the ovary, and is apparent in the lateral view of the flower with the lateral sepal removed (Figure 6). The length and width of the basal calli (16) refers to the mean length and mean basal width, respectively, of the two structures on a single lip. The lateral width of the anther sac (18) refers to its width as viewed from the side, while the dorsal width (24) refers to the width as viewed from above. The basal and middle lateral widths of the flower (6 and 7, respectively) are widths measured 1 mm from the base and at the midpoint along the length of the flower respectively, with the lateral sepal removed and viewing the flower from the side.

The numerical taxonomy system of multivariate statistical programs (NT-SYS) written by F. J. Rohlf, J. Kishpaugh and D. Kirk (1974, State University of New York, Stony Brook) was used to produce a character-by-character correlation matrix based on standardized data. This correlation matrix involving 24 characters

Table 1. Units, means, standard deviations and character weights for 24 floral characters measured in 22 pickled flowers of *S. ochroleuca* and 22 of *S. cernua,* all from the type locality, Mt. Washington, Massachusetts, OCHR=*S. ochroleuca,* CERN=*S. cernua.** *To the discriminant function add the constant 0.720.*

| Character | Units | Means |  | Standard Deviations |  | DFA Character Weights* |
|---|---|---|---|---|---|---|
|  |  | OCHR | CERN | OCHR | CERN |  |
| 1. Separation of sepals | mm | 0.9 | 0.5 | 0.3 | 0.2 |  |
| 2. Sepal length | mm | 8.8 | 8.8 | 0.7 | 0.5 | — |
| 3. Sepal width | mm | 2.6 | 2.7 | 0.3 | 0.2 | — |
| 4. Length of aperture | mm | 0.8 | 0.6 | 0.1 | 0.2 |  |
| 5. Width of aperture | mm | 0.6 | 0.4 | 0.1 | 0.1 | — |
| 6. Basal lateral width of flower | mm | 3.4 | 3.1 | 0.3 | 0.3 | — |
| 7. Middle lateral width of flower | mm | 2.7 | 2.7 | 0.2 | 0.3 |  |
| 8. Angle of curvature of lip from basal stalk | ° | 55.8 | 31.0 | 9.9 | 11.0 | 0.051 |
| 9. Petal length | mm | 9.5 | 9.0 | 0.7 | 0.6 | — |
| 10. Petal width | mm | 2.2 | 2.5 | 0.2 | 0.2 | —4.677 |
| 11. Dorsal sepal length | mm | 9.5 | 9.2 | 0.8 | 0.5 |  |
| 12. Dorsal sepal width | mm | 3.2 | 3.0 | 0.3 | 0.2 |  |
| 13. Lip length | mm | 9.2 | 8.9 | 0.7 | 0.5 |  |
| 14. Maximum lip width | mm | 4.8 | 4.8 | 0.5 | 0.5 | 1.460 |
| 15. Length of basal calli | mm | 1.2 | 0.9 | 0.2 | 0.1 | 3.621 |
| 16. Width of basal calli | mm | 0.8 | 0.8 | 0.2 | 0.2 | — |
| 17. Length of anther sac | mm | 2.2 | 2.4 | 0.1 | 0.2 | 8.528 |
| 18. Width of anther sac (lateral) | mm | 1.0 | 0.8 | 0.1 | 0.1 | 12.215 |
| 19. Length of stigmatic surface | mm | 1.3 | 1.1 | 0.2 | 0.1 |  |
| 20. Width of stigmatic surface | mm | 1.7 | 1.8 | 0.2 | 0.1 |  |
| 21. Column length | mm | 3.9 | 3.6 | 0.4 | 0.3 | 1.616 |
| 22. Angle of basal curvature of lip | ° | 46.3 | 22.2 | 8.9 | 15.5 |  |
| 23. Length of disc (rostellum) | mm | 1.5 | 1.5 | 0.1 | 0.1 |  |
| 24. Width of anther sac (dorsal) | mm | 1.2 | 1.1 | 0.1 | 0.2 | — |

(see Table 1) was subjected to a Principal Components Analysis. In this procedure individuals are ordered along uncorrelated axes, while variation in all characters among all the individuals is considered simultaneously (Sneath & Sokal, 1973, pp. 245–247). Any major groupings in the sample data are elucidated through this technique.

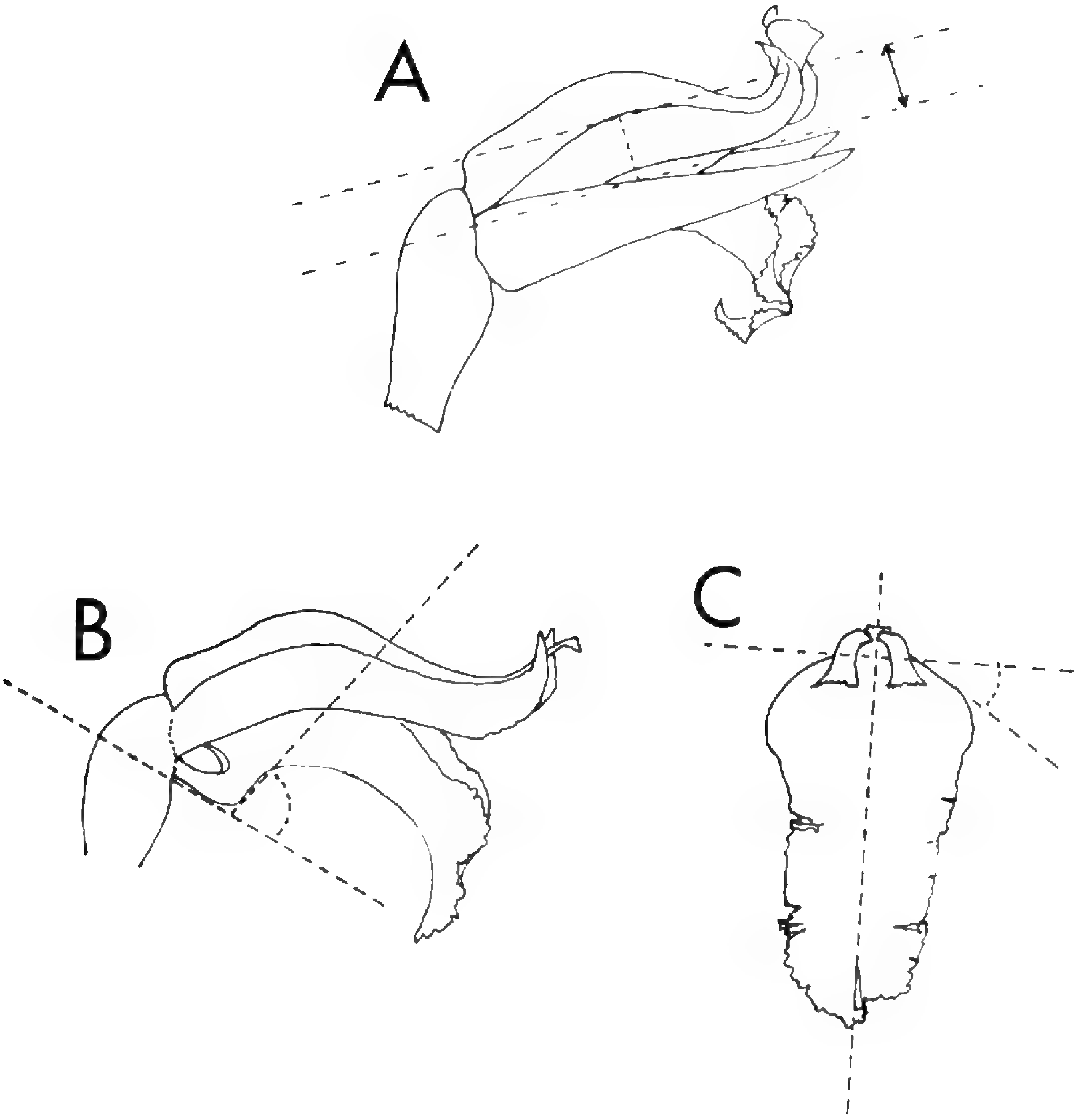


Figure 4. Method of measurement of A, separation of dorsal and lateral sepal; B, the angle of curvature of the lip from the basal stalk; and C, the angle of basal curvature of the lip.

A stepwise Discriminant Function Analysis program (BMDP 7M) developed by P. Sampson (1975, University of California, Los Angeles) was used to maximize discrimination between identifiable groups. This multivariate procedure maximizes intergroup differences with respect to intragroup differences through the development of weighted character combinations. The discriminant scores for each specimen are obtained by multiplying each measurement by the appropriate discriminant weight and adding the resulting values. Unknowns may be identified by applying the weighted character combination (see Table 1) derived from the DFA reference samples, the latter representing specimens of known affinity. Multivariate statistical programs were run on the University of Toronto IBM/370 computer.

### 5. Statistical analysis of dried material

In addition to a statistical treatment of flowers from the type locality, it was thought that a statistical analysis of dried material covering a wide geographical area would help to elucidate further the nature and variation of *Spiranthes ochroleuca*, and assist in the development of means for the determination of herbarium specimens with an acceptable misdetermination rate.

For this analysis dried material collected by the authors and known to be referable to either *Spiranthes ochroleuca* or *S. cernua* on the basis of flower colour, habitat, and various qualitative features was chosen for measurement. For some of this material chromosome numbers were also known (Table 3). Eleven measurements were made of each of 30 individuals of *S. ochroleuca;* 37 of *S. cernua;* and two of specimens, from mixed populations, which could not be readily determined. The collection localities and corresponding number of specimens of each group measured are given in Table 3; the characters, units of measurement, means and standard deviations are shown in Table 2. Various type material was also considered in these analyses. The angle of ascension of the flower (7) refers to an angle measured from a line perpendicular to the main axis of the plant. Again, all floral measurements refer exclusively to basal flowers. The same statistical techniques and programs were employed for the analysis of dried specimen data as for the study of flower morphology described above.

Table 2. Units, means, standard deviations, and character weights for 11 characters measured in 30 dried specimens referable to *S. ochroleuca* and 37 referable to *S. cernua*, representing a wide geographical area of the northeast. OCHR = *S. ochroleuca*, CERN = *S. cernua*. *From the first discriminant function subtract the constant 4.362 and from the second subtract 3.589.

| **Character** | **Units** | **Means** | | **Standard Deviations** | | DFA Character Weights* | |
|---|---|---|---|---|---|---|---|
| | | OCHR | CERN | OCHR | CERN | 1 | 2 |
| 1. Length mid-stem bract | mm | 49.3 | 33.5 | 15.4 | 7.6 | 0.017 | 0.027 |
| 2. Length of spike | mm | 83.0 | 58.3 | 35.6 | 23.2 | 0.024 | — |
| 3. Flower number | — | 29.0 | 20.1 | 9.3 | 6.6 | 0.000 | — |
| 4. Plant height | mm | 264.0 | 239.3 | 81.6 | 60.9 | —0.004 | — |
| 5. Ovary length | mm | 5.2 | 6.2 | 0.7 | 1.2 | —0.491 | —0.527 |
| 6. Separation of lateral and dorsal sepals | mm | 0.8 | 0.3 | 0.3 | 0.2 | 2.425 | 3.742 |
| 7. Angle of ascension of flower from ovary | ° | 110.7 | 100.9 | 11.5 | 13.7 | 0.016 | — |
| 8. Length lowest floral bract | mm | 13.3 | 11.2 | 2.7 | 1.8 | 0.240 | 0.297 |
| 9. Length lateral sepal | mm | 8.3 | 8.4 | 0.9 | 0.9 | —0.257 | — |
| 10. Width lateral sepal | mm | 2.1 | 2.1 | 0.3 | 0.4 | 0.220 | — |
| 11. Basal curvature of lip from basal stalk | ° | 46.3 | 15.1 | 14.4 | 10.1 | 0.055 | — |

Table 3. Subjectively determined categories, number of specimens, chromosome numbers, and collection sites of dried material used in statistical analyses.

| | *S. ochroleuca* | Indet. | *S. cernua* |
|---|---|---|---|
| ILLINOIS | | | |
| Iroquois Co. (*Sheviak 699*) | | | 1 ($2n=60$) |
| Will Co. (*Sheviak 470*) | | | 1 ($2n=60$) |
| MASSACHUSETTS | | | |
| Berkshire Co. (*Catling* 4 Sept. '75) | 1 | | 2 |
| (*Sheviak 1076*, TOPOTYPE) | 2 ($2n=30$) | | |
| (*Catling 831c*, TOPOTYPE) | 10 ($2n=30$) | | |
| (*Catling 83a*) | | | 5 ($2n=ca. 60$) |
| Middlesex Co. (*Sheviak 821*) | | | 2 ($2n=ca. 60$) |
| Worcester Co. (*Sheviak 891*) | | | 2 ($2n=60$) |
| Worcester Co. (*Sheviak 922*) | | | 1 ($2n=60$) |
| MAINE | | | |
| Sagadahoc Co. (*Sheviak 870*) | 1 ($2n=30$) | | |
| Sagadahoc Co. (*Sheviak 915*) | 1 ($2n=30$) | | |
| York Co. (*Sheviak 888*) | | | 2 |
| York Co. (*Sheviak 1113*) | | 1 ($2n=45$) | |
| York Co. (*Sheviak 1070*) | 1 | | |
| MICHIGAN | | | |
| Saginaw Co. (*Gunn* 15 Sept. '73) | 2 | | |
| Saginaw Co. (*Sheviak 1065*) | 1 ($2n=30$) | | |
| Saginaw Co. (*Sheviak 1155*) | | | 1 |
| NEW HAMPSHIRE | | | |
| Belknap Co. (*Sheviak 1022*) | 2 ($2n=30$) | | |
| Cheshire Co. (*Sheviak 1041*) | 1 ($2n=30$) | | |
| Coos Co. (*Catling* 1 Sept. '76) | 1 ($2n=30$) | | |
| Merrimack Co. (*Sheviak* 875) | | | 2 ($2n=60$) |
| Sullivan Co. (*Sheviak* 877) | 1 ($2n=30$) | | |
| Sullivan Co. (*Sheviak 1063*) | | 1 ($2n=45$) | |
| Sullivan Co. (*Sheviak 1036b*) | | | 1 ($2n=61$) |
| Sullivan Co. (*Sheviak 1036g*) | | | 1 |
| Sullivan Co. (*Sheviak 1035*) | 1 | | |
| Sullivan Co. (*Sheviak 1034*) | | | 1 ($2n=45$) |
| NOVA SCOTIA | | | |
| Shelburne Co. (*Catling* 25 Aug. '75) | 1 | | |
| ONTARIO | | | |
| Haliburton Co. (*Catling* 12 Sept. '71) | | | 1 |
| Kent Co. (*Catling* 18 Sept. '76) | 1 | | |
| Muskoka Dist. (*Whiting* 10 Sept. '70) | | | 1 |

*Table 3 continued*

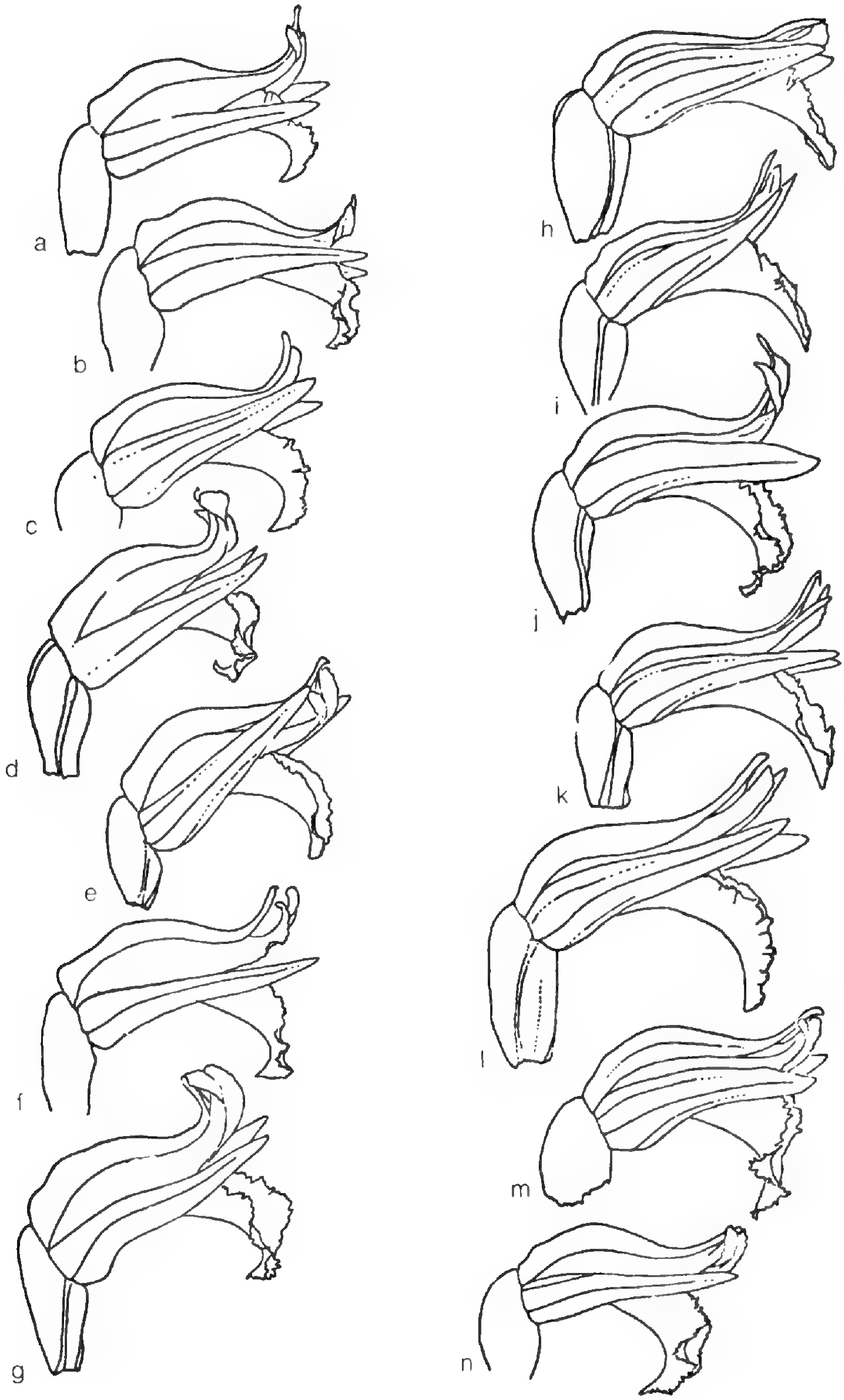
| | | |
|---|---|---|
| Norfolk Co. (TRT 153068) | | 3 |
| Ontario Co. (*Catling* 13 Sept. '70) | | 1 |
| Wentworth Co. (TRT 85372) | | 1 |
| York Co. (*Catling* 21 Sept. '72) | | 1 |
| PENNSYLVANIA | | |
| Bradford Co. (*Catling* 13 Aug. '76) | 1 | |
| Erie Co. (*Sheviak* 988, *I. incurvum, TOPOTYPE)* | | *3* |
| QUEBEC | | |
| Sherbrooke Co. (*Catling* 5 Sept. '74) | | 2 |
| VERMONT | | |
| Windham Co. (*Sheviak 1043a*) | | 2 |
| Windham Co. (*Sheviak 1044*) | 2 | |

| | Number of OTU's |
|---|---|
| *Spiranthes cernua* (including 3 *Ibidium incurvum* topotypes) | 37 |
| *S. ochroleuca* | 30 |
| Indeterminates | 2 |
| Total | 67 |

RESULTS AND DISCUSSION

## The Types

Citation of the type of *Gyrostachys ochroleuca* has not been made in the literature; it may be significant that Ames, despite his emphasis on proper typification, never mentioned a type. Examination of the collection of the New York Botanical Garden revealed only a single specimen from the type locality old enough to have served as the type of *G. ochroleuca*. This small, poorly preserved specimen (*W. M. Whitfield s.n.*, 30 August 1889) shows no signs of ever having been seen by Rydberg, and is apparently referable to *Spiranthes cernua*. Another collection by Whitfield, made a few days later on 5 September, does appear to represent *S. ochroleuca;* this specimen is in the herbarium of the University of Minnesota (MIN *94418*) and similarly cannot be connected with Rydberg.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The New York Botanical Garden collection (NY), however, includes a drawing labeled "*Gyrostachys ochroleuca* Rydberg *ined.* Britton's Manual 1901. Drawings by Mrs. Long, Mt. Washington, Mass. 1897" (Figure 1). Significantly, an additional series of drawings, also at NY, is labeled "Drawings by Mrs. Long of *Spiranthes cernua.* Mt. Washington, Mass. September 1897." It appears that the drawing labeled *G. ochroleuca* is Rydberg's type. This conclusion, suggested by the labeling of the drawing, is supported by the correlation between the characteristics of the drawing and those attributed to *G. ochroleuca* in Rydberg's description. Additionally, comparison with archival materials indicated a strong possibility that the label is in Rydberg's hand, although a relationship could not be established with certainty.

The drawings of *Spiranthes cernua* illustrate rather well some of the previously suggested distinguishing characteristics of this species, such as nodding flowers and basally dilated lips. In contrast, the drawing of *Gyrostachys ochroleuca* shows a plant with ascending flowers and an ovate-oblong, non-dilated lip. The basis for Rydberg's description of the spike in *G. ochroleuca* as acute is also revealed in this drawing. The larger plant illustrated is in very early flower and, like all northeastern *Spiranthes* in this stage of development, the upper part of the inflorescence is composed of erect pointed buds of decreasing size resulting in an acute tip. The five drawings of *S. cernua* represent plants all fully in flower, and not surprisingly the inflorescences appear obtuse. This is, additionally, a significant early suggestion of a slightly later flowering time for *S. ochroleuca* at the type locality. The lower floral bracts in the

Figure 5. Camera lucida drawings made from pickled flowers of *S. ochroleuca* and *S. cernua*. Flowers viewed laterally.

**a-g**, *Spiranthes ochroleuca*. a,b,c, Mt. Washington, near Hunts Pond, Berkshire Co., Mass., 10 Sept. 1976. d, 10 miles E of Lee, Berkshire Co., Mass., 4 Sept. 1975. e, 2 miles W of Jordan Falls, Shelburne Co., Nova Scotia, 25 Aug. 1975. f, Armenia Mt., S of Sylvania, Bradford Co., Penn., 10 Sept. 1976. g, 1 2 mile N of Thamesville, Zone Tp., Kent Co., Ont., 18 Sept. 1976.

**h-n**, *Spiranthes cernua*. h,i, Mt. Washington near Hunts Pond, Berkshire Co., Mass., 10 Sept. 1976. j, 10 miles E of Lee, Berkshire Co., Mass., 4 Sept. 1975. k, Toronto Island, York Co., Ont., 24 Sept. 1976. l, 1 mile SW of Lake St. Nora, Stanhope Tp., Haliburton Co., Ont., 29 Aug. 1976. m, Mont Orford Park, Sherbrooke Co., Quebec, 5 Sept. 1974. n, 1 mile NE of Erroll, Coos Co., New Hampshire, 1 Sept. 1976.

illustration of *G. ochroleuca* are, as described by Rydberg, ovate-lanceolate, acuminate, and longer than the flowers. Those illustrated for *S. cernua,* in contrast, are quite variable, but often shorter than those of *G. ochroleuca* and more ovate, with an aristate, rather than acuminate, apex.

Typification of *Spiranthes cernua* is easily established. In the Linnaean herbarium in London is a specimen (LINN *1056.9:* Figure 2) on which Linnaeus has written *"cernua"* and "K" (*i.e.* Kalm). Although Linnaeus did not directly indicate the basis for the description of his new species *Ophrys cernua* in Species Plantarum in 1753, he did state "Habitat in Virginia, Canada". Since Linnaeus had Kalm's collection of "Canadian" material prior to 1753, and any reference to Canada by Linnaeus refers exclusively to Kalm's work, a Kalm collection would be a suitable choice for a lectotype. There are two plants on the sheet (LINN *1056.9*). The right hand specimen bears a highly characterisic inflorescence of densely arranged, nodding flowers. This specimen does not include roots. The left hand specimen, bearing roots, has a less well developed inflorescence of rather ascending flowers, with only a few nodding flowers interspersed. This condition is found in *S. cernua* when it is grown in dense vegetation, and in cultivation such plants produce inflorescences of horizontal or nodding flowers. Linnaeus' description included reference to both nodding flowers and roots, so we must assume that he based his concept on both of these specimens.

Asa Gray annotated the right hand specimen "*Romanzoviana* A. Gray" and the left hand specimen "*cernua auctor.*" Oakes Ames later wrote on the sheet, "Gray is most certainly mistaken—this is *S. cernua*, Oakes Ames, Nov. 14, 1905." Dr. L. A. Garay has kindly

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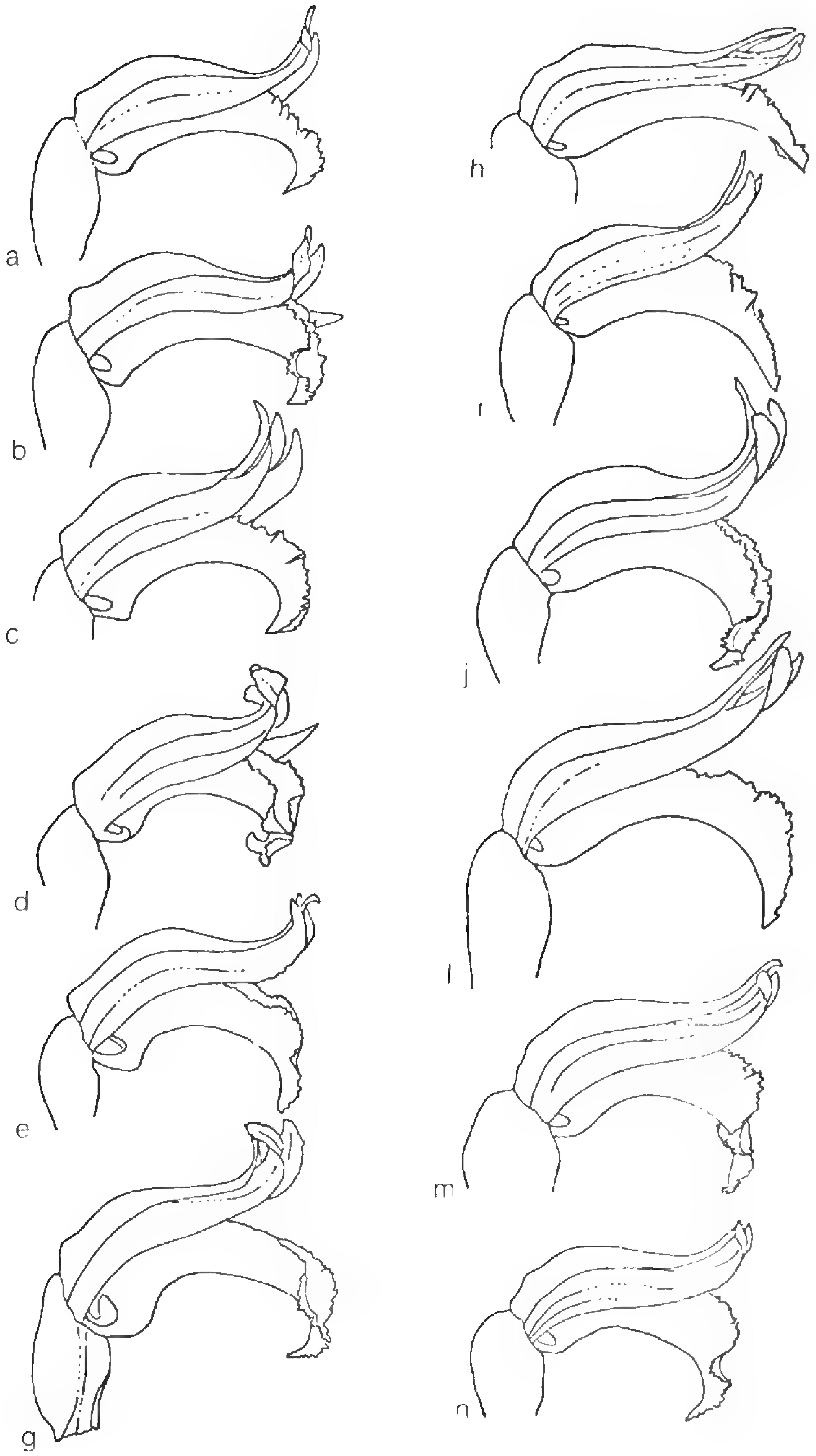
Figure 6. Camera lucida drawings made from pickled flowers of *S. ochroleuca* and *S. cernua*. Flowers viewed laterally with the lateral sepal removed.

a-g, *Spiranthes ochroleuca*. a,b,c, Mt. Washington, near Hunts Pond, Berkshire Co., Mass., 10 Sept. 1976. d, 10 miles E of Lee, Berkshire Co., Mass., 4 Sept. 1975. e, 2 miles W of Jordan Falls, Shelburne Co., Nova Scotia, 25 Aug. 1975. g, 1/2 mile N of Thamesville, Zone Tp., Kent Co., Ontario, 18 Sept. 1976.

h-n, *Spiranthes cernua*. h,i, Mt. Washington, near Hunts Pond, Berkshire Co., Mass., 10 Sept. 1976. j, 10 miles E of Lee, Berkshire Co., Mass., 4 Sept. 1975. l, 1 mile SW of Lake St. Nora, Stanhope Tp., Haliburton Co., Ontario, 29 Aug. 1976. m, Mont Orford Park, Sherbrook Co., Quebec, 5 Sept. 1974. n, 1 mile NE of Erroll, Coos Co., New Hampshire, 1 Sept. 1976.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provided us with drawings of the flowers from each of these specimens. It is clear from these drawings (Figure 3) that neither plant represents *Spiranthes romanzoffiana*, which is characterized by a pandurate lip.

The measurements accompanying Garay's drawings of the type material enable the length of the calli to be calculated. These calli lengths range from ca. 0.8 to 1.0 mm and are therefore more like *Spiranthes cernua* than *S. ochroleuca* (Table 1). A correlation exists between lip length and calli length; larger lips have larger basal calli. Therefore it is convenient to express the calli length in relation to the lip length. Ratios of the length of the lip to the length of the calli are usually less than 7.5 in yellow-flowered upland plants referable to *S. ochroleuca*, but average 8.0–9.0 in *S. cernua*. The ratios for the three lips illustrated by Garay are ca. 9.0–9.4.

The floral bracts measuring ca. 10.3 mm in the left hand specimen of LINN *1056.9* and ca. 12.5 mm in the right hand specimen are well within the usual range of white-flowered plants generally called *S. cernua*, and the leaves are all basal, the stem bearing only cauline bracts. Therefore the type material of *S. cernua* does not display characteristic features of *S. ochroleuca* as described originally by Rydberg. In fact, LINN *1056.9*, which we designate as lectotype of *S. cernua*, clearly represents the taxon treated as *S. cernua* by recent American authors.

### The type locality

Yellow-flowered plants in drier sites referable to *Spiranthes ochroleuca* and white-flowered plants of more moist habitats

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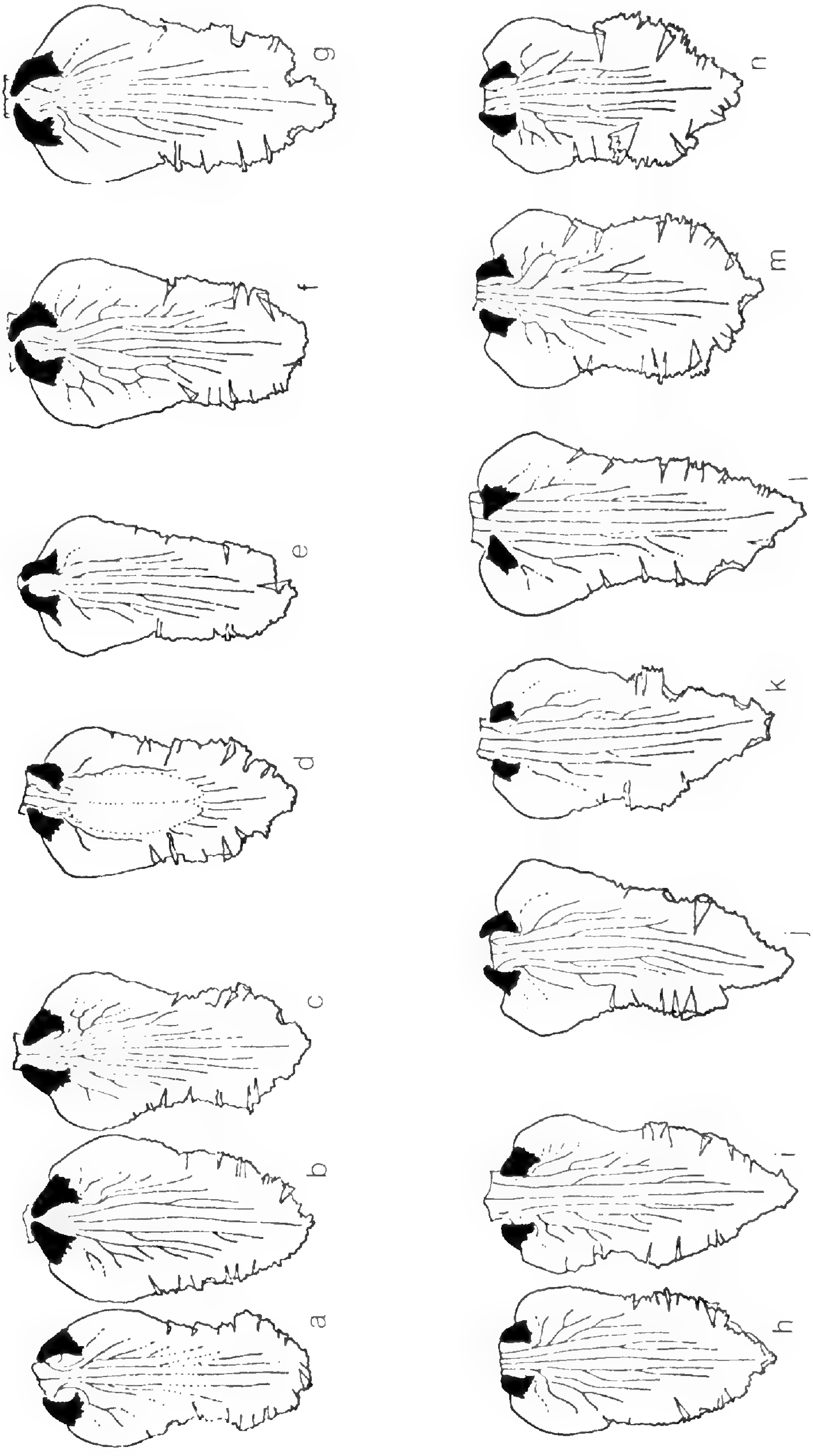
Figure 7. Camera lucida drawings made from pickled flowers of *S. ochroleuca*. Upper surface of lip pressed flat.

