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TAXONOMIC CONCEPTS

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The Linnean period; deduction and diagnosis.
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INTRODUCTION

Whatever, and however little, we may think about such things, we are all of us bound to have some taxonomic concepts. They are in effect the clips with which we put together in the most significant manner (we hope) our knowledge about many aspects of birds or any other organisms. They are far from being only nomenclatorial or only in relation to the limits of species; they include ideas about how things should be grouped at all and for what purposes, how they should be analysed and in consequence described —and that is quite a large field of study. Ornithology has been responsible for many important and, in their day, startling changes in taxonomy generally, and a review of some outstanding concepts, how they came to be what they are, and what should now be done about it, is by no means out of place in this celebration.

RAY AND WILLUGHBY ON COMPARISON

I cannot do better than begin with a quotation from Ray and Willughby (1678), not only because this is a centenary celebrated in Cambridge of a society founded by Cambridge men (mainly), and Ray is one of the ornaments of Cambridge, indeed of European biology, but because he and his brilliant associate realized clearly one of the outstanding difficulties of taxonomy. In his introduction to the ' Ornithology ', Ray writes of Willughby as follows.

" For my part I know no man who hath seen more Species, been more exact in noting their differences, and inventing Characteristic Marks whereby they may be certainly distinguished; or more curious in dissecting them, and observing the make and constitution of their parts as well internal as external. Howbeit I do not deny but some have been more accurate in anatomizing one or two particular Animals. The reason of this his diligence was, because he observed that some of the descriptions of former Writers of this kind, either by reason of their brevity, or because they contained only general notes, were very obscure, and gave occasion to many errours and mistakes, but chiefly unnecessary multiplications of *Species*; the Readers often mistaking several descriptions of the same Animal, which they meet with in divers Authors, by reason of their generality and obscurity, for so many descriptions of several Animals. Now that he might clear up all these obscurities, and render the knowledge and distinction of Species facile to all that should come after, he bent his endeavours mainly to find out (as I before intimated) certain Characteristic notes of each kind. But if in any kind no singular mark occurred whereby it might be certainly distinguished from all others, he did minutely and exactly describe all its parts, that at least a Collection of many accidents, which all together could not be found in any *Species* else of the same kind, might serve for a Characteristic: That the Reader should not by a general and ambiguous description be left in suspense, nor incur the danger of error. But because a prolix and operose description is tedious to most Readers, and to the unattentive seems rather to obscure than illustrate the thing described, to relieve and gratifie such, besides the description he often adds some short notes, by which the Animal described may be distinguished from others of the same kind like to it, and wherewith it is in danger to be confounded. Now though I cannot but commend his diligence, yet I must confess that in describing the colours of each single feather he sometimes seems to me to be too scrupulous and particular, partly because Nature doth not in all Individuals (perhaps not in any two) observe exactly the same spots or strokes, partly because it is very difficult so to word descriptions of this sort as to render them intelligible: Yet dared I not to omit or alter anything." [In fact he puts in his own comments between square brackets.]

The difficulties that Willughby & Ray experienced three centuries ago are still with the taxonomist working on the less well-known groups (i.e. most of the Animal Kingdom). They often did not know whether several descriptions in the literature were of different species, or of individual variants or of different ages and sexes of the same. So they described after the fashion indicated, from their own specimens wherever possible, had figures made (which often did not satisfy Ray), and worked out an arrangement of the birds which as far as possible in those days grouped allied forms together. A sample of their difficulties can be seen from (for example) the account of the Golden-eye. This (i.e. the drake in nuptial plumage) in the English version is described well. Then comes

" Our smaller reddish-headed Duck, which it seems is no other than the Female of the precedent . . . "

" Since the finishing of the *Latine* History we have been informed that this Bird is no distinct kind, but only the Female *Golden-eye.* And truly, the shape of the body, the make of the Bill, the length, number of feathers, figure and colour of the Tail, the fashion and colour of the Feet, and other accidents induce us to think so, neither is there more difference in weight than is usual between different Sexes. Besides, that this was a Female the want of the labyrinth proves; but in the next Article I shall shew some reason to doubt whether of the *Golden-eye* or not. Mr. *Willughby* also was suspicious that it might be the Hen *Golden-eye* ."

The next Article is the " greater reddish-headed Duck, perchance the same with the last described, or the Male thereof. . ." This is described, and then Ray says " I should take this Bird to be the very same with the precedent, not only in *Species*, but in Sex, notwithstanding its difference in bigness, were it not that it had a labyrinth on the Wind-pipe, which I suppose is proper only to the Males. So that either this is the Male of the precedent, and both different in species from the *Golden-eye*: Or, which I rather incline to believe, this must be a young *Cock-Golden-eye*, that had not moulted its chicken-feathers; and the precedent an old *Hen Golden-eye*: And so these two supposed *Species* are reduced to the *Golden-eye*; they being all three the same." The latter supposition was in fact correct, Willughby and Ray having described the drake, the duck, and the drake in eclipse in that order. They give several notes on variation, an interesting one being on the Buzzard. " In some birds of this kind, we observed many white spots in the covert feathers of the Wings; which in the Wings spread made a kind of white line: The like white spots it had in the long feathers springing from the shoulders which cover the whole back. The edges of these feathers were of a dirty yellow. . . But whether it come to pass by reason of Sex, or Age, or other accident, certain it is they differ very much one from another in this respect: For whereas some have no white feathers neither in head, back, nor wings; others have very many." This quotation recalls Ray's comment in a letter to Martin Lister that in the birds of prey, nature seems to play with us, in respect of plumage, there being so much variation, and his *cri de coeur* about ducks in the ' Synopsis methodica Avium ': " Verum colores in hac & aliis Anatibus variant nonnihil in diversis individuis ".

Ray and Willughby often used behavioural characters in their accounts of species; and by this careful association together of the different plumages and variants of the same species, they were doing work of the utmost importance for that period, in establishing firmly the biological idea of the species. Ray, as Raven (1942) says, deeply influenced Linnaeus in this respect (and others). But the point I wish to emphasize is the Description. They were aiming not only at identifying, always the first requisite in any subject whatever (you must know that you and others are talking about the same thing), but also at giving a reasonably complete characterization which would serve also to show the place of the thing classified in a natural classification. And straightway comes up the principal dilemma of biology. On the one hand, a brief description leaves out so much, and may not be sufficient even for simple identification (particularly in an age of multitudes of new discoveries). On the other, the drawing-up of a really detailed description takes much time and labour. Only those who have tried, I think, really appreciate the mode of excellence proper to a good description. Moreover, too minute a description may be so much wasted labour for a specific purpose; a feather-by-feather account of a single skin—when what is wanted is the specific description (i.e. those characters reasonably constant in the species)—may be useless if the skin is of an abnormal individual, although for studying variation within the species it may be just what is required. But we cannot know what will be required some hundred years hence; consequently it may often be only sensible to give what is required at the time, and work away at the current problem. This attitude can degenerate only too easily into merely sloppy work on the current problem. But it is true indeed that art is long and life fleeting, and some sort of economy of effort must be made.

