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The biosystematic species concept

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> Es ist mit Meinungen, die man wagt, wie
> mit Steinen, die man im Brette voranbe-
> wegt: Sie können geschlagen werden, aber
> sie haben ein Spiel eingeleitet, das ge-
> wonnen wird.
> G o e t h e

Taxonomy in all its phases is among the most fascinating of biological sciences. It is, also, the most important of botanical disciplines because its conclusions are fundamental to other approaches in general and to the study of evolution in particular. The impact of taxonomical studies in plants and animals on the theory of evolution is incalculable, since this idea was very strongly documented by observations of variation of living beings (LAMARCK 1809; DARWIN 1859, 1868). Antithetically, however, the evolutionary argument has of late become directed toward the definition of the taxonomical categories. Although this first resulted in morphological and chorological definitions of the basic concept of species that produced an immense confusion as to the real nature of this category, the evolutionary argument has lately become the strongest supporter of a sound and scientific species concept: no other means of study is as effective in explaining the causal factors in the creation of the hierarchy of natural categories as is the analytical and synthetic approach to the study of evolution of all groups of biota.

When LINNAEUS (1751) decided upon the standard of species to be followed in biological taxonomy, he accepted a category which is a greater reality in nature than are other taxonomic groups and which is, therefore, most distinct to human observation. In selecting this standard, LINNAEUS followed a judgment originating in dim antiquity. It was evidently his intention that the species of animals and plants ought to be of the same indisputable distinction as are man and ape, cat, dog, horse and sheep, or apple and pear, barley, rye and wheat. Although he did not define his standard from this point of view, probably because he was convinced that the number of species must be limited since they were an act of creation, it is evident from his publications, especially on the Swedish flora and fauna, that he regarded the category of species to coincide largely with the cessation of hybridization possibilities or miscibility.

Because LINNAEUS did not feel a need to define his species standard very sharply, other botanists soon ventured to do this in order to obtain a distinct guide to determine this category. The definition most closely related to the works of LINNAEUS himself was phrased by DE CANDOLLE (1813), who regarded the species as "la collection de tous les individus qui se ressemblent plus entr'eux qu'ils ne ressemblant à d'autres; qui peuvent, par une fécondation reciproque, produire des individus fertiles; et qui se reproduisent par la gé-

nération, de telle sorte qu'on peut par analogie les supposer tous sortis originairement d'un seul individu." If this definition had been strictly adhered to by all biologists studying the variation of species even within the heavily explored regions of Europe, then no confusion in the concept of this category would have ever arisen.

It was the Linnaean species that was the basis of the theory of evolution as explained by DARWIN (1859), though he was also the first evolutionary biologist to become confused and deviate from the Linnaean standard. Therefore, he proposed a vague morphological definition of this category: "I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms." Elsewhere in the same book, DARWIN even went so far as to affirm that "in determining whether a form should be ranked as a species of a variety, the opinion of naturalists having sound judgment and wide experience seems the only guide to follow." This may appear reasonable to those knowing and recognizing the Linnaean standard, whereas it must be utterly confusing to those who try to follow the Darwinian definition of this category.

Botanists studying the variation within the Linnaean concept of species soon discovered that morphological characters alone are not always an easy means by which to distinguish species from the category immediately above or below. It also became evident that the limit between species is not always sharp and that, furthermore, some species include considerable morphological variations that may also be geographically or ecologically distinct. Even LINNAEUS (1751) knew this and included such variations in his concept of variety. When EHRHART (1788) realized that such variations within a species actually may be at different levels, he proposed the category of subspecies as a name for a major geographical race that is composed of varieties or minor geographical races. Although this was a very reasonable solution that did not require any change in the Linnaean standard, some students of these variations preferred to deviate from the classical approach and use the species category not only for the Linnaean species but also for these geographical variations. This trend had started somewhat earlier, but it reached one of its extremes by the time that SENDTNER (1854) accepted as distinct species two morphologically very similar ecological races of *Pinus montana* only because he felt it unlikely that they could belong to the same species since each grew in such markedly different habitat, *P. Pumilio* in mires and *P. Mughus* on limestone respectively. The same tendency to use the species category for small splits from the Linnaean species, though retaining it also in the classical sense for other taxa, was strongly advocated by KERNER (1866), who, quite correctly, pointed out that the difficulty to distinguish morphologically between the Linnaean species and its lower categories must be a result of a continuous evolutionary process. Instead of accepting the proposal by EHRHART (1788), however, he preferred to give each of such variations a species name, provided that they could be distinguished morphologically, described, and then again recognized. WETTSTEIN (1895, 1896a, b, 1898), who broadened the studies of KERNER (l.c.) and provided additional details concerning the chorological effects on the evolution of variations, continued the use of the species category not only for the Linnaean standard but also for closely allied, smaller taxa of

undoubtedly more recent origin though chorologically somewhat distinct.