**a-g**, *Spiranthes ochroleuca*. a,b,c, Mt. Washington, near Hunts Pond, Berkshire Co., Mass., 10 Sept. 1976. d, 10 miles E of Lee, Berkshire Co., Mass., 4 Sept. 1975. e, 2 miles W of Jordan Falls, Shelburne Co., Nova Scotia, 25 Aug. 1975. f, Armenia Mt., S of Sylvania, Bradford Co., Penn., 10 Sept. 1976. g, 1/2 mile N of Thamesville, Zone Tp., Kent Co., Ont., 18 Sept. 1976.

**h-n**, *Spiranthes cernua*. h,i, Mt. Washington, near Hunts Pond, Berkshire Co., Mass., 10 Sept. 1976. j, 10 miles E of Lee, Berkshire Co., Mass., 4 Sept. 1975. k, Toronto Island, York Co., Ont., 24 Sept. 1976. l, 1 mile SW of Lake St. Nora, Stanhope Tp., Haliburton Co., Ont., 29 Aug. 1976. m, Mont Orford park, Sherbrooke Co., Quebec, 5 Sept. 1974. n, 1 mile NE of Erroll, Coos Co., New Hampshire, 1 Sept. 1976.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referable to *S. cernua* were found abundantly at the type locality, i.e. Mt. Washington, Berkshire County, Massachusetts (ca. 42°05′ N., 73°27′ W.).

The *Spiranthes ochroleuca* plants had distinctly yellowish flowers. (4d, 8d; Royal Horticultural Society colour chart, 1966). The central portion of the lip was deep straw yellow (13c). The *S. cernua* plants had essentially white flowers (155c) with the central portion of the lip at most a very pale creamy-white (6d,9d).

The yellow-flowered plants were found exclusively in drier sites associated with species characteristic of well-drained soil (e.g. *Plantago lanceolata, Rubus flagellaris, Hypericum perforatum, Pedicularis canadensis, Botrychium dissectum* var. *dissectum, Vaccinium angustifolium, Achillea millefolium, Aster ericoides, Solidago nemoralis, Solidago bicolor, Viola fimbriatula, Fragaria virginiana, Danthonia spicata,* and *Polytrichum* sp.).

The white-flowered plants were found always in wet humic soil with typical species of open mesic to wet sites (e.g. *Prunella vulgaris, Ranunculus* spp., *Plantago major, Viola* spp., *Lycopus americanus, Carex* spp., *Juncus* spp.).

Similar observations of habitat and associates of *Spiranthes ochroleuca* and *S. cernua* have been made consistently. *Spiranthes ochroleuca* is characteristically a colonizer and commonly invades roadcuts and old fields. Large populations may develop in open herbaceous communities, especially in sporadically mowed situations in full sun or occasionally in light shade. It occupies mesic to somewhat xeric sites usually on acidic sandy or rocky soils. Organic mats on acutely drained outcrops are sometimes utilized; there is also some evidence for its occurrence in finer textured soils.

In disturbed sites, *Spiranthes ochroleuca* frequently associates with *S. cernua,* but the two species show distinct moisture preferences. Under the wettest conditions, the latter species occurs alone. In typical roadcut colonies, *S. ochroleuca* is found abundantly on the upper slopes, whereas *S. cernua* occupies ditches. Some mixture occurs on the basal portions of slopes, and *S. cernua* may occur locally about seepages far up the slope. Conversely, a few *S. ochroleuca* may be found in drier situations atop mounds and rocks along the base of the slope.

A phenological difference between *Spiranthes ochroleuca* and *S. cernua* was apparent at Mt. Washington. *Spiranthes ochroleuca* was just coming into its peak of flowering (maximum number of fresh flowers) when *S. cernua* was slightly past its peak. We have noticed a similar and sometimes more pronounced separation in peak flowering period elsewhere in New England, in Ontario, and in Pennsylvania in those locations where both species occur together.

In summary, the plants of *Spiranthes ochroleuca* at the type locality were the same in general appearance, ecology, and phenology as plants we had come to call *S. ochroleuca* over a wide area of the northeast.

## Distinguishing features of Spiranthes ochroleuca

Having established the identity of *Spiranthes ochroleuca* on the basis of the original description, the literature in general, the type drawing, and a visit to the type locality, it became obvious that the main source of confusion was *S. cernua*. Other *Spiranthes* species do apparently contribute to the problem, but to a much lesser extent. *Spiranthes laciniata* (type locality: Eustis, Florida) is a taller (to 9.5 dm), more southern coastal plain species with a longer, more loosely spiraling inflorescence and shorter floral bracts. *Spiranthes magnicamporum* Sheviak (1973, type locality: Greene Co., Illinois) occurs mostly to the west of *S. ochroleuca* and is readily distinguished by the absence of basal leaves at flowering time, relatively thick roots (ca. 1 cm), long and narrow perianth parts (ca. 1 cm), and smaller basal calli (ca. 0.5 mm) on the lip. *Spiranthes casei* Catling and Cruise (1974, type locality: Muskoka District, Ontario) occurs mainly to the north of *S. ochroleuca* and differs in having a more loosely flowered spike of relatively smaller flowers with wider lateral sepals, and in its shorter cauline and floral bracts.

Although distinguishing *Spiranthes cernua* was clearly the main problem, it was quite possible to assign most specimens to either *S. ochroleuca* or *S. cernua* and to evaluate their salient characteristics as well as to search for additional ones. Drawings of pickled flowers collected by the authors and examination of living plants over a wide geographical area indicated many characters to be useful to a greater or lesser extent in separating these species.

*Spiranthes ochroleuca* is most readily recognized in the field by its creamy to ochroleucous flowers which are in sharp contrast to the characteristic white of *S. cernua*. Structurally, they are quite constant and characteristically distinct from those of *S. cernua* in bearing lateral sepals without any curvature as viewed from above. In *S. ochroleuca* these sepals are commonly appressed to the other floral segments or but slightly spreading and extend stiffly forward, whereas the other segments reflex and curve apically. In *S. cernua,* the lateral sepals nearly always spread slightly from the base and then incurve apically to approach the apices of the dorsal sepal and petals.

The more ascending nature of the lateral sepals and greater separation of the lateral and dorsal sepals in *S. ochroleuca* is clear in Figure 5. The flowers of *S. ochroleuca* also tend to have a greater curvature, both dorsally and ventrally. The ascending nature of the flowers of *S. ochroleuca* and this increased curvature may help to account for the increased separation of the dorsal and lateral sepals as well as for the somewhat larger aperture formed by the basal lip and basal lateral petal. A somewhat greater area of attachment at the top of the ovary, a more downward orientation of the lip stalk, and a more prominent basal hump on the dorsal sepal in *S. ochroleuca* makes these flowers relatively wider basally, and the tube therefore has a greater basal diameter. These features are more or less clear in Figures 5 and 6.

The lips of *Spiranthes ochroleuca* and *S. cernua* differ in some respects and the observed range of variation is illustrated in Figure 7. *Spiranthes ochroleuca* consistently has larger basal calli and exhibits a tendency for the basal parts of the lip to be more gradually tapered resulting in a larger angle of basal curvature (Figures 4c & 7). The basal dilation of the *S. cernua* lip results in a relatively smaller angle of basal curvature and a "hunched shoulders" appearance. The lip of *S. cernua* is often, but not always, more gradually tapered distally, the tapering involving the apical half to third of the lip, whereas in *S. ochroleuca* the tapering is usually limited to the apical quarter of the lip.

In addition, the texture of the lip can be useful in identification. The lip of *Spiranthes ochroleuca* is thick and fleshy, even in softened herbarium material, while in *S. cernua* it is usually membranaceous in such material and only slightly fleshy in fresh condition. The increased fleshiness of the *S. ochroleuca* lip frequently makes the venation difficult to see except through the use of transmitted light. These lip characters must be used with caution in the determination of dried material. Natural senescence of the flower or poor preservation may sometimes produce apparent basal dilation in lips originally without it, and often alter the fleshy condition to a membranaceous one. Hence, only in well preserved herbarium material should floral characters be used for determination.

As the name implies, the flowers of *Spiranthes cernua* are nodding. This is a nearly constant characteristic and only occasionally do specimens of this species produce horizontal or ascending flowers. These are confined to obviously depauperate, often somewhat etiolated specimens and to a few peculiar forms which show various other abnormalities. In contrast, *S. ochroleuca* exhibits an intrinsic potential for the production of ascending flowers. Often field-grown specimens, especially robust plants in exposed situations, bear nodding basal flowers, but when cultivated under more moderate conditions, such plants in following seasons produce inflorescences with ascending flowers. Certain other characters which are of use in separating *S. ochroleuca* from *S. cernua* are dealt with in the statistical analyses below.

Inflorescences of *Spiranthes ochroleuca* bearing ascending flowers are more slender than those of *S. cernua* bearing nodding flowers of the same size. The comparatively slender inflorescence of ascending flowers in *S. ochroleuca* is distinct in the herbarium and hence can be of use in determination. This would seem to be in opposition to the spike measurements given by Rydberg, but it is difficult to account for the measurements he attributed to *S. cernua*, since only rarely do members of either of these species exhibit such slender inflorescences. In fact the ranges given by Rydberg are much too restrictive. Both species exhibit a similar range in inflorescence diameter, although *S. ochroleuca* averages somewhat smaller than *S. cernua*.

The more slender appearance of the *Spiranthes ochroleuca* inflorescence is often enhanced by a higher angle to the parastichy in this species, which contributes a more open aspect to the inflorescence than in most plants of *S. cernua*. Especially in small specimens, the insertion of flowers in *S. ochroleuca* may be in a rather evident spiral with the vertically superposed flowers so removed as to eliminate obvious orthostichies. Such a situation is known in *S. cernua* only in a few forms from restricted parts of its range. Robust specimens of *S. ochroleuca*, especially in exposed sites, however, commonly exhibit inflorescences as dense and obviously ranked as those of *S. cernua.*

The floral bracts of *Spiranthes ochroleuca* are generally somewhat longer than in northeastern material of *S. cernua.* They tend to be narrower and more gradually tapered. In *S. cernua* they are often widest at a point approximately one third the distance from the base to the apex; above this point they taper abruptly to a long, rather aristate tip. The longer, more acuminate bracts of *S. ochroleuca* together with a more open inflorescence make the inflorescence of this species appear greener and more "leafy." These features of the floral bracts are best evaluated in qualitative terms because they exhibit a good deal of overlap.

Foliar characters may also serve to distinguish these species. Under favorable conditions leaves of *Spiranthes ochroleuca* are sessile to short-petiolate, arcuate-spreading, oblanceolate to elliptical, canaliculate, and of a curious rough-flexible texture. A few may be borne on the lower portion of the stem. In *S. cernua,* in contrast, leaves are more typically petiolate, often notably so, ascending, linear-lanceolate to oblanceolate, conduplicate, and membranaceous. They are only rarely borne on the stem. Variation toward *S. ochroleuca* in all of these features is sometimes seen, however.

Both authors have maintained plants referable to *Spiranthes ochroleuca* and *S. cernua* in cultivation under uniform conditions. With the few exceptions noted above, all distinctive characteristics including flower colour, morphology, and phenology have been maintained. Significantly, uniform cultural conditions have been found to enhance the expression of distinctive characters over their manifestation in the field. Correlation of the characteristics of individuals in the field, under cultivation, and in the pressed condition has been of great importance in assessing the potential phenotypes and variability in these species.

## Geographical Distribution

Figure 8 shows the distribution of *Spiranthes ochroleuca* based on collections of the authors and readily determinable material from a number of herbaria. It is interesting to compare this distribution with the ranges determined by Swamy (1948). Swamy showed the "sexual race of *S. cernua*" to be confined to the northeast from New England south through New York and Pennsylvania. This compares

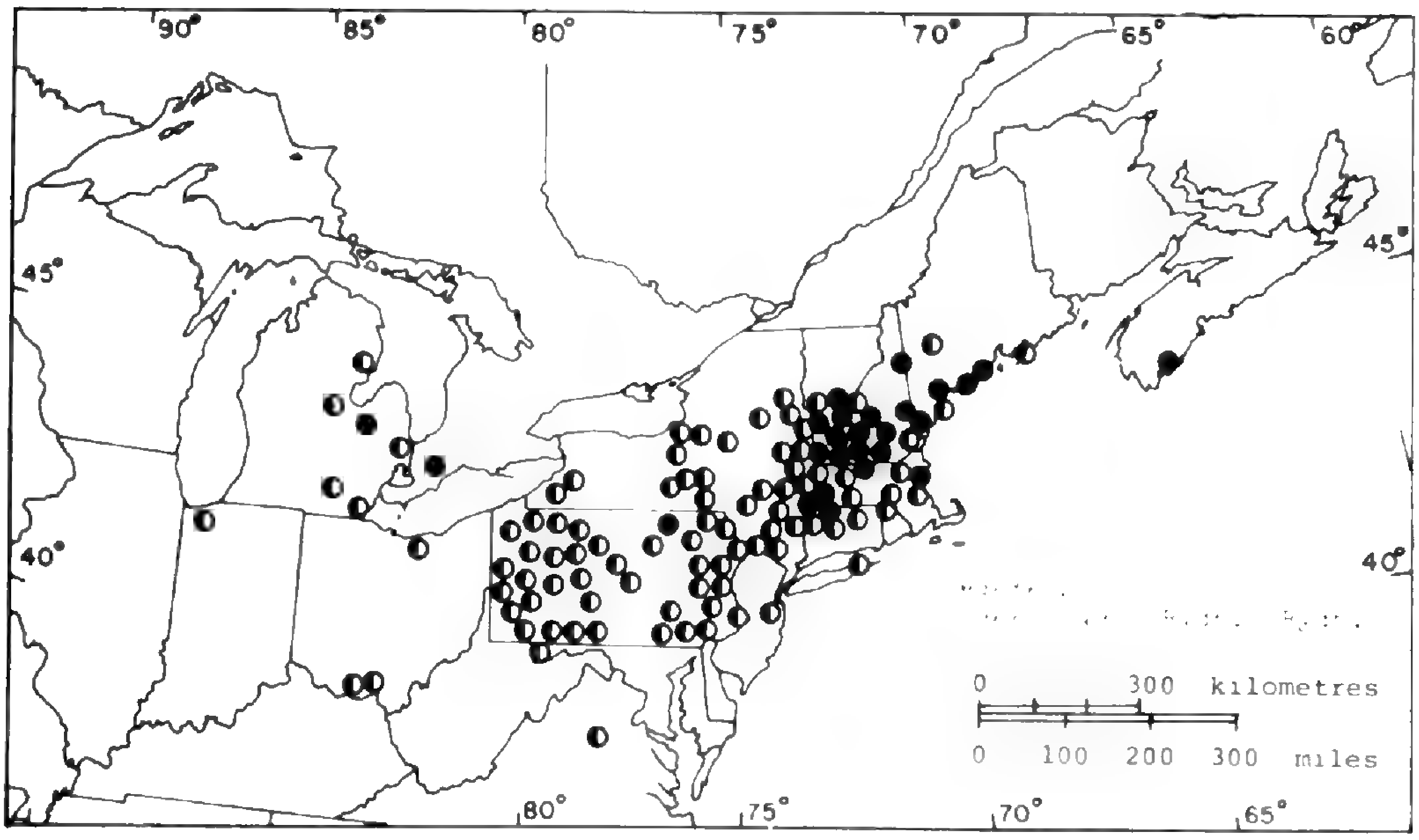

Figure 8. The distribution of *Spiranthes ochroleuca* (Rydb.) Rydb. in the northeast based on personal collections of C. J. Sheviak and P. M. Catling (solid dots) and on well preserved and easily assigned herbarium specimens (half dots).

closely with our map of the distribution of *S. ochroleuca*. Swamy found a much wider distribution of the "asexual and intermediate races of *S. cernua*" to the north, west, and south corresponding with our determination of the range of *S. cernua*. Swamy's races were based on reproductive mode and embryo number, whereas our map reflects study of morphological characters.

## Seeds, chromosomes, and pollen

It should be clear from this discussion that typical *Spiranthes ochroleuca* is readily distinguished from most *S. cernua* when living material is being considered; greater difficulty is encountered with dried material. In the herbarium some specimens cannot be satisfactorily placed through consideration of any commonly cited gross morphological characters. This situation drove Ames to conclude that the only reliable character was embryo number. Correll (1950) commented on the ultratechnical nature of this character and, indeed, it it undesirable to be forced to such extremes. However, our experience indicates that it does provide a clear distinction between the species: *Spiranthes ochroleuca* pro-

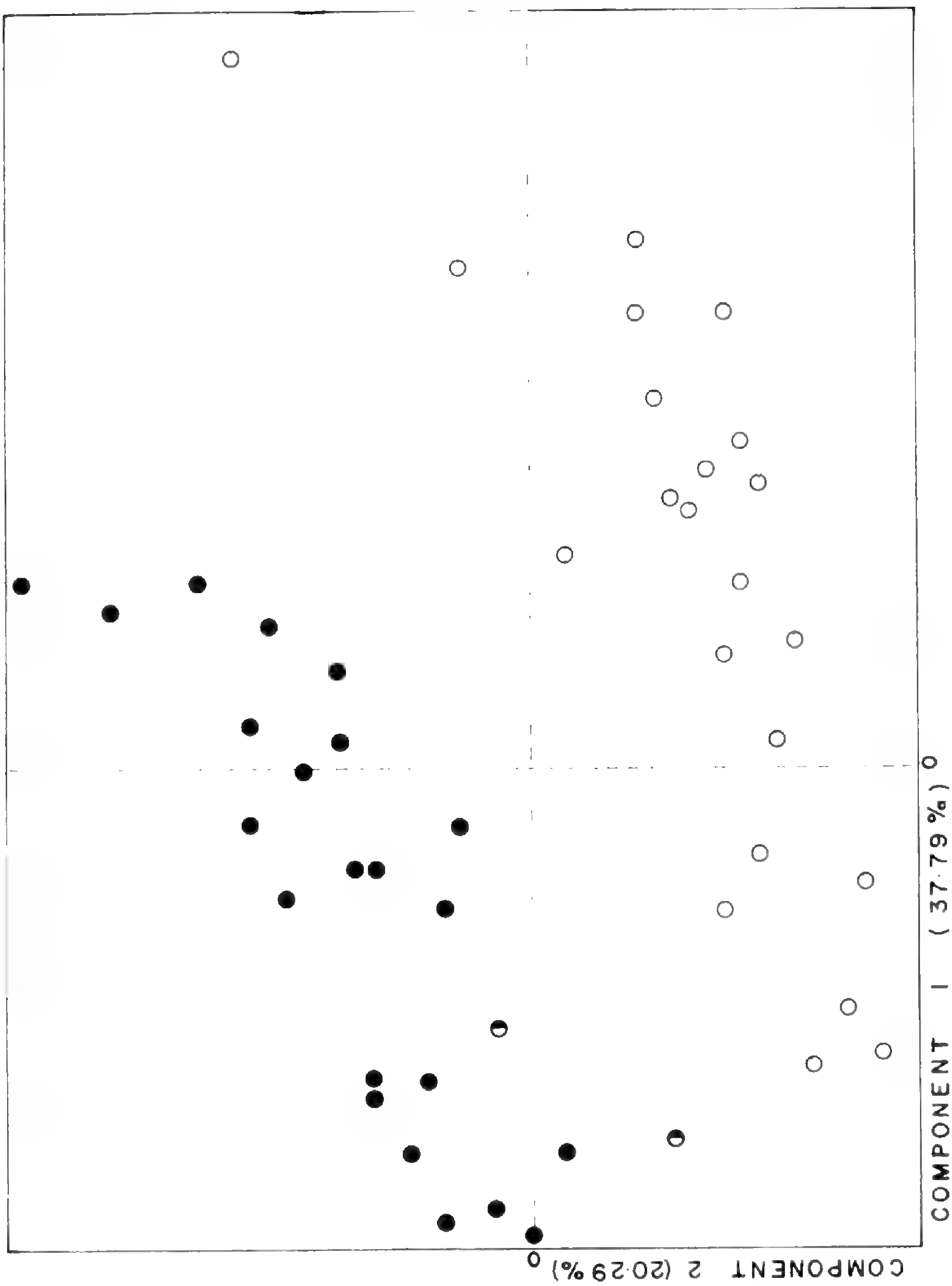

Figure 9. A 2-dimensional view of the position of 22 pickled flower specimens of *S. ochroleuca*, 22 of *S. cernua* and 3 "intermediates", on principal components 1 and 2 extracted from the matrix of correllations among 24 characters measured in material from the type locality, Mt. Washington, Mass. Open circles — *S. ochroleuca*, darkened circles — *S. cernua* and half-darkened circles — "intermediates".

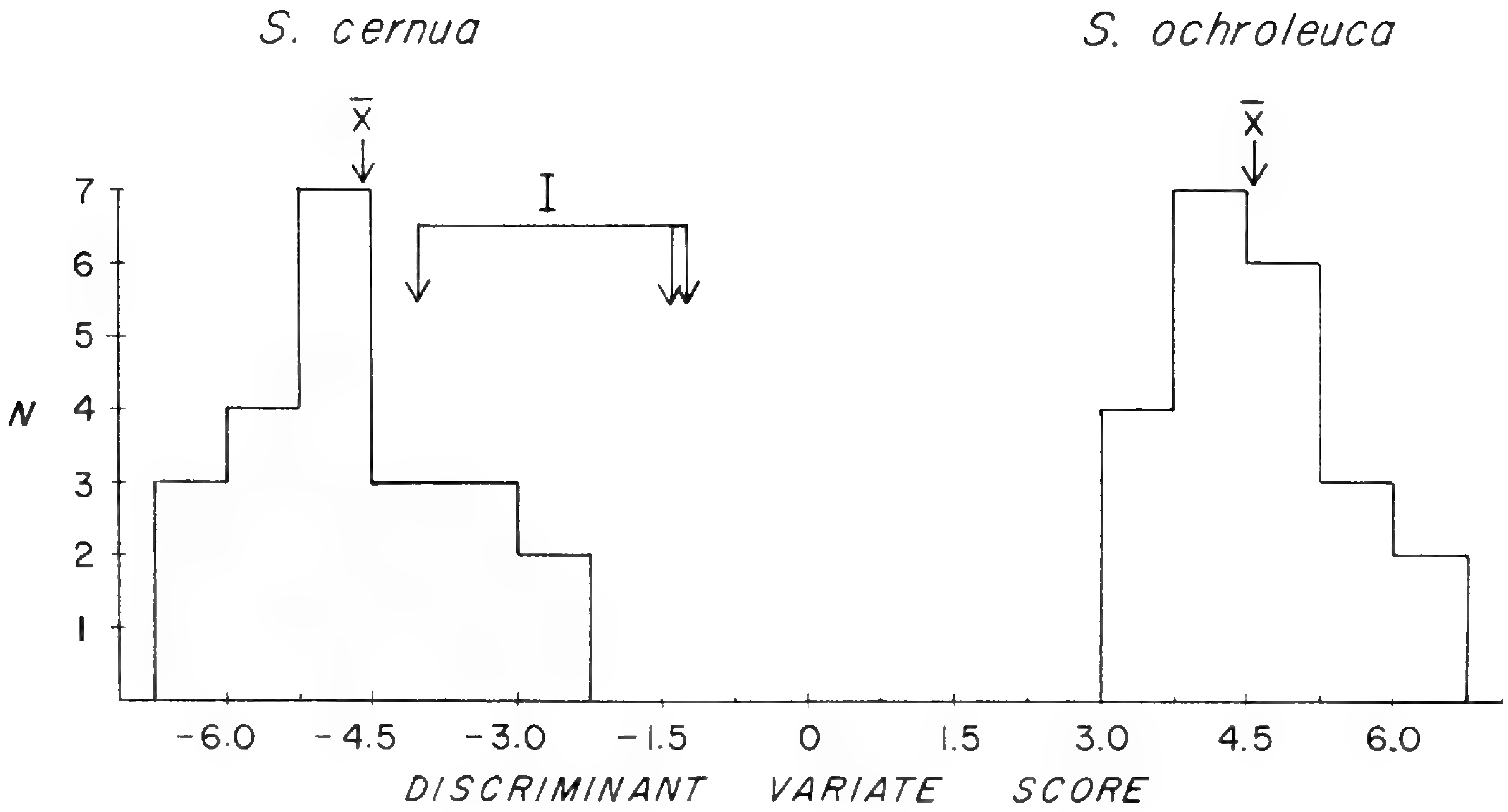

Figure 10. Histograms of discriminant scores of 22 pickled flower specimens of *S. ochroleuca* and 22 of *S. cernua*. The position of 3 apparent intermediates (I) is indicated. The plot is based on the "best" discriminant function incorporating 7 floral characters derived in stepwise fashion from 24 (see Table 1). For *S. ochroleuca* the group mean ($\overline{X}$) is 4.65 and the standard deviation of scores is 0.86. For *S. cernua* the group mean ($\overline{X}$) is 4.65 and the standard deviation is 1.12.

duces strictly monoembryonic seeds, whereas different forms of *S. cernua* yield varying percentages of polyembryonic seeds. Swamy has shown sexually reproductive plants to produce monoembryonic seeds and polyembryony to result from adventitious embryony. Detailed work on the *S. cernua* complex (Sheviak, unpubl.) has shown diploids to be sexually reproductive, whereas all polyploids exhibit apomictic potential. In the present study, we have obtained strictly diploid counts ($2n = 30$) on specimens determined as *S. ochroleuca,* and only polyploid counts ($2n = 60$ or rarely 45) on *S. cernua* (see Table 3). Hence embryo number appears to be an important character which serves to separate the diploid *S. ochroleuca* from the polyploid *S. cernua*.

Care must be taken with seed characters, however, since some obligately apomictic races of *Spiranthes cernua* exhibit a low percentage of polyembryony. A casual examination is therefore insufficient. Observation of polyembryony requires some patience. If herbarium material is being studied, seeds should be softened before examination, as this greatly aids resolution of closely overlapping embryos. Additionally the lack of understanding of the mechanism regulating reproductive mode in *Spiranthes* dictates caution, and seed characters are best used in conjunction with others.

Swamy (1948) reported pollen degeneration in asexual *Spiranthes cernua* and noted normal behavior in the sexual race, i.e. *S. ochroleuca.* Pollen abortion appears to be influenced by the environment; in our greenhouse studies we have observed this phenomenon and in addition irregularities of stipe and disc formation to be associated with high ambient temperatures. *Spiranthes ochroleuca* and various other species exhibit the same anomalies as *S. cernua*. Although different races of *S. cernua* show differing susceptibility to such conditions and the causes of the phenomenon are unknown and deserve further study, it appears that pollen degeneration is of little taxonomic significance.

## Statistical analysis of flower morphology

In Principal Components Analysis (Figure 9) flowers from *Spiranthes ochroleuca* determined on the basis of flower colour, general aspect, and habitat cluster together. None of the *S. cernua* clusters with *S. ochroleuca* and vice-versa. This clustering, based on a matrix of correlations among 24 features of flower morphology, is very important since it demonstrates clearly that these taxa, previously separated on the basis of various qualitative characters may also be separated quantitatively on the basis of floral structure alone.

The means, standard deviations, and units of the various characters are given in Table 1. The most powerful discriminating characters are the length of the stigmatic surface, length and width of lateral petal, length and width of anther sac, length of sepal, angle of curvature of lip from basal stalk, length of basal calli, separation of dorsal and lateral sepal, and the angle of basal curvature of the lip "shoulders," which measures basal dilation. Some of these are the same characters that were found to be most significant in separating the two species over a broad geographic area.

The Discriminant Functions Analysis (Figure 10) clearly separates *Spiranthes ochroleuca* from *S. cernua*. The "intermediate" plants in both PCA and DFA are more closely associated with *S. cernua* than *S. ochroleuca*, reflecting a morphological similarity that was evident even in the field. This clustering of the intermediates with the tetraploid *S. cernua* is a predictable result of dilution of the *S. ochroleuca* genome in allopolyploids; the entirely comparable results of the analysis of dried material, which included known triploids (see below), supports this hypothesis.

### Statistical analysis of dried material

Collection locality, number of specimens, and chromosome numbers are provided in Table 3. The specimens represent a wide geographical area; in the case of *Spiranthes ochroleuca*, 23 percent are topotypes. Of the *S. cernua* specimens, 35 percent are from outside the principal range of *S. ochroleuca* in the northeast. Units, means, standard deviations, and DFA character weights are given in Table 2.

Again in PCA (Figure 11), *Spiranthes ochroleuca* specimens determined as such on the basis of flower colour, various qualitative characters, and habitat formed a fairly well-defined cluster distinct from the *S. cernua* cluster. All diploid plants are located in the *S. ochroleuca* cluster while triploids and tetraploids are confined to the *S. cernua* cluster. Topotypes of *Ibidium incurvum* cluster with *S. cernua* and topotypes of *S. ochroleuca* cluster with plants referable to *S. ochroleuca* from elsewhere. Based on this morphological analysis, *I. incurvum* is not distinguishable from *S. cernua*, and *S. ochroleuca* from the type locality corresponds to *S. ochroleuca* over a broad geographical area.

Since the clusters are formed on the basis of quantitative morphology alone, and correspond to nominant *Spiranthes ochroleuca* and *S. cernua*, it is suggested that dried material can be correctly determined without weighting characters. We have been convinced of this for some time, and indeed our distribution map is based on the determination of herbarium material without character weighting.

The most useful characters in determining dried specimens were found to be the distance of separation of the dorsal and lateral sepals, and the curvature of the lip from the basal stalk. The length of the lowest floral bract and length of midstem bract are also useful. However, there is moderate overlap in all of these characters as might be expected with pressed and dried material. Certain characters that have already been discussed qualitatively can be evaluated in quantitative terms for the dried material in Table 2. One that has not been discussed previously is the tendency toward a somewhat larger ovary in *S. cernua* flowers at anthesis, a condition probably related to the early development of adventitious embryos (Swamy, 1948).

