

MORPHISM AND EVOLUTION

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I. INTRODUCTION

EARLY in his career, William Bateson showed the preoccupation with discontinuity which lasted the rest of his life. He became convinced that discontinuous was often more important than continuous variation in producing new forms in evolution, and amassed the huge volume of data included in *Materials for the Study of Variation* (1894) in order to prove it.

On page 76 of this work, he pointed out that "so long as systematic experiments in breeding are wanting, and so long as the attention of naturalists is limited to the study of normal forms, in this part of biology [the occurrence of discontinuous variation], which is perhaps of greater theoretical and even practical importance than any other, there can be no progress." He thus, by a natural transition, became interested in the inheritance of discontinuous variations and was, one might almost say, pre-adapted to become the protagonist and apostle of discontinuity in inheritance, after the rediscovery of Mendel's work in 1900.

He further pointed out (p. ix) the danger of discussing "the causes of Variation and the nature of 'Heredity', a subject of extreme and peculiar difficulty", without adequate knowledge of the actual "modes of Variation or of the visible facts of Descent." In passing, we may note the curious fact pointed out by Darlington (1953) that, though Bateson was fascinated by the idea of inheritance being discontinuous, he resisted the idea that it was particulate.

Later, in his *Problems of Genetics* (1913) he was busy noting examples of discontinuous genetic variation and inheritance in nature; and towards the end of his life was attracted to the problems of discontinuity posed by such curiosities of variation as those of chimaeras, rogue peas and root-cuttings.

It is perhaps not unfair to say that he preferred his problems to retain an element of strangeness and inexplicability, tending to lose interest in them when simple principles of explanation became available. However that may be, it is a matter of record that he stood out against the chromosome theory of heredity for years after all other geneticists had accepted it, until finally convinced by the demonstrations set before him in Morgan's laboratory †; and that

* Based on the Bateson Lecture delivered at the John Innes Horticultural Institution on Friday, 8th July 1953.

† As an example of Bateson's attitude to cytology in 1894 I cannot refrain from quoting his remark on pp. 21-22 of the *Materials*, where he briefly anticipated D'Arcy Thompson and other modern biologists in stressing the importance of a proper consideration of *pattern* in biology. "If anyone will take into his hand some complex piece of living structure . . . and will ask himself how it has come to be so, the part of the answer that he will find it

he never could bring himself to the reconciliation between the idea of continuous variation and evolution and that of discontinuous inheritance, between the essentially selectionist approach of the pure biometrician and the essentially anti-selectionist view of the pure mutationist—the reconciliation which was initiated by Morgan's young men in the '20's and was made the corner-stone of future advance in evolutionary genetics by R. A. Fisher in his great book in 1930.

Even in 1894, however, he anticipated some modern geneticists' views on selection by writing:—"while the only test of [biological] utility is the success of the organism, even this does not indicate the utility of one part of the Economy, but rather *the nett fitness of the whole*" (italics mine).

But Bateson's instinct was correct in two important respects. First and foremost, in the conditions prevailing in the biological world around the turn of the century, emphasis on discontinuity was not only desirable but necessary for progress. Without the discovery of the discontinuous or, as we now say, the particulate basis of inheritance, the biometrical approach would have remained sterile. By a strange paradox, although continuous variation and gradual evolution are the rule, they could not be properly analysed or understood except in terms of discontinuous genes and abrupt mutations.

And secondly, it was necessary to go to the facts of evolution, as revealed by the comparative study of variation in nature, to jolt the then leaders of biological thought out of their armchairs and enlarge their horizon beyond the limits of the assemblage of forms they chose to introduce into their laboratories.

Both of these aspects of his work are still extremely relevant. His belief in the evolutionary importance of markedly discontinuous variations has turned out to be justified, even though the phenomena and their explanation are very different from anything which he could have imagined at the time: and it is only by going to the facts of nature, as revealed in the natural history of all groups of animals and plants, and analysing them on a comparative basis, that we are reaching this new understanding of the importance of discontinuity.

Bateson (1894, p. 20), introduced into the study of variation the useful terms *merism* and *meristic*. I propose to introduce the term *morphism* and its derivatives, *morphic* and *morph*. I make no apology for this. Brief terms for genetic polymorphic variance are badly needed; *form* is too general, and *phase*, though sometimes used, especially by ornithologists and mammalogists, for colour-morphs, hard to give, is that which relates to the perfection of its pattern. And it is not only in large and tangible structures that the question arises, for the same challenge is presented in the most minute and seemingly trivial details. In the skeleton of a Diatom, . . . the scale of a Butterfly . . . *in the wreaths and stars of nuclear division* (italics mine), such patterns again and again recur, and again and again the question of their significance goes unanswered." It is only fair to add that Bateson's view of distinctive patterns or alternative forms as being what, following Galton, he called *positions of organic stability* (pp. 36, 42, 65), foreshadows many important modern ideas and discoveries concerning developmental mechanics, and helps us to understand the alternative canalisation of various morphisms (see p. 28).

has other connotations, and is, I think luckily, not generally accepted. *Polymorphism* is not merely unnecessarily lengthy, but unduly general in sense. We speak of *forms*, not *multiforms*, of a species; and provided we define the term accurately, we can conveniently employ a brief and convenient word like *morph*.

I restrict the term *morphism* to genetic polymorphism, as defined by Ford (1945a), in which (usually sharply distinct) genetic variants or *morphs* coexist in temporary or permanent balance within a single interbreeding population in a single spatial region, and in such frequencies that the rarer cannot be due solely to mutation, or to the spread of selectively neutral mutants. It is important to have a term applicable in this restricted sense, since the evolutionary implications of other phenomena often loosely included under the head of polymorphism—geographical, seasonal, and all non-genetic cases, as well as mere high recombinational variance, whether with or without previous hybridisation, are very different.

In *Materials for the Study of Variation*, Bateson had already noted many cases of real or supposed genetic morphism in nature. These include the "high" and "low" forms of beetles like *Xylotrupes* and of earwigs like *Forficula* (in the latter case, he notes the geographical variation in morph-ratio; see p. 25): the colour-morphism of various common beetles, such as *Phratora* and *Telephorus* (which would well repay investigation by modern methods); of Lepidoptera such as the Clouded Yellow, *Colias* (see p. 12), the Crimson Underwing, *Catocala nupta*, and the Burnet Moth, *Zygaena* (foreshadowing the work of Bovey, 1941); of the egg-colour of various Copepods (curiously enough, he overlooks the mimetic egg-colour morphism of Cuckoos); of tibia-colour in grasshoppers, foreshadowing the work of Nabours (see below); of plants such as the Pimpernel, *Anagallis arvensis* (which I discuss on p. 15), the Daffodil, *Narcissus corbularia*, and other species (in flower-colour), and the Yew, *Taxus baccata*, and the Raspberry, *Rubus idaeus* (in fruit-colour): the pattern- and colour-morphism of molluscs like the Dog-whelk, *Purpura lapillus*, the Periwinkle, *Littorina rudis*, and some species of *Chiton* (but curiously not of *Cepaea*; see p. 9); of butterflies like *Hipparchia tithonus* and *Satyrus hyperanthus*; of beetles like the Ladybirds, *Coccinella bipunctata* and *decempunctata* (as against its absence in *C. septempunctata*; and see Dobzhansky, 1951, pp. 130, 152); of the butterflies *Pyrameis cardui* (in Australia) and *Terias*, and the cryptic Leaf-butterfly, *Kallima inachys*: of petal-number in various flowering plants (possibly not genetic); and the dextral-sinistral dimorphism of certain Gastropods.

He rightly compares the "discontinuity of sex" with discontinuous (morphic) variation in general. But he confuses the discontinuity of true genetic morphism with that of meristic variation, of gynandromorphism, of sporadic mutation, and of developmental abnormalities of various kinds.

I would here like to record my thanks to various colleagues. First and foremost to Dr E. B. Ford, F.R.S., and his co-worker Dr P. M. Sheppard for their invaluable

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In addition, I wish to pay tribute to those who, by their special contributions to the subject, have established the evolutionary importance of morphism. Bateson I have already mentioned: he was the precursor. R. A. Fisher must without doubt be acclaimed as the founder of the genetical theory of morphism, with his demonstration, twenty-six years ago, that morphism cannot exist in nature without a selective balance between the morphs concerned. E. B. Ford in his brilliant surveys has followed up Fisher's ideas and their applications, and J. B. S. Haldane has made valuable contributions to morphic theory.

Erwin Stresemann in his *Mutationsstudien* first showed the importance of morphism in the micro-evolution of birds, and Ernst Mayr has extended his work and related it to modern genetical theory. Various botanical geneticists have unravelled the complexities of the special type of morphism seen in the incompatibility mechanisms of plants. Cyril Darlington has done much to demonstrate the importance and widespread occurrence of chromosomal and chromosomegmental polymorphism, while Theodosius Dobzhansky, following up his penetrating study of inversion-morphism in *Drosophila*, has contributed notably to the general theory of morphism. But the subject has not always received due attention. Thus it is not specifically mentioned in Darlington's *Evolution of Genetic Systems*, in Srb and Owen's *General Genetics*, or Grüneberg (1947), though he cites several examples.

At the outset, I would like to stress the extremely widespread occurrence of morphism. Among animals, I have found reference to its occurrence in all classes of Vertebrates, and in the Urochorda, among Chordates; among Insects, in the Coleoptera, Diptera, Lepidoptera, Hymenoptera, Odonata, Dermaptera, Hemiptera, Orthoptera, and possibly Isoptera; among Arachnida, in Spiders; among Crustacea, in Copepoda, Isopoda, and Decapoda; among Echinoderms, in Asterozoa, Holothurozoa and Ophiurozoa; among Molluscs, in Gastropoda and Lamellibranchia; among Coelenterates, in Anthozoa and possibly in Leptomedusae; among Sponges, in Demospongiae; and I have doubtless missed other occurrences. Among plants, my references include cases among various Orders both of Dicotyledons and Monocotyledons, and several groups of Fungi; and I am sure botanists will know of many other cases of morphism in many other groups.

The characters involved in morphism are equally varied. They include colour, pattern, structure, sex-chromosomes, secondary sexual characters, caste in certain insects, essential oils in certain trees, reproductive incompatibility, clutch-size in birds, blood-groups, blood-diseases, chromosomal and chromosomegmental variation, migratory behaviour, heterokaryosis in fungi, sensory thresholds, general habit, temperature-tolerance, disease-resistance, cancer-proneness—indeed probably every conceivable character of every developmental stage.

2. ADAPTIVE MORPHISM

After a survey such as this, the question inevitably arises why morphism is so widespread. The answer, I think, is that it provides a method of intraspecific differentiation for adapting the species to sets of sharply distinct environmental conditions. We often speak as if the environment of a species were uniform, whereas in the great majority of cases it presents marked fluctuations in all its major components—temperature, humidity, availability of food, abundance of enemies, shelter, and many other factors—both in space, from habitat to habitat and from one geographical area to another, and also in time, from day to day, from season to season, and from year to year. A species must accordingly be adapted not only to the constant factors of its environment, or to its mean conditions, but to its variations.

Adaptation to environmental variation may involve better avoidance of or greater resistance to extreme conditions, or may consist in the exploitation of a wider range of habitats or niches. In highly mobile species avoidance of extreme conditions may be effected by migration ; but greater resistance to or fuller exploitation of contrasting conditions can only be effected by greater differentiation of the species. Much of this differentiation may be non-genetic. It may be purely modificational, as in the case of plants with high plasticity ; or it may be physiological and reversible, as in the adaptive colour-changes of chameleons or flounders ; or it may be developmental (ontogenetic), as in the adaptation of larvae and adult to different conditions, or the exploitation of different environmental conditions for feeding and reproduction, as in salmon or eels ; or it may be cyclical, as in the alternation of generations in ferns, or cyclomorphosis in Cladocera, or seasonal polymorphism in butterflies, or the phases of locusts (see p. 52).