This first step towards accuracy and adequacy in the description of birds (which certainly was not originated by Ray and Willughby) had most important consequences. Careful description of different plumages and of variant individuals is the beginning of the realization that plumages and moults are themselves worthy of study, that they have their own regularities of distribution in different groups of birds, and their exceptions. One of the principal ways in which biology progresses is the more careful description of things already known in part or vaguely, which brings out regularities asking for explanation and often of great taxonomic value.

A second consequence was the fastening of attention on anatomical characters, as in the discussion of the female Golden-eye quoted above, as less liable to vary from one sex to the other, or in different age-groups. This trend was later taken to ridiculous extremes when anatomical characters were regarded as *necessarily* more important than plumage characters in the classification, not the identification, of birds.

THE LINNEAN PERIOD; DEDUCTION AND DIAGNOSIS

Unfortunately, the excellent example of Willughby and Ray was not followed up with sufficient care, mainly because the spate of new discoveries had broadened to a flood. New discoveries advance science; but not if there are too many at once. What was needed fifty years after Ray was a good handy, easily worked key, and it is precisely this which Linnaeus produced. I have described Linnaeus's theory of taxonomy elsewhere (Cain 1958). His attitude was vastly different from Ray's. Ray, like Linnaeus, was trying to get at the real natures of things, in the Aristotelian sense, their essences, and as he tells us (1703) he used any constant character as an indication of the essence. Linnaeus, however, was more Aristotelian, at least as far as his botanical classification went. It was standard doctrine that the reproductive system must on the Aristotelian system of physiology, be of great importance for classification (Cain 1958, 1959 b), and he used it, therefore, not only for his admittedly artificial classification of plants, but also for his attempt at a natural classification. He was less fond of the reproductive system for classifying animals, partly from motives of propriety, and very much, one suspects, because it was unhelpful. His classification of birds, therefore, in spite of his theory, was not so very different from Ray's and may (*pace* Raven) have been easier to use as a key. But in order to encompass the whole of the Animal, Vegetable and Mineral Kingdoms, he had to cultivate conciseness almost to the point of silence. His names were keys within each genus, limited to twelve words (a far from unnecessary reaction against the page-long names that some had employed for plants). But how could such brevity deal with the various plumages of the Golden-eye, for example? Yet even if one could run down any Golden-eye with his key, one might well want to know if the bird under examination was a drake, a duck, or a drake in eclipse. I give as an appendix Linnaeus's paragraph on the Pochard, together with Willughby's and Ray's description for comparison; the corresponding descriptions in the ' Catalogue of Birds ', Witherby's ' Practical Handbook ', and the ' Handbook of British Birds ' should also be compared.

The Linnean period marked a deterioration in taxonomic description, probably necessary for the sake of identification. It continued with gradually decreasing self-confidence right down to the time of Darwin. Cuvier, Lamarck, de Candolle and other great systematists were still *deducing* what must be more and what less important, and classifying animals accordingly (Cain 1959 b); and although there was a wholly excellent movement towards taking all sorts of characters into consideration when producing a natural classification, in the hands of all but the best systematists classifications were still really keys, modified here and there when it would be quite ridiculous to separate off a particular species because of a single aberrant character. This modification has often been acknowledged explicitly. Bowdler Sharpe, for example, cataloguing the Ploceidae (1890), adds a footnote to the key to the Viduinae " In some respects the present ' Key ' is an artificial one, and I have slightly altered the arrangement of some of the genera in the detailed sequence of the *Viduinae*, by placing *Chlorura* near to *Erythrura* [an excellent move], *Pyromelana* and *Urobrachya* close to *Penthetria*, &c." But nevertheless, many ostensibly natural classifications have really been keys constructed on one single group of characters believed to be of most importance. The convenience of a natural classification which is also a key is very great; if a new form is found, it will be run down to a place near its true relatives, which in general will not happen with an artificial key—indeed the results may often be grotesque. Nevertheless, a natural classification and one designed for identification are not the same thing, and require different techniques, as Willughby knew perfectly well, and Ray pointed out in the quotation from the 'Ornithology' given above.

However, there is one thing that remains to us from the Linnean period which requires further examination. That is the binomial nomenclature. It was designed by Linnaeus as an unimportant abbreviation (unimportant, that is, from the point of view of taxonomic theory) assisting what he regarded as the proper nomenclature of organisms. For Linnaeus, for various reasons which I have discussed elsewhere (Cain 1958), the genus was the most important practical unit in taxonomy. Provided a man knew his genera, he could always work out from the literature what his species was, and he was not tied down to the use of one particular arrangement of genera. Therefore, although Linnaeus regarded the species as a natural true-breeding entity (and occasionally added notes on behaviour, as in the common earthworm—"*adscendit noctu*") it was treated as a subdivision of the genus, and was named differentially within it (Cain 1956, 1958, 1959 a). The generic name was placed first, because one needs to know what kind of thing one is dealing with before specifying the exact sort; and the specific name which qualified it (and the trivial name, which was a mnemonic for or abbreviation of the specific name) naturally followed it.

The downfall of deduction, the abandonment of the attempt to pretend that we know enough about the design and construction of animals, so to speak, to classify on that basis, was slow. Many different classifications were proposed, but so often the characters chosen for the basis were manifestly useless in some one group or other. Where they were not, it was often the case that in fact they had been arrived at by induction from obviously natural groupings first, and then on the grounds of physiological or other importance, were used to divide up the group in question on principle (Cain 1959 b). The coming of evolution did little at first to alter this state of things. In general, the groups as already arrived at were simply taken over and declared to be monophyletic. This was a much too simple procedure. But in addition, new principles were enunciated to be used in classification; the important characters now were those least likely to be altered in the course of evolution, and they could often be recognized because, as Darwin said, they will be the constant ones within a group, not readily modified for particular modes of life. But do we know this for certain in any particular group, and is it always true that the characters common to a group at the present day are the ancestral ones? How far has convergence occurred, and can we always detect it? These are difficult questions to answer, and in fact the simple imposition of evolutionary theory to explain pre-evolutionary taxonomic groupings is not really possible; it raises a large number of problems, some of which have been as yet hardly discussed (Cain 1959 b).