Although the chorological approach has strongly influenced even moderate taxonomists outside Central Europe, even in Scandinavia, Britain, and the Netherlands where botanists adhered most conservatively to the Linnaean standard, it has nowhere reached such an extreme as in the so-called "KOMAROV School" in the Soviet Union (cf. JUZEPCZUK, 1958). The value of the major product of the ideas of this School, the otherwise exemplary Flora SSSR, is greatly diminished by the fact that, in some genera, even small morphological variations showing some slight degree of chorological distinction, are classified as species. The most starting example to be cited in this instance is the genus *Astragalus* with 849 so-called species filling a volume of its own.

The morphological-chorological method was not accepted by all taxonomists, although the concepts of many have been confused by it. One of the strongest dissenters to these ideas was ČELAKOVSKÝ (1873), who firmly advocated both the need for a synthetic approach and the necessity of maintaining the Linnaean standard. This may be the reason why Czech botanists never went to the same extremes as did some of their Austrian colleagues with the result that the flora of the western Carpathians has never been split up into as many microspecies as has the equally variable flora of the Alps.

It ought to be emphasized that the morphological-chorological approach is wholly based on the theory of evolution. Its imperfection seems, however, to be caused by overemphasis on comparative morphology combined with studies on distribution and too weak an emphasis on differential analysis combined with experimental synthesis. This is just what should have been expected at a time when the theory of evolution had not yet been studied from the point of view of the mechanisms and processes of evolution that were later to be explained with the aid of cytology and genetics. Before these processes were discovered, morphological comparison was the only method available. As long as it was kept separate from the observations on the ceasing of hybridization possibilities, so important from the point of view of LINNAEUS and DE CANDOLLE, a confused use of the category of species could scarcely be avoided.

Although the KERNER—WETTSTEIN—KOMAROV species concept has had greater influence on taxonomists than any other concept, save the Linnaean, many related definitions have been proposed in the past to lessen the apparent gap between these two approaches. These cannot be discussed here, but references to many of these will be easily found in the fairly comprehensive reviews by SEMENOV-TIAN-SHANSKY (1910), DU RIETZ (1930), DOBZHANSKY (1937, 1951), MAYR (1942, 1957), MANSFELD (1949), CAMP & GILLY (1943), ROTHMALER (1955), VAN STEENIS (1957), JUZEPCZUK (1958), LAMPRECHT (1959), BEAUDRY (1960), and GRANT (1960). Although differently enunciated and with emphasis on various characteristics of the species, most of these definitions first fail to recognize the simple and basic biological characteristics of the Linnaean species standard and then, try to alter the standard to fit the definition, without reducing the confusion the least.

A more definite return to the Linnaean standard has been strongly accentuated by the more recent approach we name biosystematics. This is the study of the taxonomic categories and their distribution based on the analytic and synthetic methods of cytogenetics combined with the classical morphological and chorological endeavour. This approach has led to interpretations of the

species based on studies of the interrelationships and total pattern of each system of detectable components and the history of evolutionary divergence and its causes. It is from this approach that we have been able to conclude that there are four essential and independent processes of evolution: mutation, genetic recombination, natural selection, and reproductive isolation. The importance of each and all of these processes for the development of the characteristics of different categories is becoming increasingly more evident. It has also been possible to demonstrate that although all these processes are of great significance in the development of the Linnaean species, reproductive isolation is most important because the emerging of the species as such coincides largely with the occurrence of a barrier to miscibility (cf. MAYR, 1942; LÖVE, 1960a, d). This has made it possible to find a biological norm for a clear definition of the species standard of LINNAEUS based on present evolutionary knowledge.

