

THE TAXONOMIC ASPECT OF THE SPECIES QUESTION

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1. HISTORIC

THE ancients knew and described plants by generic names. Their knowledge of them was general and superficial. According to Adanson,¹ Conrad Gesner, 1559, was the first to indicate the distinction of plants into genera and species, although this advance is also claimed for Columna. Subsequent authors in general, for about a century, arranged species of plants under generic names, but without definite rules for the limitations of genera. Morison (1655), Ray (1682), and Tournefort (1694), defined genera with reference to their fruits and were followed by Linnæus.

Ray regarded specific differences as those that are somewhat notable and fixed and not due to cultivation and which cultivation does not change. The way to determine these, according to him, is to grow them from seed, because all the differences which are found in different plants grown from the same seed are accidental and not specific, but he was not always exact in following this rule.

Tournefort declared that it troubled him very little whether the plants he cited were species or varieties as long as they differed in remarkable and perceptible qualities; Adanson approves this view, remarking that it seems to him sufficient and reasonable.

From Linnæus, *Philosophia Botanica*, 1751.

We enumerate as many species as different forms were originally created.

¹ *Fam. des Plantes* 1: 102. 1763.

There are as many species as the Infinite Being originally produced different forms; and these forms, following the laws of reproduction imposed upon them, have produced more, but always similar to themselves. Therefore, there are as many species as there are different forms or structure met with to-day.

From Adanson, Familles des Plantes, 1763.

The moderns define a species of plant as a collection of several individuals which resemble each other perfectly, yet not in everything, but in the essential parts and qualities, without, however, giving attention to the differences caused in these individuals either by sex or accidental varieties.

According to Linnaeus (Phil. bot., p. 99) "the species of plants are natural and constant, as their propagation either by seeds or cuttings is only a continuation of the same species. Individuals die, but the species does not."

But we wish to make a distinction between reproduction by seed and that by shoots, offsets, corms, cuttings, suckers or by grafting. These last simply continue the individual from which they are taken and consequently are opposed to the production of new species in plants; *whereas seeds are the source of a prodigious number of varieties, sometimes so changed that they may pass for new species.* He cites, among other examples:

"In 1715 Marchant found in his garden a new species of *Mercurialis* and the following year it came from self-sown seed; again, four resembled the parent and two were so different that he made another species of *Mercurialis*. These two new plants were cultivated and continued to grow each year."

It is well known that without foreign fecundation in plants that reproduce by seed, similar changes are induced either by reciprocal fecundation of two different individuals or owing to cultivation, the soil, the climate, dryness or moisture, light or shade, etc. These changes are more or less prompt, more or less durable, disap-

pearing in one generation or perpetuating themselves through several generations, according to the number, the force, the duration of the causes which united to form them, etc., according to the nature, the disposition, the customs, so to speak, of each plant, for it is to be noted that some families do not vary except in the roots, others in the leaves, others in height, pubescence, and color, whereas others change more easily their flowers or their fruit.

It is difficult to define a primitive species and which those are which have originated by successive reproduction or been changed by accidental causes. It is without doubt for this reason that we do not find nowadays a number of plants described by ancient botanists; they have disappeared, either by returning to primitive forms or by changing their form in the multiplication of species. For this reason the ancients knew fewer species; time has brought novelties! And for the same reason future botanists will be *overwhelmed* by the number of species and be obliged to abandon them and be *reduced solely to genera!*

From Lamarck, *Encyclopedie Methodique*, Vol. 2, 1786.

Species; in botany as in zoology, a species is necessarily constituted of the aggregation of similar individuals which perpetuate themselves, the same, by reproduction. I understand similarity in the essential qualities of the species, because the individuals which constitute it offer frequently accidental differences which give rise to varieties and sometimes sexual differences, which belong however to the same species, as the male and female hemp, in which all the individuals constitute the common cultivated hemp. Thus, without the constant reproduction of similar individuals, there could not exist a true species.

From Rees, Abraham, *The Cyclopædia*, Vol. XXXIII, 1819.