However, from the point of view of this paper, evolution made little difference to the practice of most taxonomists. The most constant characters were still sought for to define groups. They were now explained as primitive, where previously they had been called "more essential" and the groups were said to be monophyletic rather than just natural; but the taxonomic procedures remained virtually the same. Species on the whole were distinct from one another; intermediates must have occurred in the course of evolution, but few if any were known. The old nomenclature could be used with great advantage, since it indicated not only which species was under discussion but to which genus it belonged; and moreover, the construction of new names and the elimination of homonyms was facilitated by having only the generic name unique within each Kingdom.

Darwin's great point in the 'Origin' was the necessity of studying variation, and of breaking away from the old idea that every species had its own immutable essence and therefore could vary only unimportantly and within rigid limits. (This was also Lamarck's idea, but he spoilt his case by fantastic speculations about the physico-chemical nature of the organism.) It is remarkably ironical, therefore, that the principal effect of the ' Origin ' on those taxonomists that accepted its thesis, was to confirm them in their search for constant characters, as just mentioned.

POPULATIONS; BIOSPECIES AND CLINES

I do not think I need to tell an audience of ornithologists what happened next. The taxonomic description of organisms, because of the labours of the Parisian taxonomists especially, had recovered to some extent from the Linnean depression, which, however, continued to exert a not too desirable influence by giving prestige to mere brevity as such, regardless of the circumstances. The second major advance in taxonomic accuracy and adequacy came when it was fully realised that the locality of collection was an important piece of information about a specimen, not because of the necessity for recording the range of that form, but because of geographical variation. It was for a long time the custom (we have many specimens in the Oxford University Museum that suffered from it), to give on the label attached to a skin the specific name then current, and not the locality of capture but the range, usually called the habitat; for example " Pyranga aestiva Linn. Male. Summer Redbird. Hab. S. of U.S.A. and S. America. Brydges Collection, c. 1874–5". This was formerly regarded as the most useful information. But good description of specimens, combined with extensive exploration and accurate localisation, showed clearly that certain forms, which by themselves would have been called good species unhesitatingly, intergraded with each other. The result, as we know, was the discovery of the principal mode of origin of the species of higher (and many other) animals, thanks to the labours of Wagner, Kleinschmidt, Hartert, Jordan, Mayr, and others. This was a major contribution to evolutionary theory, and in this ornithologists (not entirely alone) have led the world.

Next to be dealt with in this too short sketch of the development of taxonomy are two subjects in which ornithologists did *not* lead the world. In one they couldn't, in the other they—didn't.

Birds are very convenient in one important respect for the evolutionist. They reproduce entirely by bisexual reproduction. Other groups do the most bizarre things. They may reproduce by mere fragmentation, or special budding; they may abandon the male sex altogether and reproduce by unfertilised eggs; they may go through all the motions of sexual reproduction except that no actual fertilisations ever occur, and they are in fact parthenogenetic although it would hardly seem so at first sight; or almost any combination of these processes may occur. Now the notion of the species that Ray established scientifically so successfully, and which has always been known to practical breeders of the higher animals, is simply inapplicable to species that never reproduce bisexually at any time.

It is only too easy to think of the group that one knows best as the " real " representative on the Animal Kingdom; and I know of one book that purports to give instruction on the taxonomy of all sorts of animals, that dismisses these fascinating forms in a single sentence, presumably because of its authors' having specialised too much. But I must insist that these extraordinary reproductive antics are commonplaces over surprisingly large areas of the Animal Kingdom, and all the Plant Kingdom. It would be safer to argue that birds are rather exceptional in using only strictly bisexual reproduction, and ponder on that limitation, which necessarily precluded ornithologists from contributing to the recognition of different sorts of species. For with the discovery of non-bisexual modes of reproduction, the species ceases to be the same sort of entity throughout the Animal and Plant Kingdoms. At least two different sorts must be recognised, and while for one, the biospecies, the criteria of specific distinctness are breeding data—morphological (or better, comparative) data being used only as a substitute for breeding data—for the other, the agamospecies, none but comparative data can be used. This is a development that neither Ray nor Linnaeus could have foreseen.

The second subject is the development of techniques for describing precisely the differences between forms when taking all sorts of characters, and all sorts of intermediate forms, as required by evolutionary theory, into consideration. The approach to this problem has been very gradual. The consequences for taxonomists of the discovery of geographical speciation and its importance in evolution, were only slowly appreciated. Here almost for the first time (but palaeontological data were beginning to give trouble too) taxonomists were faced with the problem of describing *continuous* variation affecting extensive populations, while their whole attitudes of mind were conditioned to a taxonomy of *discrete* variation, and their nomenclature was based on it and other assumptions now equally inappropriate. For many species it still did not matter; they were sufficiently discrete to cause no great trouble. But one cannot help feeling that a taxonomic practice that worked only where too little was known about its subject was hardly the best possible, scientifically.

There have been two major reactions to the problem of describing geographical variation. On the one hand, many races were discovered which were sufficiently alike for no one to doubt that they belonged to the same species, and whose characters were reasonably constant and definable. These could perfectly well be named as *subspecies*, being still discrete and simply definable. Hence arose the trinomial nomenclature which has played so valuable a part in promoting the study of speciation by naming populations so that their relationships were immediately apparent. The extension of it to the superspecies, which has been equally helpful, involves no new departure in taxonomic theory.

But on the other hand, there are many populations in which variation is not as simple as all that. Very different forms intergrade smoothly, and it is almost impossible to see where to draw a satisfactory line between them; yet some nomenclaturists feel that a line should be drawn somewhere. This attitude is in fact inappropriate for such situations, and nowadays anachronistic. Moreover, different characters may vary, and not in the same directions, geographically; which should be regarded as the important variation, on the basis of which subspecific names can be bestowed? The attempt to solve this problem was really a new departure in taxonomy. Huxley (1938) proposed an auxiliary taxonomic principle, the *cline*, which I believe was the first ever proposed to cope with continuous variation. This was in effect an easily usable description of a character-gradient. But meanwhile, other modes of description of variation, especially where that variation was to be estimated from a sample, had been elaborated in very different subjects, and were slowly penetrating into taxonomy. These were the ordinary techniques of statistics; and they bear much the same relationship to the cline or the series of subspecies into which a cline can be broken by the confirmed nomenclaturist, as Willughby's and Ray's descriptions did to Linnaeus's diagnoses. They are far more exact, and take far more trouble (and material, very often). An outstanding example of their highly successful use is Moreau's study of the populations of African *Zosterops* (1957), which cast up a new rule of variation. This surely is the proper way to describe varying populations when you want to get all the information you can out of the data. But the cline remains as a most useful approximation, often far more wieldy in ordinary speech.