Flower colour, general appearance, habitat, and PCA on quantitative morphology have established the two species *Spiranthes ochroleuca* and *S. cernua* in the dried material. Using these determined groupings it is possible to find and evaluate the best means of discrimination using DFA. The results of two discriminant

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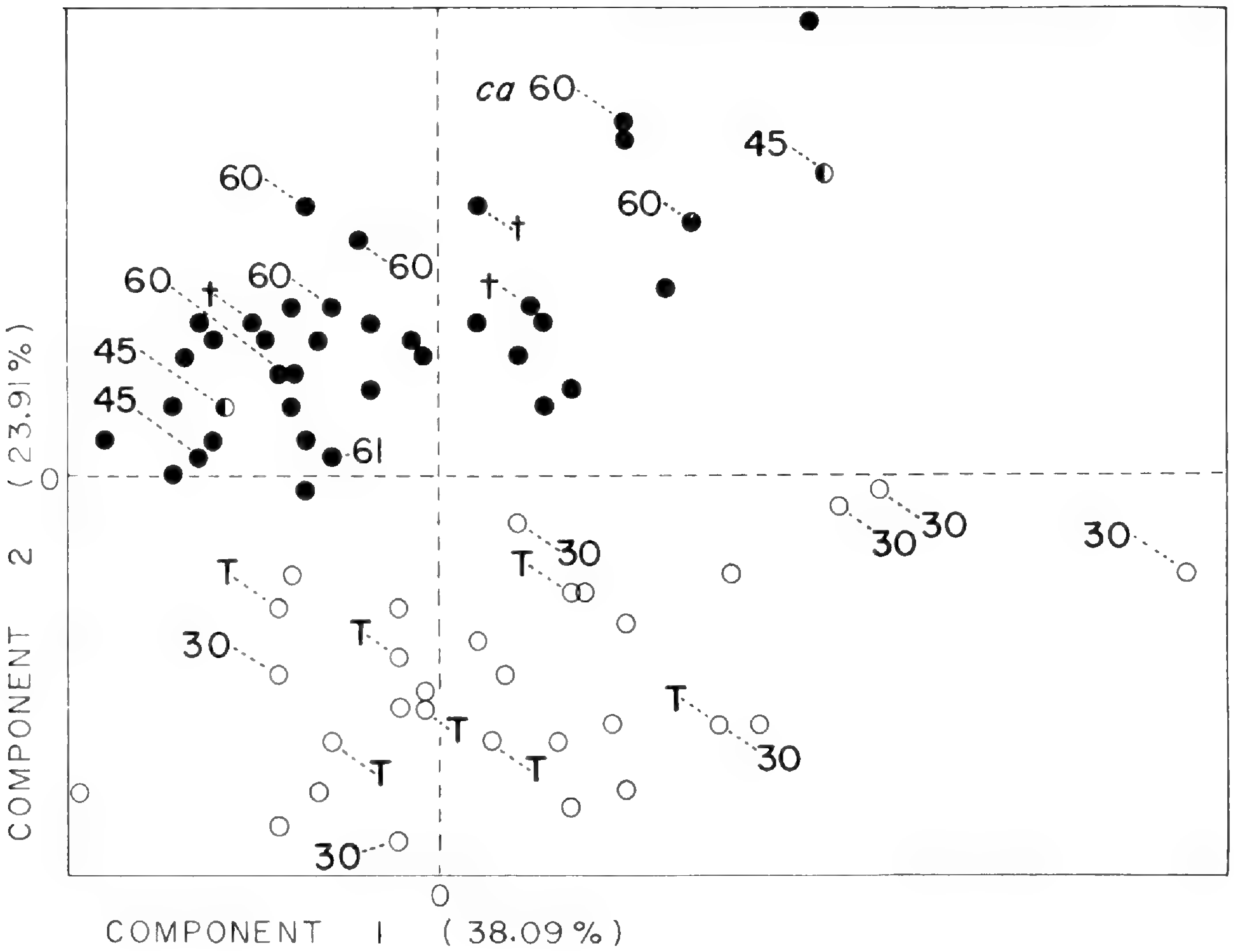
Figure 11. A 2-dimensional view of the position of 30 dried specimens referable to *S. ochroleuca*, 37 referable to *S. cernua* and 2 indeterminates, on principal components 1 and 2 extracted from the matrix of correlations among 11 characters measured in dried material from throughout the northeastern U.S. and adjacent Canada. Open circles — *S. ochroleuca*, darkened circles — *S. cernua*, half-darkened circles = indeterminates. Chromosome counts are shown for certain OTU's and topotypes of *Ibidium incurvum* (t) and *Spiranthes ochroleuca* (T) are also identified.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function analyses are shown in Figures 12 and 13. The former employs all eleven measured characters. The histogram of discriminant scores shows the scores to be distributed bimodally. The separation is more clear than in the PCA, as is to be expected with character weighting. No specimens are "misdetermined" (i.e., are placed differently than their flower colour, general appearance, morphology, and habitat would indicate). In the second analysis based on only four characters, separation is less dramatic but discrimination is complete. This function has the advantage of being more convenient for determination of herbarium material. It has, however, a disadvantage in relying more heavily on the separation of the dorsal and lateral sepals. If the flowers were withered when pressed or were very tightly pressed, this character may be difficult to use.

A limited set of measurements was available for the type of *Spiranthes cernua* (LINN *1056.9*) enabling the use of the second discriminant function. The resultant scores place the two plants representing the type of *S. cernua* in with the group representing *S. cernua* as defined by recent American authors (Figure 13). In both DFA histograms an isotype of *Ibidium incurvum* (CM *5603*) falls into the *S. cernua* group, again suggesting that the former name be placed in synonymy with the latter. Also in both of the DFA histograms the triploids fall within the *S. cernua* group as they did in unweighted analysis (Figure 11). Interestingly, two of the three triploids could not be determined in the field while one was determined as *S. cernua.* This suggests the possible occurrence of unidirectional gene flow from *S. ochroleuca* to *S. cernua,* a situation which will require detailed experimental work for proper verification.

## CONCLUSIONS

This study indicates that *Spiranthes ochroleuca* is a diploid, sexual species morphologically, ecologically, and to some extent

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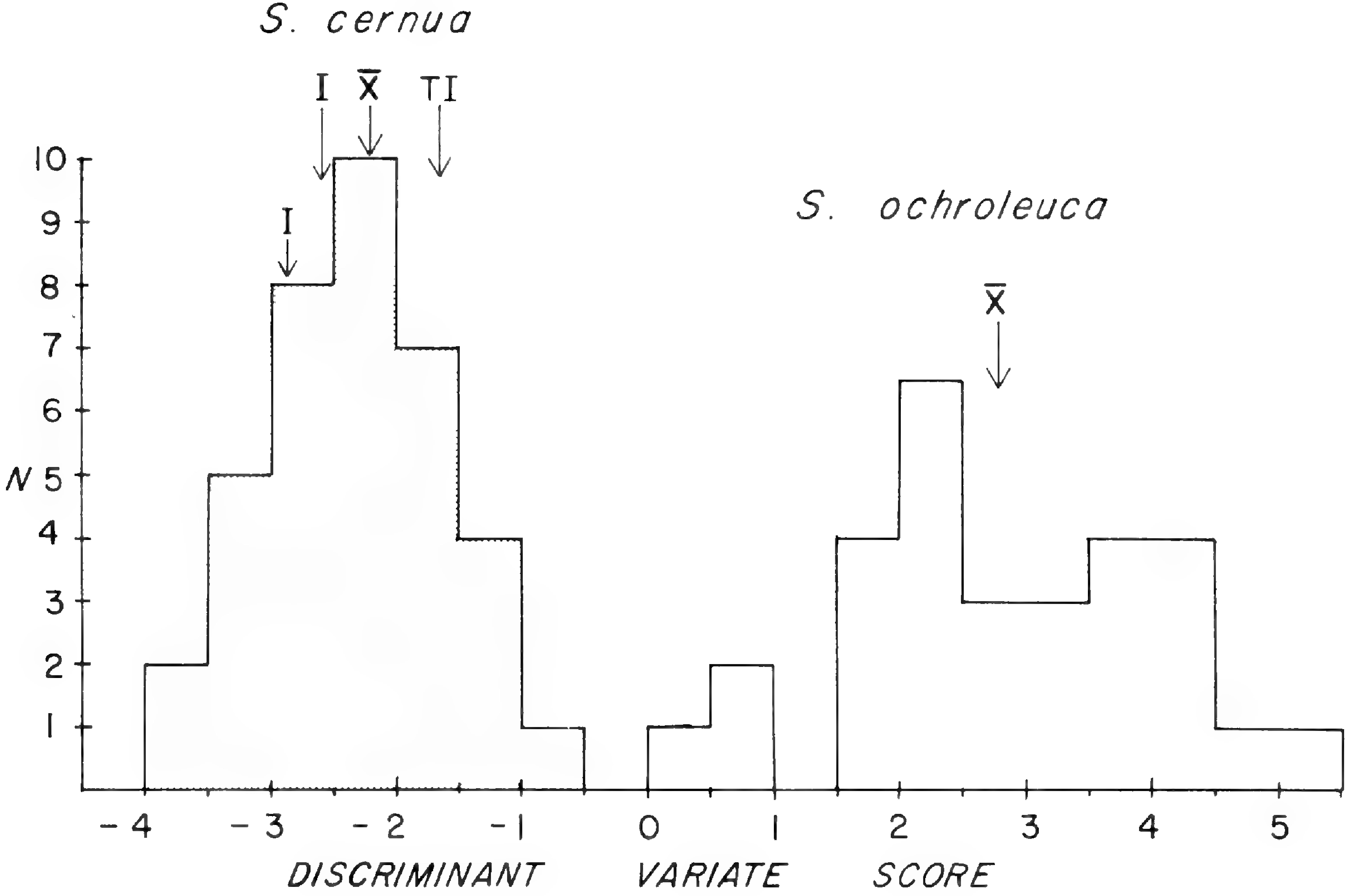
Figure 12. Histograms of discriminant scores of 30 dried specimens referable to *S. ochroleuca* and 37 referable to *S. cernua.* The plot is based on a discriminant function using all 11 characters measured (see table 2). The indeterminates, later found to be triploids, are positioned (I=—2.60, —2.84) as well as the isotype of *Ibidium incurvum* (TI=—1.68). For *S. ochroleuca,* the group mean ($\overline{X}$) is 2.78 and the standard deviation of scores is 1.24. For *S. cernua,* the group mean ($\overline{X}$) is —2.25 and the standard deviation is 0.750.


S. cernua
I
X̄
TI
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S. ochroleuca
X̄
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7
6
5
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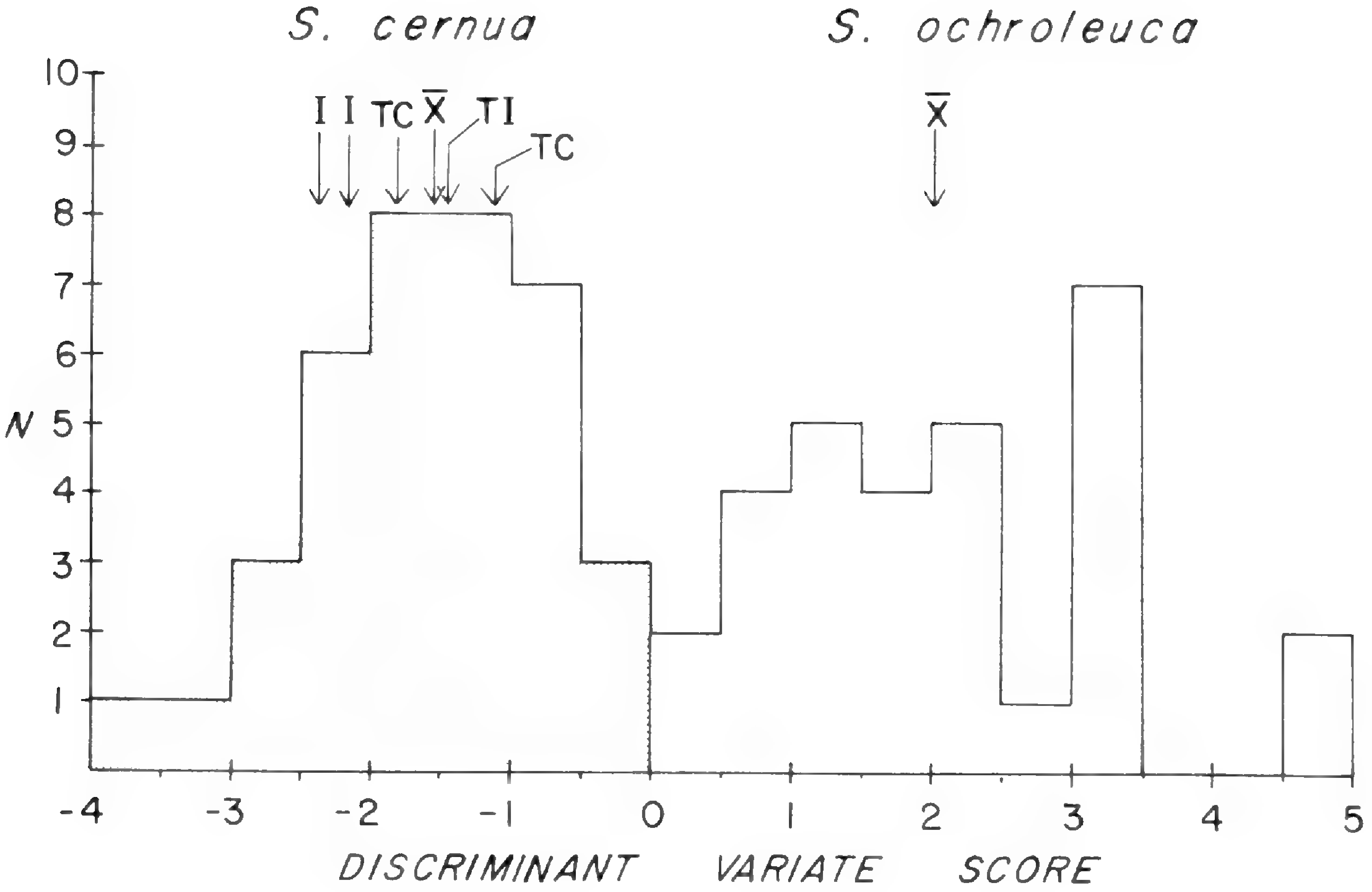
DISCRIMINANT VARIATE SCORE


S. cernua
S. ochroleuca
I
I
TC
X̄
TI
TC
X̄
N
10
9
8
7
6
5
4
3
2
1
-4
-3
-2
-1
0
1
2
3
4
5
DISCRIMINANT VARIATE SCORE

phenologically distinct from the polyploid, facultatively apomictic *S. cernua*. In contrast to the widespread *Spiranthes cernua, S. ochroleuca* exhibits a distinctive restricted distribution, occurring primarily in the northeast and becoming very rare and local westward. These differences clearly distinguish *S. ochroleuca* from *S. cernua* and justify specific rank. Topotype collections made by the authors (*C.J. Sheviak & J. Hart 1076*, 21 September 1976; and *P.M. Catling 831c*, 10 September 1976), for which data on habitat, flower colour, morphology, etc. are available, may be found at AMES, TRT, and CAN.

## ACKNOWLEDGMENTS

We are indebted to the following botanists for valuable discussion and criticisms: R.E. Schultes, L.A. Garay, R.C. Rollins, and C.E. Wood of Harvard University; J. McNeill of Agriculture Canada, Ottawa; R.S. Mitchell, New York State Museum; and F.W. Case II of Saginaw, Michigan. Measurements and drawings of the flowers of the type of *S. cernua* were kindly provided by L.A.Garay and other measurements of the same type were kindly provided by P.F. Hunt. We are grateful to F.W. Case II for providing living plants and for drawing our attention to the problem. Our taxonomic studies of the genus *Spiranthes* have received financial support from the Fernald Fund for Field Work in Systematic Botany, Harvard University; the Atkins Fund, Harvard University; the American Orchid Society Fund for Education and Research; and the National Research Council of Canada.

## LITERATURE CITED

AMES, O. 1905. A synopsis of the genus *Spiranthes* north of Mexico. Orchidaceae, fasc. 1: 122–154.

———. 1921. Notes on New England orchids, I. *Spiranthes*. Rhodora **23**: 73–84.

———. 1924. An enumeration of the orchids of the United States and Canada. American Orchid Society, Boston. 120 pp.

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Figure 13. Histograms of discriminant scores of 30 dried specimens of *S. ochroleuca* and 37 of *S. cernua*. The plot is based on a discriminant function using 4 of 11 characters (see table 2) that are easily and consistently measurable. The positions of the two plants representing the type of *Spiranthes cernua* (TC= —1.17, —1.83), two indeterminates later found to be triploids (I=—2.19, —2.24) and the isotype of *Ibidium incurvum* (TI=—1.47) are shown. For *S. ochroleuca* the group means ($\bar{X}$) is 2.01 and the standard deviation of scores is 1.18. For *S. cernua* the group mean ($\bar{X}$) is —1.63 and the standard deviation is 0.83.

Barkley, T. M. 1968. A manual of the flowering plants of Kansas. Kansas State University Endowment Association, Manhattan. 401 pp.

Britton, N. L. 1901. Manual of the flora of the Northern States and Canada. Henry Holt and Co., New York.

Case, F. W., Jr. 1964. Orchids of the western Great Lakes region. Cranbrook Institute of Science Bulletin **48**. Bloomfield Hills, Michigan. 147 pp.

Catling, P. M. & J. E. Cruise. 1974. *Spiranthes casei*, a new species from northeastern North America. Rhodora **76:** 526 536.

Correll, D. S. 1950. Native orchids of North America north of Mexico. Chronica Botanica Co., Waltham, Massachusetts. 399 pp.

Deam, C. C. 1940. Flora of Indiana. Wm. B. Burford Printing Co., Indianapolis. 1236 pp.

Fernald, M. L. 1950. Gray's manual of botany, eighth ed. American Book Co., Boston. 1632 pp.

Jennings, O. E. 1906. A new species of *Ibidium (Gyrostachys).* Annals of the Carnegie Museum **III:** 483 484.

———. 1953. Wild flowers of western Pennsylvania and the upper Ohio basin, Vol. 1. University of Pittsburg Press. Pittsburg. 575 pp.

Luer, C. A. 1975. The native orchids of the United States and Canada. New York Botanical Garden. 361 pp.

Royal Horticultural Society. 1966. Colour Chart (consisting of 202 colours each with 4 tints printed in solid colour). Royal Horticultural Society. Vincent Square, Westminster, S.W. 1, (London) England.

Rydberg, P. A. 1932. Flora of the prairies and plains of central North America. New York Botanical Garden. 969 pp.

Sheviak, C. J. 1973. A new *Spiranthes* from the grasslands of central North America. Bot. Mus. Leafl. Harvard Univ. **23:** 285 297.

———. 1974. An introduction to the ecology of the Illinois Orchidaceae. Illinois State Museum Scientific Paper **14**. 89 pp.

Sneath, P. H. A. & R. R. Sokal. 1973. Numerical taxonomy. W.H. Freeman and Co., San Francisco. 573 pp.

Steyermark, J. A. 1963. Flora of Missouri. Iowa State University Press, Ames. 1725 pp.

Swamy, B. G. L. 1948. Agamospermy in *Spiranthes cernua*. Lloydia **11:** 149 162.

Voss, E. G. 1972. Michigan flora, part 1, Gymnosperms and Monocots. Cranbrook Inst. Science and Univ. Michigan Herbarium, Bloomfield Hills, Michigan. 488 pp.

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# BRYOPHYTES OF THE PEAT MAT AT PONKAPOAG POND, EASTERN MASSACHUSETTS, WITH TAXONOMIC AND ECOLOGICAL NOTES ON *SPHAGNUM*

WALTER S. JUDD

Ponkapoag bog is located in the town of Canton in Norfolk County, Massachusetts, and occupies a little over 100 acres along the northwest shore of Ponkapoag Pond. Along its northern boundary the bog (actually a poor fen) is separated from the surrounding oak-white pine forest by an abrupt slope. Several small streams flow into the bog mat from the north and northwest, and Ponkapoag Pond itself has an outlet at its southwest corner. The mat is in contact with the mineral substrate of the pond except at its extreme outer edge.

The bog comprises several vegetation types including (1) *Chamaedaphne calyculata* thicket, (2) *Chamaecyparis thyoides* forest and (3) *Acer rubrum* swamp-forest. These vegetation types are not absolutely distinct and grade into each other. *Chamaedaphne* thickets are usually nearer the open water of the pond, while *Acer rubrum* swamp-forest is limited to the outer margin of the bog near the surrounding upland forest. *Chamaecyparis* trees have been removed from portions of the study area, and these places are now occupied by dense thickets of *Chamaedaphne calyculata. Decodon verticillatus* is abundant along the peaty shore of the pond (i.e., at the outer, unconsolidated edge of the mat nearest the pond). In each of the vegetation types occur several distinct bryophyte communities. These are discussed below, with special emphasis on *Sphagnum*, of which 15 species have been found within the study area.

Dominant vascular plants of the *Chamaedaphne* thickets include *Chamaedaphne calyculata, Kalmia angustifolia, Myrica gale, Vaccinium macrocarpon,* and the herbs *Drosera intermedia, D. rotundifolia, Sarracenia purpurea, Peltrandra virginica, Eriophorum virginicum, Rhynchospora alba,* and *Carex* spp.[1] The surface beneath these thickets is a series of hummocks, hollows, and mats of *Sphagnum*. The most abundant species include the ombrotrophic to

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[1] Here, as throughout, the nomenclature of vascular plants follows M. L. Fernald (1950), except for *Xyris* which follows R. Kral (1966).

only weakly minerotrophic *Sphagnum capillifolium, S. flavicomans, S. papillosum,* and *S. magellanicum,* which are not found in the more mineral-rich *Acer rubrum* swamp-forest (see table 1). *Sphagnum cuspidatum* and *S. torreyanum* are also common, and *S. recurvum s. stricto* is an occasional member of the community. *Dicranum scoparium* and *Aulacomnium palustre* sometimes occupy hummock tops, and lower on the hummock sides the *Sphagna* may be mixed with *Drepanocladus uncinatus* or *D. fluitans.* On disturbed and/or eroded hummocks, *Mylia anomala, Cladopodiella fluitans, Cephalozia connivens,* or *Aulacomnium palustre* are often found. The species of *Sphagnum* occurring in these hummocks and hollows can be arranged in a series in relation to their position above (or below) the water level (see Figure 1). *Sphagnum torreyanum* always occurs in the deepest portions of pools, while *S. cuspidatum* is found in shallow pools and depressions, around the margins of deeper pools, or in low mats. *Sphagnum recurvum* can occur in hollows (but only rarely under water) or in low mounds around clumps of vegetation (base of shrubs, trees, etc.). *Sphagnum papillosum* and *S. magellanicum* occur at slightly higher levels and characteristically form dense mats or low to moderately high (i.e., to 30 cm.) hummocks. The highest portions of the hummocks (i.e., to

Table 1: **The distribution of species of** *Sphagnum* **occurring at Ponkapoag Bog. (Note: **** = abundant, *** = common, ** = locally common, * = occasional, + rare, 0 = not present).**

| Species | *Chamaedaphne* thicket | *Chamaecyparis* forest | *Acer rubrum* forest |
|---|---|---|---|
| *S. papillosum* | **** | ** | 0 |
| *S. magellanicum* | *** | ** | 0 |
| *S. palustre* | 0 | + | **** |
| *S. henryense* | 0 | + | *** |
| *S. imbricatum* | 0 | 0 | **** |
| *S. recurvum* | * | **** | ** |
| *S. fallax* | 0 | + | *** |
| *S. cuspidatum* | ** | ** | ** |
| *S. torreyanum* | ** | ** | ** |
| *S. fimbriatum* | + | **** | **** |
| *S. girgensohnii* | 0 | 0 | + |
| *S. capillifolium* | **** | ** | 0 |
| *S. russowii* | 0 | 0 | + |
| *S. flavicomans* | *** | ** | 0 |
| *S. squarrosum* | 0 | 0 | * |

ca. 60 cm.) are occupied by *Sphagnum flavicomans* and/or *S. capillifolium.* However, both species are sometimes rather variable in position, and occasionaly occupy low flat mats with *S. papillosum* or *S. magellanicum.* Similar zonations of species have been reported by Andrus (1974), Moss (1953), Ratcliffe and Walker (1958), Rose (1953), Spearing (1972), Vitt, Crum, and Snider (1975); and Vitt and Slack (1975). The vertical zonation of species probably results from the galacturonic acid content (and thus cation-exchange capacity) of individual species and their differential ability to hold (and conduct) water.

*Cladopodiella fluitans, Cephalozia connivens* and *Mylia anomala* are common in low depressions and around small pools in rather low, open thickets of *Chamaedaphne calyculata, Kalmia angustifolia,* and *Vaccinium macrocarpon* (with various sedges, *Drosera* spp., and *Xyris difformis*). They are often mixed with *Sphagnum cuspidatum* and *S. papillosum.*

*Chamaecyparis thyoides* forest can be quite open and sunny with many shrubs such as *Vaccinium corymbosum, Kalmia angustifolia, Chamaedaphne calyculata, Rhododendron viscosum, Pyrus (Aronia) arbutifolia, Ilex verticillata,* and *Nemopanthus mucronata,* or quite dense with little other than closely spaced *Chamaecyparis* trees. A distinctive assemblage of species including *Tetraphis pellucida, Microlepidozia sylvatica, Cephalozia connivens, Dicranum flagellare, Mylia anomala*, and *Odontoschisma denudatum* occurs on rotted, decorticated cedar stumps (and logs). Humus at the bases of such stumps (or on living trees) is often covered with *Sphagnum fimbriatum* (especially at densely shaded sites), *Mylia anomala, Cephalozia connivens, C. macrostachya,* or *Drepanocladus fluitans. Sphagnum recurvum* and *S. cuspidatum* often occur in depressions between hummocks, and *S. torreyanum* is found in the deepest pools. *Sphagnum recurvum* becomes dominant in more open portions of *Chamaecyparis* forest and reaches its greatest abundance in this vegetation type. In these areas it forms low to slightly raised mats between the various trees and shrubs and forms small hummocks around their bases. It is often mixed with *S. papillosum, S. magellanicum,* and *S. fimbriatum.* Other common bryophytes at the bases of trees and shrubs in these areas are *Dicranum flagellare, D. scoparium, Tetraphis pellucida,* and *Hypnum pallescens* (all usually well above water-level), along with *Cephalozia* spp., *Aulacomnium palustre,* and *Drepanocladus flui-*

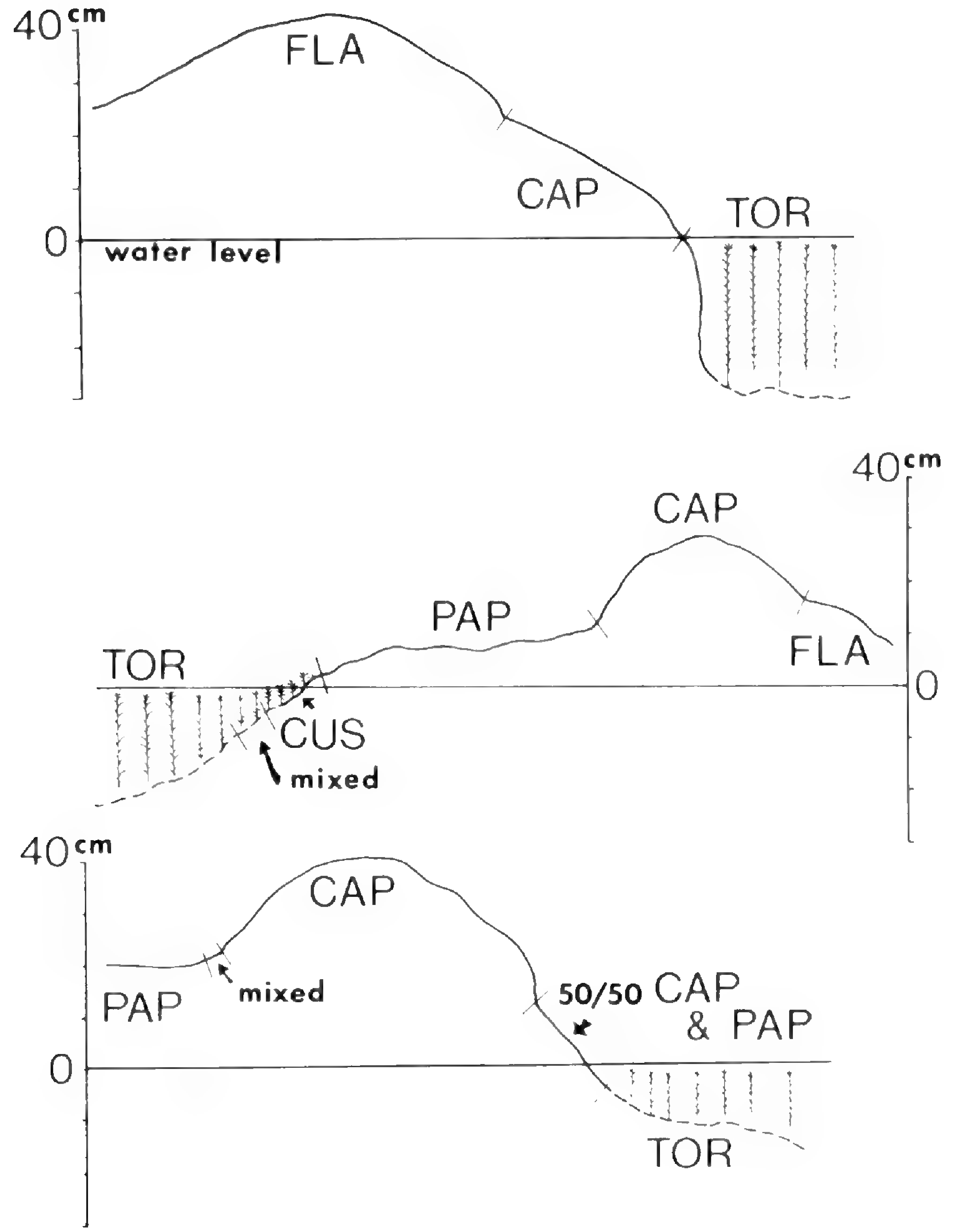

Figure 1.: Selected hummock-hollow diagrams of *Sphagnum* species at Ponkapoag Bog. Scale shows height above (or below) water level (in 10 cm units). CAP = *Sphagnum capillifolium;* CUS = *S. cuspidatum;* FLA = *S. flavicomans;* PAP = *S. papillosum;* TOR = *S. torreyanum.*

*tans* (found near water-level or mixed with above). *Pallavicinia lyellii* is often found over organic material in open areas of the *Chamaecyparis* forest.

The swamp-forest at the periphery of much of the bog is composed of scattered *Acer rubrum* trees with a dense undergrowth of various ericaceous shrubs (e.g., *Vaccinium corymbosum, Leucothoë racemosa, Kalmia angustifolia, Rhododendron viscosum,* and *Lyonia ligustrina*) with *Clethra alnifolia, Ilex verticillata, Pyrus arbutifolia, Viburnum recognitum, Nemopanthus mucronata, Rosa palustris,* and *Cephalanthus occidentalis.* Moist, decorticated logs and stumps in this forest are characteristically covered with *Cephalozia* spp., *Nowellia curvifolia, Dicranum flagellare, Odontoschisma denudatum, Callicladium haldanianum, Lophocolea heterophylla, Tetraphis pellucida,* and *Aulacomnium palustre.* Species of *Sphagnum* (e.g., *S. palustre, S. imbricatum, S. henryense, S. fimbriatum,* etc.) often become established on the wettest of the logs, and eventually completely cover them to form *Sphagnum* hummocks. *Leucobryum glaucum* is often present along with *Dicranum flagellare* on dry logs.

*Sphagnum* hummocks are frequent at the bases of shrubs, trees, and ferns, and are usually composed of the minerotrophic *S. imbricatum, S. palustre, S. henryense* (all essentially limited to the *Acer rubrum* forest), and *S. fimbriatum.* Unlike in the open *Chamaedaphne* thicket or *Chamaecyparis* forest, *Sphagnum* does not form a continuous covering over the peat. *Sphagnum squarrosum* and *S. fallax* are occasionally also present, and two rare species (*S. russowii* and *S. girgensohnii*) are limited to this habitat (Table 1). *Sphagnum cuspidatum* and *S. torreyanum* also occur but are restricted to small ephemeral or permanent pools.

*Drepanocladus fluitans, D. aduncus* var. *polycarpus, Leptodictyum riparium,* and *Calliergon cordifolium* are common on twigs, organic debris, and at the base of *Decodon* clumps or other shrubs, in low, open, often inundated areas of the *Acer rubrum* swamp. *Drepanocladus fluitans* (with *Aulacomnium palustre*) is also usually present in the lower portions of the organic hummocks around the bases of trees and shrubs.

*Platygyrium repens* and *Dicranum flagellare* occur as epiphytes on the higher portions (i.e., above ca. 0.5 m.) of tree trunks. Near the base of such trees at the margin of the *Acer rubrum* swamp-forest nearest the upland forest, several other species occur, such as

*Plagiothecium denticulatum, Mnium cuspidatum, M. hornum, Thuidium delicatulum, Tetraphis pellucida, Hypnum pallescens,* and *Leucobryum glaucum. Plagiothecium laetum* and *P. latebricola* are found only at the base of trees in the drier portions of the *Acer rubrum* woods adjacent to the surrounding upland forest. *Bryhnia novae-angliae* occurs on humus in a few shaded areas along a small ditch which flows into the *Acer rubrum* swamp-forest.

The occurrence of such a high number of *Sphagnum* species in the bog (see table 1) is probably related at least in part to the diversity of suitable microhabitats which are arranged along both vertical (hummock to hollow, see Figure 1) and horizontal (ombrotrophic to minerotrophic) environmental gradients. No other genus present in the bog (with the possible exception of *Carex*) has as many species and the diversity of habitats as does *Sphagnum*.