Species of Plants, in *Systematic Botany*, appear, as

far as can be ascertained from the universal experience of those who are conversant with them, as well as from everything that can be gathered from the records of remote antiquity, to remain distinct from each other, marked by their appropriate characters and qualities, and renewing themselves periodically by sexual generation. Such being the case with all the plants of which we have any knowledge, we conclude it to be so with the rest, as well as with animals. The white blackbird of Aristotle still inhabits the Cyllenian groves and copses of Arcadia, undisturbed by the revolutions of two thousand years; and we doubt not that the banks of the Alpheus have been fringed with the same violets and primroses, through uncounted ages, as those with which they are now, every spring, adorned.

Various plants indeed, and especially domestic ones, like domestic animals, are found liable to some variations of color, luxuriance, and sensible qualities, which have led curious inquirers to doubt whether any species are certainly permanent. This doubt could arise only from a slight view of the subject. Whatever casual aberrations there may be in the seminal offspring of cultivated plants, a little observation will prove how transient such varieties are, and how uniformly their descendants, if they be capable of producing any, resume the natural characters of the species to which they belong.

From A. P. DeCandolle and K. Sprengel, *Elements of the Philosophy of Plants*, Edinburgh, 1821.

By species we understand a number of plants, which agree with one another in invariable marks.

In this matter everything depends upon the idea of invariableness. When an organ, or a property of it, is changed neither by difference of soil, of climate, or of treatment, nor by continued breeding, this organ or property is said to be invariable. When, for instance, we have remarked during centuries, that the centifolia has always unarmed leafstalks, we say correctly, that this property of the centifolia is invariable.

This idea proceeds on the supposition that the species which we know have existed as long as the earth has had its present form. No doubt there were, in the preceding state of our globe, other species of plants, which have now perished, and the remains of which we still find in impressions in shale, slate-clay, and other floetz rocks. Whether the present species, which often resemble these, have arisen from them; whether the great revolutions on the surface of the earth, which we read in the Book of Nature, contributed to these transitions—we know not. What we know is that from as early a time as the human race has left memorials of its existence upon the earth the separate species of plants have maintained the same properties invariably.

To be sure, we frequently speak of the transitions and crossings of species; and it can not be denied that something of this kind does occur, though without affecting the idea of species which we have proposed. We must, therefore, understand this difference.

We perceive the *Transitions of a Species*, when it loses or changes the properties, which we had considered as invariable in the character. Thus, it would be a transition, if we had stated as an invariable character of winter wheat (*Triticum hybernum*), that it was biennial, and had an ear without awns; and if we should remark, that by frequent reproduction, and by very different treatment, it began to assume awns, and, when sown in spring, came to maturity during the same summer.

But this shows only that our idea of the difference between the two kinds of grains had been incorrect; for it is the universal rule, that the character does not constitute the species, but the species the character. Species, then, only appear to undergo transitions, when we have considered an organ or a property as invariable which is not so.

All properties of plants which are subject to change, form either a subspecies or a variety. By the former we understand such forms as continue indeed during

some reproductions, but at last, by a greater difference of soil, of climate, and of treatment, are either lost or changed. When the different cabbage species receive the same treatment in the same climate, they continue to be frequently reproduced, without changing their appearance. But we can not on this account maintain, that cauliflower would retain the same favorite form in very different climates, and under a complete change of treatment. It at last changes so much, that it can scarcely be distinguished from the common cabbage. This, therefore, is a subspecies. Varieties again do not retain their forms during reproduction. The variable colors—the very variable taste, and other properties of the kitchen vegetables, the ornamental plants, and the fruit-trees, show what varieties are; and the scientific botanist must therefore be particularly attentive to distinguish permanent species from the variable subspecies, degenerate plants and varieties.

To this discrimination belongs, above all things, a careful, continued, and unprejudiced observation of the whole vegetation of the same plant during its different ages, and amidst the most different circumstances which have an influence on it. When, for instance, in the common *Lotus corniculatus*, on whatever soil it may grow, we uniformly observe that it has a solid stem, even and erect divisions of the calyx, and expanded filaments, we must of necessity distinguish, as a particular species from it, another form which grows in bogs and in watery meadows, which has a much higher, and always hollow stalk, the divisions of its calyx spread out into a star-shape and hairy, and which has uniformly thin filaments; and we must name this latter species either *Lotus uliginosus* with Schkuhr, or *Lotus major* with Scopoli and Smith. As, on the other hand, the *Pimpinella Saxifraga* grows sometimes quite smooth, and sometimes in woods and shady meadows, considerably hairy; as it displays sometimes simple and small stem-leaves, sometimes half and even doubly pinnated leaves; and as these

forms vary according to the situation of the plant and during reproduction, we can not regard these forms by any means as distinct species, but we must view them as corruptions.

