## INFRASPECIFIC CLASSIFICATION IN THE CAROLINA FLORA

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The taxonomic treatment of infraspecific variation is one of the more troublesome problems confronting the systematic botanist. Judging from numerous recent articles concerned with this subject, the topic is no less controversial among zoologists nor is it apparently any closer to satisfactory resolution. For example, Wilson and Brown (Syst. Zoo. 2: 100., 1953) "are convinced that the subspecies concept is the most critical and disorderly area of modern systematic theory — more so than taxonomists have realized or theorists have admitted."

A comparison of the infraspecific taxa recognized in two recently completed floras of temperate North America will emphasize something of the diversity in current taxonomic practice. Steyermark (1963) recognized 517 subspecies or varieties within Missouri and an additional 297 forms. Radford et al. (1968) included 174 subspecies or varieties within North and South Carolina but no forms. The Carolinas possess a total of 3360 recognized species compared to 2438 known from Missouri. Although the Carolinas together have an area approximately one fifth larger than Missouri, their greater number of species is perhaps better attributed to their greater diversity in topography, geology, climate and ecology than exists in Missouri. There is a ratio in the Carolina Flora of 18.7 species to every subspecies or variety recognized while the Missouri Flora has only 4.7 times as many species as it has subspecies or varieties. If one included all infraspecific taxa recognized in Steyermark's Missouri flora, there is an accepted subspecies, variety or form for every three species included. It is safe to conclude that the greater richness of the Missouri flora in

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recognized infraspecific taxa in comparison to that of the Carolinas is due more to the difference in taxonomic outlook of the respective authors than it is to differences in the frequency of infraspecific variation within the two areas. It would not appear that either of the two taxonomic publications is exceptional in their treatment of infraspecific variation but merely illustrate something of the diversity existing in current taxonomic practice. As has been suggested elsewhere (Wilbur, 1968), greater effort should be made towards achieving a greater degree of uniformity by taxonomists before such major works as the projected Flora North America and Flora Neotropica are prepared.

Three infraspecific categories are most frequently encountered in botanical taxonomic literature: subspecies, variety and form. It is no more possible to define the proper use of each of these taxonomic ranks than it would be to summarize completely the great diversity in current taxonomic usage. The following statements perhaps sketchily outline the principal trends in botanical practice.

- 1) infraspecific taxa are incipient species and the taxonomist can and should utilize the hierarchy of *subspecies*, *varietas*, and *forma* to present an estimate of how far the population has diverged towards the status of species.
- 2) it is futile to attempt categorizing the great array of variation encountered within most wide-ranging species, hence, one should restrict oneself to naming formally only recognizable populations occupying either different geographic areas or ecological sites.
  - a) Since the category variety has been applied to so many different kinds of variation from slight genetical variant, or even habitat modifications to the morphologically distinctive representative of the species in a major geographic and/or ecologic area, its continued scientific use is rendered undesirable since it is too imprecise. Consequently one should designate these geographically and/or ecologically recognizable units as subspecies—a practice

- which also has the added virtue of being in closer accord with the prevailing zoological procedure.
- b) The category variety ought to be employed for these geographically and/or ecologically recognizable units since it has been historically far more frequently employed botanically. Consequently the necessary bibliographic and nomenclatural paperwork would be reduced to a minimum in contrast to the numerous changes required if one were to adopt subspecies a category whose botanical usage has been just as varied and imprecise as variety.
- 3) Both subspecies and varieties are useful infraspecific categories for geographically and/or ecologically distinctive populations with the category subspecies employed for particularly distinctive taxa while variety is to be applied to those somewhat less strongly delimited or, perhaps less subjectively, the subspecies might be employed as a collective taxon for a group of varieties apparently more closely related to each other than to another variety or a group of varieties within the same species.