But, finally, it may be genetic. In this case, two or more distinct genetically-determined forms co-exist in balance in the population, each adapted to, and therefore enjoying differential survival in, one distinct set of conditions confronting the species, or one habitat of the many available. The result is balanced genetic polymorphism—morphism.

Morphic differentiation is able to originate so frequently (i) because so many mutants are ambivalent—*i.e.* have both selectively favourable and unfavourable effects (see p. 25) ; (ii) because inversion and translocation provide the gene-complex with sets of distinct “supergenes” incapable of crossing-over and therefore capable of independent evolution in different adaptive directions ; (iii) because variations in chromosome-number and -type may persist within a population, as with supernumeraries in plants, and as in chromosomal sex-determination ; (iv) because some genetically-determined differences produce sharp meristic discontinuity (*e.g.* in egg-number in birds) ; (v) because in certain circumstances extremely high variability is an asset. In any case, the sharply distinct environmental conditions with which most organisms are confronted may be better met by the

sets of sharply distinct characters provided by morphism than by unimodal adaptation to the mean conditions. Morphism thus frequently serves as an adaptation to the extremes of environmental variation.

At the outset, we must make a distinction between *phaneromorphism*, in which the morphs are *manifest* or readily distinguishable by inspection, and *cryptomorphism*, in which they are not; and also between the phenotypic *phenomorphs* and the *genomorphs* which are their genetic basis. From the genetic or genomorphic point of view, we may distinguish *genic* morphism, in which the differences between morphs depend on one or a few single genes; *continuous* morphism (p. 20), where so many genes are involved that the sharp distinctness of the morphs is submerged in excessive continuous variability, *chromosomal* morphism, in which the differences between morphs depend on sections of chromosomes; and *meristic* morphism, in which they depend on genetic thresholds determining a series of large meristic characters.

I will begin with the most interesting type of morphic adaptation, adaptive genic phaneromorphism. An obvious example is the mimetic morphism of butterflies (Ford, 1953; Carpenter, 1925; Eltringham, 1910; Beebe, 1955; Goldschmidt (1945), whose anti-selectionist review of the subject, however, is very one-sided). It is an advantage for a Batesian mimic to have more than one model, for this spreads the risk and increases the potential total population; but clearly an appearance intermediate between two sharply distinct models would be of no selective value. Some such species have two, others three or more mimetic morphs. The selective value of the resemblance is shown by the way in which the geographical variation of the models is followed by that of the mimetic morphs, and conversely by the breakdown of the resemblance in areas where the model is absent or rarer than the mimic.

In some species non-mimetic as well as mimetic morphs are found. This indicates a general tendency to morphism. Any resemblance of some of the original morphs to a nauseous species would then be improved by natural selection.

A further point of interest is that in the great majority of cases, mimetic morphism is confined to the female sex, the males being non-mimetic. Ford suggests that this is due to sex-recognition being dependent on the visual recognition of males by females.

Genetically, the appearance of the mimetic morphs depends on a large number of genes, all controlled by a single switch-gene which is in selective balance with the other main morphic gene or genes. If a morphism is of adaptive value to the species, it is important that the morphic genes concerned shall be preserved in balanced co-existence within the population, and that none shall be lost to the species by differential adverse selection in extreme conditions. In mimetic morphism, this balance could theoretically be maintained by variations in external selection-pressure, for the selective advantage enjoyed by a mimetic morph decreases as its abundance increases,

and vice versa (Ford, op. cit.). However, in practice, the balance appears to be also secured genetically, the homozygous dominants being at a marked selective disadvantage, and the heterozygotes enjoying a selective advantage.

This heterotic type of genetic stabilising mechanism, in which the co-existence of morphic partners is maintained by means of some intrinsic selective advantage enjoyed by the heterozygote, is found in most morphisms, but in various forms. In genic morphism, the balance is usually preserved by a mechanism which I shall call *double-dose disadvantage*. This is preferable to *over-dominance* (Crow, 1952; Hull, 1952), as it is unrelated to dominance in the accepted sense. Alternatively the term *dosage heterosis* might serve. One of each morphic pair then depends on a dominant mutant, which in single dose confers a selective advantage over the recessive (normal) type, but when in double dose is either lethal, sublethal, or, to use a term to denote slightly subnormal general fitness or viability, subviable. In such cases, the favouring of the heterozygote does not depend on an advantage due to increase of "vigour" or fitness arising from the fact of its heterozygosity, but from the advantage of the mutant over the normal when in single dose, combined with its disadvantageous subviability when in double dose; (see also p. 50).

When genic polymorphism occurs, all the morphic genes except one usually show double-dose disadvantage, so that we have a so-called "universal recessive" together with a number of dominant morphs.

Since it is advantageous to make the balance mechanism as strong as possible, any other mutant in loci close to the primary morphic gene and possessing both double-dose disadvantage and either single-dose advantage or neutrality will tend to be preserved. Further, as R. A. Fisher pointed out many years ago (1930), selection will automatically operate to produce closer linkage between all mutants concerned with a given morphism, which happen to arise in the same chromosome. And finally, as Ford has stressed, genes with strong double-dose disadvantage will provide genetic shelter to any recessive lethal mutations which happen to arise close to them, and the recessive lethals will then increase the double-dose disadvantage of the system. Thus in all these ways, a morphic balance-mechanism which originally consisted of a single gene-pair with double-dose disadvantage will tend to be converted into a system of closely linked genes whose total double-dose disadvantage is much stronger, and its stability or resistance to disruption therefore much increased.

In all cases of mimetic morphism in butterflies so far investigated, double-dose disadvantage is operative. However, much more work is needed before the genetic situation is fully clarified.

A somewhat similar example is that of the egg-mimicry of the Cuckoo, *Cuculus canorus* (Southern, 1954). Here the mimetic resemblance reduces the risk of the host-parents ejecting the brood-parasite's egg, while the polymorphism provides a greater range of hosts and so permits a larger total population to exist. However,

the Cuckoo's morphic egg-mimicry differs from the adult morphic mimicry of butterflies in various ways :—(1) intermediate types are more frequent ; (2) in some areas such intermediate egg-types are much rarer, and the mimetic resemblances to host eggs are much closer ; (3) whereas in the butterflies segregation within one brood is no disadvantage, in the Cuckoo it is essential that each female should produce only one egg-type.

Southern considers that the variance here is intermediate between geographical differentiation and true balanced morphism, leading to the production of partially isolated strains or *gentes*. Where large areas of distinctive habitat exist (*e.g.* forests, reed-beds, open plains) the local *gentes* can develop a high degree of egg-mimicry for one or a few host species ; but where human interference (or other agency) has broken down the habitat areas into smaller blocks and intermingled them, as in Western Europe, the gene-systems underlying the different mimetic egg-patterns are also largely broken down through intercrossing. This implies that major switch-genes are not operative. It is not known whether double-dose disadvantage occurs.

Like various mimetic butterflies, the Cuckoo shows a general tendency to morphism (Voipio, 1953), for it shows a plumage dimorphism, barred red and unbarred grey. Among adults, the red morph is confined to a minority, all females ; among juveniles, it occurs in both sexes, but in a majority of females and a minority of males. Voipio suggests that there is a morphic rate-gene concerned with the deposition of (grey) eumelanin, which has a lower operative threshold in males, so that all adult and most juvenile males are grey. Furthermore, the distinction between the adult morphs is sharp, whereas in juveniles, presumably owing to their being in different stages of eumelanin production, there are numerous intermediates. Voipio further considers that the plumage-morphism is mimetic, the dorsal view of the unbarred grey morph resembling the Sparrowhawk, that of the barred red morph the Kestrel and Merlin. The advantage accruing to the red female morph from these resemblances lies, he suggests, in the grey male being chased away by fosterers because of its resemblance to a Sparrowhawk, leaving the coast clear for the female. In support of this he adduces some figures indicating that the frequency of the red adult morph is higher in wooded habitats, where Sparrowhawks are common. The red adult female morph also occurs in *C. saturatus* and *C. poliocephalus* from the S. Palearctic, but more commonly than in *C. canorus* ; these also are predominantly parasites of woodland host species. Many other cuckoos show egg-mimicry (Baker, 1942). Dr A. H. Sturtevant informs me that some species of *Volucella* are morphic, like some of its bee hosts. This may prove to be a mimetic morphism.

Morphic egg-mimicry could presumably only arise in species whose egg-colouration is already polymorphic or highly variable. It is worth recalling that some birds, such as the Guillemot, *Uria aalge*, the Red-backed Shrike, *Lanius collurio*, and the Tree-Pipit, *Anthus*

trivialis, show such non-mimetic egg-morphism to a much greater extent than related species. A comparative study of morphic egg-variation in birds would be of considerable interest.

The primary morphism in such cases depends on a balance of viability (intrinsic general fitness) factors. A similar secondary extrinsic adaptive utilisation of such a primary viability-morphism is to be seen in the snails of the genus *Cepaea*. Here the manifest colour and banding morphs appear to have originally been "correlated characters" in Darwin's sense—non-adaptive phenotypic effects of the morphic viability genes; but Cain and Sheppard (1950) and Goodhart (1954) have shown that they now collectively confer cryptic protection from predators, notably song-thrushes but also rabbits, over a wider range of habitats than would be possible without morphism. Thus unbanded browns are at a selective advantage in beechwoods, banded non-browns in hedgerows.

The similar morphism of the Garden Snail, *Helix hortensis*, is largely masked by uniform dark brown pigment, but Sheppard (*in litt.*) tells me that even so there is evidence of the adaptive (cryptic) value of morphism in general tint or shade in relation to variations of tint or shade of soil-colour.

Reproductive morphism may be highly adaptive. Thus the Swift, *Apus apus* (Lack, 1947-48, 1954), is dimorphic as regards clutch-size, females laying either two or three eggs. In favourable seasons the three-egg females produce a higher absolute number of fledged young than the two-egg females, but in cold and wet seasons a lower absolute number, since the smaller amount of insect food is less adequate for three than for two nestlings. The balanced coexistence of three-egg and two-egg reproductive morphs is thus an adaptation, acting as an insurance against the regular occurrence of bad seasons.

At Oxford, the two-egg morph is rather commoner, but the proportion of the two morphs varies geographically, the three-egg morph becoming somewhat more abundant in higher latitudes, where longer day-length ensures a greater total time for catching food. Such a graded geographical alteration in proportion of morphs constitutes a *ratio-cline*, and characterises many morphic systems.

Similar but usually more striking ratio-clines in egg-number morphs (which are most easily detected as a graded geographical change in mean clutch-size) occur in a great many birds (Lack, 1947-48). In any given locality, as would be expected, there are distinct egg-number morphs (Lack, 1953, Kluiver, 1951). This type of adaptive reproductive morphism thus appears to be widespread.*

While in such cases there obviously must be a genetic basis for the tendency to lay more or fewer eggs, the *discontinuity* between the

* Some species are "determinate" layers, like the Herring Gull, *Larus argentatus*, normally monomorphic for a clutch of three (Tinbergen, 1953), and thus have foregone the adaptive insurance provided by egg-number morphism. Other species, again, like the Short-eared Owl, *Asio flammeus*, have a physiological instead of a genetic mechanism for adjusting egg-number, and can markedly increase or decrease clutch-size in immediate reaction to available food-supply.

morphs is not genetic but meristic, depending on the fact that a bird's clutch of eggs consist of a few large discontinuous units. If the range of egg-number in Swifts were from 200 to 300 instead of from two to three, a sharply bimodal morphism in clutch-size could not arise, except with the aid of some special genetic switch-mechanism. It is interesting to speculate at what absolute number this failure of meristic discontinuity to provide a basis for effective morphic discontinuity would set in: I would hazard a clutch-size of between ten and twenty.