We see, that, in order to decide respecting the idea of a species, an observation of many years, and of much accuracy, is often required; and that the cultivation of plants, from the most different climates, in botanical gardens, is in the highest degree necessary for their discrimination.

From Lindley, John, *An Introduction to Botany*, London, 1832.

A *species* is a union of individuals agreeing with each other in all essential characters of vegetation and fructification, capable of reproduction by seed without change, breeding freely together, and producing perfect seed from which a fertile progeny can be reared. Such are the true limits of a species; and if it were possible to try all plants by such a test, there would be no difficulty in fixing them, and determining what is species and what is variety. But, unfortunately, such is not the case. The manner in which individuals agree in their external characters is the only guide which can be followed in the greater part of plants. We do not often possess the means of ascertaining what the effect of sowing their seed or mixing the pollen of individuals would be; and, consequently, this test, which is the only sure one, is, in practice, seldom capable of being applied. The determination of what is a species, and what a variety, becomes therefore wholly dependent upon external characters, the power of duly appreciating which, as indicative of specific difference, is only to be obtained by experience, and is, in all cases, to a certain degree arbitrary. It is probable that, in the beginning, species only were formed; and that they have, since the creation, sported into varieties, by which the limits of the species themselves have now become greatly confounded. For ex-

ample, it may be supposed that a rose, or a few species of rose, were originally created. In the course of time these have produced endless varieties, some of which, depending for a long series of ages upon permanent peculiarities of soil or climate, have been in a manner fixed, acquiring a constitution and physiognomy of their own. Such supposed varieties have again intermixed with each other, producing other forms, and so the operation has proceeded. But as it is impossible, at the present day, to determine which was the original or originals, from which all the roses of our own time have proceeded, or even whether they were produced in the manner I have assumed; and as the forms into which they divide are so peculiar as to render a classification of them indispensable to accuracy of language; it has become necessary to give names to certain of those forms, which are called species. Thus it seems that there are two sorts of species: the one, called natural species, determined by the definition given above; and the other, called botanical species, depending only upon the external character of the plant. The former have been ascertained to a very limited extent; of the latter nearly the whole of systematic botany consists. In this sense a species may be defined to be "an assemblage of individuals agreeing in all the essential characters of vegetation and fructification." Here the whole question lies with the word essential. What is an essential character of a species? This will generally depend upon a proneness to vary, or to be constant in particular characters, so that one class of characters may be essential in one genus, another class in another genus; and these points can be only determined by experience. Thus, in the genus *Dahlia*, the form of the leaves is found to be subject to great variation; the same species producing from seed, individuals, the form of whose leaves vary in a very striking manner; the form of the leaves is, therefore, in *Dahlia*, not a specific character. In like manner, in *Rosa*, the number of prickles, the surface of the fruit,

or the surface of their leaves, and their serratures, are found to be generally fluctuating characters, and can not often be taken as essential to species. The determination of species is, therefore, in all respects, arbitrary, and must depend upon the discretion or experience of the botanist.

From Nicholson, Henry Alleyne, *A Manual of Zoology*, New York, 1876.

Species.—No term is more difficult to define than “species,” and on no point are zoologists more divided than as to what should be understood by this word. Naturalists, in fact, are not yet agreed as to whether the term species expresses a real and permanent distinction, or whether it is to be regarded merely as a convenient, but not immutable, abstraction, the employment of which is necessitated by the requirements of classification.

By Buffon, “species” is defined as “a constant succession of individuals similar to and capable of reproducing each other.”

DeCandolle defines species as an assemblage of all those individuals which resemble each other more than they do others, and are able to reproduce their like, doing so by the generative process, and in such a manner that they may be supposed by analogy to have all descended from a single being or a single pair.