It would appear that the taxonomic category forma has undergone a sharp decline in botanical esteem and as a result there are far fewer minor variants such as color forms of flowers named in recent years than was the custom three or four decades ago. Taxonomists doubtless have wisely concluded that their task is overwhelming enough if they limit themselves to categorizing populations and disregard the sporadic, although often conspicuous, individual variations. Consequently one should not be disappointed that the various authors of the Carolina Manual did not emulate the author of the Flora of Missouri in naming formae.

Certainly most taxonomists would agree that if a hierarchy of infraspecific taxa is utilized then the ranks employed should indicate degrees of divergence in the named populations. It is illogical to call apparently equivalent populations *subspecies* in one genus and *varietas* in another.

Yet this easy going practice is openly acknowledged by Munz (1959) in the preface of his "A California Flora." The Carolina Manual apparently follows the same practice since subspecies are recognized only in those few genera (e.g. Nuphar, Hydrangea, Acer, Asclepias, and Phlox) in which the monographer, whose work was adopted, employed that category rather than variety (or rarely used both). The category subspecies as the sole infraspecific unit is far less frequently encountered in the literature of eastern North American botany than it is in the West but, unfortunately, that nomenclatural blight is spreading eastward with increasing momentum.

Although doubtless not a precise standard of measurement compared to those employed by the Newtonian physicists, the "biological species concept" has introduced a useful level of objectivity in helping taxonomists to delimit species in sexually reproducing organisms. One might also hope that eventually the infraspecific categories might convey a more uniform indication of similar biological significance. A small sample of the *varietas* recognized within the Carolina Flora will, I believe, disillusion anyone as to the biological meaningfulness of the category as employed. There, varieties are an extremely heterogenous assemblage. I would like to discuss some of them under the following headings.

- 1) In some cases the recognized varieties should not be recognized formally as they are either trivial genetical variants, modifications perhaps due to habitat or portions or a morphological continuum.
- 2) Other varieties are accepted or proposed which give evidence of being better considered as biological species.
- 3) And there are species possessing morphologically recognizable populations with distinct geographical ranges which are treated as taxonomically indivisable.
- 1. EXAMPLES OF VARIETIES LACKING TAXONOMIC MERIT.
- a) Monotropsis odorata var. lehmaniae (Burnham) Ahles, Jour. Elisha Mitchell Sci. Soc. 80: 172. 1964. (Manual, p. 797)

Baldwin's own observations (Rhodora 59: 259-262. 1957) coupled with the detailed study of Wolf (Amer. Midl. Nat. 8: 104-187. 1922) has, as summarized by Wood (Jour. Arnold Arb. 42: 65. 1961), "effectively disposed of M. lehmaniae Burnham as the immature fall phase of M. odorata". To my knowledge nothing has been published to refute the conclusions reached in the above papers. If new and contradictory knowledge is available, its publication would be of far greater biological interest than the reduction from specific to varietal status of what apparently has been shown to be the fall stage of growth of the spring flowering Monotropsis odorata. The striking fragrance of the flowers is detected only at anthesis in the spring and all other differences suggested as distinguishing the supposed two taxa are apparently equally transitional or ephemeral including the differences in the proportions of corolla tube and lobes. Ahles states in the Manual (p. 797) that M. odorata var. odorata flowers in February through April in the Carolinas and fruits in May and June. The var. lehmaniae flowers in the fall from September into November and is said to fruit in October and November. The supposedly diagnostic features employed by Ahles in the Manual are set forth as follows:

b) Calycanthus floridus var. laevigatus (Willd.) T. & G. (Manual, p. 476).

