

Cl. 19 (4): 23, 27, 51. 1941; Am. Midl. Nat. 24: 687, 695, 697, 1940; Ann. Mo. Bot. Gard. 27: 347-349. 1940) and by myself in a number of as yet unpublished papers and in at least two published ones (Am. Midl. Nat. 26: 69. 1941; Lloydia 4: 275. 1941). Dr. Gleason has told me that he has definitely published the proposal, for action at the next Botanical Congress, that this method be made mandatory. The last example by McVaugh, cited above, is also an excellent example of a place where the use of both categories, *subspecies* and *varietas*, is desirable within the same species.

Finally, concerning the confusion surrounding the term 'variety,' most of those who dwell upon this confusion seem to overlook the fact that the confusion is about the term 'variety' while the category in the Rules is '*varietas*.' Botanically there has been relatively little confusion of the meaning of the Latin term. If one is worried by the confusion surrounding the English translation of this word, he should look up the English translations of the words '*genus*' and '*species*' in a good Latin-English dictionary (i. e. Cassell's) and see what confusion emerges. All three terms were good Latin words long before they were adopted by botanists, and had their popular meanings and attendant confusions. It seems to serve no good purpose to disturb legitimate botanical usage by recourse to arguments based on popular, horticultural, or even past botanical confusion.

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## SUBSPECIES

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DR. FOSBERG hardly needs support; yet the following rather desultory remarks, to be regarded as in the nature of footnotes, may perhaps usefully supplement his excellent discussion.

He is, of course, right in maintaining that present usage is of more importance than past; yet something may be learned from history, if only that arguments drawn from it may be worthless. In looking over the three preceding articles, I have been struck by the fact that Clausen places his chief emphasis on definitions,



Fernald and Fosberg on practice. From the latter standpoint, the use of the term variety presents a natural and normal development. Linnaeus and his immediate successors used it for any and all groups subordinate to the species. As European floras were intensively studied, it was recognized that there were different grades of variants within species and a series of categories was accordingly worked out in the effort accurately to represent the observed facts of nature. In the "Lois" of 1867 de Candolle enumerated six such categories<sup>1</sup> and by 1905 this system had so far proceeded that there was included in the International Rules a provision designating variety and form as the terms primarily to be used for categories below the species, with a number of others, including subspecies, to be inserted, if desired, above, below and between them, and allowing authors full liberty to interpolate new categories as needed. This section (11) remains unchanged in the present rules<sup>2</sup>. In America, with larger areas to cover and much less detailed knowledge of their floras, a simpler system has for the most part been followed; but as early as 1856, in the second edition of his *Manual*, Dr. Gray was distinguishing major and minor varieties<sup>3</sup>. In both continents, as accumulating material in herbaria came to show ranges with reasonable reliability, geography, as a convenient test of the probable validity of varieties, came more and more into use. From the point of view of practice, all this development, though of course not even and symmetrical, has proceeded hand in hand with the increase of knowledge. The division of the Linnaean variety into several categories is roughly analogous to the division of aggregate Linnaean genera and species, and the addition of the geographic idea to the concept of variety comparable to the redescription of the older groups by the addition of newly discovered characters.

To Clausen, looking mainly at definitions, differences and developments in practice appear only laxity in the use of terms,

<sup>1</sup> See Weddell's translation, with comment by Asa Gray, in *Am. Journ. Sci.* ser. 2, xlv. 63-77 (1868).

<sup>2</sup> As Fosberg points out, this is a flexible system, accommodating readily both authors who use only a single category and Ascherson & Graebner with their ten.

<sup>3</sup> His method of distinguishing them, by paragraphing and typography, was not altogether a happy one, since it was obvious to the eye alone and allowed the use of the same spoken term for both. It was, of course, to correct this that the term *forma* came into use for essentially his lesser varieties.



