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# The Genus in Evolutionary Taxonomy

A. J. CAIN

THE idea of the genus as the smallest "kind" of plant or animal that can be recognised without close study was an extremely important one in the earlier periods of taxonomy (Bartlett, 1940). The species was a subdivision of it, often requiring expert examination both before it could be recognised and before it could be named, since the specific name was at once a qualification of the generic name and a differentiation from all other specific names within that genus. Hence the custom of putting the generic name first. More than a trace of this same attitude to the genus can be seen in the results of Anderson's minor census (1940) of botanical opinion, which revealed a high proportion in favour of the view that the genus is more natural than the species. It is presumably the extreme usefulness of the genus taken in this sense that leads Just (1953) to affirm that "from a purely systematic point of view, the genus still comprises [sic] the most effective taxonomic unit on which new classifications of higher groups can be based. . . ."

Linnaeus seems to me to stand halfway between this earlier practice and more modern ones. For naming, he retains the older ideas and states emphatically (*Critica Botanica*, Hort's translation, Aphorism 257, for example) that "the Genus must be established before the [specific] name is settled, so that in each genus we may recognise the species which we are supposed to be distinguishing. For the specific name is not given us alive, unless it has a head: the head is the generic name." It is not merely fanciful, surely, to believe that such an attitude was necessary in days when the production of keys, and sound rules for name-

formation, the operation of which would produce agreed synonymies, was of the first importance.

But on the other hand, his attitude to the species is much more modern. Ramsbottom (1938) has given an excellent survey of Linnaeus's opinions and Svenson (1945) has discussed much of their historical background. Svenson points out that, as soon as (and not until) the doctrine of a general and frequent transmutation of species had been brought into disrepute, the species could be regarded with confidence as a morphologically stable group of individuals, "breeding true." It then became a unit within the genus, equally susceptible of definition. The idea of its constancy, the doctrine of the immutability of species, has been of great use in the development of modern taxonomy. That Linnaeus in later years came to consider that species were not wholly immutable, as Ramsbottom has pointed out, does not mean that he returned to a chaos, comparatively speaking, of fluctuating forms within each genus. He, like his predecessors, knew far too many distinct species, apparently immutable apart from phenotypical variation. Hybrids were to be recognised as such, but if they achieved relative constancy, then they merited the status of species.

These views are well expressed in his method of nomenclature. The generic name was a single word, denoting a general kind of plant or animal. His name for a species was a phrase, not exceeding twelve words and preferably as short as possible, which was descriptive. It either referred to some striking character by which the species could be distinguished

from all others of the genus so far discovered—this was best—or gave several characters, the combination of which served to distinguish it. Such names require re-examination and amendment every time a new species is introduced into the genus. The binomial name was only supplementary to the polynomial phrase-name.

In consequence, Linnaeus found it necessary to consider species as separate entities, while naming them as parts of genera. His ideas on the nature of the genus are of special interest. Svenson quotes him as saying, in the preface to *Genera Plantarum*, "Genera . . . therefore, are as many as there are common attributes next [in rank] to those of distinct species, such as were created in the beginning: this is confirmed by revelation, experiment and observation. Hence *all genera and species are natural*." Svenson remarks that "natural" here means that genera and species were created units, "and it was the duty of man to group together those species which belonged to a genus." He continues:

As Spring and others have pointed out, most of our genera are not natural units; but merely represent a stage of classification above that of the species. Nor did the doctrine of descent with modifications of Lamarck and Darwin ease the Genus problem, since it introduced the additional element of time into a system which had been preeminently concerned with the nomenclature of plants and animals as they are distributed in space. To this problem of the Genus, Linnaeus seems to have given a good answer. "The limits of a genus cannot be determined until all the species of the genus are known." In the author's opinion, the attempt to make all genera "natural," without some conventional limitations, would be destructive to nomenclature, which is built up primarily on a basis of history and usage.

That Linnaeus was much interested in the production of a natural classification, based on the relationships of all parts, not on one (e.g. the fructification) is well known. Apparently, from Svenson's quotation given above and from many remarks in the *Critica Botanica*, he believed

that all species could be grouped into genera between which there were definite discontinuities of attributes. The final definition of each genus as a natural group would have to wait until all the species in it were known. Presumably the genera which seemed separate only through ignorance would then be duly interconnected by newly discovered species, and exactly which attributes were merely shared by a few species and which were indeed characteristic of particular genera could then be determined.

We may well smile (and sigh) at the idea that all our problems in classification at the generic level would be over if we could discover all the separate created forms of life. On the contrary, the more that is known of a group and its past history, the more will evolutionary continuity appear and the less will enumeration of forms supposedly distinct, or actually distinct at any one period, help us. We must face up to at least four problems.