Nicely concluded (Castanea 30: 67. 1965) that within C. floridus there exist "two populations, or varieties, which are more or less distinguishable by the glabrous or pubescent undersurface of the leaf" with "each having a more or less distinct geographical range." His map (p. 70) shows a considerable overlapping range of plants with or without

pubescence. Personal observations and Niceley's own admission that both the twigs and leaf undersurface of var. laevigatus could be slightly pubescent would suggest that the two are at least not "ideal" varieties. Populations admittedly exist in which "both extremes of pubescence as well as various intermediates are present." It would appear that the differences were of a slight genetical basis and the taxonomic utility of recognizing such as taxa on the basis of existing knowledge seems highly questionable. It seems unlikely that we are concerned here with biologically distinctive populations. Instead the pubescence types are apparently no more deserving of taxonomic recognition than the striking glaucous form of Fothergilla major L. (sometimes segregated as F. monticola Ashe) or the non-glaucous form of Zenobia pulverulenta (Bartr. ex Willd.) Pollard (formerly often designated Z. cassinefolia (Vent.) Pollard), which now are both rightfully not allotted taxonomic recognition.

c) Clethra alnifolia var. tomentosa (Lam.) Michx. (Man-ual, p. 793).

A recent study (Jour. Elisha Mitchell Sci. Soc. 83: 82-88. 1967) demonstrated, at least to my satisfaction, that "there seems no basis whatsoever to recognize taxa of any rank" within C. alnifolia. The variation in amount of pubescence on the abaxial leaf surface ranges from glabrate or sparingly strigillose along the principal veins to so copiously stellate-tomentose that the lower epidermis is masked from view. That study also indicated that the reputed differences in pubescence of style, capsule size and orientation and shape of sepals which in the past had been thought to be correlated with the striking difference in foliar pubescence were either not diagnostic or based upon faulty observations. The extremes of variation are so striking that it is not surprising to find taxonomists disinclined to submerge the tomentose individuals with the more abundant sparingly strigillose types. There seems, however, to be no biologically meaningful criteria by which the pubescence types can be recognized as separate taxa. There is an earlier

varietal name, *C. alnifolia* var. *pubescens* Ait., which should be employed by those who wish to persist in naming segments of a continuum.

2. EXAMPLES OF VARIETIES BETTER TREATED AS SPECIES.

Sabatia dodecandra (L.) B.S.P. (Manual, pp. 838-839). Ahles (Jour. Elisha Mitchell Sci. Soc. 80: 173. 1964) reduced to varietal status without discussion the very distinctive Sabatia kennedyana Fern. (= S. dodecandra var. kennedyana (Fern.) Ahles) and S. bartramii Wilbur (= S. dodecandra var. coriacea (Ell.) Ahles). Ahles also placed S. harperi Small, a synonym of S. foliosa Fern., in the synonymy of S. dodecandra var. dodecandra. Four taxa of which three were considered species in the most recent monograph of the genus (Rhodora 57: 1-23, 43-71, 78-104. 1955) were consequently reduced by Ahles to three varieties of a single species. It now appears probable that I erred in reducing S. foliosa to varietal status since it differs from S. dodecandra morphologically and possesses a distinctive range and a very different habitat. Perry's studies (1967) suggest that the chromosome number of the two taxa (S. dodecandra s.s. and S. foliosa) differs as well. Consequently I now believe all current evidence would favor the recognition of four species in this complex and not three as I recognized in 1955 and certainly not one species and three varieties as Ahles suggests. Sabatia bartramii and S. foliosa are largely sympatric but natural hybrids are unknown. They differ greatly both morphologically and apparently ecologically. Perry's extremely thorough work has shown that their chromosome numbers differ and that artificial crosses between the two result in vigorous but sterile progeny. These facts are certainly more suggestive of specific than varietal status. Sabatia dodecandra s.s. is a plant of brackish marshes from Connecticut as far south at least as North Carolina while S. kennedyana is a plant of open stream banks and margins of fresh water ponds with a three-parted, disjunct range: 1) Nova Scotia, 2) Massachusetts and Rhode Island, and 3) North Carolina and northeastern South Carolina. Morphologically the two seem