M. de Quatrefages defines species as “an assemblage of individuals, more or less resembling one another, which are descended, or may be regarded as being descended, from a single primitive pair by an uninterrupted succession of families.”

Müller defines species as “a living form, represented by individual beings, which reappears in the product of generation with certain invariable characters, and is constantly reproduced by the generative act of similar individuals.”

According to Woodward, “all the specimens, or individuals, which are so much alike that we may reasonably

believe them to have descended from a common stock, constitute a *species*."

From the above definitions it will be at once evident that there are two leading ideas in the minds of zoologists when they employ the term species; one of these being a certain amount of resemblance between individuals, and the other being the proof that the individuals so resembling each other have descended from a single pair, or from pairs exactly similar to one another. The characters in which individuals must resemble one another in order to entitle them to be grouped in a separate species, according to Agassiz, "are only those determining size, proportion, color, habits and relations to surrounding circumstances and external objects."

On a closer examination, however, it will be found that these two leading ideas in the definition of species—external resemblance and community of descent—are both defective, and liable to break down if rigidly applied. Thus, there are in nature no assemblages of plants or animals, usually grouped together into a single species, the individuals of which *exactly* resemble one another in every point. Every naturalist is compelled to admit that the individuals which compose any so-called species, whether of plants or of animals, differ from one another to a greater or less extent, and in respects which may be regarded as more or less important. The existence of such individual differences is attested by the universal employment of the terms "varieties" and "races." Thus a "variety" comprises all those individuals which possess some distinctive peculiarity in common, but do not differ in other respects from another set of individuals sufficiently to entitle them to take rank as a separate species. A "race," again, is simply a permanent or "perpetuated" variety. The question, however, is this—How far may these differences amongst individuals obtain without necessitating their being placed in a separate species? In other words: How great is the amount of individual difference which is to be considered

as merely “*varietal*,” and at what exact point do these differences become of “*specific*” value? To this question no answer can be given, since it depends entirely upon the weight which different naturalists would attach to any given individual difference.² Distinctions which appear to one observer as sufficiently great to entitle the individuals possessing them to be grouped as a distinct species, by another are looked upon as simply of varietal value; and, in the nature of the case, it seems impossible to lay down any definite rules. To such an extent do individual differences sometimes exist in particular genera—termed “*protean*” or “*polymorphic*” genera—that the determination of the different species and varieties becomes an almost hopeless task.

The second point in the definition of species—namely, community of descent—is hardly in a more satisfactory condition, since the descent of any given series of individuals from a single pair, or from pairs exactly similar to one another, is at best but a probability, and is in no case capable of proof.

Upon the whole, then, it seems in the meanwhile safest to adopt a definition of species which implies no theory, and does not include the belief that the term necessarily expresses a fixed and permanent quantity. Species, therefore, may be defined as *an assemblage of individuals which resemble each other in their essential characters, are able, directly or indirectly, to produce fertile individuals, and which do not (as far as human observation goes) give rise to individuals which vary from the general type through more than certain definite limits.* The production of occasional monstrosities does not, of course, invalidate this definition.

From Gray, Asa, *Structural Botany*, Ed. 6, 1879.

Species in biological natural history is a chain or series

² As an example of this, it is sufficient to allude to the fact that hardly any two botanists agree as to the number of species of willows and brambles in the British Isles. What one observer classes as mere varieties, another regards as good and distinct species.

of organisms of which the links or component individuals are parent and offspring. Objectively, a species is the totality of beings which have come from one stock, in virtue of that most general fact that likeness is transmitted from parent to progeny. Among the many definitions, that of A. L. Jussieu is one of the briefest and best, since it expresses the fundamental conception of a species, *i. e.*, the perennial succession of similar individuals perpetuated by generation.

The two elements of species are: (1) community of origin; and, (2) similarity of the component individuals. But the degree of similarity is variable, and the fact of genetic relationship can seldom be established by observation or historical evidence. It is from the likeness that the naturalist ordinarily decides that such and such individuals belong to one species. Still the likeness is a consequence of the genetic relationship; so that the latter is the real foundation of species.