Those who were specially impressed with the (undoubted) usefulness of the subspecies have made many gallant efforts to cope with the sort of situation which requires statistical or clinal treatment. Doubts began to be expressed about the value of breaking up continuous variation into apparently discrete subspecies; Lack (1946), for example, working with the robin *Erithacus rubecula* (L.), found many difficulties in the application of trinomials, devoted a section of his paper to " The Subspecies Concept ", and ended " One therefore begins to wonder whether subspecific trinomial terminology is not beginning to outlive its usefulness and validity. Certainly, in the case of *Erithacus* *rubecula*, it is both simpler and more accurate to describe subspecific variations in terms of geographical trends, and to omit altogether the tyranny of subspecific names." Since then much has been said for and against the trinomial, which, one must admit, has done valuable work, and is often applicable but often inapplicable. I think the time has come when we should regard it as one attempt to deal with geographical variation, applicable to some rather uncomplicated cases, the cline as a much more accurate one, especially useful where quick communication is desired (like the notes of special characters put by Willughby after his detailed descriptions), and the full statistical treatment, by far the best, and capable of discovering new regularities when the material and time are available.

Meanwhile there has been arising in two different ways a problem that threatens to overshadow all those so far discussed, and be the outstanding feature of the next period of taxonomy. At the level of the subspecies, there has been much trouble and many discussions about the amount of difference necessary before a population should be given a subspecific name. Some have given names on the slightest perceptible difference (some, indeed on less) while others, not in the least denying the existence of these slight differences, have felt that there was no point in their receiving nomenclatural recognition. How different must one subspecies be, then, from its nearest relative? Amadon's paper on the 75% rule (1949) deals with this point, and Mayr, Linsley & Usinger's useful textbook (1953) also discusses it. It is a matter for arbitrary definition and agreement among taxonomists. This may seem a small thing, but we have only to think of the usefulness of that well-known object in Paris, the standard metre, to see what arbitrary agreement may lead to.

But the same problem arises in a more acute form on the other side of the species, so to speak. How different overall must a species be from its nearest relatives before it must be put into a different genus, or a genus into a different family? Two subspecies may well differ in only a single character, and a single measurement may be sufficient to distinguish them. But species, genera, and higher groups differ simultaneously in respect of many characters, and many sorts of characters. Is it possible to get an agreed arbitrary figure for overall difference, in order to separate genera or higher groups as subspecies are separated? This question will be dealt with later; in the meanwhile the question of what is meant by a genus has arisen. To Linnaeus the genus was the main unit of taxonomy, divisible into species. At the present day, however, it is only a collection of related species (Cain 1956). It need not be definable by any single character or complex of characters, and species may well exist that are exactly half way between two genera, and cannot be included in one rather than in the other. The real practical importance of the genus at the present day is purely nomenclatorial. No species can be officially named until it is put into one genus or other. But this arrangement was made by Linnaeus, working with a very different theory of taxonomy from what is permissible at the present day. Ornithologists have certainly not led the world in recognising this point.

It is worth while taking stock here of the present situation in taxonomic theory.

(i) The different sorts of organisms, including birds, are grouped together by Ray's practice of taking many characters into account and putting together those forms most like each other overall; but this procedure is modified to take into account any sort of evidence whatever that suggests that convergence has occurred. Very often we simply do not know whether it has or not, and the classification then must be purely natural.

(ii) The genus, like the family or order, is no more than a natural collection of species, hoped to be monophyletic. It is not at all the primary unit in taxonomy, as it was to Linnaeus.

(iii) The species is no longer equivalent throughout the Animal Kingdom. In some groups, it can be defined only comparatively, with no reference to breeding data (Cain 1954, 1956), and the degree of difference needed to recognise a species is a matter for arbitrary convention. This happens not to worry ornithologists, but it is an important point for general taxonomic theory.

(iv) We now have a much clearer picture of the situation as far as the species based on breeding data (the old familiar species) is concerned. The terms biospecies, superspecies, genetical allopatry and sympatry (Mayr 1942, Cain 1953), and the subspecific, clinal and statistical description of geographical variation enable us to describe the situation in any species with far greater accuracy (where necessary) than was possible before. This accuracy has again cast up further problems which is all to the good; how can we settle the biospecific status of wholly allopatric populations (a matter of great interest to ornithologists), what do we do with hybrid swarms, etc.?

(v) Nevertheless, the binomial system is still with us, and indeed more firmly entrenched than ever, by international agreement. I have pointed out elsewhere (Cain 1959 a) how it became accepted just when the theoretical basis for which it was elaborated by Linnaeus had finally been revealed as insufficient. It is not a good thing now that a species cannot be named before it is assigned to a genus, and this applies especially in birds. There are far too many examples of species put into separate genera simply because they could belong equally well to one of several, and no one knows what to do with them. Binomials give the impression that genera are as well known, neat and tidy as in Linnaeus's day, which is nonsense, and actively discourage work on the status of many species.

(vi) Although a beginning has been made with the proposal of arbitrary conventions, they have not yet been produced where they are most needed, because the complexity of the comparisons to be made has so far defied their quantification. Consequently, the weighting of characters phylogenetically is also still purely non-quantitative, and there is much divergence of opinion about them.

NEW CHARACTERS

At all times there has been a strong tendency on the part of those who know their animals in the field, to use characters of behaviour, food, detailed ecology etc., as much as or even in some groups more than plumage or anatomical characters, to characterize their species, and to recognise groups of species as well. But such characters are often far more difficult to observe, and still more to describe accurately, than those observable in the peace and quiet of the museums on skins. Bad descriptions are worse than none at all; descriptions that do not take into account variation may be most misleading; and descriptions based on no insight into the thing decribed may confound very different things.