A precisely analogous reproductive insurance is provided by the morphism of "hard" and "soft" seeds in various plants, "soft" seeds germinating immediately, "hard" seeds only after considerable delay (see Crocker and Barton, 1952). The phenomenon is well-known, but has not been scientifically investigated save in a few cases. *E.g.* in the Rockrose, *Helianthemum guttatum*, Juby and Pheasant (1933) find that a single plant may produce some seeds germinating after a few days, others only after much longer periods, which would delay growth until the following spring, and thus be of advantage in severe winters. The difference in germination is determined by variation in the permeability of the seed-coat. The "hard" seeds show a multimodal frequency for their germination-time, indicating that several genes are operative; while failure to obtain strains pure for any particular germination-delay implies the existence of a genetic balance-mechanism underlying the morphism.

In *Nicandra*, germination-time morphism depends on the number of isochromosomes present (Darlington and Janaki-Ammal, 1945). A minority of plants have one instead of the more normal two isochromosomes. One-isochromosome seeds show delayed germination. Darlington has suggested to me that the variation of many plants in supernumerary or B-chromosome number, provides a balanced switch-mechanism for morphic adaptation in germination-date, drought-resistance, etc. The grasshopper, *Melanoplus differentialis*, shows egg-dimorphism, one morph developing directly, the other with an obligatory diapause (Bodine; Bodine and Boell; H. C. Burdick). Further investigation would be profitable.

A similar insurance mechanism is provided by the morphism in migratory behaviour of many birds (Lack, 1943). Single populations (and even single broods (Nice, 1937, 1943, *Trans. Linn. Soc. N.Y.*, 4, 6)) contain individuals which remain resident throughout the winter, and others which develop the migratory urge. Further, there are well-marked ratio-clines, the percentage of non-migrators often falling to zero in the north, and rising to 100 per cent. in the southern parts of the birds' range.

In most areas there is a simple dimorphism between migrators and non-migrators. In Britain, however, a trimorphism has been evolved since the end of the last glacial period, there being two quite distinct migrator morphs, the presumably original southward migrators and those which migrate westward to the mild climate of western

Ireland. Migratory morphism is also known in song-sparrows and other North American birds, and presumably occurs in all migratory Passerines and Limicolines.

My examples so far have all been phaneromorphic: however, cryptomorphism also can be highly adaptive. Cryptomorphism was discovered by Dobzhansky in *Drosophila* (see his admirable summary, 1951, Ch. V and VI). Interestingly, this large genus shows only one or two phaneromorphisms (e.g. the abdomen pattern of *D. polymorpha*; de Cunha, 1949, 1953). However, many, perhaps most, species are morphic for chromosomegmental inversions, which are detectable by inspection of salivary gland preparations. Inversion prevents crossing-over between the chromosomegments concerned, so that the inverted and "normal" chromosomegments can behave as supergenes in Darlington's sense. Cordeiro and Dobzhansky (1954, *Amer. Nat.*, 88, 75) find that all "wild" chromosomes differ in selective value, both when homozygous and in various heterozygous combinations.

In all cases investigated, the two chromosomegmental morphs of each such inversion-morphism have evolved divergently so as to adapt their possessors to two sharply alternative conditions—summer and winter, low and high altitudes, urban and rural habitats, favourable and unfavourable years, etc. Thus *D. pseudoobscura* in California contains third chromosomes with morphic chromosomegments, called *Standard* and *Chiricahua*. In the high temperatures of summer the frequency of Standard decreases, while that of Chiricahua increases, and conversely in the lower temperatures of spring and autumn. If the population were pure for Standard, it might be unable to survive exceptionally hot summers, and vice versa. In order to prevent the elimination of one or other temperature-adapted chromosomegment in exceptional seasons, the two alternative chromosome-morphs are automatically tied together in a balanced morphic system: the heterozygous combinations enjoy a marked selective advantage, and this prevents the elimination of either member. This *euheterosis*, to use Dobzhansky's useful term, is not a necessary consequence of the heterozygosity of inversions, for it is not found when inversions from distant areas are brought together and combined artificially. It must therefore have been evolved co-adaptively as a stability mechanism for securing the permanence of the morphic system. Inversion morphisms have been detected microscopically in various other Diptera (White, 1954).

Inversion (chromosomegmental) morphism thus differs from genic morphism in several interesting ways. First, the permanence of the balance-mechanism is provided for by a specially evolved euheterotic co-adaptive system of genes in the two chromosomegmental partners, conferring on the heterozygotes a marked positive selective advantage in respect of viability or other aspect of intrinsic general fitness; whereas in genic morphism the same result is obtained, but by the different method of double-dose disadvantage. Secondly, whereas

euheterotic advantage has to be evolved, some degree of double-dose disadvantage appears to be present from the start in genic morphisms, though it may be strengthened later (see above). Further, whereas in most genic morphisms one allele of a morphic pair is a simple dominant and there are thus only two distinct phenomorphs, in inversion morphism neither supergene is dominant and there are three phenomorphs—the two homozygotes, each adapted to one of two contrasting environmental conditions, and the heterozygote adaptively equipped with an advantage in general fitness (p. 27).

The efficiency of such a system in securing an equilibrium between the morphs concerned has been experimentally demonstrated by Dobzhansky. When different proportions of two inversion-morphs are used to set up a number of breeding populations, their frequencies will change, tending after about ten months to a certain constant ratio. The precise final ratio will vary with varying conditions of temperature, food, etc., but in any one set of conditions the final ratio is the same, whatever the ratio at the beginning of the experiment.

As would be expected from these facts, both altitudinal and geographical ratio-clines for inversion-morphs occur in nature. The geographical ratio-clines present a rather complicated picture. It is significant that in different *Drosophila* species, wide range and biological success are correlated with abundance of inversion-morphisms.

White (1954) cites numerous cases of morphism in chromosome-number, but their underlying stability-mechanisms are mostly uninvestigated and their selective implications unknown.

The morphism exhibited by the Clouded Yellow butterflies, *Colias*, is of exceptional interest since it has been studied in all its aspects—taxonomic, genetic, ecological, and evolutionary (Hovanitz, 1953; Komai and A , 1953; and see Ford, 1945). Most species of the genus are monomorphic yellow in the male sex, but dimorphic yellow and white in the female. The monomorphism of the males is presumably due to the need for a uniform sign-stimulus for sex-recognition, as in polymorphic mimicry (see above). The white morph is determined by a single dominant allele, with sex-limited manifest effect. This is closely linked with a "recessive lethal"—i.e. a gene with extreme double-dose disadvantage, so that crosses give a 2 : 1 instead of a 3 : 1 ratio in F₂. This gene presumably enjoys some single-dose advantage, as it is present in all wild populations in the same frequency as the white allele. It is to be expected that the white allele itself has some double-dose disadvantage, but this has not yet been proved. However, since monomorphic white populations occur near the northern limit of the range of some species, its linkage with the lethal can be broken naturally as well as experimentally, and any double-dose disadvantage of white must be small enough to be capable of being buffered by compensatory modifiers.*

* In the Japanese subspecies of *C. hyale*, Komai and A  (1953) find only a probable small subviability of homozygous whites, indicating that the adjacent recessive lethal is not present; but a considerable deficiency of homozygous yellows occurs.

The two morphs differ in their behaviour with regard to temperature, the whites being more active at lower temperatures, so that in California they fly (and oviposit) mainly in the mornings and evenings, the yellows mainly in the midday hours. This behaviour-difference is reflected in corresponding ratio-clines, both altitudinal and geographical. Geographically, white frequency increases with north latitude, or rather with decrease of temperature, but the precise form of the cline differs in different species of the genus, showing that the basic behaviour-difference has been quantitatively modified in the course of speciation.

The adaptive value of the morphism clearly consists in increasing the range of environmental conditions and habitats which can be profitably occupied, both by any given population and by the species as a whole. However, this fact would probably never have been discovered if the biologically important character of differential temperature-reaction had not been associated with the manifestly visible but biologically unimportant "correlated character" of colour-morphism. The classical case of female dimorphism in the Silver-washed Fritillary, *Argynnis paphia*, is similar in genetic basis and possibly in behavioural result, but differs in being geographically localised (Ford, 1945*b*).

The existence of all-white populations in the northern parts of the range of various species shows that a primary dimorphism shared by many or all species of a genus may give rise to *secondarily monomorphic* populations. If these then become isolated from the rest of the species, they could readily differentiate to the subspecific or specific level. Such secondarily monomorphic groups would then constitute a hitherto little-recognised category of taxonomic units, produced by a peculiar mode of evolution.

We have already met with secondary monomorphism in migratory birds. It occurs also in many other groups: a classical example is the Australian Goshawk, *Accipiter novae-hollandiae* (Southern and Serventy, 1947; Stresemann, 1926). This species is dimorphic, with white and dark morphs in very variable frequency. Near the southern boundary of Queensland about 80 per cent. darks occur; from here an irregular double ratio-cline extends along the coast, northwards to New Guinea (where the picture is complicated by the presence of a different dark allele, producing rufous or brown instead of grey plumage, and by a separate dimorphism in juvenile plumage: Mayr, 1940), and round to the north coast of Western Australia, and southwards to Tasmania. In New Guinea, whites are moderately frequent, but totally absent on some islands, presumably due to their colonisation by dark birds only. In Tasmania the entire population is secondarily monomorphic white, possibly because whites are favoured by humidity.

In this case the secondarily monomorphic white population has not undergone further taxonomic differentiation as a result of its isolation on an island. But in the dimorphic Great Blue Heron of

America, *Ardea herodias*, the white morph shows an increasing ratio-cline eastward from Yucatan to culminate in 100 per cent. white on the Florida Keys. This all-white population has usually been separated as a distinct species, *A. occidentalis*, but is almost certainly a subspecific specialisation of a secondarily monomorphic population of *A. herodias* (E. Mayr, 1955).

Mayr (1942, p. 78 ff.) cites other examples. However, only that of the Lory, *Charmosyna papou*, in which three of four subspecies are dimorphic for melanism but one is monomorphic and lacks the melanic morph, would seem to illustrate this process. None of the others are morphic in any single population; they merely show subspecific divergence in respect of sharply distinct characters. In the Bulbul, *Microcelis leucocephalus*, this is further demonstrated by the existence of hybrid zones, containing "a medley of hybrid forms" (recombinations), where pairs of the very distinctively plumaged subspecies have come secondarily into contact. Such facts are a salutary warning not to confuse the recombinational polymorphism due to secondary hybridisation with true balanced morphism. Another case where polymorphism is probably due to hybridisation is the African Barbet, *Lybius torquatus* (Mayr, 1940, p. 77).

Secondary monomorphism is found also in some Pacific land-snails, such as *Partula otaheitana* in Tahiti (Crampton, 1932). This species is dimorphic as regards direction of coiling, but monomorphic dextral and monomorphic sinistral microraces occur. Such secondary monomorphism, which is also found in respect of colour and pattern in forms like *P. clara*, *suturalis* and *mirabilis*, which are expanding their range in a region with many small habitat-areas, is to be expected as the result of random sampling during the colonisation of new areas. For similar phenomena in other oceanic land-snails see Huxley, 1932, pp. 232-4; and in flatfish, etc., p. 50 of this paper.