## THE BRYOPHYTE FLORA

Although the area surveyed is small, the several distinct habitats present support an interesting bryophyte flora of 60 species (i.e., 44 mosses and 16 liverworts). The catalog which follows is based almost exclusively on my own collections (made between September 1975 and July 1978), and unless otherwise indicated all the collection numbers are my own. A set of voucher specimens is deposited in the Farlow Herbarium. The families are listed in phylogenetic order and follow Crum, Steere, and Anderson (1973) for the mosses and Stotler and Crandall-Stotler (1977) for the liverworts. The occurrence of each species in the vegetation zones of the bog is indicated by a code in parentheses following the collection numbers. The zone in which the species is most frequent is listed first. These zones are:

(A.) *Acer rubrum* swamp-forest
(Cc.) *Chamaecyparis thyoides* forest
(Cd.) *Chamaedaphne calyculata* thicket

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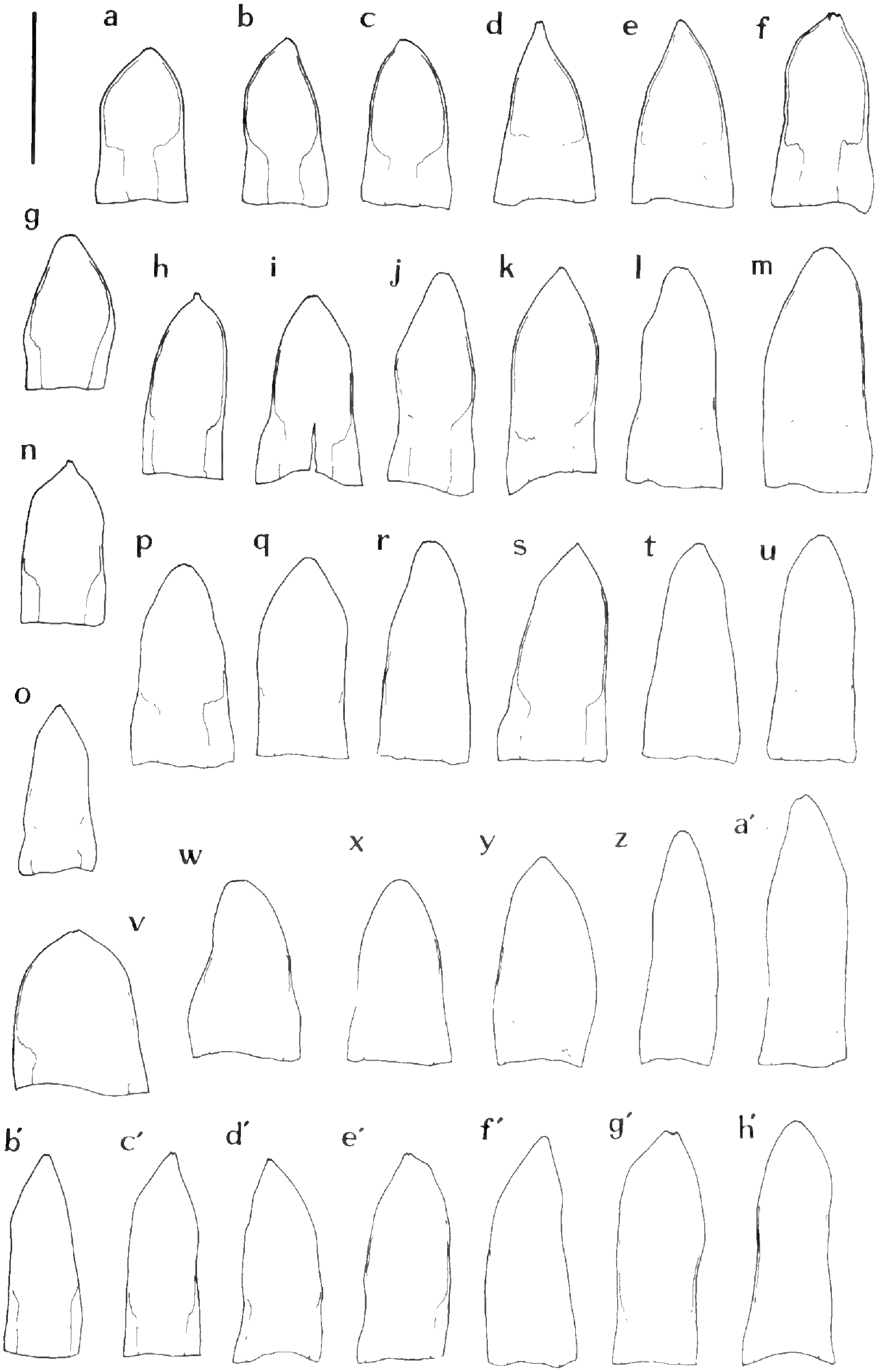
Figure 2: Variation in stem leaf shape and marginal linear cell development in *Sphagnum capillifolium* from Ponkapoag Bog. Bar equals 1 mm.

Collection numbers: **a,** *2136;* **b,c,** *1947;* **d,e,** 1960; **f,** *1020;* **g,** *1927,* top of hummock; **h,** *1974;* **i,** *1949;* **j,k,** *1943;* **1,** *1978;* **m,** *1961;* **n,** *1949;* **o,** *1954;* **p,** *1973;* **q,** *1999;* **r,** *1977;* **s,** *1916,* bottom of hummock; **t,** *1977;* **u,** *1978;* **v-x,** *967;* **y,** *1915,* bottom of hummock; **z,** *1977;* **a′**. *1978;* **b′**, *1949;* **c′***1927,* bottom of hummock; **d′**. *1915,* top of hummock; **e′**, *1872;* **f′**, *1961;* **g′,h′**, *1927,* bottom of hummock.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The distribution of the 15 species of *Sphagnum* occurring within the study area was especially interesting and is summarized in Table 1 and Figure 1.

## MUSCI

### SPHAGNACEAE

**Sphagnum capillifolium** (Weiss) Schrank *967, 999, 1020, 1022, 1061, 1872, 1913, 1915, 1916, 1921, 1927, 1928, 1931, 1943, 1944, 1947, 1949, 1954, 1960 1962, 1973 1982, 1993 1999, 2101, 2136.* (Cd, Cc). This morphologically variable taxon often has been divided into several species (see Andrus, 1974, 1976), and if these segregates are recognized, then the Ponkapoag material falls chiefly within *Sphagnum rubellum* Wils. and *S. subtile* (Russow) Warnst. According to Andrus (1974) *S. rubellum* is characterized by its lingulate to lingulate-triangular stem leaves with a strong border (moderately broadened basally) and with 1–3-septate and often fibrillose cells. The branch leaves are 5-ranked. The capitulum varies from flat-topped to slightly rounded and often has a 5-parted, stellate appearance. In contrast, *S. subtile* is characterized by its triangular-lingulate to lingulate stem leaves with a very strong border (greatly broadened basally) and with smaller 1(2)-septate and usually efibrillose cells. The branch leaves are 5-ranked in coastal forms (but not 5-ranked inland) and the capitulum is flat-topped but not stellate in appearance. However I was not able to separate the Ponkapoag material into two discrete groups by using the above characters. The variation in shape of the stem leaves and the development of their marginal linear cells form a continuum (see Figure 2) among specimens collected at Ponkapoag Bog. Continuous variation was also observed in cells of the stem leaves, which vary from fibrillose to efibrillose and from 0–1-septate to 1–3-septate (see Figure 3). Also the branch leaves vary from clearly 5-ranked to imbricate and the capitula vary from flat-topped and clearly star-shaped to hemispherical. Some plants were found (e.g., *1961, 1960, 967*) with certain characters of *S. subtile* and other characters of *S. rubellum.* Much of this variation may be due to hydrologic stress and other environmental factors. For example, small plants with imbricate branch leaves and nearly hemispherical capitula are more common near the tops of hummocks than in the hollows between them. However some variation is probably genetically controlled because certain populations had consistently more clearly 5-ranked branch-leaves, or developed consistently smaller and more strongly bordered stem-leaves than other populations. It is noteworthy that mixed populations (e.g., *1995*) of deep red and pinkish-brown individuals also occur. At least until the factors resulting in the above described patterns of variation are better understood it seems best to delimit *S. capillifolium* in the broad sense (see Andrews, 1913; Crum, 1976; Hill, 1976; and comments of Nyholm, 1954, concerning genetically determined but intergrading variation patterns within this species).

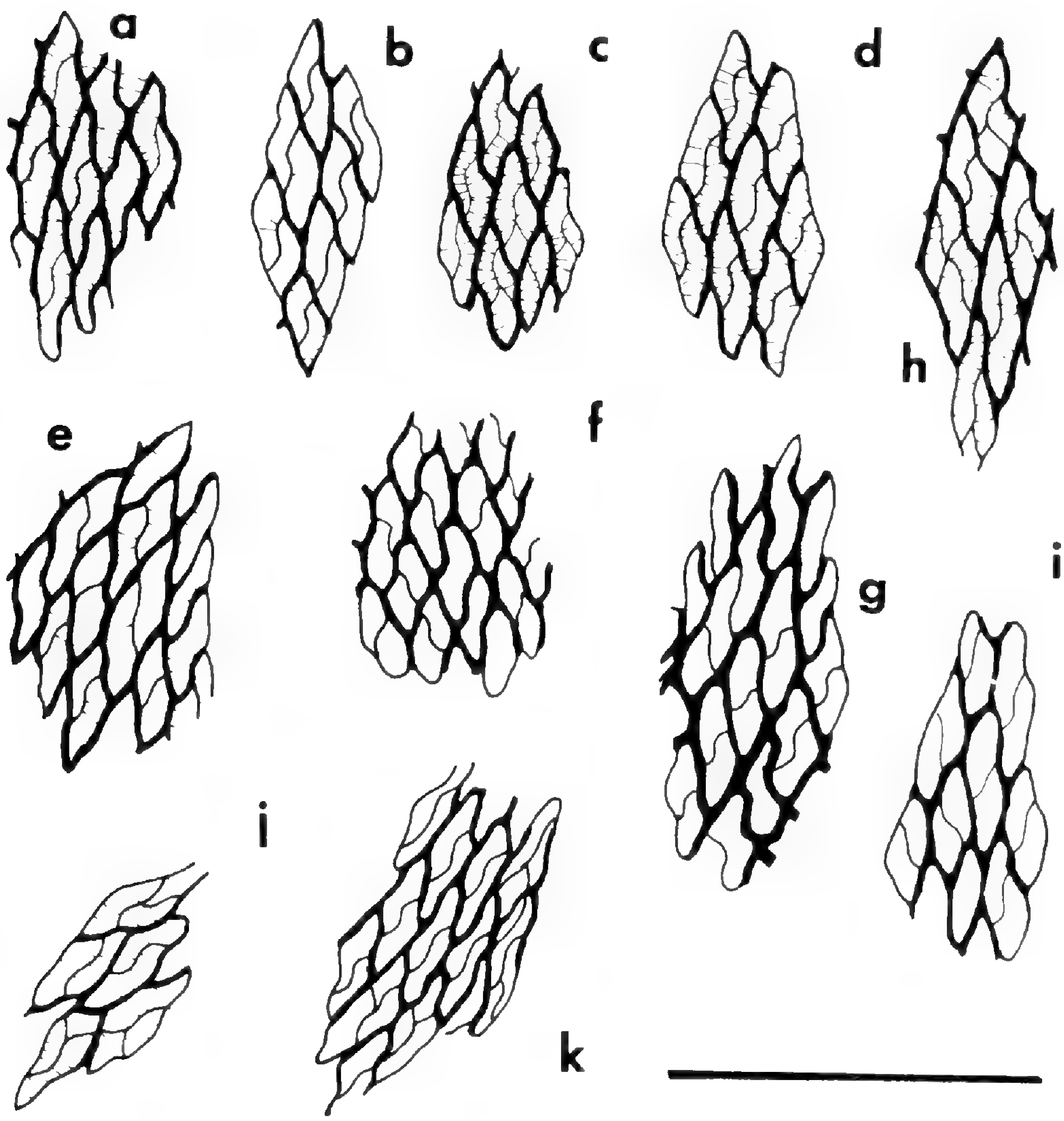

Figure 3.: Variation in cells of stem leaves of *Sphagnum capillifolium* from Ponkapoag Bog. Cells projected and traced from mid-portion of each leaf; bar equals 0.25 mm.

Collection numbers: **a,** *1916,* bottom of hummock; **b,** *1947;* **c,** *1916,* top of hummock; **d,** *1943;* **e,** *1020;* **f,** *2136;* **g,** *967;* **h,** *1872;* **i,** *1949;* **j,** *1927;* **k,** *999.*

**S. cuspidatum** Ehrh. *ex* Hoffm. — *890, 964a, 1649, 2113, 2114.* (Cd, Cc, A).

**S. fallax** (Klinggr.) Klinggr. — *1021, 1652, 1950, 2108.* (A, Cc).
This species is separated from the closely related **Sphagnum recurvum** by its smaller size, apiculate stem leaves and slightly exposed to slightly enclosed chlorophyllose cells of the branch leaves (as seen in transverse section); (see Andrus, 1974; Nyholm, 1954; Smith, 1977).

**S. fimbriatum** Wils. *ex* J. D. Hook. & Wils. — *841, 844, 891, 895, 964b, 1002, 1019, 1621, 1651, 1910, 1917, 1956, 2104 2107.* (A, Cc, Cd).

**S. flavicomans** (Card.) Warnst. — *1010, 1011, 1871, 1872, 1914, 1919, 1928, 1931, 1948, 2096-2100.* (Cd, Cc).
This species is usually easily separated from *Sphagnum capillifolium,* with which it is often found intermixed, by its usually larger size, orange-brown color (i.e., stems yellowish-green to brown and *not* purplish-red pigmented), nearly always imbricate branch leaves, and often larger stem leaves with cells nearly always l-septate (Figure 4). However, poorly-pigmented, young forms may be difficult to identify.

**S. girgensohnii** Russow — 2103. (A).

**S. henryense** Warnst. — *1879, 1881, 1911, 1912, 2129, 2133.* (A, Cc).

**S. imbricatum** Russow — *892, 1014, 1016, 1017, 1957, 2131, 2135* (A).

**S. magellanicum** Brid. — *897, 909, 1009, 1873.* (Cd, Cc).

**S. palustre** L. — *888, 889, 1878, 1880, 1908, 1909, 1951, 2130, 2132, 2134.* (A, Cc).

**S. papillosum** Lindb. — *843, 846, 851, 899, 908, 1015, 1875-1877, 1945, 2118 2128.* (Cd, Cc).

**S. recurvum** P.-Beauv. **s. stricto** — *845, 849, 893, 896, 898, 1000, 1001, 1922 1926, 1929, 1930, 1946, 2109-2112.* (Cc, A, Cd).
This species is separated from *S. fallax* by having often erose to fimbriate (apex more or less rounded) stem leaves, chlorophyllose cells of the branch leaves included in transverse section, and a larger size.

**S. russowii** Warnst. — *1003.* (A).

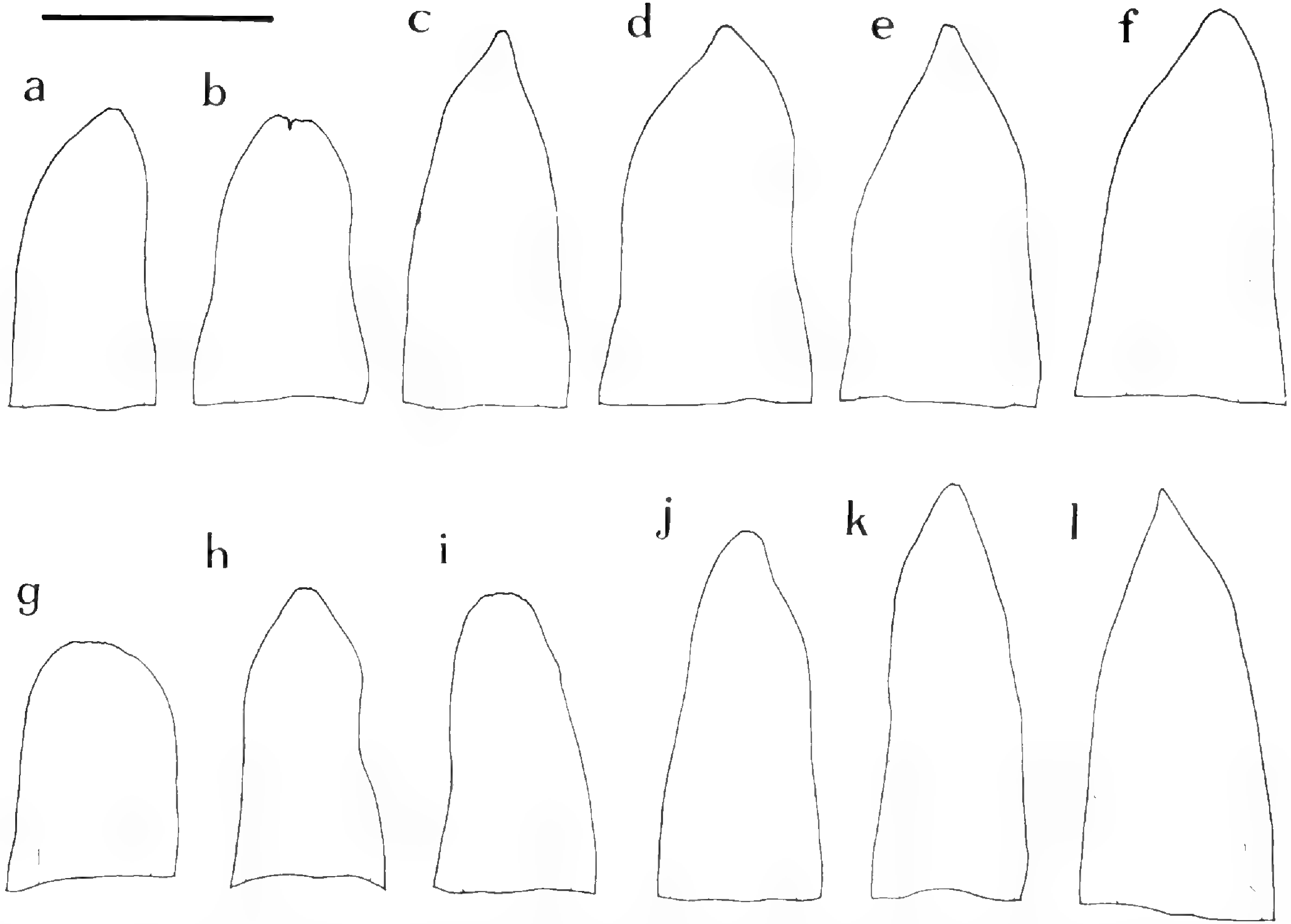

Figure 4: Variation in the shape of the stem leaves and in the development of their marginal linear cells of *Sphagnum flavicomans* in Ponkapoag Bog. Bar equals 1 mm.

Collection numbers; **a**, *1928;* **b**, *2099;* **c**, *1011;* **d**, *1919;* **e**, *1011;* **f**, *2100;* **g**, *2099;* **h**, *1928;* **i**, *2099;* **j**, *1928;* **k**, *1919;* **l**, *1919.*

**S. squarrosum** Crome — *842, 1018.* (A).

**S. torreyanum** Sull. — *900, 1036 1038, 1874, 2115 2117.* (Cd, Cc, A).

DICRANACEAE

**Dicranum flagellare** Hedw. — *833, 836, 881, 887, 894, 904, 2137.* (A, Cc).

**D. scoparium** Hedw. — *837, 903, 954, 996* (Cc, Cd).

LEUCOBRYACEAE

**Leucobryum glaucum** (Hed.) Aongstr. *ex* Fr. — *953, 961* (A, Cc).

BRYACEAE

**Pohlia nutans** (Hedw.) Lindb. — *859.* (A).

MNIACEAE

**Mnium cuspidatum** Hedw. — *1041.* (A).

**M. hornum** Hedw. *1054a, 1054b, s.n.,* 12 July 1976. (A).

**M. punctatum** Hedw. var. **elatum** Schimp. — *s.n.,* 12 July 1976. (A).

AULACOMNIACEAE

**Aulacomnium palustre** (Hedw.) Schwaegr. — *839, 848, 856, 884, 944, 949, 971, 1057* (A, Cc, Cd).

CLIMACIACEAE

**Climacium americanum** Brid. — *917, 976, 978, 1024.* (A).

THUIDIACEAE

**Helodium paludosum** (Sull.) Aust. — *920, 1055.* (A).

**Thuidium delicatulum** (Hedw.) BSG. — *1048.* (A).

AMBLYSTEGIACEAE

**Calliergon cordifolium** (Hedw.) Kindb. *857, 1647, 1650.* (A, Cc).

**Campylium radicale** (P.-Beauv.) Grout — *997.* (A).

**Drepanocladus aduncus** (Hedw.) Warnst. var. **polycarpus** (Bland. *ex* Voit) Roth — *973.* (A).

**D. fluitans** (Hedw.) Warnst — *854, 906, 1648.* (A, Cc, Cd).

**D. uncinatus** (Hedw.) Warnst. — *960, 1952.* (Cd, Cc).

**Leptodictyum riparium** (Hedw.) Warnst. – *858, 972, 1058, 1654, s.n.,* 7 July 1976. (A, Cc).

BRACHYTHEACEAE

**Bryhnia novae-angliae** (Sull. & Lesq. *ex* Sull.) Grout *s.n.,* 12 July 1976. (A).

PLAGIOTHECIACEAE

**Plagiothecium denticulatum** (Hedw.) BSG. — *1052.* (A).

**P. laetum** BSG. — *1043.* (A).

**P. latebricola** BSG. — 1050. (A).

HYPNACEAE

**Callicladium haldanianum** (Grev.) Crum *885, 918, 965, 975, 1059.* (A, Cc).

**Herzogiella turfaceae** (Lindb.) Iwats. — *835.* (A).

**Hypnum cupressiforme** Hedw. — *1653.* (A).

**H. lindbergii** Mitt. — *853, 860a, 883, 901, 1060.* (A, Cc).

**H. pallescens** (Hedw.) P.-Beauv. *880, 1053.* (A).

**Platygyrium repens** (Brid.) BSG — *1051.* (A).

TETRAPHIDACEAE

**Tetraphis pellucida** Hedw. — *850, 855, 886, 2138.* (A, Cc).

POLYTRICHACEAE

**Atrichum angustatum** (Brid.) BSG. — *1047.* (A).

## HEPATICAE

### LEPIDOZIACEAE

**Bazzania trilobata** (L.) Gray — *843a, 1006*. (Cc).

**Microlepidozia sylvatica** (Evans) Joerg. — *1004*. (Cc).

### CALYPOGEJACEAE

**Calypogeja muelleriana** (Schiffn.) K. Müller — *834, 840*. (Cc, A).

**C. sphagnicola** (Arn & Perss.) Warnst. & Loeske — *N. G. Miller 8068*. (Cd).

### CEPHALOZIACEAE

**Cephalozia catenulata** (Hüb.) Lindb. — *951a, 951b*. (A).

**C. connivens** (Dicks.) Spruce — *955, 963, 1013*. (Cd, Cc).

**C. macrostachya** Kaal. — *948, 1958, s.n.*, October 1975. (Cc).

**Cladopodiella fluitans** (Nees) Buch — *907, 1012a, 1012b, 1918, 2139*. (Cd).

**Nowellia curvifolia** (Dicks.) Mitt. — *905*. (A).

### ADELANTHACEAE

**Odontoschisma denudatum** (Mart.) Dumort. *1005, 1039*. (A, Cc).

**O. prostratum** (Sw.) Trevis. — *1041*. (A).

### CEPHALOZIELLACEAE

**Cephaloziella elachista** (Jack) Schiffn. — *840b*. (Cc).

### LOPHOCOLEACEAE

**Lophocolea heterophylla** (Schrad.) Dumort. — *952, 998, 1045*. (A).

### JUNGERMANNIACEAE

**Mylia anomala** (Hook.) Gray — *852, 902, 905, 947, 962, 1955*. (Cc, Cd).

PALLAVICINIACEAE

**Pallavicinia lyellii** (Lindenberg) Gray — *847, 945, 946* (A, Cc, Cd).

PELLIACEAE

**Pellia epiphylla** (L.) Corda — *977, 1046.* (A).

## ACKNOWLEDGMENTS

I wish to thank Dr. Norton G. Miller for his encouragement during the course of the project and for his helpful suggestions concerning the manuscript.

## LITERATURE CITED

Andrews, A. L. 1913. Sphagnaceae. North American Flora **15:** 3–31.

Andrus, R. E. 1974. The Sphagna of New York State. Ph.D. Dissertation, State University of New York, College of Environmental Science and Forestry, Syracuse, New York. 421 pp.

Andrus, R. E. 1976. Three neglected *Sphagnum* species of the section *Acutifolia.* p. 16. American Bryological and Lichenological Society. Abstracts of contributed papers presented at the annual meeting. New Orleans, La.

Crum, H. A. 1976. Mosses of the Great Lakes Forest. Revised Ed. University of Michigan, Ann Arbor, Michigan. 404 pp.

Crum, H.A., W. C. Steere, & L. E. Anderson. 1973. A new list of mosses of North America north of Mexico. Bryologist **76:** 85–130.

Fernald, M. L. 1950. Gray's Manual of Botany, ed. 8. American Book Co., New York.

Hill, M. O. 1976. A critical assessment of the distinction between *Sphagnum capillaceum* (Weiss) Schrank and *S. rubellum* Wils. in Britain. Jour. Bryol. **9:** 185–191.

Kral, R. 1966. *Xyris* (Xyridaceae) of the continental United States and Canada. Sida **2:** 177–260.

Moss, E. H. 1953. Marsh and bog vegetation in northwestern Alberta. Canad. J. Bot. **31:** 448–470.

Nyholm, E. 1954. Illustrated moss flora of Fennoscandia, vol. 2. Musci. CWK Gleerup Lund, Sweden. 799 pp.

Ratcliffe, D. A., & D. Walker. 1958. The Silver Flowe, Galloway, Scotland. Jour. Ecol. **46:** 407–445.

Rose, F. 1953. A survey of the ecology of British lowland bogs. Proc. Linn. Soc. London **164:** 186–211.

Smith, G. L. 1977. *Sphagnum recurvum.* Phytologia **36:** 171–176.

SPEARING, A. M. 1972. Caton-exchange capacity and galacturonic acid content of several species of *Sphagnum* in Sandy Ridge Bog, central New York State. Bryologist **75:** 154 158.

STOTLER, R. & B. CRANDALL-STOTLER. 1977. A checklist of the liverworts and hornworts of North America. Bryologist **80:** 405 428.

VITT, D. H., H. CRUM, & J. A. SNIDER. 1975. The vertical zonation of *Sphagnum* species in hummock-hollow complexes in northern Michigan. Mich. Bot. **14:** 190 200.

VITT, D. H., & N. G. SLACK. 1975. An analysis of the vegetation of *Sphagnum*-dominated kettle-hole bogs in relation to environmental gradients. Canad. J. Bot. **53:** 332 359.

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# TYPE SPECIMENS OF THE HODGDON HERBARIUM, UNIVERSITY OF NEW HAMPSHIRE[1]

C. Thomas Philbrick
and Garrett E. Crow

In an effort to catalog the type specimens of the Hodgdon Herbarium all materials in type folders were reevaluated as to type status. The following totals are reported: 5 holotypes, 70 isotypes, 13 syntypes, 6 paratypes, and 1 cotype.

In 1969 the Parker Cleaveland Herbarium of Bowdoin College, Brunswick, Maine, came to the University of New Hampshire on a long term loan and was incorporated into the herbarium collection. Hehre, Hodgdon, and Pike (1972) reported on this collection and noted it included a large number of specimens collected by Augustus Fendler in New Mexico in 1847, many of which are isotypes, and a large number of specimens collected by Ferdinand Lindheimer in Texas in 1843 and 1845. Thus the entire herbarium was searched for additional Fendler and Lindheimer collections which may have been overlooked as type material. The search turned up 231 Fendler specimens, 67 of which are types and 60 Lindheimer specimens, 8 of which are types. Original descriptions were examined to verify all type material.

Many of the types among the Fendler collections were cited by Asa Gray for new species he described in *Plantae Fendlerianae* (Mem. Amer. Acad. Arts, vol. **4**, 1849). Dr. Elizabeth Shaw of the Gray Herbarium kindly pointed out a problem regarding numbers appearing on Fendler specimens. Apparently, upon receiving collections from Fendler, Gray divided the specimens into duplicate sets for distribution, using his own distribution numbers on these labels, not Fendler's collection numbers. He also cited these distribution numbers with his descriptions of new species. Dr. Shaw graciously allowed us to examine Fendler's original notebooks to help clarify the problem.

The confusion which has arisen with regard to the numbers appearing on Fendler specimens is due to the numbering practices employed by Gray (1849) during the preparation of *Plantae Fendle-*

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[1] Scientific Contribution Number 986 from the New Hampshire Agricultural Experiment Station.

*rianae.* Comparison of Fendler's notebooks with *Plantae Fendlerianae* reveals that initially Gray did not use the numbers from these notebooks as specimen label numbers or in protologs. Instead, he substitued these notebooks numbers with his own numbering sequence (*Plantae Fendlerianae* numbers) which also served as distributional numbers for the specimens. This substitution by Gray continued up to the beginning of the Compositae. After this point Gray discontinued the use of *Plantae Fendlerianae* numbers as distribution numbers on specimen labels and in protologs, using Fendler's notebook numbers instead. Gray footnotes this change, but fails to note the discrepancy between the *Plantae Fendlerianae* numbers and the Fendler notebook numbers (Figure 1).

The three different numbers which are encountered when dealing with taxa described from Fendler's specimens in *Plantae Fendlerianae* are as follows:

1) *Fendler notebook numbers:* Fendler's specimen numbers which were included in the noteboks sent to Gray along with the specimens (Figure 2). It is doubtful that these are Fendler's actual field collection notebooks since the specimens are numbered and arranged sequentially by family and the numerical order of the specimens does not correspond with the chronology of collection dates in the notebooks.

2) *Plantae Fendlerianae numbers preceeding the Compositae (Nos. 1–295):* Numerical sequence of species in *Plantae Fendlerianae* (Figure 3). In preparing the original descriptions these numbers were used as specimen distribution numbers instead of Fendler notebook numbers.

3) *Plantae Fendlerianae numbers after the beginning of the Compositae (Nos. 296–462)*[1]: These numbers, starting with No. 296, continue the numbering sequence in *Plantae Fendlerianae* (Figure 5). These differ, however, in that Gray began using Fendler notebook numbers on specimen labels instead of the *Plantae Fendlerianae* numbers and cited them, in parentheses, with the description of each taxon (Figure 1).

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[1] Specimens with distributions numbers from 463 onward were not cited with taxa included in *Plantae Fendlerianae*. These numbers correspond with Fendler notebook numbers.

Information on the labels which Gray distributed with the Fendler specimens is very brief (Figures 4 & 6). The information supplied by Fendler in his notebooks, however, is much more complete, often describing the precise collection locality for each specimen (Figure 2).

Another problem arose when it was discovered that, in some cases, Gray combined two or more of Fendler's collection numbers to form a single distribution number. Consequently, when Gray described a new species he cited only the distribution number and not Fendler's collection numbers. Because of this, the actual Fendler collection number for a type specimen cannot be determined from the original descriptions of certain species.

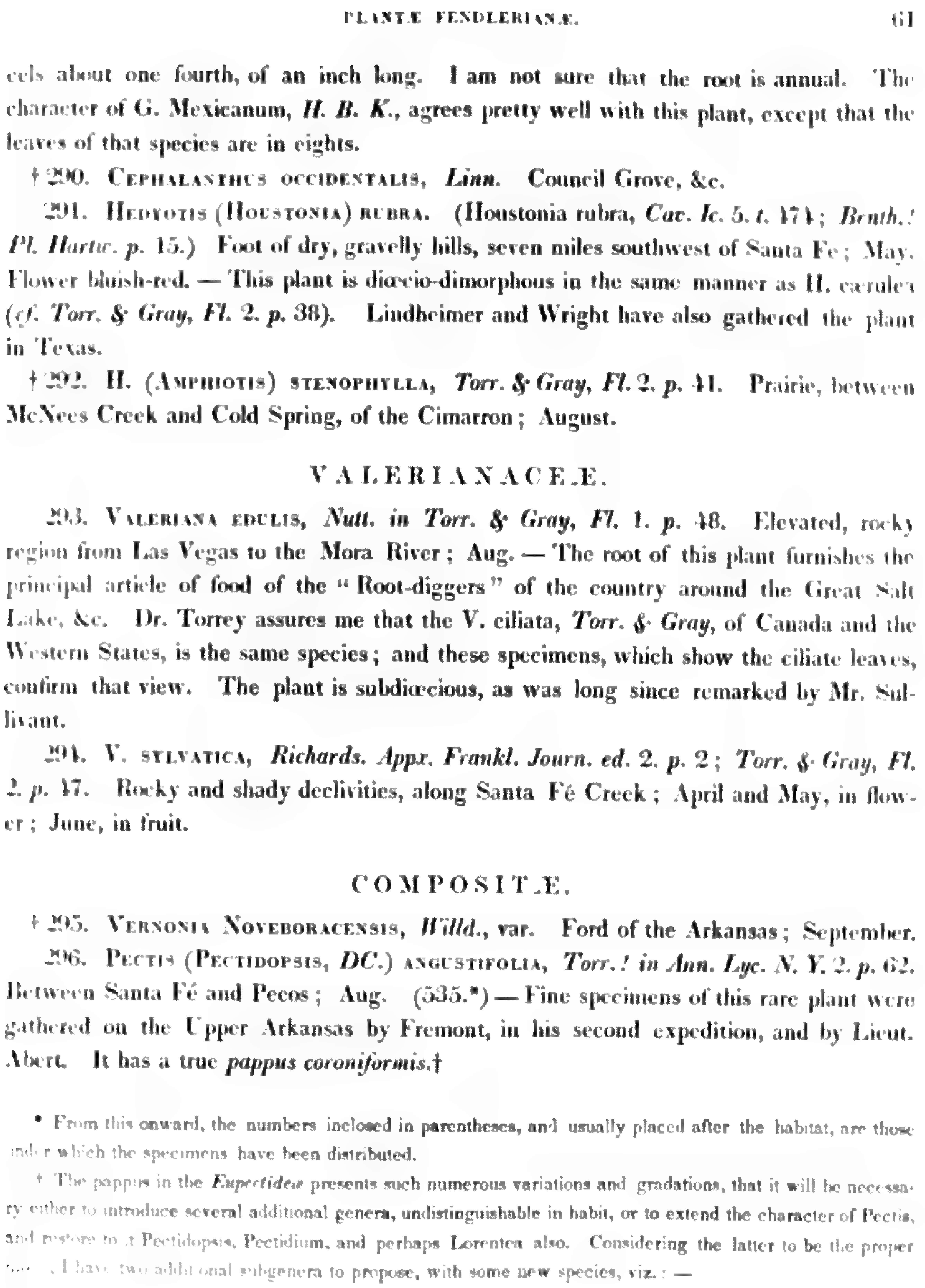
Since Gray usually based descriptions of new species on specific Fendler collection numbers this lumping is a problem in only a few cases. Gray's occasional practice of combining collections can be observed by examining Fendler's noteboks, in which Gray marked his own distribution number next to Fendler's collection numbers.