The present period of taxonomy may well be compared with the Linnean in one important respect. That was characterised by a flood of new forms, this by a flood of new characters. The former caused a real deterioration in taxonomic practice by reason of the very excess of material, and we must be careful that the same does not happen again. The outstanding researches of Lorenz, Tinbergen and their school have at last given us the means of accurate analytical description of behavioural characters, which are now available to the taxonomist, and have been eagerly seized by him. The work of Boyden, Irwin and others on comparative serology, and that of Sibley on egg proteins, bring new characters to test the old relationships. Chromosome studies have not so far been as useful as they have proved in flies or plants or earthworms, but they have not been taken very far as yet in birds. But perhaps the most spectacular example of all, of a formerly intractable complex of characters being reduced to the most accurate comparability and measurability, is Thorpe's work in producing oscillograms of song. Previous attempts to describe bird song are sometimes good when you know the song already, sometimes quite unintelligible whether you know it or not; sometimes imitative, sometimes purely by simile, metaphor, or even more poetical devices. The same could be said of descriptions of behaviour (my own favourite is Butler's description, after giving a good account of the courtship of the Diamond Sparrow, of that of the Zebra Finch as " Comic, but not unpleasing "). But the transference of the song to the sound spectrograph produces such a multitude of workable characters (rather like those of the salivary-gland chromosomes of flies) where were so few before, as to be truly dramatic.

Moreover, increased accuracy of description brings to light unsuspected examples of convergence. Morris (1958), for example, discussing behaviour in some estrildine finches, remarks of the bow of the Star Finch " The statement that a bird bobs up and down is unfortunately an extremely ambiguous description. There are so many subtly, but importantly, different ways in which it can move up and down. Each way appears to be derived from a basically different movement and the ceremonies should not therefore be compared too glibly. In the bowing of the straw-carrying male Star Finch, the movements are repeated and deliberate. The bird bows rhythmically keeping the beak horizontal both at the top and at the bottom of the bow. In this way it differs distinctly from the bowing of most other courting estrildines. Usually the ceremonial bow is derived from displacement beak-wiping and then the beak points more and more downwards as the body is lowered in the bow. The Star Finch bow is almost certainly derived from a different source, namely the intention movements of taking-off for level flights." Similarly in the allusive description of song, both Sibley and Donaghho have described birds (a cuckoo and a flycatcher in the Solomons) as whistling like a person calling to a dog; but we find the calls to be in one case a series of whistles nearly on one note, and in the other a set of rising slurs (Cain & Galbraith 1956). Both are right but the description is insufficient.

All these new characters are subject to the same limitations as those of classical taxonomy. All need to be described with sufficient accuracy (the observation of one specimen may be quite insufficient to give a description of behaviour sufficient to characterise a species or subspecies), all must be shown by appropriate analysis to be the same on each occasion they are referred to, just as morphological characters cannot be regarded as the same unless they are shown to be homologous. All need to be regarded with the same suspicion as morphological characters—that is, they may be constant in one group, and therefore of great value in defining it, and so variable in another as to be nearly useless; they may be subject to convergence in some groups and not in others; they may be primitive in some groups and not in others. Those avian taxonomists who are unaware of the difficulties of simple comparison in taxonomy and systematics as worked out by the classical anatomists will simply repeat all the previous mistakes in new fields.

COMPARISON OF CHARACTERS

The discovery of so many new sorts of character, and their expression in ways that make them suitable for taxonomic use brings up as part of the problem of estimating amounts of overall difference, the balancing of characters of one sort (e.g. behavioural) against those of others (e.g. serological or anatomical). It is obvious enough that taxonomists do take into account all sorts of characters when grouping forms, but how exactly do they do it? And after that, how do they weight characters of the same kind for their phylogenetic significance?

Here we come up against one of the most extreme examples of accuracy versus convenience in all taxonomy. The human brain is a marvellous electronic device, amazingly quick at perceiving whole constellations and configurations of characters, comparing them in an almost wholly non-quantitative way, and in weighting them by means of its own previous experiences. This very facility is a grave danger in some situations. It is very easy for a taxonomist to look at a specimen, sum up a hundred characters, decide that it is obviously a relative of another form he already knows, discount some of the differences as in his experience due to different modes of preparing the specimen, others as due to (e.g.) slight juvenility, others because they are likely to be due to convergence, yet others because although conspicuous they could be due to a single gene-difference, and fasten on one because he thinks it very important phylogenetically. And all this without realising that he has also been greatly influenced by one character or more, which has made him accept the closeness of relationship to the forms he already knows, without really considering the matter. But it is all done so quickly that far more forms can be classified than if he had to stop and describe the characters of each one carefully, measure them, and make some quantitative estimate of their resemblances. Morris (1958) says of Delacour's revision of the estrildine finches "... there are few, if any ' ideal ' characters which split the estrildines nearly up into the three tribes suggested by Delacour. Despite all this I am certain that Delacour's *tribal* separation of the species (with the single exception of the Red-browed Finch) is correct in almost all respects. This is, of course, because one includes *many complex character-relationships* in any taxonomic evaluation. Intuitively one is on guard against the ruthless use of single characters, but unfortunately their employment makes for a very tidy report. Delacour's brilliant revision of the 108 estrildine species succeeds in general, I feel sure, not because of the official reasons he gives, but despite them."

From my own studies of the estrildine finches, I would add that Delacour's classification (1943), which will certainly be the basis of departure for all future revisions, is also an example of unconscious influence. He takes two genera as being the most primitive, because they have longer first primaries (a very dubious conclusion). Those two contain rather large birds (for estrildines), with not very modified beaks, mostly brilliant coloured with black and red, and with white spots. Now nowhere does Delacour discuss the proposition that if a species is primitive in one character, it will be primitive also in its others. Yet if one lays out a complete set of the estrildines in Delacour's order, it becomes immediately obvious that he has accepted this proposition, probably unconsciously, and that with some slight modification (the relegation of very odd genera, such as *Erythrura* to the end of their groups), the birds which are largest, with " ordinary " beaks, and with most rich red, deep black, and white spots come first within each tribe or genus, or often subgenus too, and those that are smaller, brown, and barred rather than spotted, come last. There are even traces of this in the Australian grassfinches, which are so heterogeneous in their plumage that it is difficult to arrange them so as to show any trend.