A peculiar picture is presented by the eastern palearctic lady-beetle, *Harmonia axyridis* (see Dobzhansky, 1951, p. 142). In the eastern parts of its range this species is highly morphic in colour and pattern, with the yellow morph increasing in frequency eastward. In its western area, however, it is virtually monomorphic for one particular colour-pattern; most other morphs were wholly absent, but two occurred in a total of over 4000 individuals examined, and must therefore be regarded as not in morphic balance, but as rare mutants.

The common squirrel of Europe, *Sciurus vulgaris*, is dimorphic red and black. The British form, however, is monomorphic red, and has undergone subspecific differentiation (Matthews, 1952). The American Grey Squirrel, *S. carolinensis*, has a melanic morph, which in some areas once exceeded 50 per cent.; but the ratio-cline needs fuller analysis (Shorten, 1954). The dimorphic Arctic Fox, *Alopex lagopus*, is monomorphic white in Kamchatka and blue on some Alaskan islands (see Huxley, 1942, p. 103). I found Voipio's important paper (1950) too late to include his valuable facts on Squirrels, Foxes,

Hares, and Musk-rats: the spread of the apparently deleterious *Samson* mutant of the Red Fox to become an established morph in areas of dense human population is especially interesting.

In plants, the common Scarlet Pimpernel, *Anagallis arvensis*, has flowers "usually red or pink, more rarely blue or lilac" (Clapham, Tutin and Warburg, 1952, p. 809), a tetramorphism presumably due to two morphic gene-pairs. However, the form *A. a. foemina*, classed as a distinct subspecies and distinguished by minor differences in length of pedicel and calyx-teeth, and shape and hairiness of corolla-lobes, is monomorphic blue-flowered. In Britain it is rare and confined to the south and west, so that it has probably differentiated as an ecogeographical subspecies.

The rapidity with which selective balance may be altered and one morphic allele may replace its partner in certain conditions is beautifully illustrated by the facts of industrial melanism in moths (Ford, 1945, 1955). In the past 100 years, in the industrial areas of Britain and NW. Europe, forty-eight species of moth have become full melanics and some 250 others have become markedly darker. In *Biston betularia*, Haldane (1923) calculated that the coefficient of selective disadvantage of non-melanics in industrial surroundings is at least 0.33, which implies an astonishingly high intensity of selection.

Ford has shown that all industrial melanism is due to the spread of dominant genes, which occur regularly as rare mutants in normal (non-industrial) habitats: no recessive melanic mutants have spread. The selective balance is between the cryptic value of normal colouration, which is very high in rural areas but lower in the darker environment and the lower predator-frequency of industrial areas; and the greater hardiness of dominant melanics and their high resistance to unfavourable conditions such as soot- and smoke-contaminated food.

In most species, the dimorphism in any one area is transient; in the course of a few decades the population is converted from an overwhelmingly non-melanic to an overwhelmingly melanic one. The species as a whole thus comes to show what can be called geographical morphism; but this is only a special case of geographical differentiation, differing from the usual process seen in wild species merely in its greater rapidity and in the fact that only one gene with major effect is involved, instead of many genes with small or moderate effects. However, there are indications of double-dose disadvantage in some melanics, with the consequent establishment of a true balanced morphism in certain areas (Kettlewell, *in litt.*).

I may here mention other cases of morphic melanism, though the adaptive value of the black morph is not always known.

Thus the melanic morph of the fur-bearing mammal the Hamster, *Cricetus cricetus*, has increased in frequency and extended in range during the past 150 years in SW. Russia, until now in four sub-steppe (woodland steppe) areas about 25 per cent. of pelts are

black. These "black spots" are surrounded by areas of decreasing melanic frequency, until in the true steppes melanics occur only as rare mutants (Gershenson, 1945; and see Huxley, 1942, p. 103, and map in Dobzhansky, 1951, p. 143). The melanic morph appears to be favoured by moist conditions, and its spread must have been facilitated by alterations produced by human interference.

The Brush Opossum, *Trichosurus vulpecula*, is monomorphic grey in mainland Australia, but in Tasmania is dimorphic, with melanics up to 100 per cent. in some areas (Guiler, 1953; and see Huxley, 1939). Guiler finds that high melanic frequency is favoured by a combination of high rainfall and dense forest cover; where man has abolished the forest cover, a sharp fall in melanic frequency occurs. The populations of the small islands between Tasmania and the mainland show no morphism (see p. 51, and Pearson, 1938).

Melanic morphism also occurs in the Rabbit, *Oryctolagus cuniculus*, in Tasmania, but also, unlike the Brush Opossum, in wet areas of the Australian mainland (Barber, 1954). The melanics here appear to be at a cryptic disadvantage against predators when in open country, which is not the case with the black Brush Opossums. (In Tasmania, the melanic morph in the Brush Opossum appears to have reached equilibrium, but in the Rabbit appears to be still spreading. The maximum frequency of melanics is about 35 per cent., reached in the high forested plateau of the interior. As the rabbit was only introduced within the last 150 years, the spread of its melanism has been nearly as explosive as that of moths in industrial areas: Barber considers that it has taken place within the last fifty years.

It should be mentioned that on small islands off the British coast, melanic (and other mutant) rabbits are more abundant than on the mainland, though never constituting a balanced morphism. Thus R. M. Lockley (*in litt.*) found 0.5 per cent. melanic, 0.25 per cent. particoloured and 0.5 per cent. long-haired specimens among 8148 rabbits trapped on Skokholm (Pemb.)

There is a rough ratio-cline in the Common Squirrel, *Sciurus vulgaris*, in Eurasia, the frequency of melanics increasing from zero in the north to 100 per cent. in the south (Matthews, 1952, p. 201, Shorten, 1954). For other mammalian cases, see p. 51.

Similar melanic morphisms also occur in birds: e.g. the West Indian Sugarbird, *Coereba flaveola*, the New Zealand Pied Fantail, *Rhipidura flabellifera*, and the New Guinea Lory, *Charmosyna papou* (Mayr, 1942; Huxley, 1955), but here, as in Squirrels, the precise climatic conditions favouring melanics have not yet been fully analysed.

Some remarkable cases of adaptive morphism occurs in West Australian frogs (Main, 1954). *Crinia georgiana* is highly polymorphic both as tadpole and as adult, and in respect both of colour (mottled, fawn, grey and red-brown) and of skin-texture (smooth, warty, ridged, "lyrate"). All ridge-skinned forms so far collected are fawn and no lyrates are red-brown, but smooth and warty may be of any colour.

The colour-morphism seems to serve as cryptic adaptation in different backgrounds, and smooth-skinned adults are less resistant to drought, and have a lower frequency in dry habitats. The smooth-skinned forms metamorphose earlier than the three "rough" forms, indicating that thyroid activity is involved. In *Crinia signifera* adults are trimorphic for skin-character—rough, smooth, and with longitudinal ridges. All three morphs occur in areas where there are swamps but only the rough-skinned form in hot dry habitats. In genetic experiments marked deficiencies from expectation occur in certain classes. Some populations appear to consist wholly of heterozygotes. *C. glauerti* appears to have a similar morphism. *C. leai* is monomorphic smooth, but shows adult colour-morphism, while *C. rosea* is wholly monomorphic.

In *Helioporus pelobatoides* the tadpoles are dimorphic, fast-developing "normals" capable of colour-change, and slow-developing "pales" which remain pale in all conditions of background or illumination, though pituitary injection will artificially darken them. The pales thus appear to be suffering from a pituitary disadvantage which affects both their capacity for colour-change and their rate of development. The counteracting advantage enjoyed by the pale morph may possibly be a skin-character rendering adults more resistant to desiccation. J. A. Moore (1943), Goin (1947, 1950) and Moriwaki (1953) also report morphisms in various Anura.

What appears to be an analogous case of morphism related to climatic resistance is found in the large Australian land-snail, *Bothriembryon bulla* (Main and Carrigy, 1953). Near Perth, W. Australia, this has a melanic morph which differs from the normal not only in its black body-colour but in the darker ground-colour of its striped shell. In one type of habitat, where the shrub, *Jacksonia gracilis*, resists fire and provides good cover for snails even after burning, the melanic morph is present but rare (5-10 per cent.); but in another where the ground is black and bare and there are no "refuges" provided by *Jacksonia*, the population is 100 per cent. melanic. Main ascribes the advantage of the melanic in this habitat to cryptic protection from the snail-eating Western Magpie, *Gymnorhina dorsalis*.

The British pyralid moth, *Acentropus niveus*, is unique in having two female morphs, one normal and resembling the male, the other aquatic and flightless, which protrudes its posterior end through the surface-film to permit copulation (Beirre, 1952, p. 72; Meisenheimer, 1921, fig. 678). The selective advantage of the aquatic female morph apparently consists in its ability to oviposit at depths far beyond the reach of the flying morph, thus extending the ecological range of the larvæ, which feed on submerged plants. Several species of water-beetle are dimorphic for flight and flightlessness (Jackson, 1952, 1955). This demands thorough investigation. (See also p. 51.)

The Plumose Sea-Anemone, *Metridium senile*, shows a high degree of morphism, apparently based on three allelic or closely linked dominants and a universal recessive, determining different biochemical

properties of the pigments involved in its colouration (Fox and Pantin, 1941; North and Pantin, unpubl.). The different phenomorphs have different light-sensitivities, and are adapted to different conditions of illumination. Dr Pantin informs me that the New Zealand species of *Metridium* appears to be monomorphic white, and lives in low light-intensities. A comparative study of morphism in the genus should be rewarding. A similar adaptation appears to exist in *Tealia*, but here there is also a cryptic polymorphism, differently coloured morphs resembling different backgrounds. In *Sagartia* some of the numerous morphs appear to be procryptic, others anticryptic, and still others aposematic—a remarkable spread of adaptations secured by one morphic system (Walton, 1911; Fleure and Walton, 1907; and see Stephenson, 1928-35, for these and other examples).

The orchid, *Epipactis helleborine*, is trimorphic in flower-colour, the pale violet-veined form being apparently a heterozygote between the purple and the white green-veined morphs. Weijer (1952) maintains that whites are selectively favoured in more exposed habitats. Further analysis of this species would be valuable.

In the Poecilid fish, *Lebistes reticulatus*, there is an extremely high sex-limited polymorphism, the adult males having a great variety of striking patterns while the females and immature males are monomorphic dull-coloured (Haskins and Haskins, 1950, 1951). The selective advantage of the colour-patterns is unknown. They appear not to confer epigamic advantage, since in display they are masked by a special temporary display-pattern (Baerends, 1955). They are disadvantageous in exposing their possessors to predator attack. C. P. Haskins (*in litt.*) tells me that where the dangerous predator fish *Crenicichla* occurs, the *Lebistes* population includes fewer striking colour-morphs. The different colour-morphs appear to enjoy little differential selective advantage *inter se*, artificial introductions of non-indigenous morphs into a wild population remaining at a constant ratio through several seasons. All colour-morphs depend on more or less completely dominant genes, and there is no "universal recessive" among the males (though from the evolutionary standpoint the female colouration could perhaps be regarded as such).

It is good to know that this striking morphism is being carefully studied in all its aspects, as are the somewhat similar cases of *Platypoecilus* and *Xiphophorus* (Gordon, 1948; Gordon and Gordon, 1950, 1954).