and the introduction of the geographic test for varieties a violent departure from precedent. The trouble with this view is that, in so plastic and multiform an assemblage as the vegetable kingdom, precise and comprehensive definition of taxonomic categories is, in the absence of precise and comprehensive knowledge, a difficult and even dangerous business. Professor L. H. Bailey shows the wisdom of long experience when he remarks: "I define a variety as a lesser category of a species: other definitions do not hold water, being too philosophical or too subjective."<sup>1</sup> Linnaeus, inaugurating a system, no doubt felt obliged to offer some sort of explanation of his categories. He drew up a definition of variety based on certain observations of Ray (and presumably of his own) on garden plants, in which inconstancy was the important feature—and was at once compelled to force under it many groups of whose constancy or inconstancy he knew nothing<sup>2</sup>. Rather unfortunately, various more modern taxonomists (including, in a very modest way, myself) have also felt impelled to make definitions. I think it safe to say that, because of inadequate knowledge for generalization, not one, from Linnaeus to du Rietz, has been able to produce one which either he or anyone else could apply, over any wide field, with consistency or satisfactory results. This condition Clausen hopes to see corrected by the use of data provided by that immensely promising line of research, experimental taxonomy; but almost in the same breath he is forced to admit that it cannot now be done. "The biologically most important unit under the species is the ecotype, which can be determined only by experiment . . . Taxonomists, by the usual observational methods, can often detect geographic and ecologic variations which are the counterpart of the ecotype. Such variations are the taxonomic subspecies." "When the experimental part of the work has not been done, the . . . designation subspecies should be used alone." Clausen, then, is in the same position as was Linnaeus. Starting with a relatively insignificant body of experimental data, he has to deal with a vast number of plants in regard to which he has no

<sup>1</sup> Gent. Herb. v. 18 (1941).

<sup>2</sup> Dr. Clausen's account of the Linnaean varieties would perhaps have been more adequate had he taken the unnamed ones into consideration. So far as I can see, they are quite as important as the named in indicating Linnaeus's ideas; some of them, like *Eupatorium purpureum*  $\beta$ , he later raised to specific rank. There is no obvious reason why he gave names to some and not to others.



comparable information; and he can find no better method than the ordinary exercise of taxonomic judgment, as practiced by Linnaeus and every other systematist, past and present. Of course, we can and do, with the knowledge accumulated since his time, turn out a greatly better job than Linnaeus could; but until that knowledge is complete, so long, that is, as we have to use judgment at all, the accuracy and soundness of the application of any taxonomic category, definition or no definition, will be in direct proportion to the accuracy and soundness of judgment of the individuals who apply it. This situation is not affected by any shifting of terms. This, of course, is not to say that the exercise of taxonomic judgment has not produced and will not produce very excellent results. The point is that Clausen has nothing new to offer to justify a revision of terminology—still less, a disruption of it.

It may be worth while to examine in how far the contention that subspecies is a more accurate term than variety is borne out by evidence, particularly as regards recent usage in the United States. "Subspecies" did not originate with Persoon; he did not use the term in any systematic way and seems to have been referring vaguely to some previous employment of it. What he had in mind was very likely Link's "*Philosophiae Botanicae Novae Prodromus*" (1798), in which (p. 187) subspecies are defined as strains "many of which are in cultivation and have become almost hereditary", which commonly come true from seed, but originally arose from the progeny of a single individual. Varieties, in Link's view, did not come true. Sprengel (*Anleit.* i. 372-3 (1817)) makes practical application of these ideas, designating as subspecies, on a strict basis of experimental taxonomy, cauliflower and Savoy cabbage<sup>1</sup>. De Candolle's "*Lois*" of 1867 still used subspecies for the most striking modifications of cultivated species. All this is more curious than important; but it is not without interest to observe that subspecies had as lowly a horticultural origin as variety; that from the beginning it was

<sup>1</sup> Anyone further curious about the history of subspecies may consult Dampier, *Voyage*, iii. 75 (1699), "there are . . . four sorts of these longleg'd Fowls . . . as so many Sub-Species of the same kind; viz. Crab Catchers, Clocking-Hens . . .": Aikin, *Dict. Chem. & Min.* ii. 13 (1807), "Arseniat of Lead; of this there are two subspecies": *Encycl. Britannica*, ed. 9. xii. 19, "verse narrative . . . is . . . a subspecies by itself." Followers of Hall may take what comfort they can from the fact that Link also refused to give names to varieties.



used in the sense aptly characterized by Dr. Gray as a "super-variety"<sup>1</sup>; and that it has ascended the taxonomic scale *pari passu* with variety and inseparable from it.