(i) Groups discrete at the present day will become indistinguishable as we pass back in time, yet we are committed to a hierarchy of discrete groups.

(ii) There is no theoretical or practical justification at all for believing that all genera are clearly discrete at any one time, since there is no law governing and *quantifying* the angles of divergence of different stocks branching from the same evolutionary line. The discovery of new species may merely confuse the situation by supplying isolated forms half-way between two genera and equally well included in both or neither, without supplying others to connect them clearly with only one.

(iii) There is no reason to suppose that all (natural) genera will be found to have well-marked attributes both common to and peculiar to all their members.

(iv) The "natural" affinity based only on all the parts of an organism may be very misleading at the specific and generic levels. Geographical or palaeontological evidence may reveal much convergence and lead to a considerable regrouping of

forms; and when, as so often, such evidence is lacking, we are left with the uncomfortable feeling that the best we are able to do does not reflect the phyletic situation.

These points require further consideration.

#### *Discrete Groups*

The use of only discrete groups, discontinuous one from another at each level of the hierarchy, was justified as long as it was believed that all groups were in fact discrete, and that, in particular, each species was as it had always been since the Creation, or at most, as Linnaeus came to believe, had generated a clearly marked natural group of distinct forms. Such an attitude was of the greatest use as Pirie (1952) has pointed out, when the first necessity was to explore, describe, and provide means to identify the enormous wealth of material that had begun to be discovered by the immediate predecessors of Linnaeus. Good keys, clear definitions, constant diagnostic characters, and an easily memorised, simply constructed, and unambiguous reference system were the great requirements and Linnaeus was perhaps the most generally successful in producing them. To do so is still an important function of the taxonomist.

The concept of the species as the lowest category in biological classification was based on Aristotelian logic and philosophy, with its notions of real substances each with a nature and essence characteristic of its species (Crombie, 1950), and was reinforced by the notions of special creation and fixity of species, in such a way that a system of discrete groups appeared not only useful but completely sufficient in theory for classifying organisms. The establishment of the theory of evolution produced no great immediate upheaval of taxonomic theory and practice merely because the fossil record was (and in large measure still is) too fragmentary to enforce a taxonomy of continuity. The few fossils known could easily be classified into discrete species.

Moreover, the study of geographical variation was not yet so advanced as to intrude so intractable a phenomenon as the ring-species (Mayr, 1942; Stresemann and Timoféeff-Ressovsky, 1947; Cain, 1954*a*, 1955) into taxonomic discussions. At the present day, ring-species and continuous fossil series are well known and cannot be ignored. Continuity cannot well be expressed by a system using only discrete classes and the relation of inclusion of one group within another.

#### *Phyletic Lineages*

Simpson's discussion of the species concept (Simpson, 1951) leads him to consider that "a phyletic lineage (ancestral-descendent sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies, is a basic unit in evolution. The genetical definition [of species] tends to equate the species with such an evolutionary unit," at least at any one instant in time. After discussing the extreme difficulties that may beset the palaeontologist in trying to decide whether a particular series of samples of fossils is an example of such a single line, Simpson considers the purely taxonomic difficulties that arise when such lineages can be identified and are found to branch. If a chronological series of morphologically intergrading forms—*A, B, C*—forks, producing two others, *D, E, F*, and *G, H, I*, it may be impossible to draw any non-arbitrary line separating *C* from *D* and *G*, yet *D* and *G* may clearly be good species. Moreover, morphological characters do not alter in different lines at the same rate, and they must be taken into consideration in delimiting the species. If *A, B, C, D, E*, and *F* are all extremely similar, while *G, H*, and *I* show marked changes, it might well be advisable to classify the former as a single species, and *G, H* and *I* as separate ones, although *G* is as continuous with *C* as is *D*. In such situations, as Simpson remarks, the frequent occurrence of breaks in the record is very useful since, not having been put there by the

taxonomist, they are "non-arbitrary" and one can reasonably use them for delimiting species. "This is still a separation in what *was* a continuum, but it is non-arbitrary (by the special definition of that word in this paper) as regards the actually available materials being classified." Exactly the same considerations arise if the simple or branching lineage is diverse enough to be considered a genus. Where shall it be cut off from the earlier forms and how far up each branch shall it extend? Moreover, in the case of the genus and higher categories, questions of polyphyly may also arise; these are considered later.

#### *Comparative and Breeding Data*

The justification for the use of morphological data and criteria in delimiting species and genera is that (i) it allows the inclusion in the taxonomic hierarchy of forms known only from a few morphological characters (the absolute minimum of taxonomic evidence) and (ii) morphological criteria are the main example of the only class of criteria available at all in grouping asexual forms at the species level, and in classifying all phyletic lines into the higher taxonomic categories, i.e. the genus, and its sub-divisions, upwards.