The idea of defining the species through means of its reproductive isolation is not new — it was expressed already by RAY (1686), and it also constituted an integral part of the DE CANDOLLE (1813) definition. Recently, however, several attempts have been made to phrase it in such a way that it expresses the results of biosystematic knowledge while at the same time being practical. One such definition was proposed by TURESSON (1922a, b) for what he termed ecospecies, whose members are required to be able to interchange their genes without detriment to the offspring (cf. CLAUSEN, KECK & HIESEY, 1940). Another such definition was coined by DANSER (1929a, b, 1950) for what he termed the commiscuum, which is the total number of individuals that are connected genetically through miscibility (cf. VAN STEENIS, 1957). The clearest and most practical biosystematic definition, and yet at the same time equally applicable to animals and plants, was, however, formulated by MAYR (1940) in connection with his studies on birds: "A species consists of a group of populations which replace each other geographically or ecologically and of which the neighboring ones integrade or interbreed wherever they are in contact or which are potentially capable of doing so (with one or more of populations) in those cases where contact is prevented by geographical or ecological barriers". A little later, MAYR (1942) reduced this definition to the phrase: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." A better and more precise guide to the standard selected by LINNAEUS and his predecessors for the natural and distinct category of species has yet to be invented. Furthermore, a stricter adherence to such a definition would soon result in a distinct lessening of the confusion that has been caused by the lack of such recognition of the Linnaean standard.

It is evident that exact adherence to the biosystematic definition of the Linnaean species is possible only in those groups in which the occurrence of or lack of a barrier to reproduction has been established, or in taxa that are available for biosystematic studies. However, since biosystematic experiments have revealed that some character combinations are more indicative of the occurrence of a sterility barrier than are others, an experienced and critical taxonomist, when studying such species, is soon able to deduce fairly correctly what taxa are species rather than subspecies, and vice versa. This is, in fact, a method fairly similar to that used by LINNAEUS and his followers. Even though they knew little about reproductive isolation and its mechanisms, their skill in detecting real limits between species was so profound that bio-

systematic approaches only rarely will be able to improve much upon the conclusions they reached with the species they knew well. Whenever such sexually reproducing plants become available for biosystematic study, however, the conclusions from the morphological-biosystematic approach will be open to correction or, more likely, confirmation.

There are some groups of plants that never will become available for studies from the biosystematic point of view. These are the taxa that are characterized by various forms of apomictic reproduction. To classify them on the basis of reproductive isolation would lead to a confusion even greater than that created by the morphological-chorological method of study of these groups, since every individual is reproductively isolated from all its relatives. However, a taxonomist supporting the biosystematic species concept ought to be able to select in these groups as well combinations of morphological characters that differentiate the real species from its lower units and form discontinuities comparable to the reproductive gap of amphimictic groups. This possibility has recently been ventured by Löve (1960c) and Löve & Löve (1961b) for some such taxa from central and northwestern Europe. It is likely, however, that all such attempts will be defied by those few who prefer to split such groups into a legion of microspecies founded upon morphological and chorological distinctions only.

Strict application of the biosystematic definition of the Linnaean species is possible in many groups. It is applicable to most genera in the floras of central and northwestern Europe (cf. Löve & Löve, 1961b), Japan and eastern North America which have already been studied from these points of view to a considerable degree. Here studies of the development of reproductive isolation have shown that this stage is reached in either of two ways, abruptly or gradually. In the former, the irreversible reproductive barrier is formed suddenly, usually by a euploid change in chromosome number, and later followed by further morphological and chorological differentiation by aid of the processes of mutation, genetic recombination, and natural selection. In the latter, however, the establishment of the discontinuity is a continuous and slow process that will be mirrored in gradual morphological differentiation that is likely to pass through the lower intraspecific categories before reaching the species limit (Valentine, 1949). Well-established gradual species have developed a reproductive barrier so strong that hybrids are either absent or difficult to obtain, whereas others may still be able to hybridize and exchange some genes, though usually not without some detrimental effect on the progeny. In still other cases, however, it may be difficult to distinguish, even experimentally, between gradual species, which are partially interfertile, and subspecies, which are partially intersterile, since both may be equally distinct morphologically. Abrupt species, however, are strongly isolated reproductively, although polyploids at different levels may be crossable. Because abrupt species, like the categories of the gradual species, may be of different age and then likewise formed in different ways, they may show morphological distinction of all degrees from those characterizing formae of the morphological species concept through those comparable to the characteristics of varieties, subspecies, species and even genera of the group of gradual species. To classify them at these levels, as proposed by some botanists (cf. Heywood, 1958, 1960; Böcher, 1960), is, however, fallacious because of their essential character of strict reproductive isolation. Irrespective of the degree of morphological

and geographical distinction, a forma, variety, or subspecies that is reproduct-ively isolated from other such taxa of the same species is an absurdity that is incompatible with the principle of evolutionary taxonomy and which directly violates the Linnaean standard of the category of species (cf. Du Rietz, 1930; van Steenis, 1957); Valentine & Löve 1958).