In *Platypoecilus* the remarkable fact has emerged that the dominant morphic genes concerned with macromelanophore patterns produces melanotic tumours in F₁ or F₂ from crosses with the related fish *Xiphophorus helleri*. The genes concerned with micromelanophore distribution have no such effect. It may perhaps be suggested that in *Platypoecilus* all macromelanophore morphic genes have deleterious tumour-producing tendencies as well as selective advantages and that their disadvantageous effects have been buffered by modifiers, but that the buffering system is broken down by crossing. (See p. 51.)

The bee *Melipona* is unique among Hymenoptera in apparently

possessing a genetic caste-morphism, workers and queens being produced in a ratio of 3 : 1 in *M. marginata* (Kerr, 1950). Kerr explains the facts on the basis of two gene-pairs, the queens being always heterozygous for both, the workers always homozygous. In other species the ratio is 7 : 1, which Kerr ascribes to the involvement of three instead of two gene-pairs in the determination. Kerr states that the worker : queen ratios are constant, but his figures show a frequent deficiency of queens below the expected 25 per cent. in *M. marginata*. This interesting case should be further investigated. A genetic caste-morphism of this sort is clearly adaptive, but is not so flexible as the modificational determination through differential feeding found in *Apis*.

Some authorities believe that castes are genetically determined in termites, but this has not yet been proved.

Some fungi, such as *Penicillium*, possess a unique type of morphism based on heterokaryosis, or the co-existence of two genetically different types of nuclei in a single hypha, brought about by hyphal fusion and producing positive heterosis (Jinks, 1952 ; Pontecorvo, 1946). The frequency of the two nuclear types changes markedly with conditions, thus providing a flexible adjustment to environmental change. The primary sexual dimorphism (sex-ratio) of the eelworm, *Heterodera rostochiensis*, can also be adaptively adjusted to conditions (Ellenby, 1954), though the mechanism of adjustment is not known.

Adaptive morphisms involving reproductive incompatibility are widespread, the most important being sexual dimorphism in respect of sex-chromosomes. The sex-chromosomes also provide a switch-mechanism which directly or indirectly controls the appearance of all sex-limited and secondary sexual characters, and thus permits further adaptive differentiation of the two morphs.

Other incompatibility morphisms have the adaptive function of promoting outcrossing between different strains, and so increasing the species' reserve of variance. They include the visible barriers of heterostyly as in *Primula* and *Lythrum*, and the invisible ones of pollen-style incompatibility as in *Nicotiana*, *Trifolium*, cherries, etc. In the latter type, the morphic system may be very complex, involving up to forty alleles (or pseudo-alleles held together by very close linkage).

In the heterostyly of *Primula*, the genetic mechanism is of an unusual type. Instead of the usual method involving a basic switch-mechanism and a dependent canalisation-mechanism consisting of a co-adapted collection of genes in other parts of the gene-complex, there is a multiple system, consisting of a group of closely-linked genes, each controlling one of the different developmental processes involved in heterostyly, such as stamen-height and stigma-length, and together constituting the genetic switch (Ernst, 1936 ; Mather, 1950 ; and p. 52).

As showing the delicacy of the selective balance involved, I should mention the fact discovered by Crosby (1949), that in certain areas a homostyle mutant of the Primrose, *Primula vulgaris*, may spread, so establishing a transient dimorphism of homostyle and heterostyle

forms, and leading eventually to a local geographical dimorphism. The homostyles enjoy the selective advantage of being self-compatible and capable of self-fertilisation, but suffer a considerable selective disadvantage in respect of viability.

Uphof (1938) has given a review of the occurrence of cleistogamy in flowering plants. Cleistogamy is often a matter of ontogenetic differentiation, but in some cases it would appear to be morphic, genetically-determined cleistogamous and normal plants co-existing in single populations. The selective balance is then between the long-term advantages of cross-pollination and the immediate advantages of self-pollination. However, Uphof's analysis is not very clear, and the problem demands intensive investigation.

I have given enough examples of adaptive morphism to demonstrate its widespread occurrence. It remains to mention one or two special cases.

In the Sea Plantain, *Plantago maritima*, what from one angle is obviously a morphic adaptation lacks one of the criteria by which I defined morphism, namely discontinuity between the morphs (Gregor, 1938, 1939). Here a large range of forms occurs, differing in important characters such as spike-length and scape-length, the latter for instance ranging from just over 20 to nearly 50 cm. within a single population. The different forms appear to be closely adapted to the graded conditions of the sea-shore zone transitional between water-logged mud (short scapes) and dry rock (long scapes), and in nature the different forms show a ratio-cline in forms across this zone, even when its extent is only a matter of a few metres.

It appears that the species has a high genetic variance in respect of the characters involved, and that the cline results from the differential survival of those variants best adapted to the different parts of the ecologically graded habitat. The frequencies of the different morphs are thus automatically adjusted by extrinsic selection in each generation, and the only intrinsic genetic requirement is a high variance; whereas most adaptive morphisms are adaptations to sharply distinct environmental conditions, the environment here shows the unusual feature of a continuous gradation of large ecological extent within a small spatial extent.

This *continuous morphism*, as we may call it, as opposed to morphism of the usual discontinuous type, can be regarded as derived from the common phenomenon of broad ecogeographical differentiation by the spatial narrowing and compression of the ecological gradients concerned, until the allopatric populations become a single sympatric one. It is thus in a sense the converse of the secondary geographical polymorphism which may arise through the spatial extension of a morphic ratio-cline until one or both of its ends become monomorphic (p. 13).

We may expect to find many other cases where morphism becomes continuous and so grades over into high normal variability. Egg-number morphism in birds, when large clutches are involved, is one

case (p. 10). The high variability of the egg-markings of the Guillemot, *Uria aalge*, is perhaps another (p. 9; and see p. 52).

Very occasionally morphisms occur in which extrinsic advantage depends on the simultaneous presence of all the morphs concerned. Such morphisms may be called *synergic*.

One such example is the cryptic resemblance of various species of the hemipterous bug, *Flata (Phromnia)*, to flower-spikes, which is effected by a dimorphism, one morph being green like the buds, the other being coloured like that of the flower of the species copied. This synergic resemblance has deceived human observers, and must be quite effective against natural predators (see Cott, 1940, p. 344, and Gregory, 1896).

The Ruff, *Machetes pugnax*, is unique in its extreme polymorphism of male epigamic (display) characters, no two males on a mating-ground being alike. The highly developed display-characters—ruff and “ear-tufts”—are of different colour and pattern from the general plumage, and often from each other. One function of display is to stimulate psychophysiological development of the reproductive and mating system, and the stimulation is enhanced when display is communal. Ford's (1945) suggestion that the striking variety of the Ruff's display adds further to the effect, is probably correct. However, the uniqueness of the phenomenon remains unexplained. If polymorphism of display characters is advantageous, why has it not been evolved by other avian species with communal display?

Bird “duets” in which male and female sing complementary parts of a single song, either simultaneously or successively, may also be regarded as synergic morphisms (Huxley, 1955).

3. PRESUMED ADAPTIVE MORPHISM : RATIO-CLINES

There are many cases of morphism to which no adaptive value can be as yet ascribed but where we may presume that the phanero-morphism is the outward and visible sign of an inward and cryptomorphic adaptive grace, as in *Colias*. This presumption is much strengthened whenever a ratio-cline exists, for this immediately shows that the morphic balance is being affected by environmental conditions and suggests what factors to explore.

Numerous cases are mentioned in the literature (see *e.g.* Mayr, 1941; Huxley, 1942; Dobzhansky, 1951; Ford, 1945*a*, 1953, 1955). A good example is provided by the Common Guillemot, *Uria aalge* (Southern, 1951; and see Fisher and Lockley, 1954, p. 48). This is dimorphic for a white “bridle” or “spectacle” marking round the eye (var. *ringvia*). In the normal unbridled morph the position of the bridle is marked by a slight groove. In the Atlantic, bridling shows an irregularly stepped cline of increasing frequency from under 0.5 per cent. in the south to over 50 per cent. in some northern areas. This straightforward picture was upset when it was found that the bridling frequency declined from over 50 per cent. in South Iceland

to a considerably lower figure in North Iceland. However, it was then pointed out that the climate of South Iceland is markedly Atlantic, while that of North Iceland is continental. Thus the shape of the ratio-cline suggests that the environmental factor favouring the bridled morph is not merely a function of north latitude, such as lower mean temperature or longer summer day-length, but a combination of this with a threshold value for humidity.

Uria aalge is interesting in another respect: though the range of the species extends both to the North Pacific and the North Atlantic, the bridled morph occurs only in the Atlantic (though in several populations classified as distinct subspecies). One must presume that the bridled mutation occurred only in the Atlantic, after the two main populations of the species had become separated.

Southern has further shown that the allele for bridling also determines slight differences in the structure of the skull and the shape of the tail-feathers, so that here again a non-selective "visible" character is correlated with more deep-seated changes. A repetition of the census after ten years showed significant changes in bridling frequency in a number of localities, some being increases and others decreases. So far it is impossible to correlate these with the known amelioration of climate during the period, but further repetitions should eventually permit definite conclusions.

In foxes, the Arctic Fox, *Alopex lagopus*, shows dimorphism in winter (blue versus white), and there is a N.-S. ratio-cline. The Red Fox, *Vulpes fulva*, is trimorphic, the heterozygote ("cross") being distinguishable from both homozygotes, the common red and the rare "silver" (black). Here too there is a ratio-cline, silver (and of course also cross) increasing in frequency to the N. The delicacy of the selective balance is also shown by the fact that the frequency of silver changes cyclically in relation to the animal's regular ten-year cycle of abundance. All races of *V. fulva* show this morphism, but it appears to have developed independently in the Old and New Worlds, the black allele of the true silver fox occurring only in Canada, while a different black allele occurs in Alaska and Eurasia (see Huxley, 1942; Voipio, 1950).

Wild white clover, *Trifolium repens*, shows an interesting ratio-cline (Daday, 1954) in the distribution of HCN, causing bloat in ruminants. The production of HCN depends on two allele-pairs, the dominant members of which are concerned with the presence respectively of a cyanogenetic glucoside, and of an enzyme hydrolysing the glucoside. Both allele-pairs show ratio-clines dependent on winter temperature, a decrease of 10 per cent. in January mean temperature resulting in a reduction of 4.23 per cent. in frequency of the dominant glucoside allele, and of 3.16 per cent. in that of the dominant enzyme allele. The glucoside allele thus fades out slightly earlier with decrease of January temperature, but the behaviour of the two genes is sufficiently similar to give a straightforward phenocline as regards HCN-production.

A rather similar case is that of the Castor Bean, *Ricinus communis* (Harland, 1947), in Peru, where it occurs as a widespread introduced weed as well as in cultivation. Here a morphism exists involving the presence or absence of waxy bloom on the stems. Bloom is due to a dominant allele, *B*; this increases in frequency with altitude, which connotes increase of sunlight and decrease of fog, from 0·15 per cent. at sea-level to 100 per cent. at 7700 feet. The selective disadvantage of *B* plants at low altitudes is due to their much-reduced ability to fruit in sunless and foggy areas.

Doubtless numerous other character-clines, such as are subsumed under the various biological rules (see Rensch, 1954, ch. 3), will prove to have a similar genetic basis, though in many of them this is likely to be multifactorial, leading to continuous morphism.

In the Deadly Nightshade, *Atropa belladonna*, Dr J. H. Burnett tells me that unpublished work indicates the existence of a yellowish-green-flowered recessive morph which is found wild in this country only in sheltered habitats, and has less hardy seedlings than the normal purples. There is a ratio-cline, the yellow-green morph increasing in frequency eastwards; but other characters also gradually appear, so that the easternmost group of the *Atropa* population has been distinguished as a separate species, *A. lutescens*.