Now, I think it will be agreed that an activity in which we must rely on intuition to save us from error is not particularly scientific, however convenient it may be for producing what is believed to be a rough approximation to what we want. It is about as satisfactory as Morris's statement about certain estrildine markings that " Close examination reveals these to be more than just similar superficially. They also bear striking resemblances in indefinable subtleties of quality." Which is certainly intriguing, but no more. A very great deal of taxonomy is of this almost wholly cryptic description, and I can think of no other scientific subject in which it would be tolerated for a moment—partly because the subject-matter of other sciences is far less complex and less in need of such interim mystical treatment, but also because the standard of taxonomic work in ornithology is remarkably low.

It is not too much to say that because of the facility of the human brain in rapid comparison, and the undoubted truth in such remarks as those of Morris quoted above and their value in pointing out situations requiring analysis, the taxonomic concepts involved in the recognition of characters as separate, of the exact meaning of overall affinity, of the nature of a group of forms, of the qualifications for entry to a group, (and in consequence of the exact procedures for phylogenetic weighting, which presuppose all these other concepts) are in a remarkably undeveloped state, to put it no more strongly than that. When a taxonomist says of three forms that on their general similarity, or overall affinity, two are much closer together than they are to the third, he is making a quantitative judgment of a sort. Can we state exactly what he is doing? An analysis of this sort of comparison in contrast with photogenetic comparison has been attempted, with some interesting consequences (Cain & Harrison 1958 and see references in Cain 1959 a). " The taxonomist may compare, for example, different species recognised as such on biological grounds, different populations definable geographically, strains or ecotypes which can be distinguished by their different ecological preferences or occurrences, or samples of fossils from different localities. And when he says that the degree of sexual dimorphism is greater in one species than another, he is comparing the sexes within each of two species. Similarly, a remark on the profundity of a metamorphosis presupposes a comparison between successive stages in a single life-cycle. Other comparisons are often made between different polymorphs in the same population, abnormal and normal individuals, a variety of normal ones, or the effects of different allelomorphs on the phenotype within one family of progeny. All these examples have been given because it is easy to forget how various are the comparisons into which the idea of overall resemblance enters." It will be noted that in the recent periods of taxonomy, a great deal of useful energy has been put into defining the different *forms* to be recognised taxonomically (the biospecies, subspecies, age and sex-differences, populations etc.) and what is now being looked at is the method of comparing these forms when they have been distinguished.

The definition of a single character that is adopted by Cain & Harrison (1958) for comparisons such as these is perhaps rather surprising at first. It is *anything that can be considered as a variable independent of anything else considered at the same time.* For this purpose intensity of melanin in the scapular feathers (say) and length of the wing, whether correlated or not in any form or population, are separate characters. It is immaterial what correlations can be observed; all that is necessary in making these comparisons of pure affinity or overall resemblance, is to be sure not to take into account the same character twice, wholly or in part. This is so different from what goes on when one is weighting for phylogenetic comparison, that it puzzles many people.

Some have thought that this sort of comparison is doomed to failure. There are too many characters, they say. You will always introduce some bias by selecting some rather than others But it is surely possible to consider all the major parts of the animal concerned, look for the biggest differences, and especially those that can sum up a lot of others, and use them to get an estimate, drawn from all major parts, of the greatest difference between the forms compared. The advantage of this procedure is that one is certainly not grouping too closely together the forms investigated. But the real objection is by those who want only a phylogenetic classification, and say (rightly) that to use unweighted characters is simply to throw away information. This is right, but the simple overall comparison is not primarily used to get a phylogenetic classification.

PHYLOGENETIC CLASSIFICATION

Probably more pure nonsense has been talked (and published) about phylogeny in birds than in any other group of animals. People have made the most astonishing assumptions about what must be primitive in given groups, and what must have given rise to what. One ornithologist tells us that the plumage is always more reliable in a group. Another says that the vomer, being inside the mouth, is less subject to adaptive modification and therefore more reliable for ancestral characters. We must face the fact that we can achieve a purely natural classification of most groups of birds, by the sort of comparison discussed just above, and we *may* think that the natural groups so obtained are in fact also monophyletic ones, but we have no means of finding out how much convergence has gone on, and every reason to believe that it will be more considerable in more closely related than in less closely related stocks. The whole of taxonomy is an attempt to extract as much information as possible from data of very various degrees of incompleteness; and it does no good to pretend that we can find out about a given group more than we can. The feverish days when evolution seemed almost to be in peril if every known form could not be put in its appropriate position on the universal family tree have surely passed; the theory is now so strong that it will not matter if we have to say we just don't know the phylogeny of 80% of passerine birds. For such groups a "natural" classification is in fact all we can attain to, unless we wish to revert to Linnean or Cuvierian days, and decide *a priori* that some one character or complex "must" be more important. And since the "natural" classification sums up a great deal of information, it is a most useful one. It would be a great thing if ornithologists would once again lead the taxonomic world by distinguishing clearly between natural and phylogenetic groups.

But nevertheless, there are some examples even among birds, where it does seem certain that we can identify good examples of convergence at all levels. Then however natural the group may appear, if we think that some forms in it are there because of convergence, we forthwith disregard all the characters in all these forms that are convergent, and look again at what the remainder tell us. To take an example of Darwin's, the Falkland Islands diving petrel is astonishingly like a little auk. (Indeed on a natural classification it might well be grouped with it.) But once we realise that this resemblance is convergent, we disregard it, and the remaining characters put it with the petrels, not the auks. Again, if we find that several separate characters are correlated because they are all modifications for a particular mode of life, and that if any of a group of closely related animals were to take up this mode of life, they would acquire them all, then we must decide to work with only one of them. To look at any more would give us no further certainty, since if one is evolved, the rest will follow, whether by convergence or by inheritance from a common ancestor. These are examples of phylogenetic weighting which are easily expressed as modifications of the simple comparison of overall affinity mentioned above; and it is obviously desirable to systematise them as much as possible, to clarify the situation, reveal real differences of approach, and if possible get agreed procedures, just as the systematisation of the judgment of pure affinity will allow us to get a quantitative hierarchy and agree on arbitrary quantitative values for differences between genera and higher groups.

To show how easy it is to confuse overall similarity and phylogenetic classification, we can take the example of the birds of paradise. These, as everyone knows, are wonderfully diverse at first sight, far more different than species of different genera in other groups of birds. But hybrids between species are not uncommon in the wild; this has been taken to mean (rightly) that they are rather similar genetically, and have probably acquired their remarkable characters only recently. The step has then been taken of lumping them into far fewer genera than before. But we must make up our minds about what we want. Are we going to use genera to show amount of overall difference, or to reflect our views on time of divergence? The two are by no means the same; and if it is claimed that in this case the similarity of the genotypes completely outweighs the phenotypic differences, one can only say that the case is not proved at all, and cannot be until we know a lot about the differences in genotype of other genera.