There are two distinct activities of the taxonomist which are often confused; one is the recognition of phyletic lines and their separation one from another at any moment in time, and the other is the grouping of these phyletic lines according to their "natural affinities" to produce a natural classification which will show as far as possible the course of evolution in each group. The difference is indicated in Figure 1. In Figure 1*a* are represented a series of samples which on their time-relations and other evidence can be arranged in the phyletic scheme shown, which indicates only what phyletic lines are to be recognised and their time-relations—that is, only the evolutionary topology of this group of forms. In Figure 1*b* is shown the same set of samples arranged

to show *both* their phyletic relationships *and* their degrees of general morphological resemblance, or "affinity." The "natural" groups are not those shown in Figure 1*a*.

Clearly, then, the delimitation of phyletic lines as different branches from other lines, and their grouping into the natural groups of the taxonomic hierarchy are not the same activities. The assumption that the phyletic lines must be recognisable by the same criteria as is any other natural group in the taxonomic hierarchy (an assumption that lies behind any attempt to use nothing but morphological criteria for the whole of taxonomy) cannot be maintained; it is a relic of a pure Aristotelian mode of classification, and was in fact abandoned when Linnaeus, like John Ray before him, characterised species as breeding true, thereby emphasising the reproductive criterion, at the expense of the morphological. If purely morphological criteria had been employed by Linnaeus at the species level as well as elsewhere in the hierarchy, he would have been forced to separate the sexes of many species, which may differ far more than either does from the same sex of closely related species (Cain, 1954*a*). The same is true if purely physiological, ecological, or ethological, as well as morphological, characters are used. But, on the other hand, as Simpson has pointed out (1951, p. 287), *purely* morphological criteria are not used in classification. There is always some weighting of characters according to their *taxonomic importance*, not only at the species level but higher in the hierarchy as well. "Characters are always selected, weighted and interpreted." They are not merely taken at their face-value.

There is, therefore, a fundamental difference in taxonomy between *breeding data*, and all others (usually morphological) which can be grouped together as *comparative data*. The first (or indirect evidence bearing on them) are used to establish what are the phyletic lines in any sexually reproducing group, how they are interconnected and especially how

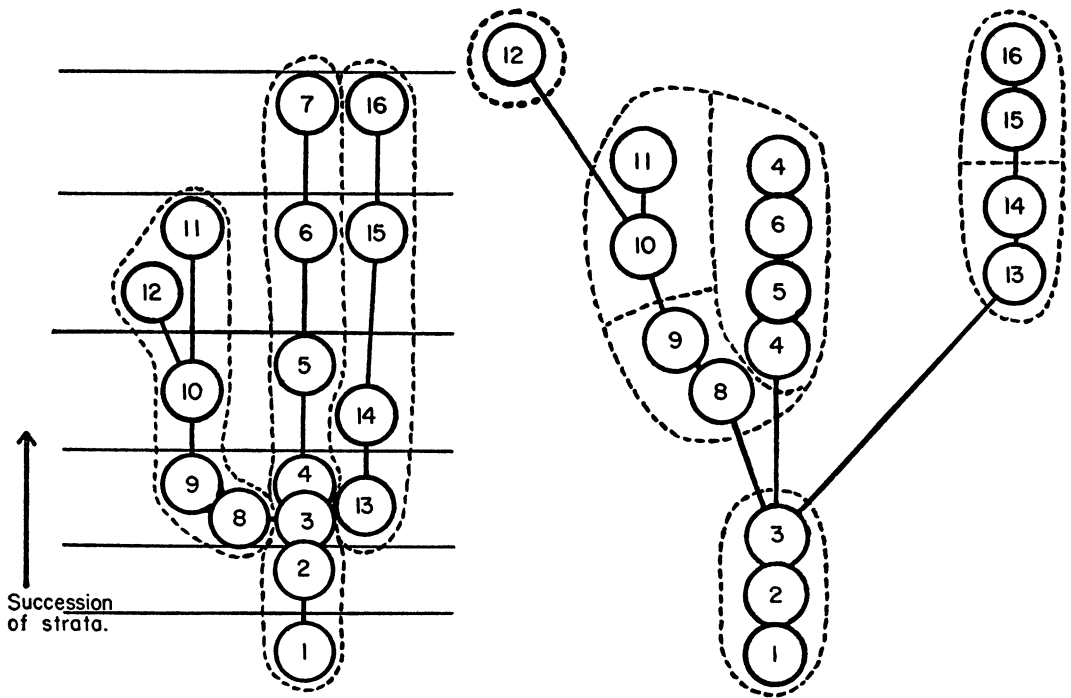


FIG. 1a (left). A number of samples of closely related fossils arranged to show their location in the strata and their presumed lines of descent.