The reason for abrupt species showing various degrees of morphological distinction is in part connected with differences in differentiation that have followed the formation of the reproductive isolation. It is, however, also due to the different methods with which such a speciation can happen. In general, abrupt species are formed either by the direct reduplication of the same set of chromosomes, or by the addition of different ones. The influence of this on the morphological distinction of the new taxon is not the same, though some morphological differences are always met with even in experimental poly-ploids (cf. Müntzing, 1953, 1955; Tischler, 1951, 1953—1957).

It is known that the first event, autoploidy, or rather its phase panautoploidy (Löve & Löve, 1949), which is the duplication of the same set of chromosomes in a more or less pure-bred popu-lation, is rare as an effective species producer, although panautoploids are probably formed at the rate of a few cases in a thousand in most populations (cf. Löve, 1944b, 1960a, d; Bowden, 1949; Kiellander, 1953). But they rarely survive in nature for more than a single or a few gener-ations, because this kind of chromosome doubling is often followed by profound meiotic disturb-ances, so they are of little significance in evolution and are taxonomically unimportant (Löve, 1960a, d). To give them a taxonomic name is, therefore, hardly advisable, since they will not even fill the requirement by Kerner (1866) that they should be recognizable later. This seems, however, to have been done by Böcher (1954) when naming the variety *duplex* of *Pulsatilla pra-tensis* on the basis of its deviating chromosome number though only occurring occasionally in some otherwise normally diploid populations. There are, however, known cases of panautotriploidy in which such individuals reproduce vegetatively and are thus able to survive and even spread. In the species *Butomus umbellatus* such triploids are generally ignored by taxonomists though they are fairly widespread (cf. Lohammar, 1931, 1954). In *Populus tremula* they have been named as var. *gigas* (cf. Hylander, 1945), whereas in *Acorus*, the Linnaean species *A. Calamus* is such a triploid that has dispersed over wide areas by aid of human agencies (Wulff, 1940, 1954; Löve & Löve, 1957a, b). These triploids are, in fact, not taxa at the Linnaean species level al-though they may have gained some morphological distinction and reproductive isolation through their unbalanced cytological condition and also have formed a geographical area of their own. They are rather to be compared with some apomicts or, equally correctly, with hybrids that are perpetuated through vegetative reproduction. If they are to be given a taxonomic rank at all, this ought to be either that of an agamovariety or, in the case of *Acorus* and other such triploids with somewhat uncertain parentage, that of a hybrid with a binary name.

In rare cases, there is some possibility of rapidly reducing the disadvantages of panauto-ploides by some selective or recombination processes. Then the new autoploid will develop in the direction of the other event (cf. Müntzing, 1943b) and produce what we name an hemiautoploid, which may survive and form an area of its own. Hemiautoploids are, other-wise, produced after hybridization of somewhat different races of the same species which have already differentiated their chromosomes enough to reduce the meiotic disturbances beyond the critical level lethal to panautoploids. Hemiautoploids have been experimentally produced in several cultivated plants (cf. Tischler, 1951, 1953—1957). It is likely that *Dactylis glomerata* (Müntzing, 1937, 1943a; Borrill, 1961), *Phleum pratense* (Nordenskiöld, 1945, 1953), the polyploid series *Acetosella* (Löve, 1943), *Anthoxanthum odoratum* (Östergren, 1942; Rozmus, 1959; Löve & Löve, 1956) and several other groups were originally formed by this process. This, however, cannot always be easily verified because the limit between hemiautoploids and certain plants belonging to the other process is never sharp.