I feel that we should continue to use the older intuitive style of classification only for want of a better, and that we should do everything we can to avoid cryptic taxonomy and unjustified weighting of the evidence. Every effort should be made to place comparison in taxonomy, and phylogenetic weighting, on as sound a basis as possible. The procedures will be far more time-consuming than simple intuitive comparison; but fortunately we have the most remarkable electrical and mechanical aids to calculation, which will vastly lighten the burden. What they will never be a substitute for, of course, is a proper procedure from which to instruct them, and a considerable experimental period is necessary first, in which different procedures are tested against undoubtedly correct phylogenetic classifications, and undoubtedly natural groups, to ensure that we are doing what we want to do. Several groups independently have begun to study these problems (e.g. Michener & Sokal 1957, Sneath 1957 a, b, Cain & Harrison 1958 and in preparation), and we can hope for a considerably increased accuracy in our concepts of comparison and grouping if a concerted attack is made.

BINOMIAL NOMENCLATURE

But there is one point that stands out from the preceding discussions in this paper, and that is the very doubtful value of the binomial nomenclature for well-worked groups of animals such as birds. It is no exaggeration to say that the most vexatious difficulties of the taxonomist stem entirely from it. We must commit ourselves to an opinion on the generic relation of every form, before we can name it at all and thus get the benefit of an internationally agreed system of reference, protected from homonymy, for what we are talking about. I have no hesitation in saying that in the passerines especially, many generic names are unnecessary, not only because so many of them are produced by gross oversplitting, but also because no one really has any idea of the generic relationships of the forms so (apparently) confidently named. It is useless to reply that everyone knows a checklist, with its imposing array of names, is really only tentative; far more users of it will take it on authority that these names are right than will understand its real nature. Probably no single factor has worked more powerfully to produce the deplorable situation that birds are perhaps the best-worked group of all at the level of the subspecies, species and superspecies, and one of the worst at the level of the genus and family. Several checklists have been published in the last twenty years, and no doubt represent the interesting opinions of reputable ornithologists; but one knows that the authors cannot possibly have gone at all deeply into the relationships of most of the groups. Often extensive alterations in large groups, with corresponding changes of nomenclature, have been made, and nothing whatever published in explanation, which is unthinkable in any other science. In some of these checklists, the expert in one group or other can see that the principles on which it has been arranged are merely idiosyncrasies of the author, and should never have been allowed to influence his arrangement. There is no doubt that, however useful the generic name may be as part of the binomial in avoiding homonymy, there is little or no justification for continuing to regard it as part of the classification of the form named, and there are some strong reasons why one should not (Cain 1959 b). When I have to publish a checklist, I shall take good care to mark with an asterisk those generic names which mean nothing whatever, but must be there to satisfy the International Commission on Zoological Nomenclature.

Even worse is the inconvenience of the specific, as against subspecific name. I have seen a distinguished ornithologist sweating as he tried to make up his mind whether a rather distinct and geographically wholly allopatric population should be given specific rank or included as a subspecies with some others. The facts of the case were not under dispute; the descriptions of the characters of all the populations concerned were sufficient, and their ranges were well known. The biology of the situation was obvious—here was a separated population which had diverged considerably, but as it nowhere met its relatives, one could not say whether it was biospecifically distinct or not. Yet it could not even be named without this impossible decision being made. Some have said that this sort of situation is comparatively uncommon; from my own work, I deny this, and envy them their perspicacity that can decide on so many situations without a qualm. Such powers of decision are not given to me. But even if it were true that the situation arose only rarely, the nomenclature that demanded an impossible decision only once must still be regarded as scientifically unsatisfactory. There is much to be said for Mayr's contention—when in doubt about an allopatric population, call it a subspecies, since then the trinomial nomenclature will at least convey its allopatry and its nearest relatives. But nevertheless, if we really don't know what the status is, we should not be forced by an anachronistic system of nomenclature into giving a status and then denying that in this particular case the status means anything. What is required is a system of reference that is not tendentious, but allows us to refer unambiguously to the things we are talking about, leaving their status to be determined when possible. Linnaeus had no difficulty of principle when inventing his reference system, since species were species, and the same in all groups, and genera were invariably characterizable, distinct from each other, and the lowest groups above species; there might often be mistakes in practice—a mere variety taken for a species, or a wrong diagnosis of a particular genus—but there could be none in principle. But almost the opposite is true today, and the system of reference is highly tendentious, forcing impossible decisions upon us, and obscuring ignorance.

The binomial nomenclature is even threatening us with a split in taxonomic practice. It is true to say that as the result of the great advances made in the study of chromosomes, many plants (and some animals too) have been revealed as complexes of different " chromosome races ", hardly differing morphologically, but isolated from each other as breeding groups. To recognise all these as separate species, which on the biospecific criteria of the species is what they certainly are, would mean the fragmentation of very large numbers of well-known species (morphological species, that is) and the introduction of hosts of specific names which the ordinary herbarium botanists could not use, since they lack the means for determining the necessary chromosomal characters. Further, it is felt that the recognition of biospecific distinctness is a matter only for the evolutionist, and does not in the least concern vast numbers of foresters, agriculturalists, gardeners and other applied botanists, who want above all things a stable nomenclature. Gilmour (1958) has stated the botanists' view with much vigour. Gilmour & Gregor (1939) and Gilmour & Heslop-Harrison (1954) have therefore proposed that the units of evolution should not be confused nomenclaturally with the units of reference, and have produced a very well-designed terminology based on the root *deme** for the units of evolution. In ornithology, on the other hand, a considerable simplification of the nomenclature and clarification of the evolutionary situation has arisen from the opposite process of adjusting the taxonomic units until they coincide with the units of evolution, i.e. making sure that the taxonomically recognised species are biospecies.

In fact, all taxonomists have two different activities (apart from identification) to pursue. On the one hand, they are producing a sort of map of the diversity of organisms, by means of a hierarchy of groups; this must be based primarily on morphological evidence, supported by all other comparative data available. On the other, they are distinguishing the different groups which are separate lines or units of evolution, and for this, when biospecies are concerned, breeding criteria, not morphological or other comparative criteria, are what is wanted. The binomial nomenclature, expressing both biospecific distinctness and morphological relationship, confuses the two, and since it is applied mainly on relational properties in plants and mainly on breeding criteria in many groups of animals, it produces an apparent fundamental divergence in practice between botanists and zoologists, which really does not extend to their principal aims. It is useless to say that such matters only concern botanists; enough is now known of some groups of animals for us to say that the botanists' problems will soon arise there too. We should take every opportunity of studying comparative taxonomy, to make the taxonomy of any one group really satisfactory.