FIG. 1b (right). The same samples as in Figure 1a, but arranged to show both their lines of descent and their degrees of over-all affinity.

many are distinct at any one time. They are the real basis for the construction of diagrams such as Figure 1a. The breeding data allow us to determine the *biospecific distinctiveness* of each separate phyletic line at any one time, and its origin from an earlier line. Of course, it is not necessary to insist on *complete* lack of cross-ability (Mayr, 1942) before one population can be regarded as biospecifically separate from another (Simpson, 1951).

Comparative data, on the other hand, give us a measure of the similarities and differences between any two known forms—broadly speaking, their “degree of affinity.” From them we can decide whether the amount of change in one phyletic line over a given period is less than, more than, or the same as, in some other line. They do not necessarily, merely as such, give us any information on breeding since, as already mentioned, they may well sepa-

rate sharply stages in the same life-history, different sexes of the same species, or different polymorphic individuals of the same population. But it is true that in the absence of breeding data, comparative data (often purely morphological) may be all that are available, and may often be used with fair certainty to indicate what are separate, non-interbreeding populations. If it were true that all phyletic lines were morphologically (or physiologically or ethologically) distinct at each instant in time, and each had unique characters by which it could be recognised, then comparative data would always be sufficient for distinguishing phyletic lines as well as for grouping them, and the same data would suffice for constructing both Figures 1a and 1b. Unfortunately this is not so. Perfectly good species, biospecifically separate at the present day, may be virtually indistinguishable mor-

phologically, and forms in one group which by observed intergradation must be ranked as only subspecies may be as distinct morphologically as good species in related groups. Comparative biochemical, physiological, or ethological evidence suffers from exactly the same limitations as comparative morphology, and Mayr has therefore rightly said that Wilhelm's "physiological" definition of the species in helminths (Mayr, 1942, p. 117) is simply the old morphological definition in a modern disguise. Biospecies are phyletic lines of sexually reproducing forms considered at any one time; the evidence necessary to establish their separateness one from another is that they are nearly or completely non-interbreeding populations (see Cain, 1954a, p. 94) and no other form of evidence is a completely sufficient substitute in all cases. But only comparative data can be used through the rest of the taxonomic hierarchy or for agamospecies. As long as it could be believed either that the species was only the lowest level in this hierarchy, or that it was a separate-breeding entity but invariably delimitable by comparative studies, then comparative data were sufficient for all taxonomic purposes. Now, it must be admitted that the homogeneity of taxonomic criteria is gone for good. At the level of the phyletic line and biospecies, the criterion relates to interbreeding and all evidence must be graded in taxonomic importance according to its usefulness in providing relevant inferences. But above the level of the biospecies, only comparative data can be used, and they are the basis of the rest of the natural classification.

The relations between breeding criteria, comparative criteria, and genetical data are not simple, and have been the cause of some confusion. It has been said, for example, that genetical data or criteria are useless in taxonomy above the level of the species. But few characters could be more genetical than the mode of sex-determination in most organisms; the fact that in the class Aves the female is the heterogametic sex, whereas it is the male

in the class Reptilia as well as in the Mammalia is of undoubted taxonomic value. A general resemblance in chromosomal morphology between two groups could equally well be described as a genetical observation of taxonomic value. But clearly, in these two examples, genetical data are valuable only as comparative data and are on exactly the same footing as morphological, physiological, or ethological comparative data. When, however, one form is found purely by examination of their chromosomes to be a simple tetraploid of another, we are immediately put in possession of a most important fact which instantly indicates

- (i) the closeness of their relationship;
- (ii) the almost certainty that the tetraploid arose from the diploid—i.e. the direction of evolution;
- (iii) the mechanism of the change, and
- (iv) the certainty that the two forms now constitute reproductively separate populations.

Although the data are purely comparative, they permit an inference about the reproductive situation so highly probable that most workers might think it unnecessary to get data on actual crossability in the field. This is a particularly clear instance of weighting for taxonomic importance—in this case, simultaneously for inferring whether a population is part of a phyletic line separate from any other existing at the same time, and how close it is to its nearest relative and what is the phyletic relation between them. In this example, the weighting is so heavy that comparative data reach the same order of importance as breeding data in assessing the separateness of phyletic lines.

Further, Rollins (1953) has pointed out that data derived from hybridisations can be valuable in determining relationships. If two species can hybridise to produce fertile offspring (even if they never do so in the field) the fertility indicates that they are more closely allied to each other than either is to any other species with

which they produce sterile or inviable hybrids. Here, breeding data are of use, not in separating phyletic lines, but in grouping them together. However, such data must be interpreted with caution. The genetical differences between interfertile and intersterile forms need not be a measure of their overall affinities but merely an indication of whether or not they have built up special barriers. Isolating mechanisms (Dobzhansky, 1951) can be evolved on particular occasions; consequently, distinct but widely separated populations may never have built up barriers, since they have never met, yet may be completely interfertile, while very closely related and similar forms which have met along a broad front for a long time may come to overlap as good species, and never hybridise in the field. An example of this has been worked out by I. C. J. Galbraith (in preparation) in the superspecies *Pachycephala pectoralis* and is briefly discussed by Cain (1954a).