The other event, or the addition of different whole sets of chromosomes, is named alloploidy. It has certainly been a much more important factor in evolution than has autoploidy (cf. Stebbins, 1950). The chromosome sets of alloploids may derive either from clearly different races of the same species in which differentiation of the chromosome sets has already commenced, or from different species which are properly isolated reproductively even

though they are characterized by the same chromosome number. When the parents are only racially distinct, then the original hybrid from which the taxon with the double chromosome number derives, will be only partially sterile. This is the only characteristic that differentiates them from hemiautoploids, which, by definition, derive from hybrids without even partial sterility. The original alloploids that have been formed in this way may have some of the properties of autoploids, although all such negative properties will soon be selected away. They are named hemialloploids, and they are supposed to be the most common kind of abrupt species (cf. STEBBINS, 1950, 1959). Many hemialloploids have been studied by biosystematists. From the taxonomical point of view, the legion of examples of such taxa that could be mentioned would range from the unequivocal to the controversial: they exhibit all grades of morphological distinction and all sizes of geographical distribution areas, depending upon their age and the distinction of their parents. Although they sometimes may display only minor morphological differences, they all certainly fill the basic requirement of the Linnaean species since they have acquired not only morphological and geographical distinction but also a strong reproductive isolation that permanently prevents their intermiscibility with other such taxa.

When the parents of alloploids are already distinct species which have differentiated their chromosomes so far as to make pairing between them difficult or even impossible, then the first hybrid will be very sterile and sometimes very difficult to obtain, whereas the plant with its duplicated chromosome number will be perfectly fertile, or nearly so. In other instances the parent species may have reached such a degree of differentiation (other than polyploidy) that hybridization is entirely excluded, though this barrier may occasionally be surpassed by a one-step production of an alloploid from the very rare coincidence of a fertilization of an unreduced female gamete of one parent by an unreduced male gamete of the other, since such unreduced gametes sometimes are able to break through an incompatibility barrier that is unbeatable by the reduced cells (cf. BERNSTRÖM, 1953). These processes are what is termed panalloploidy, and it may well be of more frequent occurrence than we suspect at present. It is very effective in the instantaneous evolution of sections, or even of genera, and is widely recognized as a producer of distinct species.

Most panalloploids are taxonomically unambiguous, as are the recently described genus *Hylandra* (LÖVE, 1961), and the three well-known species of *Triticum* (cf. SEARS, 1948, 1959; LÖVE & LÖVE, 1961a, b; SARKAR & STEBBINS, 1956; CHENNAVEERAIAH, 1960), and *Spartina Townsendii* (HUSKINS, 1931), as well as the experimentally verified *Galeopsis Tetrahit* (MÜNTZING, 1930, 1932), *Nicotiana Tabacum* (cf. GOODSPEED, 1954), and *Brassica Napus* (FRANDSEN, 1947). But some are still controversial because they exhibit differences so minute that their original detectors had difficulty in distinguishing them, as, e.g., in *Leymus arenarius* which originates from *L. mollis* and *L. sabulosus* (cf. BOWDEN, 1957), and in *Kohlrauschia Nanteuilii* which apparently originates from the hybrid between *K. prolifera* and *K. velutina* (BURNAT, 1892; HEYWOOD, 1960), although it is usually reported as only a polyploid "race" of *K. prolifera* (BÖCHER, LARSEN & RAHN, 1953; LARSEN, 1960). To classify either the parents of such polyploids as races only of the alloploid, or the alloploids as a race of one of the parents, is not only taxonomically unsound and against the requirements of the Linnaean species standard, but also directly a violation of common sense and logical taxonomical principles, as so correctly demonstrated by MÜNTZING (1930) in connection with his discussion of the morphological classification schemes proposed by some earlier taxonomists studying the subgenus *Tetrahit* of *Galeopsis*.

In the group of abrupt species, the application of the biosystematic definition of the Linnaean species standard must inavoidably produce an increase in the number of species, since taxa differing in chromosome number but ignored or

classified lower because of morphological inconspicuity will have to be raised to specific rank (cf. NANNFELDT, 1938; LÖVE, 1951, 1960d). In the group of gradual species, however, the effects of the strict application of the biosystematic definition will greatly reduce the number of taxa classified at the species level, since many post-Linnaean taxonomists tended to be deceived by the conspicuous morphological and ecological differences between some taxa that have not yet developed even the slightest degree of reproductive isolation. This is especially applicable to Central Europe where "there are still distinguished a considerable number of species which do not deserve that rank" (VAN STEENIS, 1957). There are, however, also cases of gradual species which have been generally classified at a lower level than appropriate, as recently revealed through biosystematic experiments, so that even within this group the new evidence may sometimes result in an increased number of species.