SUMMARY

1. Ray and Willughby fully understood the need for descriptions of different generality for different purposes and (Ray at least) the waste of time caused by excessive accuracy. Their principal problem was to sort out biospecies; they tried also to produce a natural classification.

* Some zoologists accustomed to think only in terms of geographically definable populations in bisexual species have wrongly used the word deme for these, thereby greatly impairing its generality and usefulness.

2. In the time of Linnaeus, a flood of material to be catalogued and identified produced a regression to a keying classification based on *a priori* principles to a large extent, the natural classifications of the time being very imperfect and inconvenient for identifying. This was the period, unfortunately, when the reference system (binomial nomenclature) was invented which is now internationally accepted.

3. The advent of evolution caused little change in taxonomic practice, the groups formerly elaborated *a priori* or by natural classification being now called monophyletic and the constant characters being the primitive ones and still important.

4. In the period of the " New Systematics ", continuous variation first became a real practical problem in a system so far devoted to discontinuous variation. It led to three things, a better understanding and description of biospecies, the idea of geographical speciation, and various techniques of differing accuracy and convenience for its description.

5. The present period is characterised by a flood of new characters, as the Linnean was by a flood of new forms. They require proper handling taxonomically (on the lines already worked out for morphological characters) and proper balancing against one another.

6. The problem of comparing wholly different sorts of characters raises again that of quantitative overall comparison in general. This, when achieved, can serve as the basis for phylogenetic weighting.

7. It is suggested that the principal development of taxonomic concepts in the past has been in the recognition of different forms (the species, subspecies, population, and the like) and that in the future those connected with exact comparison will come into prominence (the character, the natural group, etc.).

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APPENDIX. EARLY DESCRIPTIONS OF THE POCHARD

Belon, 1555.

De la Cane a la teste rousse.

Il y a vne manière de petite Cane moult semblable à vn Morillon, qui a la teste rousse: mais la poictrine & le dessous du col sont noirs. Tout le reste du corps est de couleur plombee. Son bec, ses iambes & pieds, sont noirs ressemblãts à ceux d'vne Cane, et les yeux rouges. Elle n'est de si grande corpulence qu'vne Cane.

Linnaeus, 1758. (*Anas ferina*)
ferina. 27. A. alis cinereis immaculatis, uropygio nigro. *Faun. svec.* 107
Anas fera fusca. *Gesn. av* 116. *Aldr. orn. l.* 19. *c.* 40. *Will. orn.* 288. *t.* 72. *Raj. av.* 143. *Alb. av.* 2. *p.* 87. *t.* 98.
Habitat in Europae *maritimis.*

Willughby and Ray, 1678.
The Poker, or Pochard, or great read-headed Wigeon: Anas fera fusca *of Gesner, Aldrov.* t. 3. p. 221. Penelops veterum & Rothalss *of Gesner, Aldrov.* 218. Cane a la teste rouge *of Bellonius.*

That we described weighed thirty two ounces: From tip of Bill to end of Tail was nineteen inches long, to the Claws points twenty one. It is bigger than the Common *Wigeon*, and for its bigness shorter and thicker. The lesser covert feathers of the Wings, and those on the middle of the back are most elegantly variegated with dark brown and cinereous waved lines [or ash-coloured, with very narrow, waved, cross, dusky lines]. The Rump and feathers under the Tail are black, so that the Tail is compassed with a ring of black. The lower part of the Neck is likewise black, so that the forepart of the body seems also to be encircled with a ring or swathe of black. The Head and almost the whole Neck are of a deep fulvous or red colour: the middle part of the Breast white, the sides and lower part and Belly all of the same colour with the Back, and varied with the like transverse undulated lines, but both colours paler: Toward the Vent it is by degrees darker coloured. The Tail is very short, not exceeding two inches, made up of twelve feathers, of a dark grey, the outmost the shortest, the rest gradually longer to the middlemost; yet the excess is not considerable, so that notwithstanding it is not to be reckoned among those that have sharp Tails. The quils of the Wings are about twenty five, all of one colour, *viz* a dark cinereous, though if they be carefully heeded, there will appear some diversity, for the tips of the exteriour and greater feathers are marked with black, of the middle ones with white. The interiour bastard-wing and lesser covert-feathers of the underside of the Wings are white.

The Bill is bigger and broader than in the *Wigeon*. The feathers divide the middle of the upper Mandible coming down from the forehead in form of a peak or acute angle. The upper Mandible is of a lead-colour, but its tip black: The nether is wholly black. The *Irides* of the Eyes are of a very beautiful colour, from yellow inclining to a sparkling red: The Feet lead-coloured: The membranes connecting the Toes black: The inmost toe the least, having a membranous border annexed to its outside. The back toe hath likewise an appendant membrane or fin.

The characteristic note of this Bird, is one uniform colour of its Wings, without any feathers of different colour in the middle of the Wing, as is usual in most Birds of this kind.

In another Bird of this kind (which we take to be the Female of this) the Bill was black with an ash-coloured spot of the form of a crescent a little above the tip. The back feathers and coverts of the Wings had no such transverse waved lines as those of the Male. In other points it agreed mostwhat with the Male.

BEHAVIOUR, SYSTEMATICS, AND NATURAL SELECTION

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Several review articles have been published recently on the general topic of behaviour, classification, and evolution (see J. M. Cullen 1959, Hinde 1959, Lorenz 1958, Roe & Simpson 1958). The present paper will therefore deal with a slightly different subject, and discuss, with some selected examples, the extent to which behaviour differences between taxa must be assumed to be due to natural selection. Some questions of method will also be raised. While most examples will be taken from birds, some data on other animals will also be given.

THE TAXONOMIC USE OF BEHAVIOUR CHARACTERS

It will be useful to consider first which behaviour characters can be used for taxonomic and systematic purposes, how they can be used, and what exactly are the phenomena which require an evolutionary explanation.

Analysis of behaviour "machinery".

It is now almost a commonplace to say that there *are* behaviour characters helpful to the taxonomist. Mayr (1958) has given a useful review.