Forms which reproduce totally asexually (agamospecies) can be grouped only on comparative data; no others are available (Cain, 1954a, p. 98). If no such forms existed, we could say that criteria of separateness at the specific level were based on breeding data, at all other levels on comparative data, but this pleasant correspondence simply does not hold. In any case, it does not hold for the delimitation of successive forms (palaeospecies) in a single lineage.

#### *The Palaeospecies*

The palaeospecies has been defined as a piece of a single phyletic line arbitrarily delimited as a separate species from the precedent and subsequent portions. It is the result of an unhappy attempt to impose a taxonomy of discontinuous groups on a continuous series (Simpson, 1951; Cain, 1954a, Ch. 7). If several good species of a group are known to have coexisted at any one time, then the sort of differences that are seen between them are regarded as probably indicating spe-

cific distinctiveness in close relatives as well, including successive populations in a single phyletic line, which can therefore be divided up arbitrarily into pieces, the forms in the centres of each of which differ approximately as much as do different lines coexisting at the same time. But this is to apply comparative data at the species level, and as just shown, what is required at that level for sexually reproducing forms is breeding data. It is impossible to obtain data which will allow one to decide when a given phyletic line has changed so much that the latest descendent population considered could not interbreed with the earliest one even if they could meet. It is impossible because (i) the ancestral population will have perished, so that no actual trial can be made, and (ii) as seen above, comparative data are no sure guide to the possibilities of interbreeding, even between contemporary forms. The analogy with differences between known good species is therefore uncertain; far less difference might be produced between reproductively separate populations than is actually found to occur between the known good species related to them, and conversely, in a particular line there might have been considerable change in morphology without reproductive incompatibility.

As long as biospecies and palaeospecies are both called species in some sense, the species-level in the taxonomic hierarchy is not homogeneous (even if asexual "species" are excluded) as Simpson has emphasised (1951). It will contain, without differentiating between them, both groups that are sections through different phyletic lines, delimited from each other on breeding data, and groups that are successive pieces cut out of phyletic lines, no doubt at any one time separate from all other phyletic lines then existing, but each delimited from its predecessor and successor purely on the basis of comparative data. It is standard practice to refer to both entities by specific names, each a binomen formed in accordance with the International Rules of Zoological Nomen-



clature, and no proposal for reform that requires any considerable departure from this practice can be considered practicable. The relations between these two sorts of taxonomic "species" are shown in Figure 2. *A*, *B* and *C* are biospecies, portions of different phyletic lines, distinguished primarily by lack of crossability (Mayr, 1942, p. 119) and—in this and most other examples—morphologically as well. Degrees of morphological difference between *A*, *B* and *C* being used as a yardstick, the phyletic line *ab* is divided up into sections *C*, *D*, *E*, *F*, etc., which intergrade and are palaeospecies. When good biospecies are morphologically well-nigh indistinguishable, as in the now famous case of *Drosophila pseudoobscura* and *persimilis*, or when morphological characters (or others) clearly do not keep step with reproductive distinctiveness (as would be the case if, in Figure 2, forms *L* and *M* were reproductively separate but so similar to *N* as to necessitate their being ranked as subspecies of it on comparative data), the classification of a given group into species on breeding data may be frankly incompatible with any classification on comparative data.

Figure 2 helps to elucidate the relationships between the phyletic line, the bio-

species, and the palaeospecies. Different phyletic lines that coexist at any one time are, as Simpson says, separate evolutionary units; a time-section, such as *xy*, reveals them as separate biospecies, reproductively distinct. It is not, therefore, wholly correct to say (Simpson, 1951, p. 289) that the "genetical" definition of the species tends to equate it with a single, unitary, phyletic lineage. Strictly, the reproductive definition equates it with a single lineage considered at a single instant, or rather, during a short period, the time-quantum of the biospecies (Cain, 1954a, p. 102) during which interbreeding is possible. But this definition, consistently used, would leave us no grounds for not dividing up every lineage by time-quanta wherever possible, e.g. into annual sections for forms with a single breeding season each year, and naming every division as a different species. In fact, the extreme general similarity seen in those populations within a single phyletic line that are very closely adjacent in time, leads us to believe that all the individuals within them could have interbred freely if only they could have coexisted in time. But this is to introduce comparative criteria as a substitute for strictly reproductive criteria which, by the nature of the case, cannot be applied. The palaeospecies, therefore, must be characterised as a time-series of populations known (or believed) to be connected successively by descent, reproductively separate from all other forms coexisting during the same period, and sufficiently homogeneous on comparative criteria to be included under a single specific name. It is not only the result of an attempt to impose a taxonomy of discontinuous groups on a continuous series, but also an attempt to use simultaneously two different sets of criteria, reproductive and comparative. If all that were known of the forms represented in Figure 2 were a few specimens each of *A*, *C*, *E*, and *N* (say), only comparative data could be used to classify them at all. Nevertheless, if sufficient information were to come to light later to make pos-