The followers of the American Code, in practice, applied subspecies indiscriminately to anything below the rank of species<sup>2</sup>. The work of Hall and his collaborators was, in part, a protest against the excessive splitting of Greene and his followers. In consequence, his subspecies were of very high morphological content and took no account of geography; they are the equivalent of the extreme of European usage—minor species, grouped under collective species and called subspecies. This fact, however, was obscured by Hall's failure to give any place to lesser variants which he recognized and described but would not name, partly because of uncertainty as to their nature and partly because of a prejudice against the term variety. The result is a rather curious mixture of the form of the American Code and the substance of Aschersonian systematics.

Pennell, using the three categories, subspecies, variety and form, unreservedly accepts du Rietz's purely geographic system. The result is a great lowering of the morphological content of the subspecies, as compared to that of Hall, and the almost complete disappearance of any morphological distinction between subspecies and variety. "*Lindernia dubia major* var. *inundata*", for instance, characterized by shape of leaf, length of pedicel and habit, is a variety because it occurs at more or less scattered stations within the range of the species. "*Pagesia acuminata microphylla*", distinguished by precisely the same sort and degree of variation in shape of leaf, length of pedicel and habit, is a subspecies because it is found in a single region in Alabama on the southern edge of the range of the species.<sup>3</sup>

<sup>1</sup> [Varietas] "nonnisi gradu a subspecie differt". Link. For most of these references I am indebted to Prof. A. S. Pease and Dr. H. K. Svenson.

<sup>2</sup> The use of subspecies in the American Code appears to have been an afterthought, due probably to ornithological influence. In the earlier versions of and discussions about the Code, variety was used; only in the final revision, published in 1904, was it "relegated to horticultural usage."

<sup>3</sup> It is interesting to observe that Pennell, equipped with unusually ample geographic knowledge of his group, and freely recognizing subspecies and formae, could find in eastern North America only four populations which answered to du Rietz's definition of variety, and that all four of these are estuarine. Their "local" distribution is therefore due to preference for a highly specialized habitat and is an essentially ecological, not geographic, phenomenon. Had the Atlantic coast of the United States been arranged like the Pacific, with a single large river at the north and no



Clausen, in his one major attempt to put his system into practice, keeps the exclusively geographic criterion for subspecies, but denies it to varieties, degrading that category to the level of the forma (a term which he does not use) of du Rietz, Fernald and Pennell. One might expect that this would produce a definite gap between subspecies and variety; on the contrary, any morphological difference between them again almost completely disappears. *Botrychium multifidum* ssp. *typicum*, "of medium or small size . . . the ultimate divisions usually rather crowded and sometimes overlapping", and ssp. *silafolium*, "rather large . . . the ultimate divisions rather remote and not imbricate", are treated as subspecies. *B. Schaffneri* var. *typicum*, "lax and large", and var. *pusillum*, "stout, compact and small", appear as varieties. And at least some of the varieties of *Ophioglossum nudicaule* have a far stronger morphological basis than the first two subspecies of *O. lusitanicum*.<sup>1</sup>

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estuaries elsewhere, the *Lindernia* could have occurred only at the northern edge of the range of the species and would automatically have become a subspecies. Should the *Pagesia* be discovered at an isolated station or two in the Carolinas (as a good many species have been found in the white-sand areas of Wilmington, North Carolina, and southeastern Virginia and not between), it would, equally automatically, become a variety. Nothing could better illustrate the limitations of a purely geographic criterion of infraspecific categories and, unless one denies all importance to morphological characters, the artificiality of the system which may result from its use. Geography is not a character; it is rather a reagent. Since isolation tends to preserve genetic lines, it is, in the absence of experiment, a handy test of the probable permanence of variants; it can be nothing more. (Du Rietz, *Fundamental Units of Biological Taxonomy*, in *Svensk Bot. Tidskr.* xxiv (1930), especially pp. 348-357; Pennell, *Scrophulariaceae of eastern temperate North America*, *Acad. Nat. Sci. Philadelphia, Mon.* i (1935)).

<sup>1</sup> Clausen, *Monograph of Ophioglossaceae*. *Mem. Torrey Bot. Club*, xix (1938).