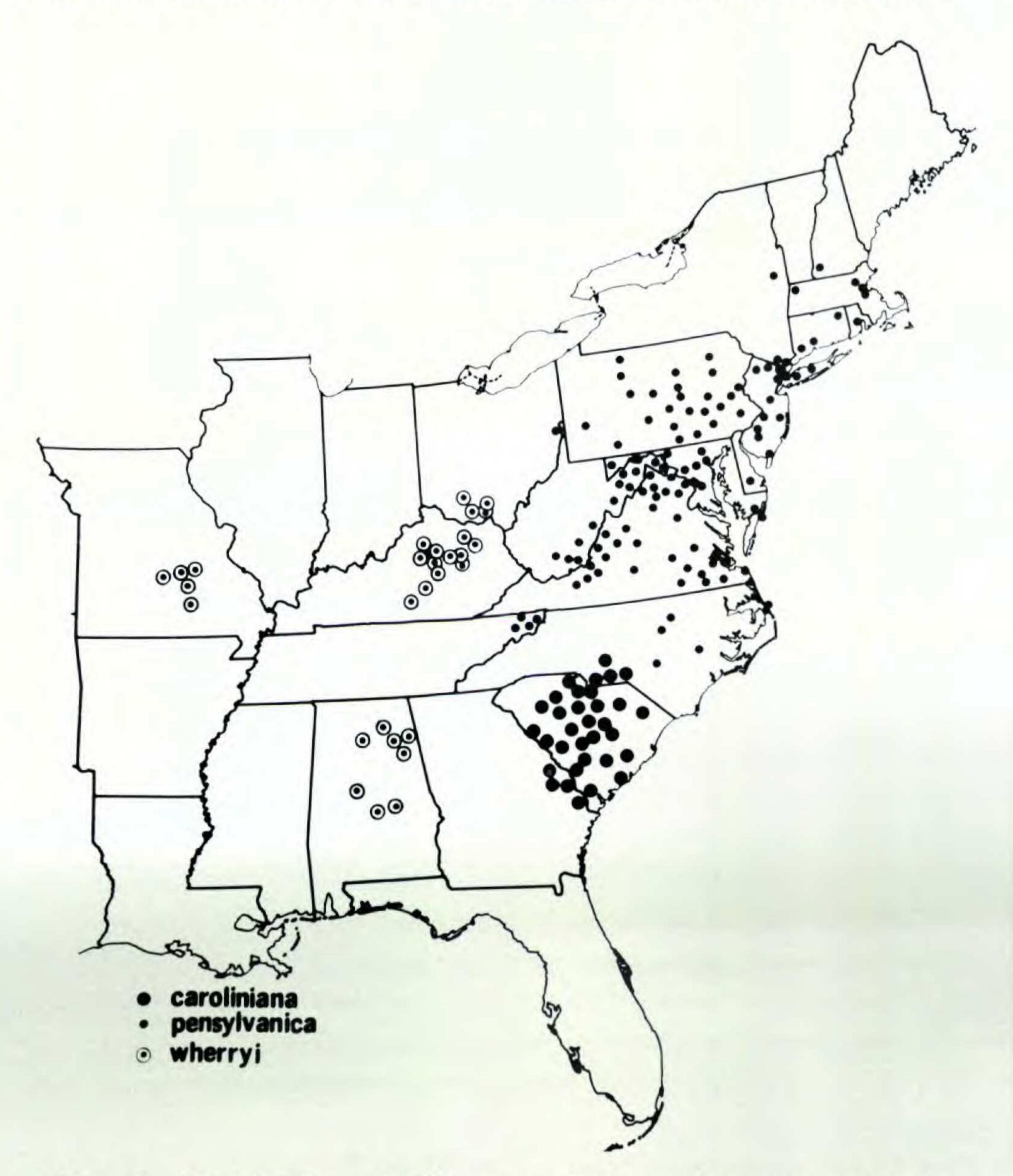
readily distinguishable. Natural hybrids are unknown. Again Perry has shown that the two taxa differ in chromosome number and that their artificially produced progeny are sterile. To treat as does Ahles four taxa such as these as three varieties of a single species obscures their biological or evolutionary divergence.

b) Utricularia inflata var. minor (L.) Chapm. (Manual, p. 969).