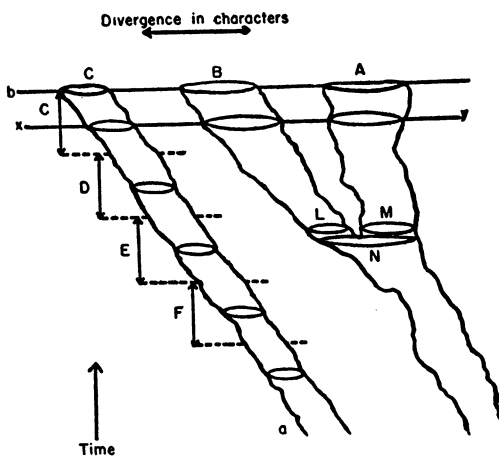


FIG. 2. The relations between palaeospecies, biospecies, and phyletic lines. For explanation see text.

sible the construction of Figure 2, the classification founded purely on comparative data must be corrected by reproductive criteria, or by comparative data weighted not purely comparatively but in relation to their value as indicators of the reproductive situation.

In fact, as the amount of knowledge about a group increases, there is a change in the criteria that can be applied to it. In a very poorly known group, only comparative data can be obtained, and they may be sufficient only to indicate in the broadest way the general affinities of the various forms, without giving the slightest clue to their exact phyletic interrelationships. As more data become available, it may be possible to obtain some evidence, direct or indirect, on the phyletic situation, and in part at any rate to construct such a diagram as Figure 2. But as soon as this happens, the natural arrangement produced solely on comparative data must be corrected to correspond as far as possible with the phyletic data, and this correction may, in fact, involve abandoning the first-produced natural arrangement.

#### *Taxonomic Importance*

From the foregoing discussion, it is obvious that taxonomic importance can be based on very different criteria in different categories.

(i) At the biospecific level, data are graded according to their reliability in providing evidence of actual or potential crossability, when the separation of forms into biospecies is being carried out.

(ii) At the species level for all kinds of species and in all higher groupings, once the different biospecies have been distinguished, the degree of resemblance in all characters is used to produce natural groups. This general degree of resemblance and differences is presumably what Linnaeus would have called affinity.

But lastly,

(iii) All other evidence that bears in any way upon the actual evolutionary

sequence of events is used to correct the arrangement made on the basis of plain affinity by distinguishing affinity due to close evolutionary relationship from that due to convergence.

This last raises an important point, clearly stated by Simpson (1945) when he says that classification must be based on phylogeny but cannot express it. The classifications used to-day must not include together in the same natural group forms whose resemblance is due only to convergence, if thereby they are separated from those forms to which they are really related. But when, as is usual, the detailed phyletic history within a group is not known, the classification used has no phylogeny to express, and when it is known, the categories available are quite inadequate to express it—only a diagram such as Figure 2 can do justice to it, and not even diagrams like these are adequate for ring-species, sibling species, or in general any forms in which morphological and reproductive distinctness do not go hand in hand. The most that the ordinary classification can do is avoid disagreeing with the phylogeny of a group as far as known.

But even this statement requires qualification. As Arkell and Moy-Thomas (1940) have pointed out, examples are known of phyletic lines, closely related and evolving in parallel, in which the characters of extreme phyletic importance that distinguish the lines are inconspicuous compared with the resemblances between contemporary forms. Judged on pure affinity, the genera (or other groups above the species) must be horizontal, not vertical, the more so because there are forms which can readily be included in such genera but whose phyletic position is uncertain, so that they cannot be assigned to one or other phyletic line. Here, different species of one genus clearly have arisen from different species of the immediately preceding one. However, it is usually considered sufficient to make sure that no genus as delimited is derived from two or more preceding genera. In gen-

eral, a group in one category is polyphyletic if it arises from more than one of its own or a higher category.