The full analysis of this case will be of great interest, as would that of the hairy- versus smooth-stemmed morphs of the Foxglove, *Digitalis purpurea* (Saunders, 1918), hairiness being dependent on a recessive allele which is at a slight viability disadvantage against the heterozygote. Both types are widely distributed over England, but the ratio varies much. Some other species of *Digitalis* are monomorphic smooth, others monomorphic hairy.

In the marine isopod *Sphaeroma* (Bocquet, Levi and Teissier, 1951), there are five main colouration phenomorphs, based on a system of alleles (or closely-linked genes); some show ratio-clines; (see p. 52).

The colouration tetramorphism of the females in the Lycaenid butterfly, *Neozephyrus taxila*, depends on a system of three alleles or semi-alleles, the two dominants suffering an intrinsic disadvantage in general fitness. The recessive appears to enjoy an extrinsic (cryptic) advantage. The morph-ratios vary geographically (Komai, 1953).

The Pied Flycatcher, *Muscicapa hypoleuca*, is broadly dimorphic in the male (black or brown) for its plumage-pigmentation (Witherby *et al.*, 1938-51; Drost, 1936). The difference appears to depend on the different rates of action of pigmentary rate-genes, as in the similar morphisms of some male Geospizidae (Lack, 1947); and there are geographical ratio-clines. For numerous other examples of morphism in birds, see Huxley, 1955.

The common British spider *Theridion ovatum (redimitum)*, is sharply trimorphic—white, red, or red-striped white. This probably depends on a single allele-pair, the heterozygous red-striped enjoying some advantage, while homozygous reds suffer some intrinsic disadvantage. Morph-ratio varies markedly: thus whites range from 50·8 to 87·1,

striped from 9.7 to 44.4, and reds from 0 to 11.8. Further, there is a ratio-cline, with white frequency increasing to the W. A puzzling result was yielded by two large collections made in one day at Brockenhurst : the afternoon collection gave abnormally high red and abnormally low striped frequencies. This case would repay further study (Bristowe, 1931).

In contrast, the anticryptic colour-dimorphism of *Misumena vatias*, which adapts the spider to the flowers on which it sits, is non-genetic, occurring physiologically in about 48 hours (Bristowe, 1941, 2, 435 ; Gabritchevsky, 1927).

The shell-colour (and -form) morphism of the Dogwhelk, *Purpura* (*Nucella*) *lapillus*, has several peculiar features (Moore, 1936). It has six phenomorphs for ground-colour and banding, and one for imbricated shell. The morph-ratios show marked but rather erratic geographical differences. Some of them are adaptively correlated with habitat ; thus the more delicate imbricate morph is almost confined to habitats below the reach of wave-action, as one would expect. But high yellow frequency shows an unexplained correlation with moderate wave-exposure, the frequency being low both in sheltered and exposed situations. Finally, the black-brown, mauve-pink, and white morphs are dependent on diet as well as on genetic factors, the two former only developing on a diet of mussels, *Mytilus edulis*, the last-named only on an acorn-barnacle diet. If black or mauve specimens are transferred to an acorn-barnacle diet, the new shell will be white. This remarkable case demands investigation by modern methods.

Limpets (*Patella*) are much less variable (Evans, 1947) ; but there is some morphism of foot-colour in some species, and of colour of shell interior ; this latter may show geographical variation in morph-ratio.

Some ratio-clines propound a puzzle rather than a clue. For instance, in the dimorphic Fulmar, *Fulmarus glacialis*, the frequency of the dark morph in the Atlantic is very low in the south of the breeding range, very high in the north. But in the Pacific subspecies the relation is reversed ! (J. Fisher, 1952).

Again, though all the smaller Skuas of the genus *Stercorarius* are dimorphic, with dark and light plumage-morphs, and the Arctic Skua, *S. parasiticus*, shows a ratio-cline with increased dark-frequency to the north, largely correlated with increasing humidity (Southern, 1943), in *S. longicaudus* the dark morph is exceedingly rare, and there is apparently no cline in *S. pomarinus* (Witherby *et al.*, 1938-51 ; Southern, 1944).

Such an absence of any ratio-cline is itself a puzzle, as one would *a priori* expect that environmental conditions would normally affect the delicate selective balance involved. However, the Gouldian Finch, *Poephila gouldiae*, in Australia is dimorphic, roughly 80 per cent. of the birds having a black mask and 20 per cent. a red one, with the gene for red a sex-linked dominant. But the frequency is stated to show no clinal alteration over all of its large range (Southern, 1945). A similar absence of true ratio-clines (as opposed to changes in

morph-ratio due to gene-diffusion after crossing) occurs in human blood-group morphisms (see later). In such cases, possibly the intrinsic selection-pressures as regards various components of general fitness are so closely balanced that the balance is unaffected by changes in extrinsic (environmental) conditions. Differences in ratio between different groups (*e.g.* in ABO ratios in human ethnic groups) could then be due either to slight allelic differences in the main morphic genes, or to different combinations of modifiers affecting their intrinsic selective values (see p. 34).

Sometimes the ratio-distribution of morphs is not regularly clinal, but yet can be correlated with some ecological factor. Thus the dimorphism of forceps-length in the male Earwig, *Forficula auricularis*, appears to be correlated with conditions favouring abundance and large size (see Huxley, 1927; and pp. 28, 52).

The morph-ratios of blue- versus white-flowered plants in *Linanthus parryae* show a curious haphazard distribution (Epling and Dobzhansky, 1942; Dobzhansky, 1951, p. 168). Dobzhansky considers that some of this is due to non-selective drift, though it must depend partly on some unknown selective factor (Wright, 1943).

4. ORIGINS AND EVOLUTION OF MORPHIC SYSTEMS

Genic balance-systems may originate from single mutant alleles which happen to have both favourable and deleterious effects: such genes may be called *ambivalent*. Further, they may show either *full ambivalence*, both effects being then exerted in both heterozygous and homozygous dosage, or *dosage ambivalence*, in which the deleterious effect is exerted only (or much more strongly) by the gene when in double dose.

In fully ambivalent genes, if the partial dominance of the favourable effect happens to be greater than that of the deleterious one, a condition of slight double-dose disadvantage will arise and will favour the heterozygote, thus tending to maintain the allele in permanent balance in the population. Furthermore, as Dr P. M. Sheppard has pointed out to me, selection will automatically operate to increase the dominance of the favourable effect and the recessivity of the deleterious one, thus further strengthening the stability system.

A good example of such ambivalent genes in morphic balance in a species is provided by the moth *Ephestia künniella* (Caspari, 1950). This species is morphic for testis-colour, a considerable proportion being *rt.rt* in constitution, with red testes, as against *Rt*, with brown testes. Testis-colour can obviously have no extrinsic adaptive significance, and the dominance of *Rt* in this respect is presumably, as Caspari suggests, a genetic accident. However, the morphic alleles do exert selective effects. Thus *rt.rt* individuals develop slightly more slowly than either *Rt.rt* or *Rt.Rt*, but enjoy a large pre-emergence viability advantage over *Rt.Rt* homozygotes and a small one over all *Rt* individuals combined (though a slight disadvantage as against the

heterozygotes). In mating behaviour (success in effecting copulation), on the other hand, *rt.rt* homozygotes are at a marked disadvantage against heterozygotes, and at a slight disadvantage against *Rt.Rt* homozygotes. *rt* is partially dominant for its favourable effect on viability, but largely recessive for its unfavourable effect on mating behaviour: the result is heterozygote advantage, with balanced morphism. Gustafsson (1953) has analysed several similar cases of "monofactorial heterosis" in barley. (See Haldane, 1954, p. 64, for biochemical implications.)

As an unexpected selective correlate of a mutant character, increased hairiness in cotton confers a (mechanical) resistance to attack by Jassid bugs such as *Empoasca* and has resulted in hairier races in various areas (Hutchinson, 1951). If the hairiness gene had shown double-dose disadvantage, a morphism would have arisen.

Teissier (1953) has shown how mutant genes in *Drosophila* may spread in certain experimental conditions. A. H. Jackson (in press) has obtained somewhat similar results with white-eyed *Drosophila* in darkness, and Waddington *et al.* (1954) with the temperature and humidity preferences of different laboratory stocks: but their suggestion that this might lead to "a relatively stable polymorphism" would only hold if inversions or double-dose disadvantages were involved.

Another type of gene capable of originating a genic morphism is one in which the heterozygote enjoys the advantage of greater flexibility because its effect is not that of one (dominant) allele alone, nor merely intermediate, but that of both allele-partners simultaneously (Smith and Smith, 1954). When this double effect is of a biochemical nature, the resultant biochemical diversity may confer marked advantage on the heterozygote, as in sickle-cell anæmia (Pauling *et al.*, 1949; Haldane, 1954, p. 121). Such genes may perhaps be called diversifiers; see p. 39.

Once a single-gene morphism is established, it may evolve in a number of ways. The double-dose disadvantage may be increased, and the stability mechanism accordingly strengthened, by the incorporation into the system of other mutants with double-dose disadvantage. Once a strong double-dose disadvantage is set up, whether by the above means or through the recessive lethality of the original ambivalent gene, further recessive lethals may become incorporated in the system, by mutations at loci close to the original morphic locus (p. 7). The selective disadvantage of dominant morphic homozygotes in the grouse-locust, *Paratettix*, is as high as 7 to 14 per cent. (Fisher, 1939).

Furthermore, all morphic alleles in the same chromosome which show double-dose disadvantage will tend to become more closely linked, since crossing-over will give selectively more unfavourable combinations. This was pointed out by R. A. Fisher nearly a quarter of a century ago (1930, p. 102 ff; and see p. 7).

The tendency to closer linkage will operate when, as with many dominant morphic genes in grouse-locusts, each shows double-dose disadvantage: it will do so with especial force when different dominant genes interact so that when present together the sum of their double-dose disadvantages is increased; or in the curious cases, also found in grouse-locusts, when co-presence converts two separate single-dose selective advantages into a joint selective disadvantage.

Since selective interaction is more likely to occur with genes affecting the same type of character, close linkage is frequently found between many members of a single morphic system.

Fisher (op. cit., p. 110) further showed that closer linkage will be favoured between loci having similar quantitative effects on metrical characters. Accordingly, if any such gene exists close to a morphic gene, other metrical genes in the same chromosome will tend to become closely linked with the morphic gene-system. Sheppard has pointed out that translocations containing genes of these types will also be favoured.

As a result of these tendencies, many species come to possess morphic systems of closely-linked genes. Thus in *Paratettix texanus* 24 of 25 morphic genes behave as semi-alleles: in *Apotettix* almost all the many genes concerned with morphic patterns are in one chromosome, and mostly in a few extremely closely linked groups (Nabours and Stebbins, 1950). Similar morphic gene-groups are known in other grouse-locusts (Fisher, 1939), and in grasshoppers (Rubtsov, 1935), in mammals for blood-group characters, in snails for shell-characters, in Cyprinodont fish for colours and patterns, and in various other organisms; and may show semi-allelism (Komai, 1950). In the grouse-locust *Acridium* (Nabours *et al.*, 1933) the 12 morphic genes are all in one chromosome, but not closely linked.

A quite different type of origin for morphism is provided by inversions, as in *Drosophila*, and this may lead on to euheterosis (see p. 11).