The parenthetical inclusion of Linnaeus in the above trinominal is an error, for Linnaeus' taxon is a very different species; Chapman's varietal name was new and not a transfer. Reinert and Godfrey (Amer. Jour. Bot. 49: 213-220. 1962) have, I believe, admirably demonstrated that U. inflata and U. radiata Small (= U. inflata var. minor Chapm.) are specifically distinct. According to Reinert and Godfrey's thorough and beautifully illustrated study, the two taxa are sympatric throughout most of their collective range and often grow intermixed in the same pond. They found the two taxa to be "easily distinguishable" "on the basis of 5 hitherto-neglected, morphological characters... and on the basis of 3 reinvestigated quantitative criteria." The two taxa are not known to intergrade and the differences were maintained in culture. Eight distinguishing characters between two taxa is in itself impressive to anyone not a numerical taxonomist but more significant in determining their status in the taxonomic hierarchy is the obvious and highly effective reproductive isolation existing between the two. Infraspecific classification is not intended to be applied automatically to taxa which are difficult for the biologist to distinguish but for populations which lack the hallmark of a species. Utricularia radiata clearly seems to be, as Reinert and Godfrey have demonstrated, specifically distinct; there seems to be ample indirect evidence in the lack of intermediates that the two are most effectively reproductively isolated.

3. SPECIES TREATED AS INDIVISIBLE IN WHICH INFRASPECIFIC TAXA OUGHT TO BE RECOGNIZED.

Silene caroliniana Walt. appears in the Carolina Manual without designated infraspecific taxa. In fact S. caroliniana var. pensylvanica (Michx.) Fernald is placed in synonymy and the inclusion of Alabama in the southeastern distribution of the species suggests that even S. caroliniana ssp. wherryi (Small) R. T. Clausen is synonymized since it is the only element of the complex known from that state.



Map 1. Distribution of Silene caroliniana. S.c. var. caroliniana, large solid dots; S.c. var. pensylvanica, small solid dots; S.c. ssp. wherryi, open circles with small central dot.

The infraspecific variation of S. caroliniana was the subject of a very thorough study by Professor Clausen (Rhodora 41: 575-584. 1939) whose findings have not been fundamentally enlarged upon in the past three decades. In the following year Fernald transferred Clausen's subspecies to varietal status without additional botanical comment. That paper (Rhodora 42: 239-276, 281-302. 1940) was prefaced, however, by a lengthy discussion of the proper and improper use of subspecies, variety and form. The tenor of Fernald's arguments can be gleaned from the following quotation: "The modern fad of certain botanists, to substitute the heretofore clear term subspecies, erroneously used and often misunderstood by them, for the long established varietas, as used correctly for more than two centuries, is . . . a practice which cheapens the status of true subspecies and makes for inaccuracy and misunderstanding."

Hitchcock and Maguire (Univ. Washington Publ. Biol. 13: 1-73–1947) accepted Clausen's concept of *S. caroliniana* and also treated the three major variants as subspecies. They stated, however, that "in the absence of obvious intermediate material and confluence of characters, it is not improbable that this (ssp. wherryi) might ultimately have to be recognized as a distinct species . . ." In passing it might be noted that their almost impossibly small maps with many different symbols are most confusing — so much so that at least two errors are apparent for *S. caroliniana* (Map 1): Silene caroliniana ssp. wherryi is mapped for the inner coastal plain of North Carolina where it is not known and ssp. caroliniana is shown as occurring in the mountains of Tennessee where only ssp. pensylvanica has been found.

Kruckeberg (Brittonia 16: 95-105. 1963) found, excepting S. caroliniana and S. virginica, that "the species east of the Mississippi River have undergone sufficient genetic divergence to have developed salient morphological gaps reinforced by strong internal barriers to crossing." Artificial crosses result in vigorous but sterile hybrids. Although S. caroliniana and S. virginica may be artificially crossed (and a few natural crosses are known) Kruckeberg felt it

best to "defer to common regional floristic practice and keep

them as separate species."