In those cases in which Gray did combine several collection numbers to form a single distribution number there seems to be no way of determining which specimens relate to specific Fendler collection numbers. Apparently when Gray described a new taxon he based his description on all the collections he combined under a single distribution number. It is possible that Gray also assigned distribution numbers when making up sets of Lindheimer specimens, just as he did with the Fendler collections, but this has not been confirmed.

In 1970 the herbarium of the Portland Society of Natural History, Portland, Maine, came to the University of New Hampshire on a permanent loan. Several isotypes of taxa described by Fernald were included in this collection.

The following is a list of all type material located in the Hodgdon Herbarium. Cases of lumping of collection numbers by Gray are noted.

Specimens of the Parker Cleaveland collection of Bowdoin College are identified as PCBC, those of the Portland Society of Natural History are identified as PSNH and those of the Hodgdon Herbarium are identified as NHA. However, the collections of PCBC and PSNH are regarded as an integral part of the Hodgdon Herbarium and any of these specimens cited in publications should be designated as NHA.



cels about one fourth, of an inch long. I am not sure that the root is annual. The character of G. Mexicanum, *H. B. K.*, agrees pretty well with this plant, except that the leaves of that species are in eights.

† 290. CEPHALANTHUS OCCIDENTALIS, *Linn.* Council Grove, &c.

291. HEDYOTIS (HOUSTONIA) RUBRA. (Houstonia rubra, *Cav. Ic.* 5. *t.* 474; *Benth.! Pl. Hartw. p.* 15.) Foot of dry, gravelly hills, seven miles southwest of Santa Fe; May. Flower bluish-red. — This plant is diœcio-dimorphous in the same manner as H. cærulea (*cf. Torr. & Gray, Fl.* 2. *p.* 38). Lindheimer and Wright have also gathered the plant in Texas.

† 292. H. (AMPHIOTIS) STENOPHYLLA, *Torr. & Gray, Fl.* 2. *p.* 41. Prairie, between McNees Creek and Cold Spring, of the Cimarron; August.

## VALERIANACEÆ.

293. VALERIANA EDULIS, *Nutt. in Torr. & Gray, Fl.* 1. *p.* 48. Elevated, rocky region from Las Vegas to the Mora River; Aug. — The root of this plant furnishes the principal article of food of the "Root-diggers" of the country around the Great Salt Lake, &c. Dr. Torrey assures me that the V. ciliata, *Torr. & Gray*, of Canada and the Western States, is the same species; and these specimens, which show the ciliate leaves, confirm that view. The plant is subdiœcious, as was long since remarked by Mr. Sullivant.

294. V. SYLVATICA, *Richards. Appx. Frankl. Journ. ed.* 2. *p.* 2; *Torr. & Gray, Fl.* 2. *p.* 47. Rocky and shady declivities, along Santa Fé Creek; April and May, in flower; June, in fruit.

## COMPOSITÆ.

† 295. VERNONIA NOVEBORACENSIS, *Willd.*, var. Ford of the Arkansas; September.

296. PECTIS (PECTIDOPSIS, *DC.*) ANGUSTIFOLIA, *Torr.! in Ann. Lyc. N. Y.* 2. *p.* 62. Between Santa Fé and Pecos; Aug. (535.*) — Fine specimens of this rare plant were gathered on the Upper Arkansas by Fremont, in his second expedition, and by Lieut. Abert. It has a true *pappus coroniformis.*†

* From this onward, the numbers inclosed in parentheses, and usually placed after the habitat, are those under which the specimens have been distributed.

† The pappus in the *Eupectideæ* presents such numerous variations and gradations, that it will be necessary either to introduce several additional genera, undistinguishable in habit, or to extend the character of Pectis, and restore to it Pectidopsis, Pectidium, and perhaps Lorentea also. Considering the latter to be the proper course, I have two additional subgenera to propose, with some new species, viz.: —

Figure 1. A page from *Plantae Fendlerianae:* nos. 290 295 do not correspond with Fendler notebook numbers, but appear on the specimen labels; no. 296 continues the numbering sequence but does not appear on the specimen labels; no. (535) cited under no. 296 corresponds with the Fendler notebook number and also appears on the specimen labels.

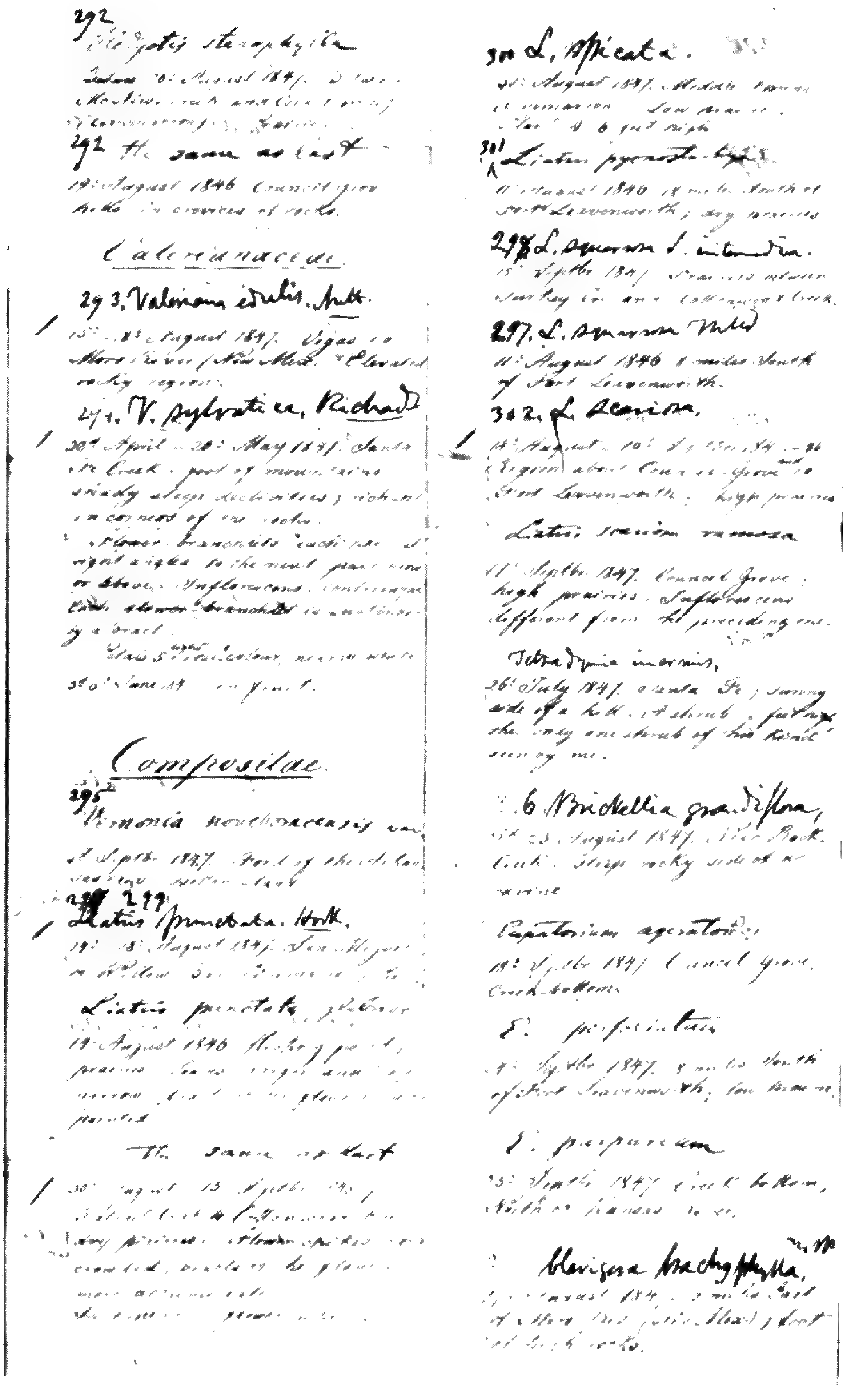


Figure 2. A page from Fendler's notebook.

## TYPES

### ACANTHACEAE

**Dipteracanthus nudiflorus** Engelm. and Gray. Boston J. Nat. Hist. **5:** 229. 1845. "Near Houston, Texas," *F. Lindheimer 157* (1843). PCBC. ISOTYPE.

### ALISMATACEAE

**Lophotocarpus spathulatus** J. G. Smith. Mo. Bot. Garden Eleventh Rept. p. 149 150. 1900. "Merrimack River, Newburyport, Massachusetts." *A. A. Eaton s.n.* September 1898. NHA. ISOTYPE.

### APIACEAE

**Thaspium montanum** Gray. Mem. Amer. Acad. Arts **4:** 57. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 276. PCBC. ISOTYPE.

### AQUIFOLIACEAE

**Ilex verticillata** (L.) Gray var. **verticillata** forma **hodgdonii** Seymour. Flora of New England, p. 377. 1969. "Northern side of Oyster River, toward its mouth, Durham, Strafford Co., New Hampshire." *A. R. Hodgdon 6637* (7 July 1950). NHA. HOLOTYPE.

### BERBERIDACEAE

**Berberis fendleri** Gray. Mem. Amer. Acad. Arts **4:** 5. 1849. "Near Santa Fe, New Mexico." *A. Fendler*, 1847, Distr. no. 15. PCBC. ISOTYPE.

### BORAGINACEAE

**Eritrichium multicaule** Torr. U. S. and Mexico Boundary Survey p. 140. 1858. "New Mexico." *A. Fendler,* 1847, Distr. no. 636. PCBC. ISOTYPE.

**Mertensia fendleri** Gray. Amer. J. Sci. II **34:** 339. 1862. "New Mexico." *A. Fendler,* 1847, Distr. no. 625. PCBC. ISOTYPE.

## COMPOSITAE

**Actinella argentea** Gray. Mem. Amer. Acad. Arts **4:** 100. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 457. PCBC. ISOTYPE (2).

**Actinella richardsonii** Nutt. var. **floribunda** Gray. Mem. Amer. Acad. Arts **4:** 101. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 460. PCBC. ISOTYPE (2)

**Antennaria marginata** Greene. Pittonia **3:** 290. 1898. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 523. PCBC. SYNTYPE.

**Bidens tenuisecta** Gray. Mem. Amer. Acad. Arts **4:** 86. 1849. "Between Bent's Fort and Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 449. PCBC. ISOTYPE

**Brickellia fendleri** Gray. Mem. Amer. Acad. Arts **4:** 63. 1849. "Near Santa Fe, New Mexico." *A. Fendler*, 1847, Distr. no. 347. PCBC. ISOTYPE.

**Erigeron cinereum** var. *α* Gray. Mem. Amer. Acad. Arts **4:** 68. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 374. PCBC. SYNTYPE (2).

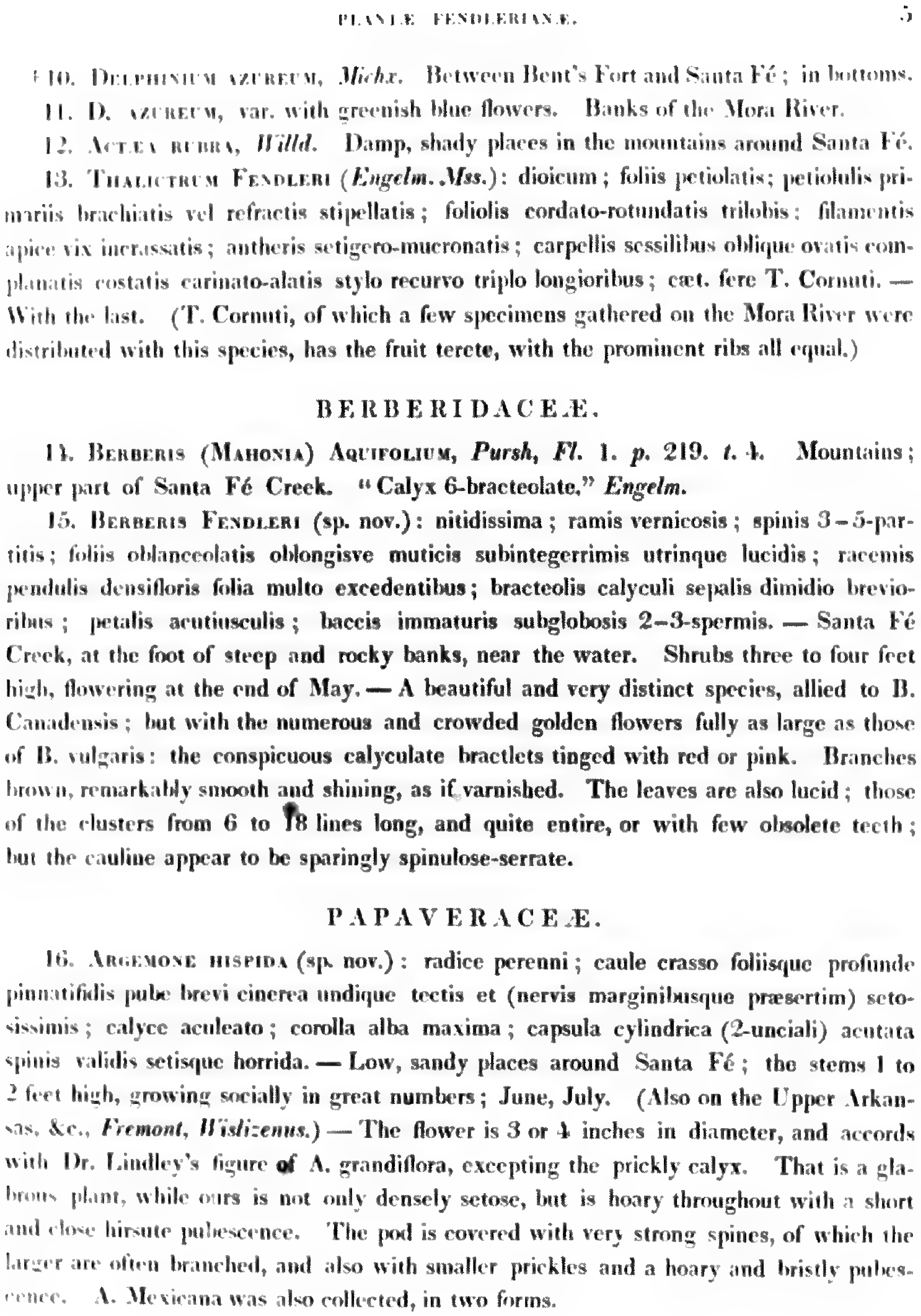
**Senecio fendleri** Gray. Mem. Amer. Acad. Arts **4:** 108. 1849. "Near Santa Fe, New Mexico." *A. Fendler*, 1847, Distr. no. 478. PCBC. SYNTYPE.

## CRUCIFERAE

**Arabis holboellii** Hornem. var. **fendleri** Watson. Gray's Synoptic Flora **1:** 164. 1895. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 27. PCBC. SYNTYPE.

**Cardamine cordifolia** Gray. Mem. Amer. Acad. Arts. **4:** 8. 1849. "Near Santa Fe, New Mexico." *A. Fendler*, 1847, Distr. no. 28. PCBC. ISOTYPE.

**Cardamine longii** Fern. Rhodora **19:** 91. 1917. "Valley of Cathance River, shaded rocky-pockets and crevices, covered at high tide, Bowdoinham, Sagadahoc Co., Maine." *Fernald and Long 13698.* PSNH. ISOTYPE.



PLANTÆ FENDLERIANÆ. 5

+ 10. Delphinium azureum, *Michx.* Between Bent's Fort and Santa Fé; in bottoms.

11. D. azureum, var. with greenish blue flowers. Banks of the Mora River.

12. Actæa rubra, *Willd.* Damp, shady places in the mountains around Santa Fé.

13. Thalictrum Fendleri (*Engelm. Mss.*): dioicum; foliis petiolatis; petiolulis primariis brachiatis vel refractis stipellatis; foliolis cordato-rotundatis trilobis; filamentis apice vix incrassatis; antheris setigero-mucronatis; carpellis sessilibus oblique ovatis complanatis costatis carinato-alatis stylo recurvo triplo longioribus; cæt. fere T. Cornuti. — With the last. (T. Cornuti, of which a few specimens gathered on the Mora River were distributed with this species, has the fruit terete, with the prominent ribs all equal.)

### BERBERIDACEÆ.

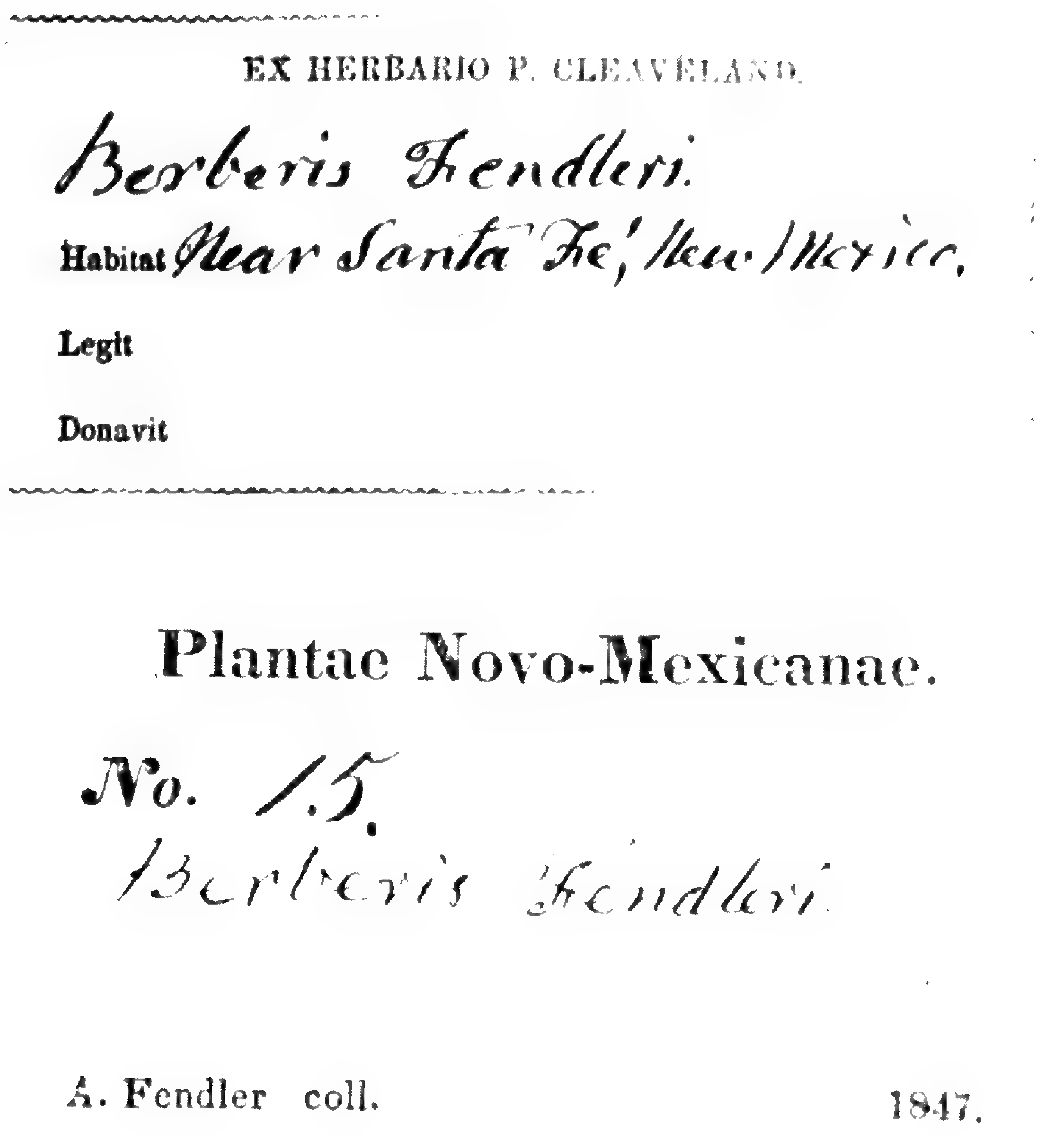
14. Berberis (Mahonia) Aquifolium, *Pursh, Fl.* 1. *p.* 219. *t.* 4. Mountains; upper part of Santa Fé Creek. "Calyx 6-bracteolate." *Engelm.*

15. Berberis Fendleri (sp. nov.): nitidissima; ramis vernicosis; spinis 3–5-partitis; foliis oblanceolatis oblongisve muticis subintegerrimis utrinque lucidis; racemis pendulis densifloris folia multo excedentibus; bracteolis calyculi sepalis dimidio brevioribus; petalis acutiusculis; baccis immaturis subglobosis 2–3-spermis. — Santa Fé Creek, at the foot of steep and rocky banks, near the water. Shrubs three to four feet high, flowering at the end of May. — A beautiful and very distinct species, allied to B. Canadensis; but with the numerous and crowded golden flowers fully as large as those of B. vulgaris: the conspicuous calyculate bractlets tinged with red or pink. Branches brown, remarkably smooth and shining, as if varnished. The leaves are also lucid; those of the clusters from 6 to 18 lines long, and quite entire, or with few obsolete teeth; but the cauline appear to be sparingly spinulose-serrate.

### PAPAVERACEÆ.

16. Argemone hispida (sp. nov.): radice perenni; caule crasso foliisque profunde pinnatifidis pube brevi cinerea undique tectis et (nervis marginibusque præsertim) setosissimis; calyce aculeato; corolla alba maxima; capsula cylindrica (2-unciali) acutata spinis validis setisque horrida. — Low, sandy places around Santa Fé; the stems 1 to 2 feet high, growing socially in great numbers; June, July. (Also on the Upper Arkansas, &c., *Fremont, Wislizenus.*) — The flower is 3 or 4 inches in diameter, and accords with Dr. Lindley's figure of A. grandiflora, excepting the prickly calyx. That is a glabrous plant, while ours is not only densely setose, but is hoary throughout with a short and close hirsute pubescence. The pod is covered with very strong spines, of which the larger are often branched, and also with smaller prickles and a hoary and bristly pubescence. A. Mexicana was also collected, in two forms.

Figure 3. A page from *Plantae Fendlerianae* prior to Compositae (cf. specimen label in Figure 4).



EX HERBARIO P. CLEAVELAND.

Berberis Fendleri.

Habitat Near Santa Fe, New Mexico.

Legit

Donavit

Plantae Novo-Mexicanae.

No. 15.

Berberis Fendleri

A. Fendler coll. 1847.

Figure 4. Specimen label showing *Plantae Fendlerianae* number, not corresponding with Fendler's notebook number (cf. Figure 3).

**Draba aurea** var. **stylosa** Gray. Amer. J. Sci. II **33:** 242. 1862. *Draba neomexicana* Greene. Pittonia **4:** 18. 1899. "Near Santa Fe, New Mexico." *A. Fendler*, 1847, Distr. no 43. PCBC. ISOTYPE (2).

**Lesquerella alpina** Watson var. **intermedia** Watson. Gray's Synoptic Flora **1:** 117. 1895. "Near Santa Fe, New Mexico." *A. Fendler*, 1847, Distr. no. 38. PCBC. ISOTYPE (2).

### CYPERACEAE

**Carex fendleriana** Boeckeler. Linnaea **39:** 135. 1875. "New Mexico." *A. Fendler,* 1847, Distr. no. 878. PCBC. ISOTYPE.

**Cyperus fendlerianus** Boeckeler. Linnaea **35:** 520. 1867–1868. "New Mexico." *A. Fendler,* 1847, Distr. no. 865. PCBC. ISOTYPE.

### ERICACEAE

**Daphnidostylis fendleriana** Klotzsch. Linnaea **24:** 80. 1851. "New Mexico." *A. Fendler,* 1847, Distr. no. 546. PCBC. ISOTYPE (2).

### EUPHORBIACEAE

**Euphorbia bicolor** Engelm. and Gray. Boston J. Nat. Hist. **5:** 233. 1845. "Near Houston, Texas." *F. Lindeimer 174* (1844). PCBC. ISOTYPE.

**Euphorbia fendleri** Torr. and Gray. Exploration of a Route for the Pacific Railroad, vol. 2, p. 175. 1854. "New Mexico." *A. Fendler,* 1847, Distr. no. 800. PCBC. ISOTYPE (2).

**Euphorbia montanus** var. $\alpha$ Engelm. U. S. and Mexico Boundary Survey p. 192. 1858. "New Mexico." *A. Fendler,* 1847, Distr. no. 786. PCBC. SYNTYPE.

**Pilinophytum lindheimeri** Engelm. and Gray. Boston J. Nat. Hist. **5:** 232. 1845. "Houston to the Brazos [River], Texas." *F. Lindheimer 171* (1843). PCBC. ISOTYPE.

### FAGACEAE

**Quercus douglasii** var. **novo-mexicana** A. DC. Prodromus **16**(2): 24. 1864. "New Mexico." *A. Fendler*, 1847, Distr. no. 809. PCBC. SYNTYPE.

### GRAMINEAE

**Aristida fendleriana** Steud. Syn. Pl. Glum. **1:** 420. 1855. "New Mexico." *A. Fendler,* 1847, Distr. no. 973. PCBC. ISOTYPE.

**Aristida longiseta** Steud. Syn. Pl. Glum. **1:** 420. 1855. "New Mexico." *A. Fendler,* 1847, Distr. no. 978. PCBC. ISOTYPE (2).

**Eragrostis fendleriana** Steud. Syn. Pl. Glum. **1:** 278. 1855. "New Mexico." *A. Fendler,* 1847, Distr. no. 932. PCBC. ISOTYPE (2).

**Poa bigelovii** Vasey and Scribn. Contr. U. S. Nat. Herb. **1:** 270. 1893. "New Mexico." *A. Fendler,* 1847, Distr. no. 931. PCBC. ISOTYPE.

### JUNCACEAE

**Juncus oronensis** Fern. Rhodora **6:** 36. 1904. "Alder swamp, Orono, Penobscot Co., Maine." *Fernald 330* (21 July 1892). PSNH. ISOTYPE. (Original publication cites no. 300 as holotype; however this is presumed to be a misprint since the specimen at the Gray Herbarium marked as the type is no. 330 and no specimen bearing no. 300 can be found.)

### LABIATAE

**Monarda lindheimeri** Engelm. and Gray. Boston J. Nat. Hist. **5:** 228. 1845. "Texas." *F. Lindheimer 151* (1843). PCBC. ISOTYPE.

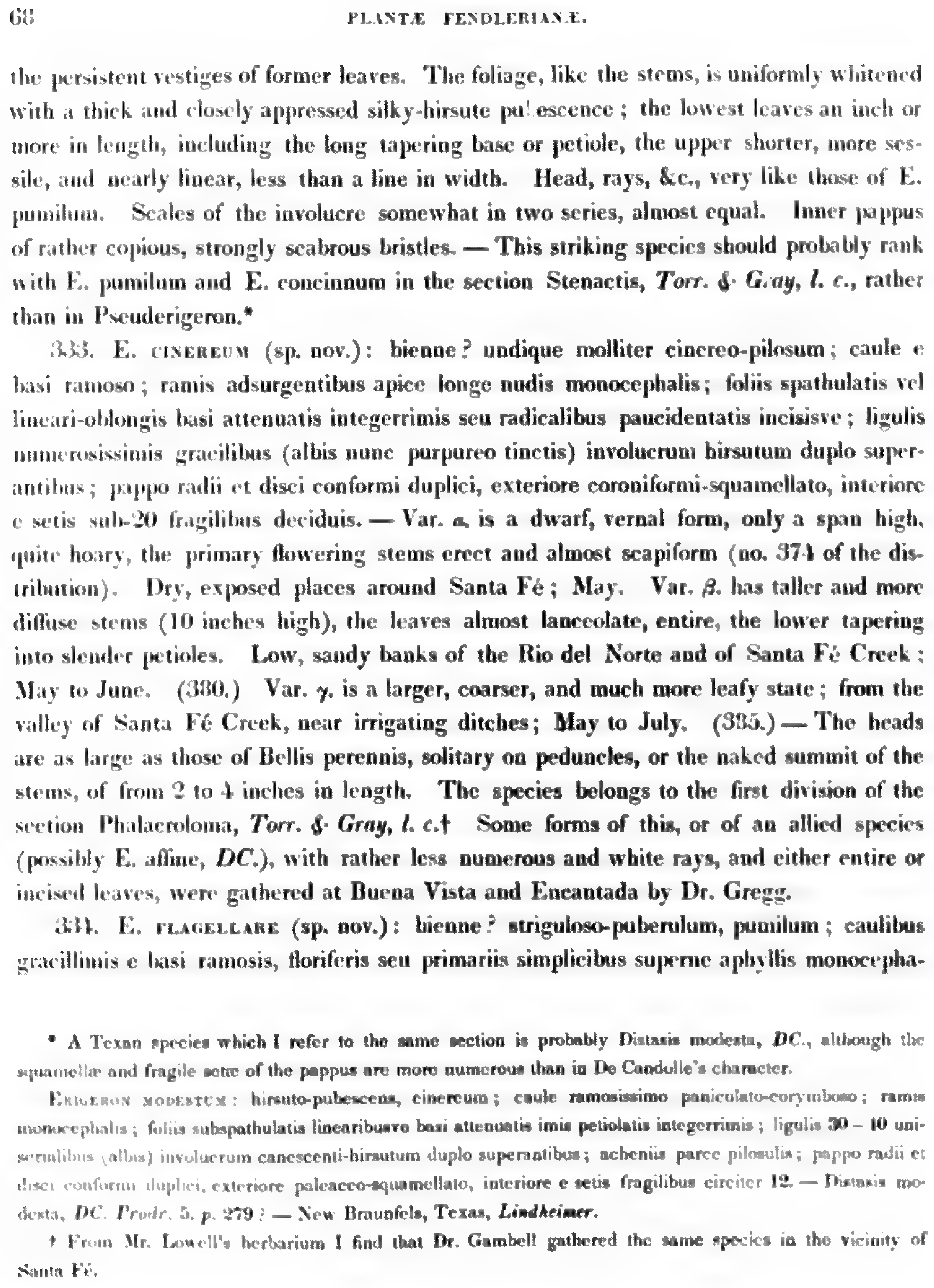
**Scutellaria cardiophylla** Engelm. and Gray. Boston J. Nat. Hist. 5: 227. 1845. "Near Houston, Texas." *F. Lindheimer 144* (1843). PCBC. ISOTYPE.

### LEGUMINOSAE

**Astragalus cyaneus** Gray. Mem. Amer. Acad. Arts **4:** 34. 1849. "Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 148. PCBC. ISOTYPE (2).

**Astragalus diphysus** Gray. Mem. Amer. Acad. Arts **4:** 34. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 146. PCBC. ISOTYPE.

**Phaca macrocarpa** Gray. Mem. Amer. Acad. Arts **4:** 36. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 160. PCBC. ISOTYPE.



68 PLANTÆ FENDLERIANÆ.

the persistent vestiges of former leaves. The foliage, like the stems, is uniformly whitened with a thick and closely appressed silky-hirsute pubescence; the lowest leaves an inch or more in length, including the long tapering base or petiole, the upper shorter, more sessile, and nearly linear, less than a line in width. Head, rays, &c., very like those of E. pumilum. Scales of the involucre somewhat in two series, almost equal. Inner pappus of rather copious, strongly scabrous bristles. — This striking species should probably rank with E. pumilum and E. concinnum in the section Stenactis, *Torr. & Gray, l. c.*, rather than in Pseuderigeron.[*]

333. E. CINEREUM (sp. nov.): bienne? undique molliter cinereo-pilosum; caule e basi ramoso; ramis adsurgentibus apice longe nudis monocephalis; foliis spathulatis vel lineari-oblongis basi attenuatis integerrimis seu radicalibus paucidentatis incisisve; ligulis numerosissimis gracilibus (albis nunc purpureo tinctis) involucrum hirsutum duplo superantibus; pappo radii et disci conformi duplici, exteriore coroniformi-squamellato, interiore e setis sub-20 fragilibus deciduis. — Var. α. is a dwarf, vernal form, only a span high, quite hoary, the primary flowering stems erect and almost scapiform (no. 374 of the distribution). Dry, exposed places around Santa Fé; May. Var. β. has taller and more diffuse stems (10 inches high), the leaves almost lanceolate, entire, the lower tapering into slender petioles. Low, sandy banks of the Rio del Norte and of Santa Fé Creek; May to June. (380.) Var. γ. is a larger, coarser, and much more leafy state; from the valley of Santa Fé Creek, near irrigating ditches; May to July. (385.) — The heads are as large as those of Bellis perennis, solitary on peduncles, or the naked summit of the stems, of from 2 to 4 inches in length. The species belongs to the first division of the section Phalacroloma, *Torr. & Gray, l. c.*[†] Some forms of this, or of an allied species (possibly E. affine, *DC.*), with rather less numerous and white rays, and either entire or incised leaves, were gathered at Buena Vista and Encantada by Dr. Gregg.