The sort of evidence that can be used to correct a classification based on pure affinity varies greatly from group to group. Two examples from birds, actually just below the generic level, may be of interest. The well-known rules of geographical variation due to Bergmann and Gloger lead us to expect that subspecies, and often closely related species also, in cold damp areas will be larger and darker than their relatives in hot dry ones. In the fruit-pigeons of the genus *Ptilinopus*, there is a striking similarity between two geographical representatives, *Pt. regina* of Australia and the Lesser Sunda Isles, and *Pt. roseicapilla* 35° of latitude away, in the Marianas, and it has been suggested that they are closely allied in spite of the enormous distance between them which is occupied by related but less similar forms. Suspicion is aroused when we find that the resemblance extends only to the southernmost subspecies of *Pt. regina*, i.e. the subspecies in the coolest and wettest part of the range, and that these two forms are the furthest from the equator, to south and north, respectively, of all the forms in the species-group. It is very likely indeed that much of the resemblance between these forms (although not all) is due to the convergent effects of selection by similar climates. At all events an arrangement placing *Pt. roseicapilla* next to the southernmost subspecies of *Pt. regina* is almost certainly not sound phyletically (Cain, *Proc. 8th Pacific Sci. Congr.*, in press).

Geographical evidence is often of value in detecting convergence irrespective of geographical rules and similar regularities that suggest convergent selection. The genus *Myiagra* comprises a very natural group of flycatchers distributed from the Lesser Sunda Isles to Tasmania, the Marianas, and Samoa. All are geographical representatives except that three overlap in Australia and southern New Guinea

and two occur in Fiji. The mountain-forest form in Fiji, *M. azureocapilla* is unique in that the male has a bright blue cap. It was duly separated as the genus *Lophomyiagra*. But in all other respects it agrees so closely with the Samoan form next door that they must be closely related, and the Samoan bird, except that it is hen-feathered, is a quite typical member of the genus. The genus *Lophomyiagra* cannot be upheld. More interesting is the remarkable resemblance between the Samoan form, *M. albiventris* and that in the Lesser Sunda Isles, *M. ruficollis*. I showed this genus recently without geographical data to a class in taxonomy and told them to group it by pure affinity; all agreed in placing *ruficollis* with *albiventris* and *azureocapilla*. But by examining ranges they found that its affinities must be with its nearest neighbours in the Tenimber Isles and northern Australia, which do indeed resemble it, and that it is cut off from *albiventris* by the full east to west range of the genus (about 4000 miles) and by ten other forms distributed in between. The chances that these two are really more closely allied phyletically to each other than each is to its neighbours are extremely remote.

In a similar way actual sequences of fossils, when available, can be used to correct a classification and show what characters do indicate separate phyletic groups. The classic example is the horse and cow. With the knowledge available in his time, Linnaeus was probably right to group them together. The possession of one digit or two on each foot, for example, need not be thought of great importance; after all, pigs have four and cows two, yet they are obviously allied. Yet the known fossil history shows clearly that this trifling character is indeed of great importance as an indicator, separating the Paraxonia from the Mesaxonia. Here is yet another meaning of taxonomic importance, with its own separate criteria. This by no means exhausts all the meanings (Cain and G. A. Harrison, in preparation).

### *Characteristics of the Genus*

From what has been said above, it is obvious that the present idea of the genus differs somewhat from Linnaeus's. Its constituents are far from unitary, equivalent and monotypic. The biospecies itself, the best-defined sort of species, is unitary in a reproductive sense, as Simpson says. But it often cannot be described by a single monotypic description when it includes considerable geographical variation, and in the case of extreme siblings may not be separable on morphological characters (see, e.g., Cain 1954a, Ch. 6). Reproductive distinctness does not always correspond to morphological distinctness—i.e., pure affinity may be misleading. Agamospecies and successive palaeospecies in a single line must be distinguished on comparative criteria, since for them nothing else is available. The genus is the lowest obligate category for which invariably only comparative data, corrected as far as possible from all data bearing on actual phylogeny, are available. It is a natural group of species, monophyletic in the sense explained above, and arbitrarily delimited at any one moment in time when either it merges backward and forward into phyletically continuous forms, or phyletic lines exist halfway in their affinities between it and a contemporary related genus and could be equally well included in either. Since the entities it contains are so far from being monotypic units, it is not surprising that some genera are known which are clearly natural groups yet cannot be diagnosed at all, since every character confined to them is lost or modified in one or more forms, the remainder of whose characters suffice to establish their membership in the group. An example is the genus *Ptilinopus* (Cain 1954b). Some examples in flowering plants are given by Sherff (1940). Since, as remarked above, there is no evolutionary law quantifying divergence, there is nothing to prescribe the degree of difference which calls for generic separation, as against familial or ordinal. Ranks other than the individual, the biospecies at any

one instant in time (and not even then if there is continual hybridisation), and that containing all living things, have only a positional value (Cain 1954a).