No two individuals are exactly alike; and offspring of the same stock may differ (or in their progeny may come to differ) strikingly in some particulars. So two or more forms which would have been regarded as wholly distinct are sometimes proved to be of one species by evidence of their common origin, or more commonly are inferred to be so from the observation of a series of intermediate forms which bridge over the differences. Only observation can inform us how much difference is compatible with a common origin. The general result of observation is that plants and animals breed true from generation to generation within certain somewhat indeterminate limits of variation; that those individuals which resemble each other within such limits interbreed freely, while those with wider differences do not. Hence, on the one hand, the naturalist recognizes *varieties* or differences within the species, and on the other *genera* and other superior associations, indicative of remoter relationship of the species themselves.

From Darwin, *Origin of Species*, new edition, from the sixth English edition, New York, p. 33, 1883.

No one definition has satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species. . . . The term variety is almost equally difficult to define; but here community of descent is almost universally implied, though it can rarely be proved.

From Britton and Brown, *Illustrated Flora* 1: VI., 1896.

A species is composed of all the individuals of a kind capable of continuous successive propagation among themselves.

From De Vries, *Species and Varieties*, p. 32, 1905, under Elementary Species in Nature.

“What are species?” Species are considered as the true units of nature by the vast majority of biologists. They have gained this high rank in our estimation principally through the influence of Linnæus. They have supplanted the genera which were the accepted units before Linnæus. They are now to be replaced, in their turn, by smaller types, for reasons which do not rest upon comparative studies but upon direct experimental evidence.

2. DISCUSSION

Any method of evolution makes difficult the establishment as a general conclusion, that all the progeny of a species must belong to that species. The paleontologists have always faced this difficulty; their species have of necessity been assumptions, and theoretically, at least, if the complete representation of any line of descent could be assembled it would be seen at once that the whole series of forms were in some way connected. The induced mutation effected by MacDougal in *Raimannia odorata*, in which plants so different from their immediate parent as to appear, at least, specifically distinct

from it, as compared with other feral species, is a notable addition to the difficulty of maintaining such a conclusion.

As long as species were generally understood to be relatively fixed in characters, their delimitation was relatively simple, but the general understanding that all living organisms are descended from others which were different from them has greatly complicated the subject.

Whether the evolution has been by imperceptible progressive modifications of structure, or by mutations, or by both methods, the result is essentially the same from the practical standpoints of taxonomy; from these standpoints, then, similarity of individuals must remain the consideration to which most weight will be given in taxonomic usage. It has been conclusively proved that many mutants and elementary species or races breed true in enough instances to establish the rule for at least a number of generations; this should not, however, in my opinion, admit them to the category of species, which, though necessarily difficult in delimitation, will still remain the practical taxonomic groups, recognizing, nevertheless, that they are made up of either relatively constant or of widely fluctuating elementary components, which, in turn, will presumably yield the species of future geologic ages.

The recognition of the existence of incipient or elementary species or races within the composition of species, explains, in large part, the multiplication of species and of groups of assumed lower rank, in many of the larger genera, nearly every taxonomist, except the most conservative, having taken more or less part in thus increasing the number of descriptions and of names. They have been variously denominated species, subspecies, varieties, subvarieties and forms, according to the point of view of the investigator.

Geographic distribution has been invoked as a very useful aid in determining the limits of species. It is a well-recognized fact that certain areas of the earth's surface, some large, some small, are characterized by types

of plants which differ from those of other areas, either contiguous or widely separated, and, in cases where types inhabiting different areas so characterized are apparently similar, though different, their separation or isolation has been given weight in regarding them as specifically distinct. No doubt this is a rational course to pursue if it is not carried to extremes. The question whether the environments to which the ancestors of such types have been exposed have been the cause of their differentiation, or whether the elementary species have been perpetuated which were best adapted to the soil, climate or other features of the environments, is one of the most interesting of unsolved problems. That similar types have for the most part come from common ancestors we must regard as most probable, even if now inhabiting widely separated regions, segregated by the disappearance of related types in intervening space, being thus remnants of the more general distribution of the ancestral forms in earlier geologic eras.