Kruckeberg stated that "crosses among the three subspecies of S. caroliniana are likewise highly fertile" but his table of crosses shows that only two subspecies were available to him: ssp. wherryi and ssp. caroliniana. The identity of the last seemed unlikely as S. caroliniana s.s. is not known from central North Carolina. (In fact no specimen of S. caroliniana s.l. is yet known to me from Orange County, the alleged source of the collection). Another collection reported upon by Kruckeberg in an earlier paper (Madroño 15: 205-215. 1960) as ssp. caroliniana from Franklin Co., N. Carolina is ssp. pensylvanica, unless it differs from all other collections known from that area. Kruckeberg felt that the subspecies of S. caroliniana "are still valid as they coincided with geographic and morphologically distinct variants within the species." Therefore in spite of the hopes expressed by Clausen, biosystematic studies have not as yet provided a new dimension to our understanding of the complex. Such studies have apparently confirmed the fact that the three taxa are more closely related to one another than they are to the other eastern species and that the morphological differences are maintained primarily through geographic isolation.

Unsurprisingly enough my examination of more than eight hundred herbarium specimens\* has confirmed the existence of three morphologically distinguishable taxa within the species and reaffirmed the allopatry of each of these taxa. Unlike Clausen, who found that "intermediates do occur, indicating continuity in the series", I found the three taxa to be remarkably clearly delimited. I was not as impressed with the differences in shape of the apex of the basal leaves as have been Clausen and others and found that the specimens could be better correlated geographically if

<sup>\*</sup>I am indebted to the curators of the herbaria listed below who loaned the specimens which made my study possible. The herbaria are indicated by their Index Herbariorum symbols: DUKE, GA, GH, KY, MO, NCU, NSC, NY, PAC, TENN, US, VBD, VPI and WVA.

the importance of the shape of the apex was not weighed as heavily as the pubescence on the surface of the basal leaves. The difference in pubescence of the calyces seems to me to be more fundamental. I therefore feel that the difference between the *wherryi* is greater than that between the eastern taxa, *caroliniana* and *pensylvanica*.

Consequently neither rigid adherence to the category subspecies advocated by Clausen nor to that of varietas practiced by Fernald would allow one to indicate the apparent greater evolutionary divergence between wherryi and the two eastern taxa in contrast to the lesser differentiation between caroliniana and pensylvanica. Silene caroliniana appears then to be an excellent example in which two levels of the taxonomic infraspecific hierarchy are required to express our present knowledge of the biological relationship.

Key to the variants of Silene caroliniana.

- - 2. Basal leaves glabrous on both surfaces, mostly narrowly oblanceolate and acute ... 1b. var. pensylvanica.
- 1. Silene caroliniana ssp. caroliniana

Calyces, pedicels and upper portion of stems densely glandular-pubescent. Calyx narrowly tubular. Surface of basal leaves glabrous or spreading short-pubescent. Range: primarily confined to the Appalachian Mountains or to the area to the east of the Mountains  $i.\ e.$  the Atlantic drainage slope.

There are two morphological variants of this subspecies and they can best be recognized by the spreading shortpubescence on the surfaces of the basal leaves of the more southern element in contrast to the glabrous surfaces of the basal leaves of the northern populations. These seem clearly differentiated and, since I do not feel that variation in the apices of the basal leaves is evidence of hybridization or introgression but part of the expected range of variation, the morphologically delimited populations are clearly allopatric.

1 a. S. caroliniana ssp. caroliniana var. caroliniana.

Basal leaves usually broadly oblanceolate to spatulate and typically with a broadly rounded apex, often (0.5) 1.5-3 cm wide, rather densely spreading short-pubescent on both surfaces. Calyces 1.5-1.8(2.0) cm long. Blades of petals reportedly 0.8-1.3 cm long, claws slightly longer than the calyx.