We may agree with Svenson that most of our genera are not natural units but merely represent a stage of classification above that of the species, in the sense that many are merely easily keyed-out groups and thus artificial, while many more are "purely natural" because no data bearing on phylogeny are available. This must very often be the case in insects, for example. The theory of evolution has indeed not eased the problem; nor should it, since it has rightly brought out the difficulty of applying a taxonomy of discrete groups to a dendritic assemblage in which every twig and branch are ultimately interconnected. We cannot hope to remove the accepted taxonomic system, which is far too firmly entrenched, yet a taxonomy of continuous groups should be designed, for maximum efficiency, only with regard to the problem, not to history as well. We need to express *relationships* such as those between agamospecies and their parent biospecies, or two sibling species, or the various forms in a ring-species, when necessary, while retaining the magnificently non-committal inclusiveness of the Linnean categories for poorly known forms. Moreover, as Linnaeus himself pointed out, the reference system must be such that it does not change as ideas on the interrelationships of particular groups change; this immediately means that the names of groups must remain stable—i.e. that we should be able to move them about in our schemes as units, which more or less imposes the view of them as discrete.

The key to a solution lies in the word "relationships." It is noticeable that all the recent developments at or about the specific level that have been proposed are designed to introduce relationships. Examples are the cline (Huxley, 1938), the subspecies as a geographical race (not in its earlier meaning as merely a well-marked form within the species), the su-

perspecies and its predecessor the *Artenkreis* (Mayr, 1931, 1942), the ecotype and ecospecies (see Baker, 1952; Valentine, 1949), the agamospecies, morphospecies, and palaeospecies (Cain, 1953, 1954a), the sibling species (Mayr, 1942), and the sets of symbolic prefixes proposed by Kiria-koff (1948), and Huxley (1942). Such proposals are characteristic of the "New Systematics." Of particular interest is the admirably designed set of terms proposed by Gilmour and Gregor (1939) and elaborated by Gilmour and Heslop-Harrison (1954). I cannot agree with the latter when he states (1953) that the aims of "classical taxonomy" are to describe all existing "kinds" of organisms, to classify them according to their resemblances and differences, and to name them according to a body of internationally agreed rules, contrasting this with "experimental taxonomy," the aims of which are to identify evolutionary units, and by experiment to determine their genetical inter-relationships and the rôle of the environment in their formation. Surely there is no distinction, or rather it is the distinction between the  $\alpha$ -taxonomy of groups so far only inadequately worked, and the  $\omega$ -taxonomy of really well-worked ones. Surely all taxonomists aim at doing both as far as their material and circumstances will allow. The problem now before us all is to find the best method for supplementing the classical taxonomy and correcting it, so that, as information becomes available, it becomes based upon everything that is known about each group, and allows the maximum number of generalisations to be made about the course of evolution.

### Summary

1. The genus as used by Linnaeus was the smallest "kind" or "sort" recognisable without much expert study. Each genus was a natural, discrete group, separable from those most closely allied by some definite attribute, recognisable when all the species in it had been discovered, if not before.

2. The species was regarded as unitary but still named by differentiation within the genus. Species were monotypic, morphologically distinct, and equivalent, no different kinds of species being recognised.

3. The same sort of comparative criteria could be used for distinguishing both species and genera, except that for species the criterion of breeding true had been accepted in addition for some time.

4. Examination of criteria now used leads to a sharp distinction being drawn between *breeding data* and *comparative data*. Confusion has arisen because the latter must often be used for want of direct evidence in place of the former, and genetical data may appear under either heading. Moreover, comparative data are not always consistent with breeding data and may be contradicted by them.

5. A review of the interrelationships of different sorts of species and the evolutionary tree shows that the genus cannot now be regarded as a naturally discrete group either in relation to its ancestors and descendants, or at any one time. It is not necessarily definable by one single peculiar attribute, nor are its constituents monotypic, equivalent, essentially merely subdivisions of it, or themselves wholly discrete. It is monophyletic, but purely positional in rank, and a collection of phyletic lines, not an entity subdivisible into species.

6. Only comparative criteria are applicable at the level of the genus (and other higher categories). Within the genus, they only are applicable to agamospecies and successive palaeospecies, while breeding criteria are appropriate for biospecies.

7. The available taxonomic information varies greatly from group to group, and a comprehensive classification must include both poorly known groups to which only comparative criteria can be applied, and very well-known ones in which phylogenetic and biospecific (breeding) criteria can be used with some approach to certainty.

8. The obvious course is to continue to

use the Linnean system as a universal basis but to supplement it as information becomes available by indications of the relationships between the constituents in each group. The whole trend of the "new systematics" is toward this supplementation by means of relators, words or symbols specifying relationships and mitigating the discreteness of the groups in the Linnean system.

9. In view of the differences between Linnean and present-day taxonomy, it is worth while considering whether the latter can still be said to be Linnean.

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