Geographic distribution must, however, in cases of contiguous land districts, be cautiously used as a determining factor. There are many instances in which a species with certain well-marked characters in one region is, apparently, at least, completely connected through intermediate characters with what is readily regarded as a perfectly distinct species in another region. Instances of this kind are within the experience of every one who has given attention to geographic distribution of plants. I say this is apparently the case; the conclusion is based on long series of herbarium specimens and on field observations made over large areas of country. Neither of these methods of information is wholly satisfactory, because the herbarium series must necessarily be limited in the number of specimens, and also because the field observations have to be taken at different times and usually at widely separated intervals. Still, the consensus of opinion of plant geographers leans strongly to the existence of intermediate forms in intermediate regions.

Some of these are almost certainly hybrids, but it would not be safe for us to conclude that they all are. Some light has been thrown on this question by the growing of the extreme forms side by side, and more information can doubtless be thus obtained, the principal difficulty being that the environment of the one is often fatal to the other. A better method would be to grow the two apparent extremes within the natural environment of the apparent intermediates.

3. THE TAXONOMIC TREATMENT OF GROUPS ASSUMED TO BE OF LOWER RANK THAN SPECIES

There is perhaps no taxonomic subject on which greater diversity of opinion and practise exists than in the arrangement and nomenclature of groups of individuals not accorded full specific value. The relationships of these groups to the group assumed to constitute the species proper, and the nomenclature of these subsidiary groups, vary all the way from regarding them all as species, to regarding some of them as subspecies, some as varieties, some as subvarieties, others as forms, while even finer distinctions have been attempted, and elaborate monographs of many genera have been written in the attempt to express descriptively these interrelationships. It has been very evident that these described groups are of unequal value, some resembling the assumed typical group more, some less, and in a good many instances very little. The general result of these attempts to dissect nature has been embarrassing, because when a subsequent student takes up the group he is wholly unable to determine from any descriptions that can be written where any given individual would have been grouped by the previous author, unless he has access to the actual specimens which the previous author studied, and the subsequent student also finds that the examination of a large number of different individual specimens from those studied by his predecessor contains some which

do not fully agree with any one of his predecessor's descriptions, or he finds that some of his specimens agree about as well with one of the groups recognized by the previous author as they do with another. This result shows conclusively that for practical taxonomic purposes it is not desirable to attempt to define a great many of these minor groups. The tendency has been brought about, I believe, by the instinct of many investigators that everything in nature must be named and described, but nothing is to be gained by permitting this laudable purpose to run to extremes.

It is evident, I think, that our taxonomy has been based on the fundamental error that the plant world is to be regarded as divisible into smaller and smaller groups, rather than following nature and proceeding on the theory that it is built up of greater and greater ones; the science should be synthetic rather than analytic. The synthetic theory will give our observation and experimentation a different significance and enable us to comprehend some of the phenomena now masked by the analytic method of attack.

If, as now seems more probable than a few years ago, species are made up of elementary species, or races, and that these are being increased by mutation, there can be no end to the number of such groups produced. As to the designation of these groups, I suggest that the term race be employed. This has long been used to designate what have been called self-perpetuating varieties, which appear to me to be identical with the present conception of elementary species, and its application may readily be widened. The term variety loses its significance, because it is usually quite impossible to tell how any given individual or group of individuals has arisen, or from which species it has sprung. The term form could be used instead of either race or elementary species, but it has had such a trivial significance in literature that race seems to be preferable. Subspecies implies divisibility, and is, therefore, an undesirable term.

In conclusion, I submit the following propositions:

1. The individual is the taxonomic unit, usually undesignated.

2. Similar individuals constitute a race.

For general taxonomic purposes races need not be designated; the conception and description of the species is broad enough to include all races of which it is composed. There will never be complete uniformity of agreement as to the distinction between races and species, any more than there will ever be complete agreement as to the limitations of genera. It is futile in science to attempt to lay down principles which interfere with individual judgments. For special purposes the races may be designated numerically, as, *Quercus alba*, race 2; *Oenothera biennis*, race 12; *Bursa Bursa-pastoris*, race 17; *Draba verna*, race 104. There are doubtless many instances where the species is composed of only one race, just as we have monotypic genera composed of but one species.

3. Similar races constitute a species, the species designated binomially.

4. Similar species constitute a genus, the genus designated monomially.