Not only are the characters of ssp. *silafolium* the same as those of varieties in other species; they are exactly the sort of modification one would expect to appear in the milder climate and more favorable growing conditions of the more southern area which it inhabits. It is true that experiment in California has shown that some large and small forms of the same species occurring at different altitudes remain unchanged when transplanted to other environments. Nevertheless, this and such cases as *Asplenium platyneuron* var. *bacculum-rubrum*, *Dryopteris fragrans* var. *remotiuscula*, and *Botrychium virginianum* var. *intermedium*, offer inviting subjects for experimental testing. I hope someone can apply it to them.

I am, of course, aware that the same character may have very different degrees of taxonomic importance in different groups. But in the instances cited from Pennell and Clausen, there is no evidence that they perceived anything of the sort or paid attention to any but purely geographic considerations. In any case, I am only applying, from the morphological point of view, the same test which Clausen applies, from the geographic, to the varieties of Gray's Manual. I hope I have done it more carefully and candidly than the anonymous colleague who "analyzed" 105 "unselected" varieties of the Manual without ever noticing whether they were major or minor varieties. Had he confined himself to the criticism that some varieties were geographic and some not, no exception could have been taken to his procedure; but



Irmscher, attempting to apply du Rietz's system to Chinese Begonias, arrived at results like those of Pennell and Clausen, but, unlike those authors, was far from pleased with them. Groups, he says, which he could only regard as of equal phylogenetic rank became, according to their ranges, partly subspecies, partly varieties. Even du Rietz's test for species, discontinuity of biotypes, broke down in this group when tried out from the morphological angle. Irmscher became so disgusted with the "gemischtrangige Sippenreihe" which emerged from the du Rietz system that he threw it overboard altogether, substituting a primarily morphological one of his own and in the process discarding the term subspecies as (of all things) *too confused*, and putting a new term, *turma*, in its place.<sup>1</sup>

Finally, there is a contemporary instance of the classical use of subspecies which deserves brief attention because of its exceptionally clear-cut character. Tryon has recently published a revision of the genus *Pteridium*.<sup>2</sup> His point of view is conservative; it would have had the approval of Prof. Hall. He reverts to the old concept of *Pt. aquilinum* as a polymorphic cosmopolitan species. He finds, however, that it breaks up into twelve varieties, distinguished by relatively minor characters, all geographic and all intergrading where their ranges touch. These varieties in turn fall into two larger groups, also geographic and also not sharply disjunct, but connected, morphologically and seemingly genetically, by var. *yarrabense* (southeastern Asia to northern Australia), which produces intermediates with both (though their extremes do not cross where they meet in the American tropics) and cannot be dismissed as a hybrid swarm since it is reasonably uniform over a wide area where no possible parent exists. Under the system of du Rietz, Pennell and Clausen, Tryon would have had to call his lesser groups subspecies;<sup>3</sup> yet he could not have called the larger ones species because they lack the required discontinuity. On the other

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when he complains that some are mere modifications and others equivalent to subspecies and fails to mention that an attempt (however unsuccessful he may consider it) to grade varieties on just this basis was made, he is not playing fair.

<sup>1</sup> Irmscher in Mitth. Inst. Bot. Hamburg, x. 459 (1939).

<sup>2</sup> In RHODORA xliii. 1-31, 37-67 (1941) (Contrib. Gray Herb. 134). Tryon's work was done as a candidate for the doctor's degree under my general supervision; but his taxonomy is wholly his own.

<sup>3</sup> Hultén, Fl. Alaska in Lunds Univ. Arsskr. N. F. Avd. 2, xxxvii. no. 1, 44 (1941), has done so.



hand, had he followed Hall's practice, or any other using only one category below the species, he would either have had no place for his lesser, geographically distinct, groups, or would have had to put them in a single series with no indication of their relative affinities. It is sometimes difficult to distinguish between the moving up and down of categories in the morphological scale attendant on splitting and lumping and a shifting which actually disrupts the taxonomic series and diminishes its responsiveness to the varied facts of nature. *Pteridium* and cases like it are good testing agents.<sup>1</sup>

From this rather casual survey, it appears that subspecies began as a term for minor horticultural strains and that all recent redefinitions of it are quite as reprehensible departures from the original as are those of variety; and that, in the fifty years since its comparatively peaceful and consistent development was disturbed by the American Code, it has acquired quite as many different uses (except the horticultural) as variety. It has been all-inclusive and highly specialized; of morphological content so high as to be equivalent to the Englerian subspecies and so low as scarcely to differ from the classical forma; it has been geographic and non-geographic, experimental and non-experimental; finally, it has achieved the ultimate ignominy of being cast into an outer darkness even blacker than that prepared for variety by the American Code. There is little here to support the contention that it has any inherent superior accuracy.