334. E. FLAGELLARE (sp. nov.): bienne? striguloso-puberulum, pumilum; caulibus gracillimis e basi ramosis, floriferis seu primariis simplicibus superne aphyllis monocepha-

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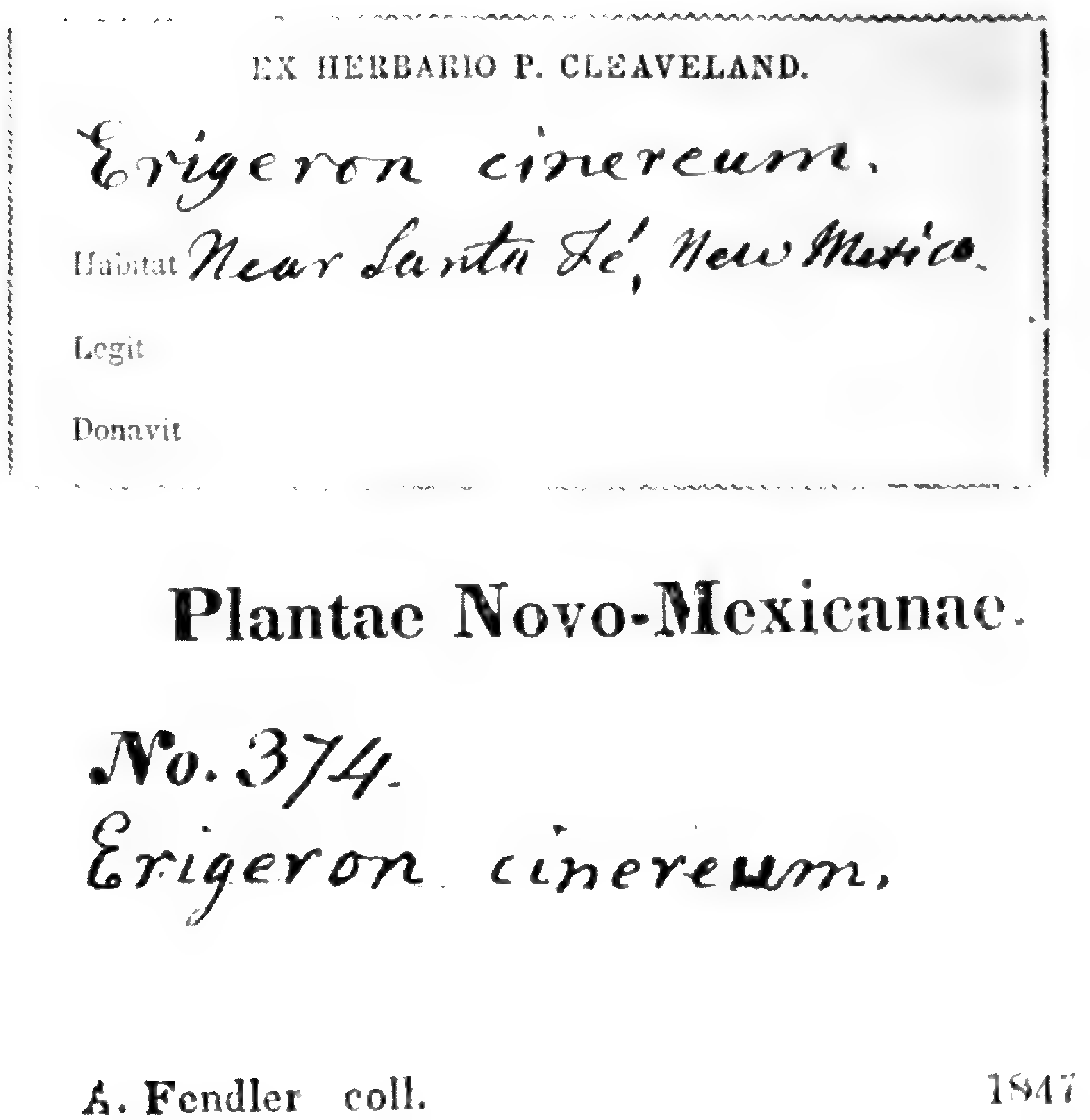
[*] A Texan species which I refer to the same section is probably Distasis modesta, *DC.*, although the squamellæ and fragile setæ of the pappus are more numerous than in De Candolle's character.

ERIGERON MODESTUM: hirsuto-pubescens, cinereum; caule ramosissimo paniculato-corymboso; ramis monocephalis; foliis subspathulatis linearibusve basi attenuatis imis petiolatis integerrimis; ligulis 30 – 40 uniserialibus (albis) involucrum canescenti-hirsutum duplo superantibus; acheniis parce pilosulis; pappo radii et disci conformi duplici, exteriore paleaceo-squamellato, interiore e setis fragilibus circiter 12. — Distasis modesta, *DC. Prodr.* 5. *p.* 279? — New Braunfels, Texas, *Lindheimer.*

[†] From Mr. Lowell's herbarium I find that Dr. Gambell gathered the same species in the vicinity of Santa Fé.

Figure 5. A page from *Plantae Fendlerianae* showing *Plantae Fendlerianae* numbers after no. 296. The numbers in parentheses correspond with Fendler notebook numbers and specimen label numbers (cf. Figure 6).



EX HERBARIO P. CLEAVELAND.

Erigeron cinereum.

Habitat Near Santa Fé, New Mexico.

Legit

Donavit

**Plantae Novo-Mexicanae.**

No. 374.
Erigeron cinereum.

A. Fendler coll. 1847

Figure 6. Specimen label bearing no. 374, which corresponds with Fendler's notebook number, not the *Plantae Fendlerianae* number, rather is cited in parentheses with the protolog (cf. Figure 5).

**Phaca picta** Gray. Mem. Amer. Acad. Arts **4:** 37. 1849. "Rio del Norte, New Mexico." *A. Fendler,* 1847, Distr. no. 161. PCBC. ISOTYPE (2).

**Sophora chrysophylla** ssp. **glabrata** (Gray) Chock var. **ovata** Chock subvar. **ovata** Chock forma **maunakeaensis** Chock. Pacific Sci. **10:** 136. 1956. "South slope of Mauna Kea, 2.1 miles north of Humuula, Hawaii." *Chock, Lohman, Hodgdon and Lamberton 580* (30 August 1952). NHA. PARATYPE.

### LENTIBULARIACEAE

**Utricularia purpurea** Walt. forma **alba** Hellquist. Rhodora **76:** 19. 1974. "Southeast of Dorr Pond on N. H. Rt. 153, Wakefield, Carroll Co., New Hampshire." *Hellquist 8935* (29 August 1972). NHA. HOLOTYPE.

### LINACEAE

**Linum rigidum** var. **puberulum** Gray. Plantae Wrightianae **1:** 25. 1852. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 85 (includes coll. nos. 93, 94, 95, 96). PCBC. ISOTYPE (2).

### LORANTHACEAE

**Arceuthobium cryptopodum** Engelm. Boston J. Nat. Hist. **6:** 214. 1850. "Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 283. PCBC. ISOTYPE.

**Phoradendron juniperinum** Engelm. Mem. Amer. Acad. Arts **4:** 58. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 281. PCBC. ISOTYPE.

### LYCOPODIACEAE

**Lycopodium annotinum** L. var. **acrifolium** Fern. Rhodora **17:** 124. 1915. "Deciduous woods, Dover, Piscataquis Co., Maine." *Fernald s.n.* 22 July 1895. PSNH. ISOTYPE.

### MALVACEAE

**Sidalcea candida** Gray. Mem. Amer. Acad. Arts **4:** 24. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 80. PCBC. ISOTYPE.

### OLEACEAE

**Menodora scabra** Gray. Amer. J. Sci. ser. 2, **14:** 44. 1852. "New Mexico." *A. Fendler,* 1847, Distr. no. 693. PCBC. SYNTYPE.

**Syringa×josiflexa** Preston *ex* Pringle. Baileya **20:** 96–97. 1977. "Katie Osborne Lilac Garden, Royal Bot. Garden, Dundas, Ontario, received from Kingsville Nurseries, Kingsville, Maryland." *Pringle 1587* (29 May 1975). NHA. PARATYPE.

**Syringa×swegiflexa** Hesse *ex* Pringle. Baileya **20:** 98. 1977. "Royal Bot. Garden nursery, Dundas, Ontario, received from Agriculture Canada Research Station, Morden, Manitoba." *Pringle 1586* (6 June 1975). NHA. PARATYPE.

### ONAGRACEAE

**Epilobium nesophilum** Fern. var. **lupulinum** Hodgdon and Pike. Rhodora **66:** 149. 1964. "East Wolf Island, New Brunswick, Canada." *Hodgdon and Pike 1000* (27 July 1962). NHA. HOLOTYPE.

**Gaura lindheimeri** Engelm. and Gray. Boston J. Nat. Hist. **5:** 217. 1845. "Houston to the Brazos [River], Texas." *F. Lindheimer 61* (1843). PCBC. ISOTYPE.

**Oenothera fendleri** Gray. Mem. Amer. Acad. Arts **4:** 45. 1849. "Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 230 (includes coll. nos. 245, 246). PCBC. ISOTYPE.

**Ludwigia linearis** var. **puberula** Engelm. and Gray. Boston J. Nat. Hist. **5:** 217. 1845. "Houston, Texas." *F. Lindheimer 58* (1843). PCBC. ISOTYPE.

### PAPAVERACEAE

**Argemone hispida** Gray. Mem. Amer. Acad. Arts **4:** 5. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 16. PCBC. ISOTYPE.

### POLYGONACEAE

**Polygonum sagittatum** L. forma **chloranthum** Fern. Rhodora **19:** 134. 1917. "Valley of the Cathance River, tidal mud flats of the river, Bowdoinham, Sagadahoc Co., Maine." *Fernald and Long 13559* (14–19 Sept 1916). PSNH. ISOTYPE.

**Sidalcea neo-mexicana** Gray. Mem. Amer. Acad. Arts **4:** 23. 1849. "Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 79. PCBC. ISOTYPE.

### NYCTAGINACEAE

**Abronia fendleri** Standley. Contr. U. S. Nat. Herb. **12:** 324. 1909. "New Mexico." *A. Fendler,* 1847, Distr. no. 739. PCBC. ISOTYPE.

### POLYPODIACEAE

**Cheilanthes fendleri** Hook. Species Filicum **2:** 103. 1858. "New Mexico." *A. Fendler,* 1847, Distr. no. 1015. PCBC. ISOTYPE.

### PRIMULACEAE

**Dodecatheon radicatum** Greene. Erythea **3:** 37. 1895. "New Mexico." *A. Fendler,* 1847, Distr. no. 549. PCBC. ISOTYPE.

### RANUNCULACEAE

**Thalictrum fendleri** Engelm. Mem. Amer. Acad. Arts **4:** 5. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 13. PCBC. ISOTYPE.

### RHAMNACEAE

**Ceanothus fendleri** Gray. Mem. Amer. Acad. Arts **4:** 29. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 106a. PCBC. ISOTYPE.

### ROSACEAE

**Potentilla crinata** Gray. Mem. Amer. Acad. Arts **4:** 41. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 199. PCBC. ISOTYPE (2).

**Potentilla diffusa** Gray. Mem. Amer. Acad. Arts **4:** 41. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 198. PCBC. ISOTYPE.

**Prunus gracilis** Engelm. and Gray. Boston J. Nat. Hist. **5:** 243. 1845. "West of the Brazos [River], Texas." *F. Lindheimer 237* (1844). PCBC. ISOTYPE.

**Rubus allegheniensis** Porter forma **rubrobaccus** Wolfe and Hodgdon. Rhodora **53:** 30. 1951. "East Foss Farm, Durham, Strafford Co., New Hampshire." *Wolfe and Hodgdon 88* (16 August 1949). NHA. HOLOTYPE (on 2 sheets), PARATYPE (3).

**Rubus idaeus** L. var. **nesophilus** Hodgdon and Pike. Rhodora **66:** 148. 1964. "Edge of Shingle Beach, South Wolf Island, New Brunswick, Canada." *Hodgdon and Pike 500* (15 August 1960). NHA. HOLOTYPE.

### SALICACEAE

**Salix coactalis** Fern. Rhodora **8:** 22. 1906. "Shore of Penobscot River, Bangor, Maine." *O. Knight 2019* (17 May, 3 June, 29 August 1906, all on one sheet): *O. Knight 4814* (8 May, 31 May 1905). PSNH. COTYPE (3 sheets).

**Salix fendleriana** Anders. Salices Boreali-Americanae (North American Willow section, p. 8). 1858. "New Mexico." *A. Fendler,* 1847, Distr. no. 816. PCBC. SYNTYPE.

**Salix irrorata** Anders. Salices Boreali-Americanae (North American Willow section, p. 11). 1858. "New Mexico." *A. Fendler,* 1847, Distr. no. 812. PCBC. ISOTYPE

### SAXIFRAGACEAE

**Philadelphus microphyllus** Gray. Mem. Amer. Acad. Arts **4:** 54. 1849. "Near Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 266. PCBC. ISOTYPE.

### SCROPHULARIACEAE

**Euphrasia purpurea** Desf. var. **randii** Robinson forma **albiflora** Fern. and Wieg. Rhodora **17:** 88. 1915. "Turfy crests, Elwell Point, South Thomaston, Knox Co., Maine." *Bissell, Fernald and Chamberlain 10404* (15 August 1913). PSNH. ISOTYPE.

**Euphrasia purpurea** Desf. var. **farlowii** Robinson forma **iodantha** Fern. and Wieg. Rhodora **17:** 189. 1915. "Matinicus Island, Maine." *Norton s.n.* 22 August 1905. PSNH. ISOTYPE.

**Euphrasia williamsii** Robinson. Rhodora **3:** 272–273. 1901. "Stony ground and crevices of rocks, Alpine Garden, Mt. Washington, New Hampshire." *Robinson and Williams s.n.* 5 August 1901. NHA, PSNH. ISOTYPE (2).

**Penstemon jamesii** Benth. Proc. Amer. Acad. Arts **6:** 67. 1862. "New Mexico." *A. Fendler,* 1847, Distr. no. 575. PCBC. SYNTYPE.

### SELAGINELLACEAE

**Selaginella rupestris** L. var. **fendleri** Underwood. Bull. Torr. Bot. Club **25:** 127. 1898. "New Mexico." *A. Fendler,* 1847, Distr. no. 1024. PCBC. SYNTYPE (2).

### SOLANACEAE

**Lycium pallidum** Miers. Ill. S. Am. Pl. **2:** 108. 1849–1857. "New Mexico." *A. Fendler,* 1847, Distr. no. 670. PCBC. ISOTYPE.

**Physalis fendleri** Gray. Proc. Amer. Acad. Arts **10:** 66. 1874. "New Mexico." *A. Fendler,* 1847, Distr. no. 683. PCBC. SYNTYPE.

### UMBELLIFERAE

**Cymopterus fendleri** Gray. Mem. Amer. Acad. Arts **4:** 56. 1849. "Santa Fe, New Mexico." *A. Fendler,* 1847, Distr. no. 274. PCBC. ISOTYPE.

The list of Fendler isotypes published by Hehre, Hodgdon and Pike (1972) for the Parker Cleaveland collection was determined by comparing specimens with type localities and collection numbers cited in Wooton and Standley (1915). However, after consulting original descriptions for all our Fendler specimens the following specimens were found to have no type status:

*Sphaeralcea fendleri* A. Gray, *Fendler 78*
*Physalis similas* A. Nels., *Fendler 575*
*Oreocarya fulvocanescens* (S. Wats.) Greene, *Fendler 632*
*Eupatorium fendleri* A. Gray, *Fendler 347*
*Diplopappus ericoides* Torr. and Gray var. *hirtella* A. Gray, *Fendler 460*
*Agroseris purpurea* (A. Gray) Greene, *Fendler 487*

### ACKNOWLEDGEMENTS

We would like to thank especially Dr. Elizabeth Shaw for making available Fendler's original notebooks and helping to interpret Fendler's collection numbers and Gray's distribution numbers. Dr.

Otto Solbrig, Director of the Gray Herbarium, kindly granted permission for us to have Fendler's notebook photographed for Figure 2, which was prepared by Mr. John J. Lupo. We would also like to thank Dr. Shaw and Dr. A. Linn Bogle for reviewing the manuscript.

## LITERATURE CITED

GRAY, A. 1849. Plantae Fendlerianae. Mem. Amer. Acad. Arts **4:** 1–116.

HEHRE, E., A. R. HODGDON & R. B. PIKE. 1972. The Parker Cleaveland Herbarium of Bowdoin College. Rhodora **74:** 80–84.

WOOTON, E. O. & P. STANDLEY. 1915. Flora of New Mexico. Contrib. U. S. Nat. Herb. Vol. **19.**

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# NEW ENGLAND FERN ALLIES, OPHIOGLOSSACEAE, HYMENOPHYLLACEAE, AND MARSILEACEAE.

R. JAMES HICKEY

This is the second paper reporting on New England pteridophytes in preparation for a set of computer documented distribution maps. An account of this project is given by A. Tryon (1978). For the most part, information on the taxa has been obtained through an examination of specimens in the Gray Herbarium (GH) and the New England Botanical Club Herbarium (NEBC). In a few cases, I have relied on recent monographs for the inclusion of the rarer taxa.

## EQUISETACEAE

### Equisetum

Much of the infraspecific variation in *Equisetum* species is a result of environmental modification and phenotypic plasticity. This is especially true of *E. arvense,* as shown by Hauke (1966). The numerous forms and varieties included by Fernald (1950) are therefore excluded from this list since they are not of systematic importance. The taxa listed are those accepted by Hauke (1963, 1978).

| | | |
|---|---|---|
| **Equisetum arvense** L. | Equis arv | Field Horsetail |
| **E. arvense** × **E. fluviatile**<br>*E.* × *litorale* Kuehl | Equis arv × fluv | Shore H. |
| **E. fluviatile** L. | Equis fluv | Water H. |
| **E. hyemale** L. var. **affine** (Engel.) A. A. Eaton | Equis hyem | Common Scouring Rush |
| **E. hyemale** × **E. laevigatum**<br>*E.* × *Ferrissii* Clute | Equis hyem × laev | |
| **E. hyemale** × **E. variegatum**<br>*E. variegatum* var *Jesupi* A. A. Eaton<br>*E.* × *trachyodon* A. Br. | Equis hyem × vari | |
| **E. palustre** L. | Equis palus | Marsh H. |
| **E. pratense** Ehrh. | Equis prat | Meadow H. |
| **E. scirpoides** Michx. | Equis scirp | Dwarf H. |
| **E. sylvaticum** L. | Equis sylv | Wood H. |
| **E. variegatum** Schl. | Equis vari | Variegated H. |

## LYCOPODIACEAE

### Lycopodium

In recent years there has been an increasing acceptance of classification systems that recognize several genera for the north temperate lycopods. The data available on sporophyte morphology, spore ornamentation, gametophyte morphology, cytology, and anatomy are suggestive of a polyphyletic origin of the boreal species. However, it is important to remember that relatively little is known about the tropical species where most of the diversity in the genus occurs. Until these tropical species are examined more closely and can be placed within one of these systems (see Tutin et al., 1964), it seems appropriate to agree with other students of the genus (Bruce, 1976a, 1976b; Øllgaard, 1975, 1979; Boivin, 1950; Wilce, 1972) who continue to recognize a single genus *Lycopodium*.

Recent works by Wilce (1965), Hickey (1977) and Beitel (1979) have clarified some of the difficult species groups in *Lycopodium*. This genus now poses relatively few taxonomic problems in the New England area with the exception of the *L. inundatum* complex. This latter group still needs considerable study before a definitive listing of its taxa can be presented. Of particular interest is the occurrence of *L. carolinianum* in the Connecticut River valley of central Massachusetts. Since this is a coastal plains species, its occurrence only in central Massachusetts rather than on Cape Cod or adjacent islands is quite surprising and it will be interesting to see if this species persists in New England. The nomenclature of Wilce (1965) is followed for *L. complanatum, L. sabinaefolium, L. sitchense,* and *L. tristachyum*. However, *L. flabelliforme* has been replaced by the older name *L. digitatum* (Hickey & Beitel, 1979).

| | | |
|---|---|---|
| **Lycopodium alopecuroides** L. | Lyco alop | Foxtail Clubmoss |
| **L. annotinum** L. | Lyco annot | Stiff C. |
| **L. carolinianum** L. | Lyco caro | Slender C. |
| **L. clavatum** L. | Lyco clav | Staghorn C. |
| **L. complanatum** ×**L. digitatum** | Lyco comp ×digit | Northern Running Pine |
| **L. complanatum** × **L. tristachyum** | Lyco comp × trist | |

| | | |
|---|---|---|
| **L. dendroideum**<br>*L. obscurum* var. *dendroideum* (Michx.) D. C. Eaton<br>*L. obscurum* forma *dendroideum* (Michx.) Blomq. & Corr. | Lyco dend | Tree C. |
| **L. digitatum** A. Br.<br>*L. complanatum* var. *flabelliforme* Fern.<br>*L. flabelliforme* (Fern.) Blanch.<br>*L. complanatum* var. *Dillenianum* Döll | Lyco digit | Running Pine |
| **L. digitatum** × **L. tristachyum**<br>*L.* × *Habereri* House | Lyco digit × trist | Haberer's Running Pine |
| **L. inundatum** L. var. **inundatum** | Lyco inun var inun | Bog C. |
| **L. inundatum** var. **Bigelovii** Tuckerm. | Lyco inun var Bigel | Slender Bog C. |
| **L. inundatum** var **robustum** R. J. Eaton | Lyco inun var robus | Robust Bog C. |
| **L. lucidulum** Michx. | Lyco luci | Shining C. |
| **L. lucidulum** × **L. Selago**<br>*L.* × *Buttersii* Abbe | Lyco luci × Sel | |
| **L. obscurum** L. var **obscurum** | Lyco obsc. var obsc | Prince's Pine |
| **L. obscurum** L. var. **isophyllum** Hickey | Lyco obsc var isop | Prince's Pine, Tree C. |
| **L. sabinaefolium** Willd. | Lyco sabin | Savin Leaved C. |
| **L. Selago** L. | Lyco Sel | Fir C. |
| **L. sitchense** Rupr.<br>*L. sabinaefolium* var. *sitchense* (Rupr.) Fern. | Lyco sitch | Sitka C. |
| **L. tristachyum** Pursh | Lyco trist | Ground Cedar |
| **L. tristachyum** × **L. alpinum**<br>*L.*×*Issleri* (Rouy) Lawal. | Lyco trist × alp | |

## SELAGINELLACEAE

### Selaginella

*Selaginella* is the only genus of fern allies in New England that does not present problems in identification. All three of the New England species are morphologically distinct and ecologically or geographically separated.

| | | |
|---|---|---|
| **Selaginella apoda** (L.) Fern. | Selag apod | Meadow Spikemoss |
| **S. rupestris** (L.) Spring | Selag rupes | Rock S. |
| **S. selaginoides** (L.) Link | Selag selag | Northern S. |

## ISOETACEAE

### Isöetes

Until a modern treatment for the New England species of *Isöetes* is proposed no listing of taxa can be considered definitive. The discrepancies between the works of Braun (1847), Engelmann (1882), Eaton (1900), Pfeiffer (1922), Proctor (1949) and Reed (1953, 1965) have led to confusion in the understanding of species limits and relationships in the New England members of this taxonomically difficult genus. For this report, six species groups have been recognized which, for the sake of simplicity, have been treated as species. These six taxa are readily distinguished by megaspore and leaf characters. It should be stressed however, that some of these taxa, especially *I. muricata* and *I. riparia*, are quite heterogenous while others, such as *I. Eatoni,* may represent local aberrant forms or hybrids. The early work of Eaton (1900) still stands as the most complete and discerning work on the New England taxa.

| | | |
|---|---|---|
| **Isoetes Eatoni** Dodge<br>*I. Gravesii* Eaton | Isoet Eaton | Eaton's Quillwort |
| **I. Engelmannii** A. Br.<br>*I. foveolata* A. A. Eaton | Isoet Engel | Engelmann's Q. |
| **I. macrospora** Dur. | Isoet macro | Large-spored Q. |
| **I. muricata** Dur.<br>*I. echinospora* var *Braunii* (Dur.) Engel.<br>*I. echinospora* var. *muricata* (Dur.) Engel. | Isoet muri | Spiny-spored Q. |

| | | |
|---|---|---|
| **I. riparia** Engel. | Isoet ripar | River Q. |
| *I. Dodgei* A. A. Eaton | | |
| *I. echinospora* var *robusta* Engel. | | |
| *I. saccharata* var. *Amesii* A. A. Eaton | | |
| **I. Tuckermanii A.** Br. | Isoet Tuck | Tuckerman's Q. |

OPHIOGLOSSACEAE

**Botrychium**

*Botrychium* is a taxonomically perplexing group because the species are morphologically simple, have a great deal of phenotypic plasticity and, for the most part, lack habitat specificity. Clausen's (1938) monograph of the Ophioglossaceae has outlined the various morphological entities involved, but additional field work and biosystematic studies are needed before a wholly adequate systematic treatment can be completed. The work on *B. minganense* by Wagner & Lord (1956) shows that this species is morphologically and cytologically distinct from *B. Lunaria. Botrychium minganense* is a tetraploid with $2n = 180$ and *B. Lunaria* is diploid with $2n = 90$. The report by Stevenson (1975) of two leaf types, each representing different taxa, attached to a single stem of *B. multifidum* points out the extensive morphological variability of *Botrychium* species. While *B. oneidense* may ultimately be accepted, the available evidence on its status is inconclusive (Clausen, 1944; Wagner, 1960, 1961a, 1961b).

| | | |
|---|---|---|
| **Botrychium dissectum** Spreng. | Botr diss | Cut-leaved Grape Fern |
| *B. obliquum* Muhl. | | |
| *B. oneidense* (Gilb.) House | | |
| *B. dissectum* forma *oneidense* (Gilb.) Clute | | |
| *B. multifidum* var. *oneidense* (Gilb.) Farwell | | |
| **B. lanceolatum** (Gmel.) Angstr. | Botr lance | Triangle G. F. |
| **B. Lunaria** (L.) Sw. | Botr Lunar | Moonwort |
| **B. matricariifolium** A. Br. | Botr matri | Matricary G. F. |

| | | |
|---|---|---|
| **B. minganense** Vict.<br>*B. Lunaria* var *minganense* (Vict.) Dole<br>*B. Lunaria* forma *minganense* (Vict.) Clute | Botr ming | Mingan Moonwort |
| **B. multifidum** (Gmel.) Rupr.<br>*B. multifidum* var. *intermedium* (D. C. Eaton) Farwell<br>*B. multifidum* forma *dentatum* Tryon | Botr multi | Leathery G. F. |
| **B. simplex** Hitch. | Botr simp | Least G. F. |
| **B. virginianum** (L.) sw. | Botr virg | Rattlesnake Fern |

### Ophioglossum

In New England there is a single taxon of the genus *Ophioglossum*. While this is a member of the *O. vulgatum* complex, its status with respect to other members has yet to be critically assessed. In view of the differences between it and other North American members of the complex (Wagner, 1971) it seems appropriate to continue to recognize it as a variety.

| | | |
|---|---|---|
| **Ophioglossum vulgatum** L. var. **pseudopodum** (Blake) Farwell | Ophio vulg | Adder's Tongue Fern |

## HYMENOPHYLLACEAE

### Trichomanes

The recent discovery (McAlpin & Farrar, 1978) of an independently reproducing *Trichomanes* gametophyte at Mt. Toby in Franklin Co., Massachusetts adds a new family to the New England flora. Since sporophytes are not produced, identification to species cannot be made for this plant. It is expected that additional locations of this gametophyte will be found when similar environments are searched.

| | | |
|---|---|---|
| **Trichomanes** sp. | Trich | Appalachian Gametophyte |

## MARSILEACEAE

### Marsilea

*Marsilea quadrifolia*, the only New England member of the Marsileaceae, is a naturalized introduction. It was first collected in 1860 from a pond in Litchfield, Connecticut but has since been reported from numerous other stations throughout southern New England. While some of these newer stations are obvious transplants, others appear to represent natural migrations, perhaps via vegetative reproduction. *Marsilea's* persistence and spread outside of cultivation indicates that it has become naturalized and can therefore be considered a part of the flora of New England.

| | | |
|---|---|---|
| **Marsilea quadrifolia** L. | Mars quad | Water Clover |

## EXCLUDED SPECIES

## SALVINIACEAE

### Azolla

In the Gray Herbarium and the New England Botanical Club Herbarium there are numerous New England collections of *Azolla caroliniana*. All of these specimens were collected between 1894 and 1902 and all apparently originated from a Lotus pond in Springfield, Massachusetts. While *Azolla caroliniana* has been included in the aquatic flora of New England by Fassett (1940), Svenson (1944) and Muenscher (1944) the collecting record of this plant indicates that it is not and never has been naturalized in New England.

### Salvinia

A single collection of *Salvinia rotundifolia* from Norfolk Co., Massachusetts, made in 1941, is in the New England Botanical Club Herbarium. As there appear to be no previous or subsequent collections of this plant from New England, this record apparently represents an ephemeral escape from cultivation and the species is therefore excluded from this list.

## LITERATURE CITED

Beitel, J. M. 1979. The clubmosses *Lycopodium sitchense* and *L. sabinifolium* in the upper Great Lakes region. Mich. Bot. **18:** 3–13.

Boivin, B. 1950. The problems of generic segregates in the form-genus *Lycopodium*. Amer. Fern J. **40:** 32–41.

Braun, A. 1847. On the North American species of *Isoetes* and *Marsilea*. J. Arts & Sci., n.s. **3:** 52–56.

Bruce, J. G. 1976a. Development and distribution of mucilage canals in *Lycopodium*. Amer. J. Bot. **63:** 481–491.

______. 1976b. Gametophytes and subgeneric concepts in *Lycopodium*. Amer. J. Bot. **63:** 919–924.

Clausen, R. T. 1938. A monograph of the Ophioglossaceae. Mem. Torrey Bot. Club **19:** 1–171.

______. 1944. On the status of *Botrychium dissectum* var. *oneidense*. Amer. Fern J. **34:** 55–60.

Eaton, A. A. 1900. The genus *Isoetes* in New England. Fernwort Papers **2:** 1–16.

Engelmann, G. 1882. The genus *Isoetes* in North America. Trans. St. Louis Acad. Sci. **4:** 358–390.

Fassett, N. C. 1940. A manual of Aquatic Plants. McGraw-Hill Book Co., New York.

Fernald, M. L. 1950. Gray's Manual of Botany. 8th ed. American Book Co., New York.

Hauke, R. L. 1963. A taxonomic monograph of the genus *Equisetum* subgenus *Hippochaete*. Beih. Nova Hedwigia **8:** 1–123.

______. 1966. A systematic study of *Equisetum arvense*. Nova Hedwigia **13:** 81–109.

______. 1978. A taxonomic monograph of *Equisetum* subgenus *Equisetum*. Nova Hedwigia **30:** 385–455.

Hickey, R. J. 1977. The *Lycopodium obscurum* complex in North America. Amer. Fern J. **67:** 45–48.

Hickey, R. J. & J. M. Beitel. 1979. A name change for *Lycopodium flabelliforme*. Rhodora **81:** 137–140.

McAlpin, B. & D. R. Farrar. 1978. *Trichomanes* gametophytes in Massachusetts. Amer. Fern J. **68:** 97–98.

Muenscher, W. C. 1944. Aquatic Plants of the United States. Cornell University Press. Ithaca, New York.

Øllgaard, B. 1975. Studies in the Lycopodiaceae, I. Observations on the structure of the sporangium wall. Amer. Fern J. **65:** 19–27.

______. 1979. Studies in the Lycopodiaceae, II. The branching patterns and infrageneric groups of *Lycopodium* sensu lato. Amer. Fern J. **69:** 49–61.

Pfeiffer, N. E. 1922. Monograph of the Isoetaceae. Ann. Mo. Bot. Gard. **9:** 79–232.

Proctor, G. R. 1949. *Isoetes riparia* and its variants. Amer. Fern J. **39:** 110–121.

Reed, C. F. 1953. Index Isoetales. Bol. Soc. Brot. **27:** 5–72.

______. 1965. *Isoetes* in Southeastern United States. Phytologia **12:** 369–400.

Stevenson, D. Wm. 1975. Taxonomic and morphological observations on *Botrychium multifidum* (Ophioglossaceae). Madroño **23:** 198–204.

Svenson, H. K. 1944. The new world species of *Azolla*. Amer. Fern J. **34:** 69–84.

Tryon, A. F. 1978. The New England Ferns (Filicales). Rhodora **80:** 558–569.

Tutin et al., eds. 1964. Flora Europaea, **I.** Lycopodiaceae to Platanaceae. University Press. Cambridge, England.

Wagner, W. H., Jr. 1960. Periodicity and pigmentation in *Botrychium* subg. *Scepteridium* in the northeastern United States. Bull. Torrey Bot. Club **87:** 303 325.

______. 1961a. Roots and the taxonomic differences between *Botrychium oneidense* and *B. dissectum*. Rhodora **63:** 164 175.

______. 1961b. On the relative development of the fertile segments in *Botrychium dissectum* and *B. oneidense*. Amer. Fern J. **51:** 75 81.

______. 1971. The Southeastern Adder's-tongue, *Ophioglossum vulgatum* var. *pycnostichum,* found for the first time in Michigan. Mich. Bot. **10:** 67–74.