There has been considerable discrepancy in the reports concerning the morphological features of the supposed type in Walter's collection in the British Museum. Fortunately the description is exceptionally full in Walter's Flora for even the obtuse and pubescent basal leaves are mentioned. Hence there can be no doubt as to the taxon to which the name should be applied. Small (Torreya 26: 67. 1926) stated that the specimen in Walter's herbarium "has the calyx distinctly though sparsely glandular." Clausen (Rhodora 41: 579. 1939) reported that Weatherby's notes on the specimen in Walter's Herbarium indicated "that the basal leaves of this specimen are oblanceolate and acutish and that the pubescence is most nearly matched by a collection from . . . Missouri" (i. e. a specimen of ssp. wherryi). The reference to "pubescence" is not clear as to whether that of the basal leaves (as Clausen assumed) or that of the calyx is being indicated. In any event Walter's description is unmistakable and would take precedence over any specimen in Walter's collection that is not in accord with the written account just as Shinners (Castanea 27: 71. 1962) has shown for Bonamia aquatica (Walt.) Gray.

1 b. S. caroliniana ssp. caroliniana var. pensylvanica (Michx) Fernald, Rhodora 42: 260. 1940.

- S. pensylvanica Michx., Fl. Bor. Am. 1: 272. 1803.
- S. caroliniana ssp. pensylvanica (Michx.) Clausen, Rhodora 41: 580. 1939.

Basal leaves usually narrowly oblanceolate and typically with an acute apex, usually 0.5-1.5(2.0) cm wide, glabrous on both surfaces. Calyces (1.0)1.3-1.8 cm long. Blades of petals reportedly 0.8-1.5 cm long, claws usually slightly longer than the calyx.

- 2. S. caroliniana ssp. wherryi (Small) Clausen, Rhodora 41: 582. 1939.
  - S. wherryi Small, Torreya 26: 66. 1926.
  - S. caroliniana var. wherryi (Small) Fernald, Rhodora 42: 260. 1940.

Calyces, pedicels and upper portion of stems densely pubescent with tapering hyaline, eglandular, wide-spreading, pilose trichomes. Calyx more broadly tubular. Surface of basal leaves glabrous. Range west of the Appalachian Mountains in south central Ohio and north central Kentucky, southern Missouri and the northern half of Alabama.

In contrast to the above contention that both subspecies and varieties can be used to advantage in expressing the degree of variation within a species, Raven (Contr. U.S. Nat. Herb. 37: 167-168. 1969) approvingly paraphrases H. L. Mason's belief that although "two of any three taxa will always be more closely related to one another than they are to the third" and questions whether it is "practical to recognize all such shades of relationship in formal taxonomy." Obviously, although it would be impossible to express hierarchially every shade of variation, I believe we can better express degrees of significant infraspecific variation if we don't assume arbitrarily that only one infraspecific category is to be recognized. Although I have not personally worked with plants in which I have found a need for more than two, I would not arbitrarily suggest that two is the absolute upper limit.

Raven also claims that the Nomenclatural Code "states explicitly that subspecies are the primary unit into which

species are divided, and it is therefore incorrect to use any other infraspecific taxon, such as variety, for the primary division of a species." Such an interpretation is, in my opinion, a complete misrepresentation of the Code. Article 4 lists twenty two categories that usually suffice in classifying plants. It is true that subspecies is listed first in the descending series of categories after species just as subfamily is listed first after family and subgenus after genus. Surely one does not conclude from such a hierarchical listing that families can not be divided into tribes unless they are first divisible into subfamilies or that sections are admissible only in genera which have recognizable subgenera. Consequently there is nothing implicit or explicit in the Code to suggest that is is mandatory to use the category subspecies if only one infraspecific taxonomic level is employed.

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## Table I Comparison of Infraspecific Usage in Two Recent North American Floras

	Species	& var.	Formae	Species/ ssp. & var.	Species/ ssp., var., formae
The Carolinas:	3360	174	0	18.7	18.7
Missouri:	2438	517	297	4.7	2.99