It ought also to be emphasized once more that the gradual differentiation itself must necessarily imply that some taxa will be found to be at the intermediate level so that even thorough experiments will be unable to conclude decisively if they are to be classified as species separated by a certain but incomplete degree of reproductive isolation, or if they are only subspecies which have gained a rather high degree of partial but variable sterility. Such cases have to be decided upon individually, and some arbitrariness in their classification cannot be avoided. This, however, does not matter much as long as the facts leading to this situation are not concealed or allowed to escape attention.

A much discussed case that may belong to the intermediate category just mentioned concerns the Linnaean species *Geum rivale* and *G. urbanum* and the taxa of the same complex later described (cf. GAJEWSKI, 1957). Ecologically, these are completely different. They also occupy somewhat different geographical regions. However, in places which ANDERSON (1948) would have called "hybrid habitats" and also under experimental conditions, hybrids are easily formed and the differential characters of both taxa seem to break down into a complete series of intermediates (WINGE, 1926; MARSDEN-JONES, 1930). Although VAN STEENIS (1957) agrees with MARSDEN-JONES (l.c.) that they are classified too high at the species level, the cytogenetic evidence still seems to be inconclusive as to their real miscibility. Though it is also the feeling of the present writer that they may be more correctly classified at the subspecific level, it is hardly possible to claim it incorrect to retain them as species. Therefore, until further investigations yield more adequate information, the continued use of the arbitrary judgment of LINNAEUS on these *Geum* taxa can as well be recommended.

It is a different matter with the two species pairs *Melandrium rubrum* and *M. album* and *Silene vulgaris* and *S. maritima*. Experiments with the former pair, carried out by a number of investigators, have clearly shown these taxa to be completely interfertile and without even a vestige of reproductive isolation. Hence, D. LÖVE (1944) concluded that they are correctly classified as the two subspecies *dioecum* and *album* of the species *M. dioecum*. This conclusion is in conformity with the Linnaean classification of both taxa as varieties only of the single species *Lychnis dioeca*. The *Silene* pair has been most intensely studied by MARSDEN-JONES & TURRILL (1957), and although they still regard both taxa as different species, the evidence as reported by them clearly supports the conclusion by VAN STEENIS (1957) and LÖVE & LÖVE (1961a, b) that they are nothing but two subspecies of *Silene vulgaris*.

In the genus *Acetosa*, experiments carried out since 1939 mainly by the present writer have shown that the four taxa *A. pratensis*, *A. alpestris*, *A. nivalis* and *A. ambigua* still have not developed a reproductive barrier, although the last two seem to be nearing the critical level of partial intersterility towards the other related taxa and *A. alpestris* shows great racial differentiation at the varietal level. From the biosystematic point of view, the four taxa are, thus,

correctly classified as subspecies of the species *A. pratensis*, whereas the related *A. thyrsiflora* apparently has produced a more distinct reproductive barrier so it is appropriately separated at the species level (cf. Löve, 1944a, 1949, 1954; Löve & Löve, 1948, 1961a, b; Swietlińska, 1960).

Innumerable experiments with the many taxa given species names within the cultivated wheats have revealed that the only reproductive barriers encountered between the different kinds of wheats are the panalloploid differences in chromosome number between the three good species *Triticum monococcum*, *T. turgidum*, and *T. aestivum* in their wider sense. All the other taxa ought, therefore, to be grouped under these species as subspecies or races of lower significance as has recently been advocated by Mac Key (1954), Sears (1959), Bowden (1959), Chennaveeraiah (1960), and Löve & Löve (1961a, b).

A need for a similar reduction of species to the level of subspecies is indicated in the recent report on the many taxa of *Dianthus* studied by Carolin (1957). The same is also the case with many other genera, especially in Central Europe where splitting on the basis of the morphological-chorological approach has been most evident, although experimental investigation still is lacking for many of these groups.

Although most of the gradually developing taxa just mentioned are ecologically rather than geographically different, some taxa that are geographically highly isolated so that they must have been separated over a long period of time have also been found to lack reproductive isolation. This is, e.g., apparently the case with the pair of Linnaean species *Platanus orientalis*, from southeastern Europe and western Asia, and *P. occidentalis* and related taxa from southeastern North America (Winge, 1917; Sax, 1933; Stebbins, 1950; Parrish, 1957; Pizzolongo, 1958), so they are probably more correctly placed as subspecies of a single species. A similar observation has recently been made in *Xanthium strumarium* by Löve & Dansereau (1959) and Löve & Nadeau (1961). This complex species seems to be made up of two variable subspecies, originating from the Mediterranean and Central and South America respectively. When the varieties of these subspecies from different parts of the world were brought together as weeds in North America and Europe, they hybridized freely and, by aid of pronounced endogamy, gave rise to more or less distinct character combinations that have greatly confused taxonomists following the morphological-chorological approach.