Wagner, W. H., Jr. & L. P. Lord. 1956. The morphological and cytological distinctness of *Botrychium minganense* and *B. lunaria* in Michigan. Bull. Torrey Bot Club. 83: 261 280.

Wilce, J. H. 1965. Section Complanata of the genus *Lycopodium*. Beih. Nova Hedwigia 19: 1 233.

______. 1972. Lycopod spores, I. General spore patterns and the generic segregates of *Lycopodium*. Amer. Fern J. 62: 65–79.

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# CENTRAL AMERICAN NOVELTIES IN THE GENUS BLAKEA (MELASTOMATACEAE)

Frank Almeda, Jr.

Current work on a treatment of the Melastomataceae for Flora Costaricensis has disclosed several new species, many of which were collected in lower elevation montane forests during the last decade. The three new species of *Blakea* presented here represent significant additions to two divergent trends of floral evolution within the genus. *Blakea chlorantha* is to be included with the small group of species characterized by pendant pedicellate flowers with green, connivent petals and copious nectar production, whereas *B. crassifolia* and *B. micrantha* are to be added to the evolutionary line having small, subsessile, nectarless flowers with expanded, tuberculate or verrucose petals.

**Blakea chlorantha** Almeda, *sp. nov.* Figure 1

Frutex vel arbuscula ad 3–5(–9) m altus. Ramuli primum obscure quadrangulati demum teretes sicut petioli pedicellique modice vel dense setosi pilis ca. 0.5 mm longis demum glabrati. Folia in quoque jugo in forma isomorphica, in dimensionibus isomorphica; petioli 1.2–1.7(–2.5) cm; lamina elliptica vel elliptico-lanceolata 6–9(–12.3) cm longa et 3–5.5(–8.7) cm lata, chartacea vel subcoriacea, integra, 5-plinervata, apice acuminata, basi acuta, supra glabra, subtus sparse vel modice setosa pilis gracilibus plerumque 0.5 mm longis. Flores 6-meri in foliorum axillus 1–3 fasciculati; pedicelli 4–10 mm longi; bracteae exteriores et interiores 5–9 × 4–5 mm ovatae vel elliptico-ovatae, apice obtuso vel rotundato. Hypanthium (ad torum) 6–6.5 mm longum extus modice setosum pilis 0.5 mm longis; calycis tubus 2 mm longus, lobis 4–4.5 mm longis triangularibus. Petala 6–8.5 × 5–6 mm crassiuscula glabra anguste-obovate, apice late rotundato. Stamina isomorphica glabra inter se non cohaerentia; filamenta 2.5–3 mm longa; antherarum thecae 3–3.5 mm longae apice dorsaliter biporosae, connectivo dorsaliter 1 mm supra basim calcari minuto elevato. Stylus 7–12 mm longus; stigma truncatum. Fructus ignotus.

TYPE: COSTA RICA. **Puntarenas:** Ca. 3–3.5 km SE of Santa Elena and 2–3 km E of Monteverde on the Peñas Blancas trail, Cordillera de Tilaran, elevation 1500–1540 m, 19 December 1973, *Almeda et al. 2005* (Holotype, DUKE!; isotypes, CAS!, CR!, F!, MO!, US!).

ADDITIONAL COLLECTIONS EXAMINED: COSTA RICA: Border of Alajuela, Puntarenas and Guanacaste Provinces: roadside along continental divide at 1550–1580 m, *Dryer 1045* (F).

*Blakea chlorantha* is presently known only from the Cordillera de Tilaran, Costa Rica, a small mountain range situated on the western edge of an old, dissected, intrusive volcanic block of mountains. This range supports a large and diverse assemblage of plant and animal species. It has been the subject of intensive conservation efforts following discovery of the Golden Toad (*Bufo periglenes* Savage), which is known from only a few hectares within the lower montane forest (Savage, 1966).

The diagnostic characters of the new species are its green pendant flowers, small (5–9 mm long) ovate to elliptic-ovate floral bracts, and entire, revolute foliar margins which are modified adaxially (at petiole-laminar junction) into pseudoformicarial flap-like pouches (mostly 2–4 mm long and 3–4 mm wide), the basal and lateral margins of which are free from but conspicuously decurrent on the lower petiolar surface. In foliar shape, vegetative indument, and shape and posture of floral organs, *Blakea chlorantha* resembles *B. austin-smithii* Standley, another Costa Rican endemic presently known only from the volcanic slopes of the Cordillera Central. These two species are readily distinguished by the latter's epiphytic habit and possession of larger (10–24 mm long) linear-lanceolate floral bracts, and elliptic-obovate, bluntly denticulate leaves.

Excepting the brief note by Spruce (1908), who suggested probable beetle pollination for an Ecuadorian species of *Blakea,* information is not yet available on pollination mechanisms in the genus. The differences in floral structure among the Costa Rican species of *Blakea,* however, strongly suggest that different groups of pollinating agents are involved. Field observations of *B. chlorantha* and *B. austin-smithii* thus appear worthy of placing on record at this time. Although natural pollinators have not been seen, these two species share several floral characteristics reminiscent of the bat-pollination syndrome summarized by various workers (Faegri & van der Pijl, 1971; van der Pijl, 1936; Proctor & Yeo, 1973; Vogel, 1958).

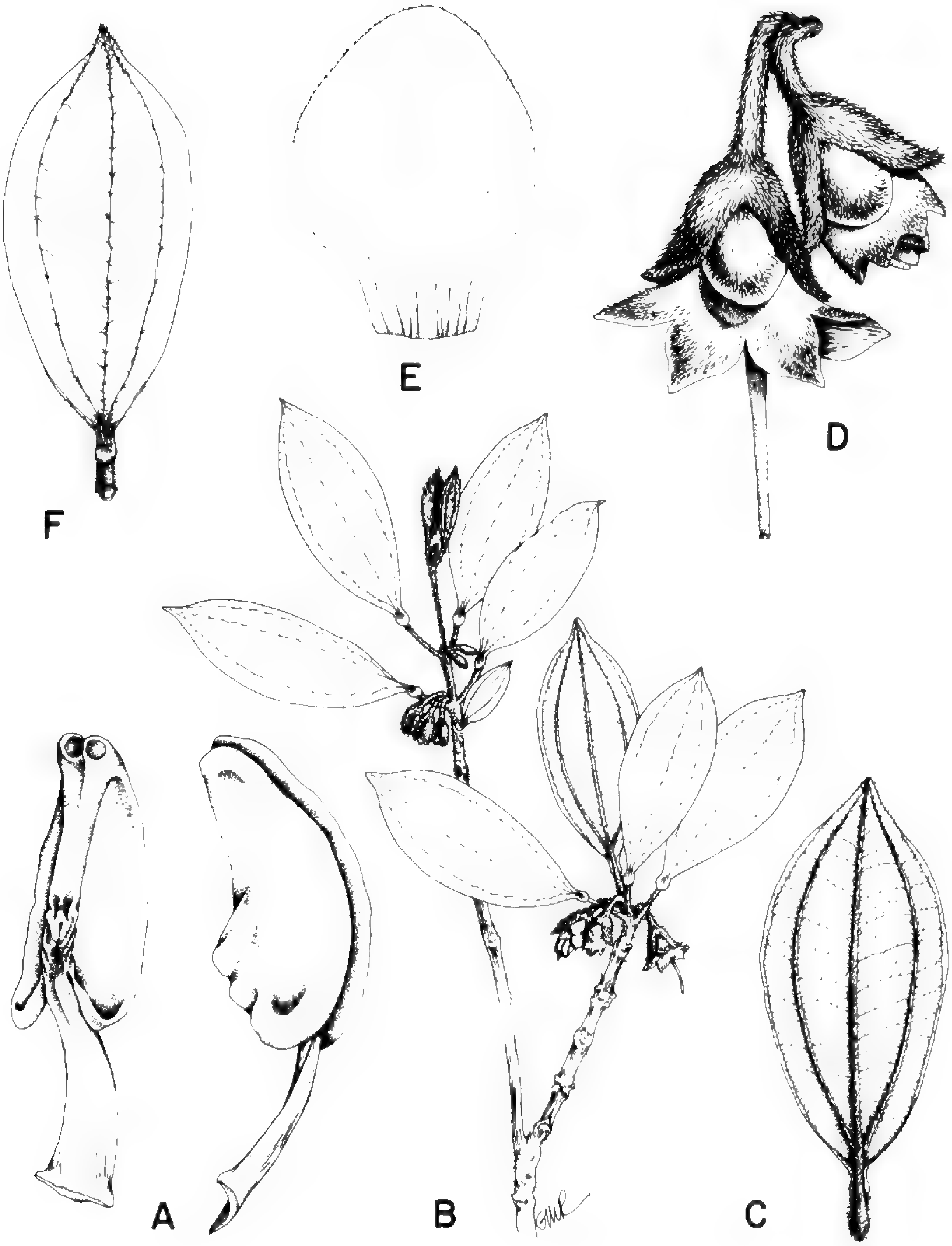

Figure 1. *Blakea chlorantha* Almeda. A, stamens, dorsal view (left) and lateral view (right), × 10; B, habit × 1/2; C, representative leaf, abaxial surface, × 1/2; D, floral bud (right) and immature hypanthium (left), × 2; E, petal, × 5; F, representative leaf, adaxial surface, × 1/2. (A–F from *Almeda et al. 2005*.)

Observed features include the following: 1) nocturnal anthesis; 2) production of a musty odor; 3) drab green petal color; 4) strong pendant pedicels which bring open flowers to an exposed ± horizontal position; 5) overlapping petal conformation to form a bell-like corolla; and 6) production of copious mucilaginous nectar.

**Blakea crassifolia** Almeda, *sp. nov.* Figure 2

Frutex epiphyticus. Ramuli glabri primum quadrangulati demum teretes. Folia rigida integra in quoque jugo in forma isomorhica, in dimensionibus isomorphica vel anisomorphica; petioli (1–)2–4 mm; lamina crasse coriacea (.5–)2–6.5 × 1–4.3 cm, glabra, ovata vel elliptico-ovata, apice acuto ad cuspidato vel mucronato basi rotundata vel cordata 3–5-nervata. Flores 6-meri in foliorum axillus 1–2(–6) fasciculati; pedicelli 1–2 mm longi; bracteae exteriores 5–8 × 2.5–4 mm elliptico-lanceolatae apice acuto vel obtuso extus sparse lanatae demum glabratae; bracteae interiores 4–7 × 2.5–4 mm elliptico-ovatae apice acuto vel rotundato. Hypanthium 3–5 × 4–6 mm glabrum; calycis tubus 1 mm longus, lobis (3–)3.5–4.5 mm longis anguste triangularibus. Petala carnosa et tuberculata 5–7 × 1.5–2.5 mm oblongo-lanceolata vel anguste oblanceolata. Stamina isomorphica glabra inter se non cohaerentia; filamenta 3.5–4.5 mm longa; antherarum thecae 2–2.5 × 0.5 mm oblongo-subulatae connectivo dorsaliter 0.5 mm supra basim calcari minuto elevato. Stigma punctiforme; stylus glaber 6 mm longus. Semina ca 0.5–1 mm longa, albida vel brunneola, clavata, lunata vel pyriformia.

TYPE: PANAMA. **Cocle:** La Mesa above El Valle in forest on both sides of junction with road to Cerro Pilon, elevation ca 800 m, 21 July 1974, *Croat 25430* (Holotype, CAS!; isotypes, MO, US!).

ADDITIONAL COLLECTIONS EXAMINED: COSTA RICA: Heredia/Alajuela Border: Colonia Virgen del Socorro along road leading from Costa Rica #9 to the Colonia, *J. & K. Utley 5629* (CAS, DUKE, F). PANAMA. Cocle: foothills of Cerro Pilon, near El Valle at 900 m, *Duke & Correa 14713* (MO); woods along trail to La Mesa about 4.5 miles beyond El Valle, *Wilbur & Luteyn 11697* (CAS, DUKE, F, MO, US).

*Blakea crassifolia* is so named because of its unusually thick leaves which become rigid and coriaceous on drying. Distinguishing characters of this species are the relative absence of an indument on

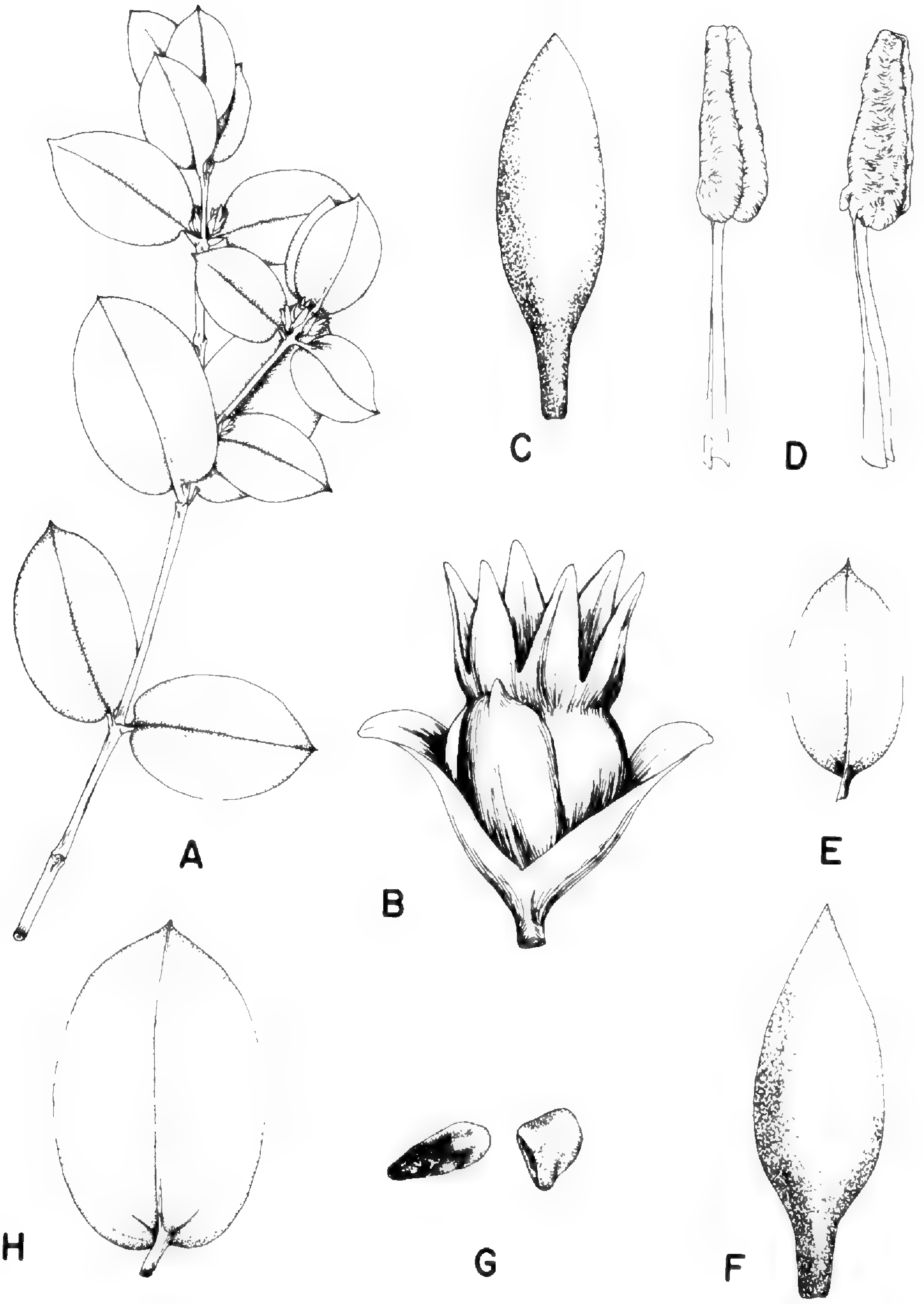

Figure 2. *Blakea crassifolia* Almeda. A, habit, × 1/2; B, hypanthium with enveloping decussate floral bracts, × 4-1/2; C & F, mature petals, × 8; D, stamens, ventral view (left) and lateral view showing dorsal appendage (right), × 10; E & H, representative leaves (abaxial surfaces), × 1; G, seeds, × 8. (A–F, H from *Croat 25430;* G from *Wilbur & Luteyn 11697.)*

mature vegetative organs, sessile or subsessile flowers, lance-triangular, tardily deciduous calyx lobes, lanceolate to narrowly oblanceolate, tuberculate petals, and apically truncate anthers.

In Gleason's (1958) treatment of the Panamanian species, *Blakea crassifolia* keys to *B. parvifolia* Gleason, a species known only from the crest of Cerro Pajita, El Valle de Anton, which differs by its conspicuous floral pedicels, basally cuneate, obovate leaves and laterally coherent stamens. With respect to floral details and type and distribution of pubescence on juvenile, vegetative and floral organs, *B. crassifolia* is most similar to *B. micrantha* (also described herein). The latter species differs in having oblanceolate to spatulate leaves, conspicuously costate outer floral bracts, sparsely verrucose, ovate to elliptic-ovate petals, and unappendaged anther connectives.

There are some noteworthy differences between the Costa Rican and Panamanian collections of the new species. The Costa Rican specimens have thinner, longer (4.8–6.5 cm) elliptic-lanceolate leaves that are acuminate apically, shorter petioles (1–1.5 cm), and pink petals (fide *Utley 5629*); the Panamanian specimens have thicker, smaller, ovate to elliptic-ovate leaves that are acute to cuspidate or mucronate apically, longer petioles (2–4 mm), and white petals (fide *Croat 25430*). Morphological differentiation of this kind is especially common among isolated populations of epiphytic plants and seems unworthy of formal taxonomic recognition. The observed differences warrant further study as additional populations are located.

**Blakea micrantha** Almeda, *sp. nov.*

Frutex epiphyticus. Ramuli sulcato-quadrangulati demum rotundato quadrangulati primum sicut folia paulo furfuracei mox glabrati. Folia in quoque jugo in forma isomorphica, in dimensionibus isomorphica; petioli 5–10 mm; lamina chartacea vel coriacea integra, 1–4 × 0.4–1.6 cm, oblanceolata vel spatulata, apice obtuso vel rotundato basi attenuata, 3-nervata. Flores 6-meri sessiles vel subsessiles in foliorum superiorum axillus solitarii; bracteae exteriores 3–5 × 2–3 mm elliptico-lanceolatae apice rotundato extus sparse lanatae demum glabratae; bracteae interiores 3–4 × 2–3 mm elliptico-ovatae apice rotundato. Hypanthium 4–5 × 3–5 mm; calycis tubus 1 mm longus, lobis 1.5 mm longis late triangularibus. Petala integra 4.5–6 × 2.5–3 mm, elliptica vel elliptico-ovata extus minute verrucosa. Stamina isomorphica glabra inter se non cohaerentia; filamenta 2–3.5 mm longa; antherarum thecae 2 × 0.5–1 mm oblongo-subulatae, connectivo non appendiculato. Stigma punctiforme; stylus glaber 6 mm longus. Fructus ignotus.

TYPE: PANAMA **Veraguas:** Cerro Tute ca. 10 km NW of Santa Fe on ridgetop in cloud forest above 1000 m, 19 June 1975, *Mori 6765* (Holotype, CAS!; isotype, MO!).

The type and only known collection of *Blakea micrantha* was gathered in an area which has received little attention by field botanists. Although closely related to *B. crassifolia*, this apparently local entity is amply distinct. In addition to the diagnostic features enumerated in the discussion of the preceding species, *B. micrantha* is distinguished by its carinate distal branchlets, thinner, basally attenuate leaves with revolute margins and longer (5–10 mm) petioles.

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## LITERATURE CITED

GLEASON, H. A. 1958. Melastomataceae. Flora of Panama. Ann. Missouri Bot. Gard. **45**:203–304.

FAEGRI, K. & L. VAN DER PIJL. 1971. The principles of pollination ecology. 2nd ed. Pergamon Press, New York.

PROCTOR, M. & P. YEO. 1973. The pollination of flowers. Williams Collins Sons & Co. Ltd., London.

SAVAGE, J. M. 1966. An extraordinary new toad (*Bufo*) from Costa Rica. Rev. Biol. Trop. **14**:153–167.

SPRUCE, R. 1908. Notes of a botanist on the Amazon and Andes. Macmillian & Co., London.

VAN DER PIJL, L. 1936. Fledermaüuse und Blumen. Flora (Jena) **131**:1–40.

VOGEL, S. 1958. Fledermausblumen in Sudamerika. Österr. Bot. Zeitschr. **104**: 491–530.

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# THE GENUS *HABENARIA* WILLD. (ORCHIDACEAE) IN THE BAHAMA ISLANDS

RUBEN P. SAULEDA AND RALPH M. ADAMS

The only reported occurrence of the genus *Habenaria* in the Bahama archipelago was made by Correll (1975), when he discovered a population of *Habenaria odontopetala* Rchb. f. on Grand Bahama Island. Our taxonomic and ecological studies of the native orchids of the Bahama archipelago, including the Turks and Caicos Islands, have resulted in the discovery of two additional species of *Habenaria* distributed within the Bahama Islands: *Habenaria alata* Hook. and *Habenaria quinqueseta* (Michx.) Eaton var. *quinqueseta*. Furthermore, we have found that *H. odontopetala* is not restricted to Grand Bahama Island as previously reported but also occurs sympatrically with *H. alata* on Andros Island.

## TAXONOMIC TREATMENT

**Habenaria** Willd., Sp. Pl. **4:** 44. 1805.

Terrestrial or semiaquatic herbs with fleshy tubers and fibrous roots. Stems erect, leafy, terminating in a raceme. Leaves entire, thin in texture, with basal part sheathing stem. Raceme loosely or densely flowered, bracts usually well developed. Ovary pedicellate, slender or broadly-winged. Sepals free, similar or dissimilar; dorsal sepal concave, forming a hood over column; lateral sepals spreading or reflexed. Petals free, simple or bipartite, connivent with dorsal sepal. Lip simple or tripartite with a spur at the base. Column short, sigmata 2, confluent, protruding around and below aperture of nectary, rostellum absent, anther 2-celled with anther canals separate. Pollinia granular on distinct caudicles.

Lectotype: *Orchis habenaria* L. (Kraezlin in Engl. Bot. Jahrb. **16:** 58, 1892).

### KEY TO THE SPECIES IN THE BAHAMA ISLANDS

1. Lip simple or obscurely dentate at base on either side, basal appendage of petals absent or short .................... 2
1a. Lip distinctly tripartite, basal appendage of petals as long as or longer than petal, ovary ribbed .......... *H. quinqueseta*

2. Petals lanceolate, acute, ovary distinctly 3-winged *H. alata*
2a. Petals oblong-quadrate to linear-oblong, apex of petals 3-lobed, ovary ribbed ................ *H. odontopetala*

1. **Habenaria alata** Hook., Exot. Fl. 3:t169. 1826. (Fig. 1).

HOLOTYPE: St. Vincent, *Guilding s.n.* (K, photograph seen*).

Plant terrestrial, erect, to 68 cm tall; roots many, fibrous, with one or two spherical to ovoid fleshy tubers; stems round, uniform in thickness throughout, simple, erect, leafy, completely enclosed by leaf-sheaths, to 46 cm tall; leaves soft and thin in texture, lanceolate to narrowly ovate, acute to subacuminate, articulated with the leaf sheaths, to 17 cm long, 2.5 cm wide, decreasing in size toward the inflorescence and base, basally becoming bract-like; inflorescence terminal, racemose, to 22 cm tall, 6–20 flowers, flowers pale green to greenish-yellow, fleshy; floral bracts ovate to linear-lanceolate, acuminate, longer than ovaries, to 3.0 cm long, 0.5 cm wide; ovary pedicellate, broadly 3-winged, to 2.0 cm long; dorsal sepal broadly ovate to suborbicular, concave, cuspidate, margins papillose, to 9 mm long, 7 mm wide; lateral sepals obliquely ovate, cuspidate, margins papillose, to 9 mm long, 6 mm wide; petals lanceolate, acute, to 8 mm long, 3 mm wide, anterior margin with a small dentiform lobe; labellum entire, directed forward, linear-lanceolate to ligulate, subobtuse, basal lobes obscure or absent, to 8 mm long, 2 mm wide, spur or nectary clavate to linear, arcuate, to 14 mm long, 1.5 mm thick; column short, to 3 mm long, 3 mm wide; capsule erect, prominently 3-winged, to 2.0 cm long, 7 mm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Northern Andros,** high coppice, 6 mi NW Love Hill settlement, *Sauleda 1974* (FTG), *1992,* (AMES, FTG, K, NY, US).

GENERAL DISTRIBUTION: **Cuba,** *Shafer 8326,* (NY); Isle of Pines, *Britton, Britton & Wilson 14568* (NY); **Haiti,** *Holdridge 851,* (NY); **Dominican Republic,** *Liogier 21290* (NY); **Jamaica,** *Harris 7526* (NY); **Puerto Rico,** *Hess 3399* (NY); **Martinique,** *Duss 4487* (NY); **Guadeloupe,** *Duss 3357* (NY); **Antigua,** *Box 557* (US); **Tobago,** *Broadway 3051* (NY); **Mexico,** *Purpus 7418* (NY); **Guatemala,** *Turckheim 1101* (US); **Costa Rica,** *Brenes 1643* (NY); **El Salvador**

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*All specimens cited have been examined unless otherwise noted.

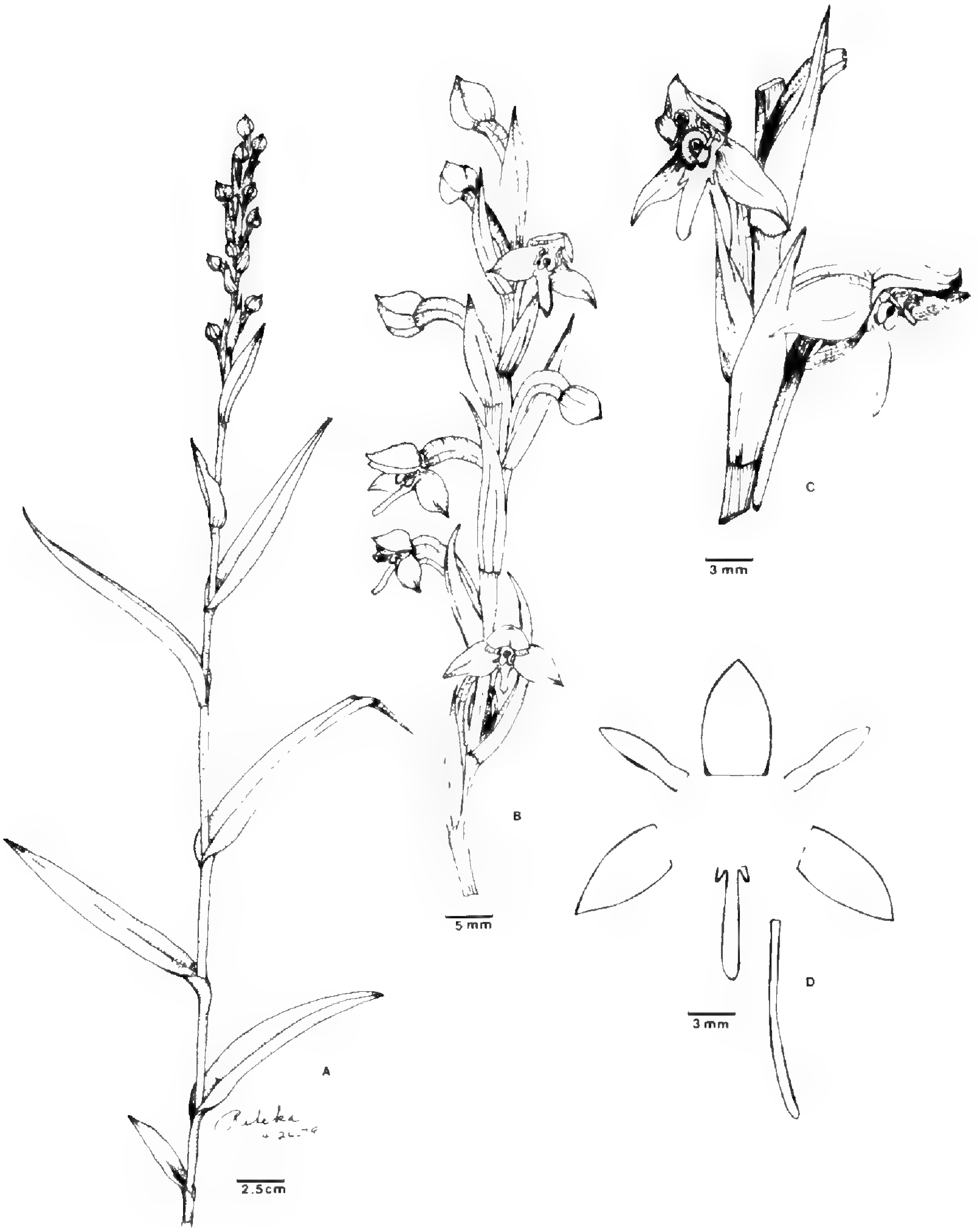

Figure 1. *Habenaria alata* Hook. A, flowering plant; B, inflorescence; C, flowers, frontal and lateral views; D, sepals, petals, labellum and nectary, frontal view.

*Calderon 1292* (US); **Honduras** *Standley 29155* (US); **Panama,** *Ebinger 784* (US); **Colombia,** *Pennell 1792* (NY); **Venezuela,** *Allart 164* (US); **Ecuador,** *Haught 3312* (US).

REPRODUCTIVE BIOLOGY: Flowers from September to November. Capsule dehiscence occurs approximately one month after pollination.

ECOLOGY: This perennial species is found growing terrestrially from April to December in soil pockets in pleistocene limestone. It grows in open, sunny, usually disturbed, areas within high coppices—high canopy (5–12 m) forests occurring on pleistocene limestone ridges and dominated by *Lysiloma latisiligua* (L.) Benth., *Swietenia mahagoni* Jacq., *Mastichodendron foetidissimum* (Jacq.) H.J. Lam., *Coccoloba diversifolia* Jacq., *Clusia rosea* Jacq., *Metopium toxiferum* (L.) Krug & Urban, and *Bursera simaruba* (L.) Sarg..

2. **Habenaria odontopetala** Rchb. f., Linnaea **18:** 407. 1844. (Fig. 2).

*Habenaria strictissima* Rchb. f. var. *odontopetala* (Rchb. f.) L.O. Williams, Bot. Mus. Leafl. Harv. Univ. 7: 184. 1939. HOLOTYPE; Mexico, *Leibold s.n.* (W).
*Habenaria garberi* Porter, Bot. Gaz. 5: 135. 1880.
*Platanthera garberi* (Porter) Chapman, Fl. S. US. ed. 3: 486. 1897.
*Habenella garberi* (Porter) Small, FL. S.E. US. 316. 1903. HOLOTYPE: Manatee, Florida, *A.P. Garber 315* (NY).

Plant terrestrial, erect to 65 cm tall; roots many, fibrous, with one or two spherical to ovoid fleshy tubers; stem round, simple, erect, leafy, completely enclosed by leaf-sheaths, to 38 cm tall; leaves soft and thin in texture, lanceolate to elliptic, acute, articulate with the leaf sheaths, decreasing in size toward the inflorescence and base, basally becoming bract-like; inflorescence terminal, racemose, to 27 cm tall, 3–25 flowers, flowers fleshy, pale green to greenish-yellow; floral bracts lanceolate to ovate, acuminate, to 2 cm long, 8 mm wide; ovary pedicellate, ribbed, to 2 cm long; dorsal sepal broadly ovate, cucullate, to 7 mm long, 5 mm wide; lateral sepals spreading or reflexed, obliquely ovate, acute, to 7 mm long, 5 mm wide; petals oblong-quadrate to linear-oblong, apex 3-lobed, to 6 mm long, 2 mm wide, anterior margin with a small dentiform lobe; labellum entire, pendent, linear to linear-clavate, obtuse, basal lobes obscure, to 1.2 cm long, 1.5 mm wide, spur or nectary cylindric, to 2.2 cm long, 1 mm thick; column short, to 3.0 mm wide; capsule ribbed, to 2.0 cm long, 8 mm thick.