The fact that a morphic chromosome contains a large number of genes, mostly producing different effects, and that the two members of the system probably differ *ab initio* in a large number of loci, makes it likely that they will show larger original differences in selective values, both quantitatively and qualitatively, than will genic systems. This will also make it possible for the morphic chromosome to show secondary adaptive evolution as wholes, by means of the incorporation of suitable mutants (supergene systems), so that each comprises both a switch-mechanism and the adaptive gene-system dependent on the switch and canalising its effects, and also half of the co-adaptive euheterosis mechanism (p. 12). With other types of origin, the switch-mechanism and the dependent canalisation-mechanism may be and usually are localised in different regions of the gene-complex. However, this need not always be so, as in *Primula* (p. 20).

In most types of genic morphism, secondary adaptive evolution will also tend to occur. Thus in polymorphic mimetic butterflies there is the mimetic adaptation of the original morphs through the evolution of switch-dependent canalisation mechanisms. These mimetic adaptations must be closely adjusted by selection (p. 6).

The cryptic adaptations of colour and pattern in the morphism of *Cepaea* appear also to be due to the selective improvement of crude "pre-adaptive" resemblances exhibited by some of the morphs (p. 9).

In general, we must expect that selection will operate on any primary intrinsic morphism in such a way that it will gradually show secondary extrinsically adaptive modifications in some or all of its morphs; the more ancient the morphism (as shown by its presence in several related species or genera) the more likely it is to show secondary adaptations. The detection of such secondary adaptation, however, is often difficult. Selection may also be theoretically expected to act so as to reduce the deleterious effects of ambivalent morphic alleles, by buffering them with modifiers. I do not know of any case in which this has been conclusively proved, but it may possibly occur in the fish *Platypoecilus* (p. 18) and in human sickle-cell anæmia (p. 39).

The original discontinuity between the morphs in all examples hitherto mentioned is genetic, provided by mutation of some sort. But in other cases it may be developmental, provided by the existence of large meristic units or of distinct growth-stages and moult-instars. I have already discussed avian clutch-size as an example of the former; other examples of meristic discontinuity as a basis for morphism doubtless exist, e.g. in vertebra-number in fish.

Instar-discontinuity is probably the basis for the dimorphism in forceps-size of male earwigs, *Forficula auricularia* (Huxley, 1927). Some sort of limitation of growth presumably underlies the continuous polymorphic variation of size and mandibles in various beetles, and of size and head of neuters in some species of ants, as well as the sharp size-dimorphism seen in others (Huxley, 1932). But much experimental analysis of such cases is still required.

The existence of alternative "mutational channels" (Mayr, 1942, p. 74), or, as they might be called, *canalisations of variance*, may enlarge the discontinuities produced by mutation. A similar large discontinuity may be provided by the existence of alternative ontogenetic processes or *canalisations of development*, such as Waddington and other experimental embryologists are now busy investigating.

However a morphism may originate, and whether its original basis is intrinsic, concerned with general fitness, or extrinsic, concerned with adaptation to external conditions, it will tend to evolve in the direction of greater stability and higher adaptive value.

5. UNEXPLORED MORPHISMS AND PROBLEMS FOR FURTHER RESEARCH

Many cases of morphism I have found in the literature have either been wholly unexplored or demand further investigation.

The well-known female dimorphism of the Currant Moth, *Abraxas grossulariata*, is unique in that the "mutant" *lacticolor* (*dohrnii*) produces a virus or virus-like body which reduces viability. The normal morph can be infected with this, but cannot produce it (Smith, 1952). Darlington suggests that the virus is a detached plasmagene to permit the permanence of the morphism. Lacticolor is not in morphic balance, but only a rare mutant. Nevertheless the case is worth citing as an example of an unexpected "correlated character" of selective import.

The frequency of melanic Leopards (*Felis pardus*) varies much. Though black Servals are not uncommon in E. Africa, black Leopards are rare except at high altitudes (Foran, 1952). They are very rare in India, but increase in frequency eastwards (T. G. Longstaff, *in verbis*). The colour-morphism of the American Black Bear, *Euarctos americanus*, differs in different subspecies. *E. a. americanus* is typically black with brown and cinnamon morphs; *E. a. emmonsu* is black or more rarely slate-grey; *E. a. kermodei* is typically white, but with a dappled reddish-yellow morph. In the Brown and Grizzly Bears, *Ursus arctos*, one montane subspecies (*U. a. isabellinus*) is markedly polymorphic, in contrast to the numerous other races.

Among birds, a unique case of morphism in habits was described by H. J. Frith at the International Ornithological Congress in 1954 for the Megapodidae (Mound-builders). Several species of *Megapodius* and *Leipoa* are di- or poly-morphic in their mound-building habits. Thus in a single population of one *Megapodius* species there are birds which dig holes in sand, others which build large mounds, either solely of organic matter or of sand enclosing organic matter, and still others which utilise volcanic heat. Geographical polymorphism also occurs.

What appears to be a unique case of vocal morphism has recently been described in the Tawny Owl, *Strix aluco*, by Muir (1954). Young birds, even from the same brood, give one or other of two quite distinct calls.

Many reptiles and amphibians are morphic, including all species of snakes, lizards, *Anura*, and *Urodela* (Smith, 1951) found in Britain, though the sand lizard has a melanic morph only on the Continent. The remarkable blue-spotted morph (var. *colchica*) of the Slow-worm, *Anguis fragilis*, is found only in adult males: it shows an increasing frequency to the southward. It is interesting to note that other species of Anguidae, e.g. *Ophisaurus gracilis* and *O. harti*, are monomorphic in both sexes for this character. In *Anura* the genetic colour-morphism is complicated by the animals' capacity for physiological colour-change. In some areas, e.g. Scotland, the red morph of *Rana temporaria* is unusually frequent.

In the Alpine Newt, *Triturus alpestris*, in some high Alpine lakes "a breed has evolved in which [total] neoteny is common" (M.

Smith, *op. cit.*). This morphism may be an evolutionary development from the partial neoteny seen in the British Smooth Newt, *T. vulgaris*, where a certain proportion of individuals in steep-sided artificial ponds find emergence too difficult, and remain unmetamorphosed in the water (but do not mature sexually). A high proportion of such forms also show partial albinism (*cf.* Main's frogs, p. 17). Similar metamorphic morphism seems to occur in Axolotls (see Bateson, 1913, p. 231).

The American King-snake, *Lampropeltis zonata*, is highly variable both between and within geographical populations (Zweifel, 1952). Some of this variance is apparently morphic, but some probably due to recombination after secondary hybridisation of subspecies.

Molluscs provide an almost inexhaustible supply of morphisms; such striking cases as the four British Periwinkles, *Littorina* (Yonge, 1949). E. Mayr (*in litt.*) tells me that in *Littorina obtusata* he has found a correlation between morph-frequency and colour of substrate, as in *Cepaea* (p. 9). Among the sea-slugs, there is *Archidoris* (*Doris*) *britannica*, where some morphs appear to be procryptic, the trimorphic *Goniodoris nodosa* (Yonge, *op. cit.*), and many cases in Alder and Hancock (1845). Among Eolids, though morphism occurs in some species, like *Eolis papillosa*, it is rarer. This is presumably because many of them have aposematic colouration advertising the unpleasant properties of their stored nematocysts, so that it is of biological advantage to be monomorphic in the pattern to be learnt by their enemies.

Prof. R. Seshaiya of Annamalai University has given me a collection of shells of the marine gastropod *Umboonium vestranum* from south of Madras, which makes it clear that the polymorphism of this genus is so extreme as to rank with that of *Apotettix* or *Lebistes*.

Land-snails and slugs appear to be exceptionally polymorphic: *e.g.* Bateson (1913) cites *Helix herpennis* with 27 morphs, and *Bulimus detritus* with 18 morphs; and see Komai (1954) on *Bradybaena*.

Among Lamellibranchs, Sowerby (1847-82), Step (1901), and Yonge (*op. cit.*) record a number of morphisms affecting either shell-colour or body-colour or both, *e.g.* in common British genera like *Tellina*, *Tapes*, *Donax* and *Pinna*. Extreme polymorphism is shown by various species of *Pecten* (*sensu lato*) such as *P. proteus* and *P. tigrinum* (see Sowerby's pls. XII to XXIV, and Step, p. 85). *Tridacna elongata* and *T. marina* of the Great Barrier Reef, show a remarkable mantle-colour morphism, while others are wholly or nearly monomorphic (Yonge, 1930). Bateson (1913, p. 130) suggests that *Anodonta* is morphic as well as highly variable.

Among Crustacea, various isopods show morphism in colour and pattern, *e.g.* the common woodlice, *Armadillidium vulgare* and *Porcellio scaber*. The latter is tetramorphic, including a non-patterned morph which is presumably the universal recessive. Morph-ratio differs in different habitats (Meinertz, 1943). Howard (1953) has begun the genetic analysis of the morphism of *Armadillidium*. In the Turkish

woodlouse, *Cyclodiscus convexus* (de Lettin, 1952) there are three female reproductive morphs, producing both sexes, almost only females, and almost only males respectively. Two morphic allele-pairs seem to be involved. For *Sphaeroma*, see pp. 25, 52.

In Copepoda, Bocquet (1951) has recently analysed the pattern-morphism of the marine *Tisbe reticulata*. There are seven main phenomorphic patterns in females, three in males. They depend mainly on a genetic system of several main dominant alleles (or closely linked genes) and a universal recessive, but with the addition of two recessive genes, and other genes producing a "secondary polychromatism" affecting small groups of pigment-cells only.

The Common Shore-crab, *Carcinus maenas*, is remarkable in showing a bewildering polymorphism of colour and pattern in juveniles up to about an inch in carapace-breadth, while adults are much less variable (personal observation). Possibly the variety of patterns in juveniles is adaptive as in *Cepaea* (p. 9), by conferring cryptic resemblance in a wider range of habitats. An extensive study of the morphism of this abundant species would be of great interest.

Echinoderms reveal what is to me a surprising number of colour- and pattern-morphisms, including that of the bêche-de-mer, that much-prized holothurian (Yonge, 1930). Among British species we have the dimorphic Spring Starfish, *Marthasterias glacialis*, the polymorphic Scarlet Starfish, *Henricia sanguinolenta*, and the trimorphic Sun-star, *Solaster pappus*, in the Asteroids; and in the Ophiuroids the highly polymorphic Common Brittle-star, *Ophiothrix fragilis* and its relative *Ophiopholis aculeata* (Yonge, 1949). Frequency determination of the morphs of *Ophiothrix* in different regions could now be carried out on an extensive scale by means of under-water photography, and would be of great interest.

Among Compound Ascidians the abundant Golden-Stars sea-squirt, *Botryllus schlosseri*, is tetramorphic in colour as regards its gelatinous matrix, and dimorphic as regards its individual zooids; and among Sponges the common British species, *Halichondria panicea* and *Hymeniacidion sanguinea*, are trimorphic in colour (Yonge, 1949).

A thorough ecological, experimental, and perhaps even genetic study of morphism in sea-anemones should be rewarding.

Ford (1955) has a valuable discussion of many morphisms in moths, including the now classical *Panaxia dominula* (Sheppard, 1951).

What may possibly be a case of morphism in the Leptomedusan *Phialidium* is mentioned by Burkenroad (1931). In certain regions, a form occasionally appears in high frequency which differs from the type chiefly (but not wholly) in possessing five instead of four radial canals. This may be a meristic morph, but there are complicating details suggesting the alternative explanation that it is a distinct species or subspecies.

Among flowering plants, inspection will often reveal the existence of colour- and pattern-morphism. Thus from my own casual observations I can say that the Field Scabious, *Krautia* (*Scabiosa*) *arvensis*,

may show marked variation interpretable on the basis of two pairs of morphic alleles, one for general flower-colour, the other for paler marginal florets; that a Swiss population of Balm (*Melissa*) clearly contained at least three gene-pairs in equilibrium; that an English population of Hemp Agrimony, *Eupatoria cannabina*, was dimorphic for depth of colour both of flowers and stems; and that wild stands of the Fritillary, *Fritillaria meleagris*, always vary in intensity of flower-colour and often contain a white morph in moderate frequency.