Such examples of gradually developing taxa that have been incorrectly classified by means of the morphological method are usually of the kind mentioned above. There are, however, also cases in which biosystematic evidence has shown that low degree of morphological differentiation, though combined to a high degree of reproductive isolation, has sometimes led morphological taxonomists to classify good gradual species as varietes or subspecies only. This is evidently the case with the subspecies *palustre* and *constrictum* of *Galium palustre*, which, according to Clapham (1949), have developed a strong reproductive barrier. The latter is, therefore, more correctly classified as the species *G. debile* which has, most likely, evolved gradually from the same original stock as has *G. palustre* proper. Another such example may be *Oryza sativa* and its so-called race *japonica*, which are distinctly intersterile (cf. Hsieh & Oka, 1958), although the meiosis is quite normal. It is, however, premature to draw the conclusion from the available evidence that these taxa ought to be separated as distinct species, as recently pointed out by Kihara (1959) in connection with a review of the present knowledge of the origin of cultivated rice.

It is remarkable that the standard for the species category, which Linnaeus (1751) accepted as a concept for the most important entity in the natural hierarchy of the living world, has not weakened with time and progress of discovery. It was invented by the original method that is inevitably descriptive and designed to answer the basic question about what are the facts (cf. Löve,

1960b). It changed only a little when the descriptive approach was supplemented by the comparative, since the distinction of this category as compared with ist next lower and next higher groups also was evident from these points of view. When the implicit postulate of physical relationship that formed the basis of the comparative method became explicit with the acceptance of the fact of evolution, the result was a phylogenetic classification. Since students of the differences between the categories in this system regarded the species category only as one link in a long chain of gradually evolving groups that pass successively from one step to another, it was perhaps natural that they failed to realize that one of these steps could be more important than the others; this was also influenced by the observations by the morphological method that species show all degrees of differentiation. It was, however, the more recent and new procedure of differential analysis with experimental synthesis, which is carried out by biosystematists, that was able to reappraise the significance of different categories based on studies of the causes of their distinctions. This approach has restored the antique standard of species to its former strength as a group of indisputable distinction in the natural hierarchy. It has also demonstrated that although this stage can be reached in different ways, all good species of the Linnaean and biosystematic standard are characterized by reproductive isolation from other such taxa.

Biosystematists are fully aware of the fact that all material available to taxonomical studies has not reached the field of exact scientific evaluation that is typical of the advanced analytic and synthetic approach. They believe, however, that the classical standard of the category of species can and ought to be aimed at by those taxonomists also who need to follow the empirical art of classifying a single specimen representing the only knowledge of the living beings of a remote land. Such approaches may fail to observe the real distinctions of a species in some cases, but later studies will bring us closer to the truth. The only requirement biosystematists feel ought to be made is that whenever a more advanced stage of knowledge of an animal or a plant is reached, this ought to modify less exact classifications based on less advanced methods. This is the simple principle of progressive taxonomy. Other procedures must be branded as reactionary and unscientific.

The species of LINNAEUS was that of the obscure past without an exact definition. It has long been evident that species show different degrees of morphological variation that may blur their real distinctions. The species of the biosystematist still is a variable unit that has evolved in diverse ways. It has been the privilege of the biosystematists not only to provide explanations for the processes of evolution of species and other taxonomical categories but also to discover that the only common denominator for all good species of animals and plants, irrespective of their age or evolutionary history, is their reproductive isolation from other such taxa. The definition based on this knowledge characterizes not only man and ape, cat, dog, horse and sheep, or apple and pear, barley, rye and wheat, but also all other species that coincide with the standard that came to LINNAEUS out of dim antiquity. In that way, the new method not only adds evolutionary explanations to the concept of species but also maintains the continuation of this concept from times longer than man can remember. This is one of the reasons why taxonomy, the oldest and most important of biological sciences, remains among the fundamental and most fascinating of all approaches to biological knowledge.

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