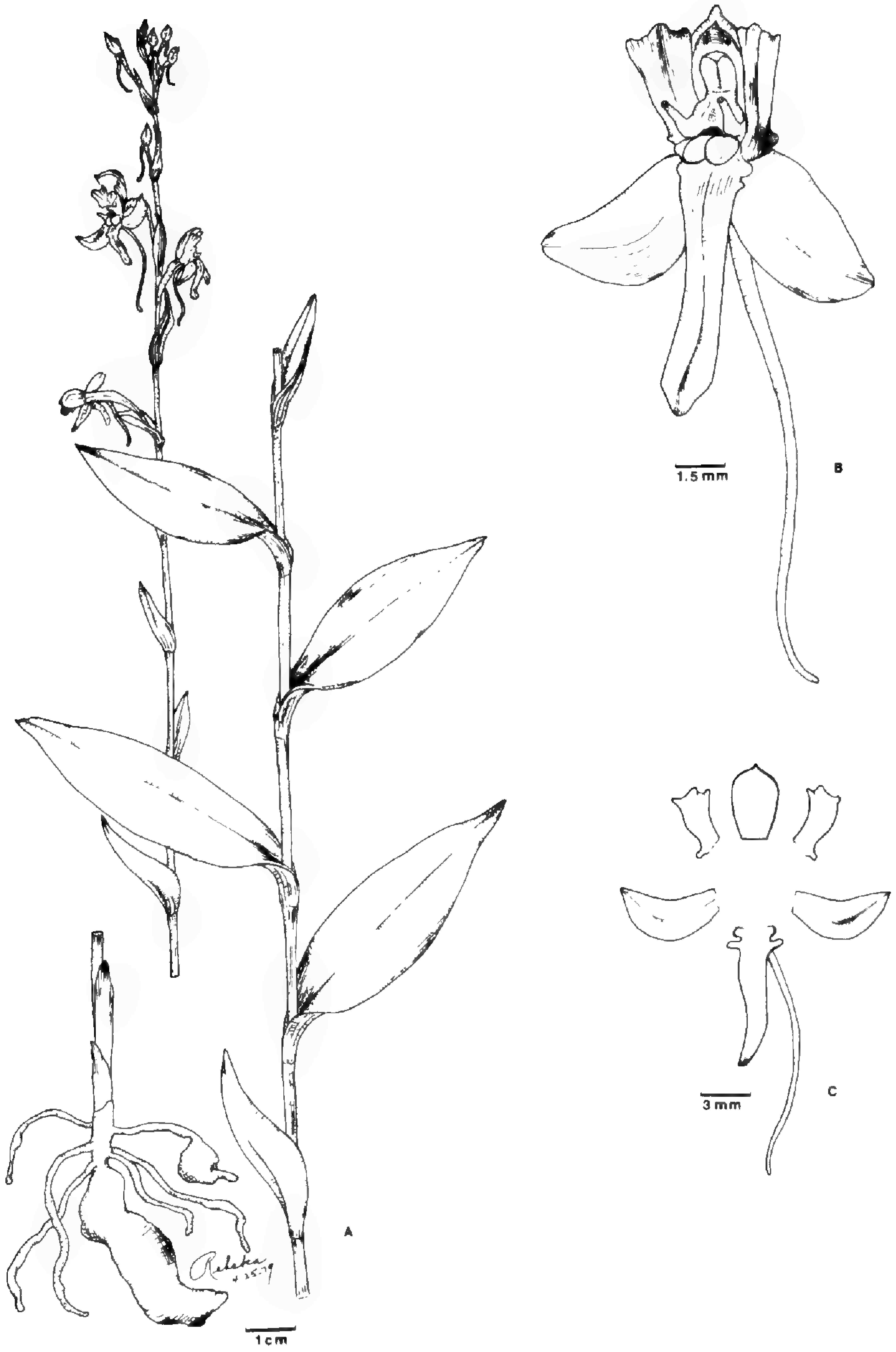

Figure 2. *Habenaria odontopetala* Rchb. f. A, flowering plant; B, flower, frontal view; C, sepals, petals, labellum and nectary, frontal view.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Northern Andros,** high coppice, 6 mi NW Love Hill settlement, *Sauleda 1993* (FTG), *1994* (FAU). **Grand Bahama,** in wet soil of hammock, north side of Sancombe Drive, 0.5 mi east of Balao Road, Freeport, *D.S. Correll, J. Popenoe & P.H. Fluck 40452* (FTG).

GENERAL DISTRIBUTION: **Florida,** *Correll 47697* (NY); **Cuba,** *Eckman 6807* (NY); **Guadeloupe,** *Stehle 2462* (NY); **Mexico,** *Dressler 1491* (NY); **Guatemala,** *Ortiz 2023* (NY); **Costa Rica,** *Brenes 1566* (NY); **Panama,** *Allen 820* (US); **Venezuela,** *Maguire 32733* (NY).

REPRODUCTIVE BIOLOGY: Flowers from September to November. Capsule dehiscence occurs approximately one month after pollination.

ECOLOGY: This perennial species is found growing terrestrially from April to December in soil pockets in pleistocene limestone. It grows in high coppices in deep shade or sunny open disturbed areas.

3. **Habenaria quinqueseta** (Michx.) Eaton, Man. ed. **5:** 253, Sept, 1829. var. **quinqueseta.** (Fig. 3).

*Orchis quinqueseta* Michx., Fl. Bor-Am. 2:155. 1803.

*Habenaria quinqueseta* (Michx.) Sw. ex Wikstrom, Adnotationes Botanicae, 46. 1829 (Month not known).

*Habenaria michauxii* Nutt., Gen. N. Am. Pl. **2:** 189. 1818.

*Mesicera quinqueseta* (Michx.) Raf. Neog. 4. 1825.

*Mesicera michauxii* (Nutt.) Raf. Fl. Tellur. 2:39. 1837.

*Platanthera michauxii* (Nutt.) Wood, Class-Book 685. 1861.

*Orchis michauxii* (Nutt.) Wood, Am. Bot. Flor. 328. 1870. HOLOTYPE: Carolina, *Michaux s.n.* (P, photograph seen).

*Habenaria simpsonii* Small, Fl. S.E. US. 315. 1903. TYPE: In dry hammocks near Manatee, Florida, *Simpson s.n.* (HOLOTYPE: NY., ISOTYPE: US).

Plant terrestrial, erect, to 48 cm tall; roots many, fibrous, with one or two spherical to ovoid fleshy tubers; stem simple, erect, leafy, completely enclosed by leaf sheaths, to 28 cm tall; leaves soft and thin in texture, oblong-elliptic to oblong-obovate, obtuse to acute, articulate with the leaf bases, usually decreasing in size toward the inflorescence and base, basally becoming bract-like, to 10 cm long, 4 cm wide; inflorescence terminal; racemose, to 20 cm tall, 1–18 flowers, flowers white to greenish-white, fleshy; floral bracts ovate-lanceolate, acute to acuminate, to 2.5 cm long, 4 mm wide; ovary pedicellate, ribbed, slender, to 2.5 cm long; dorsal sepal oblong-

Figure 3. *Habenaria quinqueseta* (Michx.) Eaton var. *quinqueseta*. A, flowering plant, distal portion; B, plant, basal portion; C, flower, frontal view; D, sepals, petals, labellum and nectary, frontal view.

elliptic to orbicular, obtuse, concave, to 9 mm long, 7 mm wide; lateral sepals obovate to oblanceolate, to 1.2 cm long, 4 mm wide; petals bipartite, posterior division ligulate, falcate, subacute to acute, to 8 mm long, 2 mm wide, anterior appendage filiform, recurved, to 1.4 cm long; labellum tripartite, posterior divisions filiform, apex recurved, to 2.2 cm long, middle division ligulate, obtuse to subacute, to 2.0 cm long, 1.5 mm wide, spur or nectary slender, linear to clavate, recurved to 3.8 cm long, 3 mm thick; column short to 2.8 mm long, 2.8 mm wide; capsule erect, ribbed to 2.5 cm long, 8 mm thick.

DISTRIBUTION IN THE BAHAMAS: **Northern Andros,** high coppice, 6 mi NW Love Hill settlement, *Sauleda 1968* (FAU), *1969* (FTG), *1970* (K), *1971* (AMES), *1972* (US), *1973* (NY); in grassy soil 3–4 mi SW Staniard Creek, near Blue Hole, in fruit, dehisced, *Correll 49375* (FTG). **Grand Bahama,** small colony at edge of hammock near Freeport, *Correll and Worsfold 50383* (FTG).

RHODORA — Sauleda & Adams — Galley 4

GENERAL DISTRIBUTION: **Florida,** *Garber 37* (NY); **Cuba,** *Howard 4699* (NY); **Haiti,** *Leonard & Leonard 11388* (NY); **Dominican Republic,** *Howard & Howard 9173*, (NY); **Mexico,** *Dressler 2500* (NY).

REPRODUCTIVE BIOLOGY: Flowers from August to October. Capsule dehiscence occurs approximately one month after pollination.

ECOLOGY: This perennial species is found growing terrestrially from March to November in low grassy open areas in direct sunlight and occasionally in partial shade at the edge of high coppices. It prefers temporarily flooded habitats or areas near permanent ponds where soil moisture content is high. In direct sunlight plants develop short stems with short internodes, the leaves forming a rosette. In partial shade the stem is more elongate with internode lengths considerably longer.

## ACKNOWLEDGMENTS

We would like to thank Dr. Peter Taylor at the Royal Botanic Gardens, Kew; Dr. Adolf Polatschek at the Naturhistorisches Museum, Wien, Austria; and the Directors, Curators, and staff members of the herbaria previously mentioned for their cooperation and help. We acknowledge the generous field assistance given by Patricia H. Adams, Kenneth and Gladys Fehling, Carol Branson, and Thomas Miller. Our thanks are due also to Rebeka Sauleda for the preparation of the illustrations. This research was supported in part by donations and grants from the Tropical Orchid Society, Delray Beach Orchid Society, and the American Orchid Society.

## LITERATURE CITED

CORRELL, D. S., 1975. Flora of the Bahama Islands New Additions, II. Fairchild Trop. Gard. Bull. **30**(2):11 12.

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# STUDIES OF AMERICAN GINSENGS

Shiu Ying Hu, Lily Rüdenberg,[1] and Peter Del Tredici

Between 1974 and 1978 four international symposia dealing with ginseng took place in Switzerland, Korea, and Singapore. A total of 79 papers were published in the proceedings of these symposia. Only one of them concerns the ecology and phytogeography of ginseng. The remaining reports deal with the isolation, identification, and characterization of the chemical composition of the root or leaves of ginseng, the biological effects of the ginsenosides, the clinical uses of ginseng products (especially for the revitalization of sick people or for the rejuvenation of elderly persons) and the management of the soil for increased production of ginseng. In researches concerning ginseng, botanists have lagged behind the phytochemists and pharmacologists. Consequently, in currently published books on ginseng, there are many myths, suppositions, and erroneous statements about the plant. In this article, chromosome counts, ecological, and biological observations of *Panax quinquefolius* L. and *P. trifolius* L. are reported. Much of the data has never been recorded before.

The material used for cytological examinations flowered in the greenhouse of the Arnold Arboretum, Harvard University. Four-year old roots of *Panax quinquefolius* were supplied by Mr. E. P. Robbins, Gardens of the Blue Ridges, Pineola, North Carolina. These roots were originally raised from seed collected locally. A colony of *P. trifolius* was carefully removed together with the soil about 40 cm. in diameter and 20 cm. in depth from the woods in Sharon, Massachusetts by Mr. Laurence Newcomb.

## CHROMOSOME NUMBERS OF TWO AMERICAN SPECIES OF PANAX

Previously reports on the chromosome numbers of *Panax quinquefolius* were made by W. Taylor (1967) $2n = 44$ for Canadian material, and by A. Blair (1975) $2n = 48$ for specimens from Virginia. Variability in the karyotype of the tetraploid species of *Panax* in America corresponds to the findings of Asian botanists for a vicarious species *P. ginseng* C. A. Meyer, T. Sugiura (1936) $2n$

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=44, and C. Harn and J. Whang (1963) $2n=48$. It is worthy of note that H. Matsuura and T. Sutô (1935) reported the gametic number 24 for *P. japonicus* A. C. Meyer. This report has been misquoted in Darlington and Jamaki Ammal (1945), in Darlington and Wylie (1955), and in Bolhovskikh (1969) as $n = 12$.

The chromosome numbers for the American species here investigated are based on n = 12. Young flowering buds with microsporocytes were fixed for 12 hours in 3:1 alcohol/acetic acid and stained in aceto-carmine. *Panax trifolius* is found to be a diploid with $2n = 24$ (Fig. 1 A), and *P. quinquefolius* is a tetraploid with $2n = 48$ (Fig. 1 B). At meiosis regular bivalent pairing was observed in both species. Specimens for documentation of these counts are deposited in the Herbarium of the Arnold Arboretum.

## ECOLOGICAL OBSERVATIONS

All the species of Panax grow on the forest floor in the shade of undisturbed deciduous woods. In New England, *Panax quinquefolius* grows in well drained soil on slopes on the northern side of hills along streams above the flood level. The associated trees are *Acer pensylvanicum* L., *A. rubrum* L., *A. saccharum* Marsh., *Betula lenta* L., *Betula lutea* Michx. f., *B. papyrifera* Marsh., *Carya ovata* (Miller) K. Koch, *Fagus grandifolia* Ehrh., *Fraxinus americana* L., *Liriodendron tulipifera* L., *Quercus rubra* L., *Tsuga canadensis* (L.) Carr., and *Tilia americana* L. The shrubs in the association are *Hamamelis virginiana* L., *Kalmia latifolia* L., *Lonicera canadensis* Bartr., *Parthenocissus quinquefolia* (L.) Planch., and *Virburnum acerifolium* L. The herbaceous species in the association include ferns and fern-allies, and many perennial dicots and monocots. Among these are *Adiantum pedatum* L., *Botrychium virginianum* (L.) Sw., *Polystichum acrostichoides* (Michx.) Schott, *Actaea pachypoda* Ell., *Allium tricoccum* Ait., *Arisaema triphyllum* (L.) Schott, *Asarum canadense* L., *Caulophyllum thalictroides* (L.) Michx., *Clintonia borealis* (Ait.) Raf., *Dentaria diphylla* Michx., *Medeola virginiana* L., *Sanguinaria canadensis* L., *Uvularia perfoliata* L., *Viola pensylvanica* Michx. and *V. rostrata* Pursh.

*Panax trifolius*, dwarf ginseng, grows very abundantly on flat wet land and along small streams. The dominant trees associated with the species are *Acer rubrum* L., *Betula lutea* Michx. f., *Cornus*

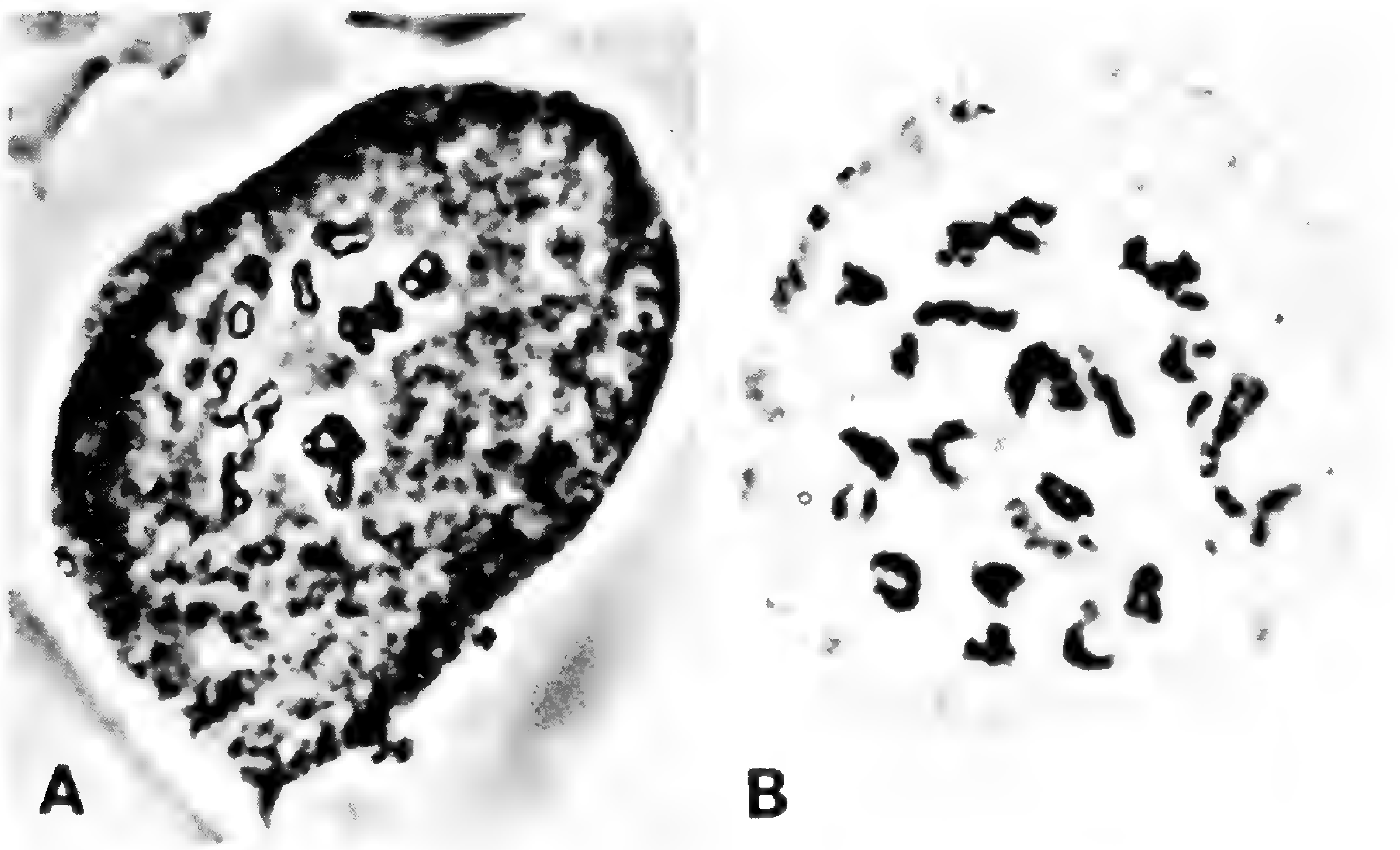

Figure 1. Dividing microsporocytes of *Panax*: A. *Panax trifolius*, $n = 12$, metaphase I (voucher specimen *S. Y. Hu 13943)*; B. *Panax quinquefolius*, $n = 24$, diakinesis (voucher specimen *S. Y. Hu 13945)*.

*florida* L., *Fraxinus americana* L., *Ostrya virginiana* (Miller) K. Koch, and *Quercus rubra* L. The shrubs in the association are *Amelanchier canadensis* (L.) Medic., *Gaylussacia frondosa* (L.) Torr. & Gray, *Hamamelis virginiana* L., *Rubus hispidus* L., *Virburnum acerifolium* L., *V. angustifolium* Ait., and *V. recognitum* Fern. The herbs in the association are *Anemone quinquefolia* L., *Arisaema triphyllum* (L.) Schott, *Impatiens capensis* Meerb., *Maianthemum canadense* Desf., *Medeola virginiana* L., *Ranunculus recurvatus* Poir, *Solidago caesia* L., and *Uvularia sessilifolia* L. The ferns and fern-allies commonly in the association are *Athyrium filix-feminia* (L.) Roth, *Dryopteris novoboracensis* (L.) Gray, *Lycopodium complanatum* L., *L. obscurum* L., *Osmunda claytoniana* L., and *O. cinnamomea* L. Some of the ferns grow very proliferously and many of them are very close to the dwarf ginseng. Fortunately for the ginseng, the ferns commence their annual development later than the ginseng, and by the time their fronds are fully grown to cover the ginseng, the latter has reached the dormant stage, with the mature fruits fallen to the soil, and the tuber hidden in the earth.

## BIOLOGICAL OBSERVATIONS

Little is known about the growing habit of the species, the structure of the population, or the longevity of the individual of ginseng. The species of ginseng are all deciduous perennial herbs, with a subapical bud on a subterranean rhizome. The aerial portion of a plant becomes yellow, dies, and disappears at the end of the growing season. Some of the Asian species of *Panax* have creeping rhizomes with slender elongated or stout short internodes without fleshy roots for storage. Both American species have fleshy roots and short suberect rhizomes. Normally one scar is added to the rhizome each year by the deciduous aerial portion, thus the scars on a rhizome serve as a criterion for estimating the age of the plant. The size of the scars on the rhizome depends upon the area of contact between the aerial growth and the rhizome. In *P. quinquefolius* the scars are usually distinct, while in *P. trifolius* the scars are very small. Moreover, the bud-scales of *P. trifolius* are quite persistent, and this condition gives added difficulty in determining the age of a plant.

The aerial portion of ginseng has been regarded as a stem, thus Fernald (1950, p. 1077) said, ". . . the erect simple stems bearing a solitary whorl of 3 palmate leaves." There are also botanists who regard the rhizome as a sympodium and the aerial growth as a compound leaf with an epiphyllous flowering umbel.

*Panax quinquefolius* resumes growth in the middle of June. The flower-buds and leaves emerge simultaneously. The flowers are relatively small, yellowish, with erect petals and anthers spreading out between them. A varying number of flowers bear one- or two-seeded fruits, which mature to a deep red color in early September. The mature fruits drop mostly near the parent plant, and in nature *P. quinquefolius* usually grows in colonies. The embryo of ginseng is poorly developed at the maturity of the fruit. When the fruits drop to the ground in September, the weather is cold. The underdeveloped embryo remains inactive during this first winter. It develops into a mature embryo at the next growing season, and passes the second winter for the chilling requirement. Germination takes place the following spring, eighteen months after the fruit has ripened. Growers know that ginseng seeds take eighteen or more months to germinate.

Figure 2. Ecological background of a colony of natural stand of *Panax quinquefolius* (see text for explanations.)

*Panax trifolius* resumes growth between mid-April and early May, with the flowers fully open by May 10th. The plants are mostly unisexual with the male plants bearing white flowers on slender pedicels 4 or 5 times longer than the obconic hypanthia, and the female plants bearing pinkish flowers on stout and short pedicels about as long as the urceolate hypanthia. By early to middle June, the three-seeded fruits mature and shatter, dispersing the seeds 1 10 mm. from the parent plant. Each seed contains an underveloped embryo which has a warm season during which it matures. The seeds of *P. trifolius* take the chilling requirement in the winter and germinate in the next growing season.

Comparing *Panax quinquefolius* and *P. trifolius* it seems that the latter species requires a shorter period of dormancy because of a difference in the timing of its seed ripening, rather than a difference in actual dormancy mechanism.

*Panax trifolius* is adapted to a very short growing season, completing its life cycle in about six weeks when the ground is warm but before the leaves of trees and ferns become fully expanded and shade out the forest floor. In general, *P. trifolius* is more tolerant of cool temperature, wet soil, and strong light than *P. quinquefolius*.

## A POPULATION STUDY

In a wooded area of northwestern Connecticut, there is an undisturbed colony of *P. quinquefolius* (Fig. 2). The largest ginseng plant in this area is over 30 years old. The data for the population study were collected there.

**An Old Ginseng:** A large ginseng plant growing by a yellow birch (Fig. 2, right front) was examined. This plant has a carrot-like taproot and four adventitious roots. The first of these emerged very early in the life of the plant and it is so close to the taproot that it appears to be a branch of it. The other adventitious roots emerged much later and at different intervals. They seem to function in supporting the rhizome, which tends to bend after attaining a certain length. The number of the scars on the rhizome shows that the plant is about 32 years old (Fig. 3).

**Vigor of American Ginseng:** An understanding of the vigor of *P. quinquefolius* helps botanists and environmentalists to evaluate whether it is an endangered species. In 1972 a quadrat of a meter

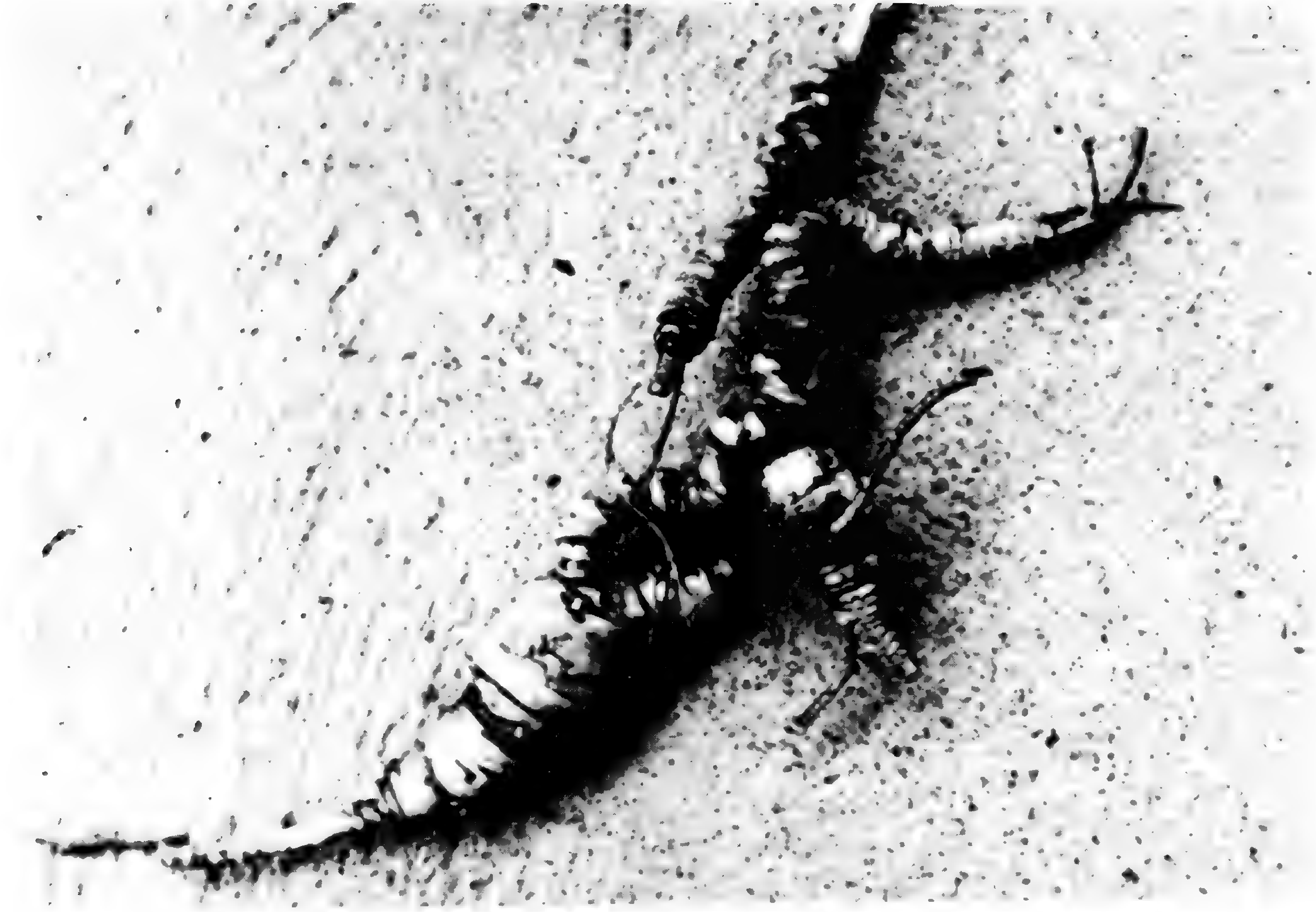

Figure 3. The subterranean portion of a 32-year old American ginseng showing the carrot-like taproot, the zigzag rhizome with adventitious roots, and a portion of the aerial growth.

square containing 24 plants of *P. quinquefolius* was mapped. The area was not disturbed in subsequent years. In 1979, only ten of the original plants remained, and one new seedling was added to the quadrat. Evidently, in an interval of seven years, 41.7% of the population survived.

The number of leaves on the aerial shoot and the number of flowers on each plant were recorded. The data of the initial and the last years are given in Table 1.

**Table 1. Vigor of Panax quinquefolius**

| Survival | 1972 | | 1979 | |
|---|---|---|---|---|
| Plants | Leaves | Flowers | Leaves | Flowers |
| 1 | 2 | 4 | 2 | 6 |
| 2 | 2 | 4 | 3 | 9 |
| 3 | 3 | 7 | 3 | 13 |
| 4 | 2 | 3 | 2 | 4 |
| 5 | 1 | 0 | 1 | 0 |
| 6 | 1 | 0 | 1 | 0 |
| 7 | 2 | 7 | 2 | 3 |
| 8 | 3 | 6 | 2 | 3 |
| 9 | 2 | 4 | 1 | 2 |
| 10 | 2 | 3 | 1 | 0 |
| 11 | | | 2 | |

The surviving plants in the plot can be grouped into four categories. Plants 1 to 4, representing 16.7% of the original 24 plants in the quadrat, have either more leaves or flowers than they had seven years ago. Plants 5 and 6 (8.3% of the original) remain unchanged. Plants 7 to 10 (16.7% of the original populations) show reduced vigor as shown in the number of the leaves or flowers. Plant number 11 (4.2% of the original population) is a new seedling.

This natural population of *P. quinquefolius* has a very high death rate (58.3% of the population of the patch), and a very low (4.2% of the original number of individuals) rate of reproduction. High death rate of cultivated *P. quinquefolius* has been observed in a plantation in Needham, Massachusetts, where approximately two thousand four-to seven-years' old ginseng disappeared in three years. The cause of such high death rate awaits further investigation. Some of the survivors in the natural population observed have increased in vigor during the seven year period, some have reduced vigor, and a small number remains unchanged. This study also shows that the number of leaves of ginseng at the flowering stage is two or three, and the number of flowers per umbel vary from two to thirteen.

## SUMMARY

Ginseng is of special interest to environmentalists because it is a rare and significant species which requires protection, to commerce because it is an high-value item in international trade, and to botanists because there is much knowledge about the species to be discovered. To environmentalists this article presents data on a high death rate and low reproduction of *P. quinquefolius* in nature. To persons interested in ginseng business we point out that there is a species, *P. trifolius,* which can tolerate colder climate, stronger light, and wetter soil, and which requires a shorter period of dormancy. To botanists we suggest the introduction of the superior characters of the hitherto neglected *P. trifolius* into the genetic system of *P. quinquefolius* and *P. ginseng* through hybridization and selection, and the investigations of its contents and possible beneficial uses for man.

## ACKNOWLEDGMENTS

We would like to extend our appreciation to Mr. E. P. Robbins for the supply of four-year old *P. quinquefolius*; to Mr. Laurence Newcomb for flowering material of *P. trifolius,* for guided tours of the site from where he transplated the colony, and for help in the identification of the major species in the Dwarf Ginseng association; to Professor R. C. Rollins for confirming the chromosome counts by Lily Rüdenberg; and to Mr. John Alexander, Propagator of the Arnold Arboretum and to his Assistant, Mr. Robert Nicolson, for taking care of the plants in the greenhouse.

## LITERATURE CITED

Blair, A. 1975. Karyotypes of five plant species with disjunct distribution in Virginia and the Carolinas. Amer. J. Bot. **62**(8): 833 837.

Bolkhovskikh, Z., V. Grif, T. Matvejeva, & O. Zakharyeva. (M. A. Fedorov ed.). 1969. Chromosome numbers of flowering plants. 1 926. (in Russian). Academy of Science, USSR.

Darlington, C. D. & E. K. Jamaki Ammal. 1945. Chromosome atlas of cultivated plants. 1 397. George Allen & Unwin, London.

Darlington, C. D. & A. P. Wylie, 1955. Chromosome atlas of flowering plants. 1 519. George Allen & Unwin, London.

Eastman, L. M. 1976. Ginseng, *Panax quinquefolius* L., in Maine and its relevance to the critical area program. State Planning Office Report **16:** 1-19. Augusta, Maine.

Fernald, M. L. 1950. Gray's Manual of Botany., ed. 8. American Book Co., N. Y. lxiv + 1632 pp.

Harn, C. & J. Whang. 1963. Development of female gametophyte in *Panax ginseng*. Korean J. Bot. **6:** 3 6.

Kurosawa, S. 1966. Cytological studies on some eastern Himalayan plants. *In:* H. Hara (ed.) The flora of eastern Himalaya. Univ. Tokyo. 661 pp.

Matsuura, H. & T. Sutô. 1935. Contribution to the idiogram study in phanerogamous plants I. J. Fac. Sci. Hakkaido Univ. **5**(5): 33 75.

Sugiura, T. 1936. A list of chromosome numbers in angiospermous plants II. Proc. Imp. Acad. Tokyo. **12:** 144 146.

Taylor, R. L. 1967. I. O. P. B. chromosome number report. Taxon **16:** 566 (ed. Löve).

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# NEW ENGLAND NOTE: CHEILANTHES LANOSA IN CONNECTICUT

BRUCE G. AITKEN[1]

On September 11, 1977, I discovered a station for *Cheilanthes lanosa* (Michx.) D. C. Eaton, in Branford, Connecticut. The colony is well established, consisting of approximately seventy mature plants which are growing in crevices of a shaded basalt cliff. At this locality, the "hairy lip fern" is associated with *Woodsia obtusa, Asplenium trichomanes, Asplenium platyneuron,* and *Pellaea atropurpurea*. The occurrence of the latter species is also of interest since, in this state, it is rarely encountered outside of the limestone areas.

*Cheilanthes lanosa* was at first mistaken for *Woodsia ilvensis*, but its identification was subsequently confirmed upon comparison with specimens of these ferns in the Yale herbarium. This record is noteworthy as it is the first for this species in Connecticut (and New England) since the original collection made at New Haven in 1892. Voucher specimens have been deposited in the herbaria of the University of Connecticut and of the New England Botanical Club.

DEPARTMENT OF GEOLOGY
STANFORD UNIVERSITY
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[1] Present Address: Mail Stop 959, U.S. Geological Survey, Reston, VA. 22092

## ERRATA VOL 82, NO. 831

p. 465 Section title: for COMENTS read COMMENTS

p. 465 second line of "COMMENTS" should read : . . . perispore overlaying a thick exospore. Spores . . .

p. 483 in table I; "= *A. oblongifolia* (Torr. & Gray) Roemer" should be reduced to synonymy under *A. canadensis* (L.) Medic, not under *A. arborea* (Michx. f.) Fern.

p. 524 omitted publication date line: "Vol. 82, No. 830, including pages 239-376, was issued April 28, 1980"

# Rhodora

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1980

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The New England Botanical Club, Inc.
Botanical Museum, Oxford Street, Cambridge, Mass. 02138

# INDEX TO VOLUME 82

New scientific names are printed in **bold face.**

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