<sup>1</sup> There are no doubt a considerable number of groups in the east-American flora in which, unless we are to disregard entirely number and kind of characters and adopt a wholly behavioristic classification—I use the adjective with apologies to the philosophers—degrees of relationship would be better shown by a three- or four-story system than by any simpler one. Three such groups with which I happen to be familiar are those of *Dryopteris spinulosa*, *Acalypha virginica* and *Eupatorium purpureum*. All are alike in that their members are obviously much more closely related to one another than to any other members of their genera and have been treated both as species and varieties by different authors in the past. In other respects, the groups are unlike. The three components of the first are geographically separated, but their ranges overlap considerably and where they do hybridization is fairly frequent. There are no very good varieties. In the second, there is no geographic and little ecological segregation, and also little crossing; two of its three members have readily recognizable geographic varieties. The third shows an intermediate condition; its four members are somewhat, but not sharply, separated geographically and ecologically, there is some apparent interbreeding and there are two regional, not very strong, varieties. All the members of all three are a bit weak as species, though they have usually been treated as such by recent authors; certainly they are not coördinate with other species of their genera. They cannot be fully accounted for by any purely geographic system, nor by any which depends at all rigidly on discontinuity; but the classical system of subspecies, variety and forma (there is some room for formae in them) puts their classification into very good order.



The zoological analogy has attracted others beside Dr. Clausen; but is it real? Is there any sound basis for uniformity of usage in vertebrate zoology and botany, or would it prove a forced and unnatural hybridization? The organisms with which the two disciplines deal are very different. It can hardly be without significance that in the best-known zoological groups the simplest series of categories has been developed, whereas the most elaborate series of botanical categories appears in the most intensively studied groups and floras. If there is to be correspondence, one would suppose that it would naturally be with that department of zoology which, in number of species and as yet imperfect knowledge of them, most nearly approximates the conditions in botany and which, moreover, in some of its families has the closest biological connection with plants—namely, entomology. Those who talk largely about uniformity between botany and zoology do not mean zoology as a whole; at most they mean vertebrate zoology and more often, I suspect, no more than ornithology.<sup>1</sup> They do not tell us that zoological usage is not uniform, that the rigidly geographic, single infraspecific category of the ornithologists does not everywhere obtain. In entomology, the botanical series of subspecies, variety and form (sometimes further elaborated) is being used in the classification of *Lepidoptera* and *Coleoptera*; in that of ants, subspecies and variety are regularly employed for different grades of variation within species. What their morphological level may be, I do not know; I am here on unfamiliar ground; but there seems no doubt that, confronted by similar conditions, the entomologists have developed a system more like the botanical than that is like the ornithological.<sup>2</sup>

In any case, if there is to be correspondence, why not have the vertebrate zoologists adopt the botanical way? They would gain a good deal.

As to horticultural usage, it is almost enough to say that the botanist who has had the longest and closest connection with it,

<sup>1</sup> Of the zoologophilous botanists who have come to my notice, only Coville and Clausen have been definite enough to say this; even they are silent as to entomology.

<sup>2</sup> For chance examples of the contemporary use of variety and of three categories (but not the term *forma*) in entomology, see articles by Normand & Vidal in *Bull. Soc. Hist. Nat. Afrique du Nord*, xxx. (1938) and by Hustache in *Bull. Mans. Soc. Linn. Lyon*, x. 5 (1941). For information as to entomological usage I am indebted to Prof. C. T. Brues.



L. H. Bailey, goes on undisturbedly using variety in his botanical work. It may be added that the horticulturalists themselves are dealing vigorously and clear-headedly with the matter.<sup>1</sup>

What Dr. Clausen really asks is that we all accept the terminology employed by the experimental taxonomists now working in California. It is not unfair to say that this terminology is a sort of ecotypical habit, characteristic of a relatively small population isolated in the United States of America. Even so, it might be the coming thing and we might, with due adjustment of the rules, accept it if it had any organic connection with the greatly promising work its protagonists are doing—as, I hope, we shall accept the really organic term *apomict* for the asexual variants in ligulate *Compositae*.<sup>2</sup> But it has no such connection; it appears, rather, to be an uncritical carrying over of Hall's personal practice to concepts different from his and set against a different nomenclatural background.

The experimental approach has, so far, wrought no revolution in taxonomy. It has, in some cases, revealed an almost terrifying complexity of forces underlying the morphological expressions we know; it has discredited, finally we hope, ill-considered splitting; but in general, save in places where taxonomists have been uncertain, it has supported their conclusions.<sup>3</sup> It has shown that the characters of gross morphology which they, of necessity, have used, really are significant. All this is immensely valuable and, to old-fashioned taxonomists, heartening. We are familiar, under other names, with *cenospecies* which cannot cross with one another, with *ecospecies* which will hybridize weakly, with *ecotypes* which cross freely, given the physical opportunity, and produce series of intermediates; but hitherto there has been an element of conjecture about them. We are grateful that a foundation of experimentally tested fact is being built under them; we are ready to welcome any readjustments of the taxonomic structure which may be proved necessary; but we do not see that these things call for any revision of taxonomic terminology.

<sup>1</sup> See, for instance, Stout in *Amer. Journ. Bot.* xxvii. 339–347 (1940) and the introduction to the new edition of *Standardized Plant Names*.

<sup>2</sup> Stebbins's system of treating these dead-end strains as *minor units* grouped around the species which they most resemble or from which they are known to have been derived seems preferable to Turesson's treatment of them as *agamic species*. See Stebbins & Babcock, *American Species of Crepis* in *Carnegie Inst. Pub.* 504 (1938).

<sup>3</sup> Cf. J. Clausen, Keck & Hiesey in *Amer. Journ. Bot.* xxvi. 104 (1939).



And we wish that the experimenters had looked into this phase of the matter far enough to perceive that clarity is not only not to be achieved by a shifting of terms, but is actually hindered thereby.

Insistence by the makers of the American Code on unessential details and disregard by them of majority usage, when a little yielding to it would not have harmed their major position, brought about thirty years of needless nomenclatural controversy. The most obvious result of a similar insistence on "subspecies" and a like disregard for the use of it by most botanists in the past has been the unedifying spectacle of one group of taxonomists busily transferring varieties to subspecies and another group equally busy making transfers in the opposite direction—a tempest in a teapot also quite needless. All difficulty not wholly illusory would have been avoided by the simple, and one would suppose the obvious, expedient of following the rules and using variety as the term primarily to be employed for subdivisions of species. If the workers in experimental taxonomy have convinced themselves that only one infraspecific category is worth while<sup>1</sup>, so be it; if they can prove it, well and good; variety would still better serve their turn and would meet with no opposition.

GRAY HERBARIUM.

### THIRD LIST OF FUNGI OF NANTUCKET<sup>2</sup>

E. F. GUBA AND E. V. SEELER, JR.

Sufficient further collections have been studied to make possible a third list of fungi of Nantucket. Several specimens collected in previous years still remain to be determined and much further work is required before the record of the fungous flora of the island can be considered fairly complete.

Certain numbers of fleshy fungi appearing in this list and indicated by an asterisk are taken from a list of names submitted

<sup>1</sup> Americans, in line with previous practice in this continent, mostly use only one. So far as I have observed, Europeans, though they have lowered more or less the morphological content of the subspecies and, in consequence, use that term more frequently than in the past, still freely employ two or three categories.

<sup>2</sup> Contribution of the Nantucket Maria Mitchell Association, Div. of Natural Science, Nantucket, Mass. For the first and second lists see *RHODORA* 39: 367–376, 1937, and 41: 508–520, 1939. The cost of publication is met by the Maria Mitchell Association.





Weatherby, Charles Alfred. 1942. "Subspecies." *Rhodora* 44, 157–167.

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