Turrill (1948) cites a number of other cases. Among these I may mention the common Comfrey, *Symphytum officinale*, which is polymorphic in flower-colour (and I believe in density of green in leaves), while other species of the genus are monomorphic; the Musk Mallow, *Malva moschata*, and the Yarrow, *Achillea millefolium*, both dimorphic for white and coloured flowers, but the latter being unusual in that the coloured morph is the less frequent; and the Cuckoo-pint, *Arum maculatum*, which is not only strikingly dimorphic for spadix-colour, but also polymorphic for leaf-spotting. Some apparent cases of morphism may be wholly or partly due to recombinational variance after hybridisation, e.g. various orchids (Heslop Harrison, 1951; and Bateson, 1913, p. 125 for *Ophrys apifera* × *aranifera* × *muscifera* in some areas) and Comfrey; and others to ploidy or apomictic variation (e.g. *Ranunculus acris* and *R. ficaria*).

Summerhayes (1951) also lists numerous examples of morphism in British orchids, including the curious case of the rare "wasp" morph of the Bee Orchis, *Ophrys apifera*, which mimics a wasp's abdomen instead of a bee's: see also Heslop Harrison's interesting studies (1951, 1953).

The gum *Eucalyptus citriodora* shows biochemical morphism. A wild population in a restricted area contained a number of morphs differing in the chemical nature of their essential oils. Similar biochemical morphisms have been found in other eucalypts and in various *Myrtaceae* and *Rutaceae* (Penfold and Willis, 1953). It would clearly be of great interest to see whether ratio-clines exist in such forms, and how chemical peculiarities are correlated with environmental conditions.

Blackman and Rutter (1950) claim that the Bluebell, *Scilla non-scripta*, exists in strains of different bulb-weight. They have not, however, analysed the share of environment and genetic constitution in determining bulb-weight, so that it is dubious whether this involves true morphism. Schütte (1949) found that *Romulea bulbocodioides* near Cape Town was dimorphic (yellow versus white) in flower-colour, and that the morph-ratio varied markedly in different localities, with considerable areas monomorphic for one or other morph. His genetical deductions, however, appear to be without foundation.

A perusal of the recent British flora (Clapham, Tutin and Warburg, 1952) reveals large numbers of definite or probable morphisms. Here I can only mention a few specially interesting examples.

The Wild Carrot, *Daucus carota*, has a very peculiar and quite

frequent morph in which the central flower of the umbel is red or purple instead of white like the rest. Some species of Milkwort (*Polygala*) are markedly dimorphic in flower-colour, others trimorphic. The subgenus *Viola* contains some species in which a white or pale flower-colour morph is absent, others in which it is present but rare, and one (*V. odorata*) in which it is about as abundant as the coloured morph. In this last species, the white morph has become more abundant in recent decades in certain areas (Turrill, 1948, p. 133 ; and see Walters, 1944).

In the subgenus *Melanium* (pansies), the colour-polymorphism is notorious, and greater than in the nominate subgenus. *Veronica*, many umbellifers, *Dianthus*, *Silene*, *Convolvulus*, *Calystegia*, *Datura*, *Verbascum*, *Limosella*, *Rhinanthus*, *Melampyrum*, *Euphrasia* show colour-morphism in many species (in the last-named genus inter-specific hybridisation may be responsible for some of the variance). Many genera of *Boraginaceae* show different degrees of morphism in different species. In some of them the phenomenon is complicated by the fact that flower-colour may change from red to blue or purple during development: this combination of genetic with developmental morphism is paralleled in birds (p. 23). The Bladder Campion, *Silene cucubalus*, is dimorphic in respect of hairy or glabrous stems. Mr Marsden Jones tells me that the Meadow Saxifrage, *S. granulata*, includes populations which are highly polymorphic for petal-size and shape (and cf. *Digitalis*, p. 23).

Field botanists will know of many other examples, and geneticists will doubtless find numerous fascinating problems for investigation in common plants.

This list of morphisms could be enormously enlarged ; but I have said enough to show what a wealth of interesting problems await analysis in this field.

6. MORPHISM IN MAN

Morphism in man deserves a special section, partly because it sheds light on human genetics and its medical, social, and ethnic applications, and partly because certain important types of morphism were first discovered and are most easily studied in our own species.

Most human polymorphism, in the general sense of high variance, is either geographical or due to hybridisation between previously isolated geographical populations. True morphism, however, is also widespread. One universal morphism is that of the blood-groups. Admirable detailed accounts of the subject are available, such as those by Race and Sanger (1950) and Mourant (1954) ; see also Boyd (1950) ; here I shall confine myself to points of general biological interest.

To begin with, some at least of the blood-group morphisms are very ancient, such as the ABO system, which exists in a somewhat

different and not yet fully analysed form in anthropoid apes as well as in *Homo* (see Boyd, 1950, p. 334; Mourant, 1954). Its origin must accordingly date back at least to the Miocene.

As already mentioned, other higher vertebrates also show analogous blood-morphisms (cattle, Stormont, 1952; ducks, McGibbon, 1945; doves, Irwin, 1953; fowls, Briles *et al.*, 1953). In doves the antigenic characters help in determining taxonomic relationships. It would be of great interest to extend such studies to other species, especially to the wild relatives of domestic forms. See also p. 52.

In general, blood-group morphisms depend on systems of allelic or more probably semi-allelic (very closely linked) genes. In fowls there is a system of four semi-alleles. In doves (*Streptopelia spp.*) there are up to nine antigenic morphs in one system. In cattle there are four such systems, two dimorphic, one with over twenty and one with over eighty morphs. This last group possibly depends on a system of up to twenty semi-alleles, and if so is one of the largest morphic systems known.

In man, there are already nine systems known, or ten if we include the secretor system, which is linked with the Lewis blood-group, and determines whether the A, B and other blood-group substances are secretable into the saliva and other secretions. Details can be found in the works already cited (and see Sheppard, 1953; Roberts, 1954a; Race *et al.*, 1954).

Different human ethnic groups show different morph-ratios and some may lack certain morphic genes of a particular blood-group system. It would be of great interest to discover if animal species show similar intra-specific variation in blood-group morph-ratios.*

It appears that these ethnic ("subspecific") differences in morph-ratio are extremely resistant to environmental influences, and remain stable even after migration to quite new habitats, thus incidentally providing one of the best indices of evolutionary relationship between different human races. A similar but lesser stability characterises other blood-morphisms such as sickling (see later), as demonstrated by Lehmann, 1954. This important field of comparative human genetics is being actively prosecuted, but there are still great gaps in our knowledge (Mourant, 1954, p. 194).

Man's blood-groups thus constitute outstanding examples of an intrinsically stable morphic balance-mechanism; and the question at once arises how this stability is achieved for the various equilibrium-points actually found. However, this is easier asked than answered. Theoretically, we must suppose that the intrinsic (general fitness) selective advantages and disadvantages of the various morphic genes in each system are so nicely balanced that a highly self-regulating equilibrium is reached—a conclusion borne out by the recent work of Allan (see later). Differences in ratio between ethnic groups would

* The present terminology of the blood-group genes is confusing and genetically barbarous. It is good news that E. B. Ford (1955; A uniform notation for the blood-groups; *Heredity*, (this issue) is proposing a satisfactory and universally applicable system which is in line with current genetic principles and practice.

then presumably be due mainly to differences in modifiers in the rest of the gene-complex affecting the expression of the various main morphic genes and so altering their effective advantages and disadvantages, as suggested by Ford (1945), though it is theoretically possible that some of it may be due to mutation of the morphic genes themselves. In any case, it seems clear that the suggestion of Wright, that the ratios originated through drift, and then remained stable, is not likely to be true.

The continual existence of a number of alternative morphic genes in equilibrium must involve a selective balance, as demonstrated by R. A. Fisher a quarter of a century ago. In spite of this theoretical necessity, almost all medical authorities have until recently maintained that the blood-group morphisms had no selective implications, and this view has been supported by leading geneticists (*e.g.* Wright, 1940; Dobzhansky, 1951, p. 157).

Recently, however, the position has changed with almost dramatic suddenness. In the first place, the Rh (rhesus) system obviously has selective implications because of the deaths from erythroblastosis fatalis due to iso-immunisation in certain genetic combinations of mother and offspring (Haldane, 1942). This would operate to reduce the number of viable heterozygotes between Rh-positive and Rh-negative, *e.g.* in such combinations as *Dd*, and so to reduce the frequency of the rarer gene—here *d*, or Rhesus-negative—in the population. Glass (1950) has shown that this tendency, is, in populations which limit family size, such as U.S. whites, compensated for by the opposite tendency to make up for deaths of offspring by adding more children to the family. It does not operate in U.S. negroes, where family limitation is little practised. This, however, cannot well be the whole story. Rh-negative genes presumably possess some as yet undiscovered intrinsic advantage which permitted them to reach morphic balance in the populations in which they originally arose. The situation is further complicated by ethnic crossing in a way which does not seem to apply to the other blood-groups.

With these too, however, evidence of differential selective value has recently been discovered. Many years ago, R. A. Fisher suggested that a determination of the morphic ratios of the blood-groups in different age-groups within a single population would probably reveal some differential viability. This challenge has now been taken up, and interesting though puzzling results have been obtained, not only on the differential viability of the ABO morphs, but also on their differential fertility (see Allan, 1953, 1954; Anon., 1954*a*). Briefly, the position is as follows: differential viability is marked, but is opposite in the two sexes. Vuori found in a large sample of Finnish children and adolescents aged eight to eighteen years that the $\frac{B}{A+O}$ ratio shows a progressive fall in males, from 0.27 to 0.18, but a progressive rise in females from 0.18 to 0.35. In both sexes there is a brief reversal of the trend in the thirteenth year at the beginning of

adolescence. The B girls developed more slowly, their average age at first menstruation being 14.7 years against 14.3 for A and O girls. The abortion rate for B mothers was nearly double that for (A+O) mothers.

Allan (1954) has independently indicated the existence of a similar state of affairs in the British population, the order of increasing fitness (viability) being $O \rightarrow A \rightarrow B$ for females, $B \rightarrow A \rightarrow O$ for males. He further found (Allan, 1953), on re-analysing Waterhouse and Hogben's data, that there is also an order of fertility as between the morphs, but as far as B is concerned, this is in the reverse sense from that for fitness. The order of increasing fertility in females is $B \rightarrow AB \rightarrow O \rightarrow A$, and the opposite in males. We may express these curious facts in a diagram, in which the arrows point in the direction of higher fertility or viability.

Group	Viability		Fertility	
	♂	♀	♂	♀
O+A	↑	↓	↓	↑
B	↓	↑	↑	↓

As regards B and (O+A) the differential, selective values are opposite in either sex for viability and for fertility, and are opposite in the two sexes in both cases.

This symmetry is not perfect when O and A are considered separately. The diagram then runs as follows :—

Group	Viability		Group	Fertility	
	♂	♀		♂	♀
O	↑	↓	A	↓	↑
A	↓	↑	O	↑	↓
B	↓	↑	B	↑	↓

Not all of these findings are fully significant statistically, but they are extremely suggestive and should be followed up on a large scale.

Meanwhile, other evidence of differential viability has been obtained. Johnstone (1954) has shown a significant difference of ♂ sex-ratio between the offspring of B mothers and non-B fathers, and the offspring of B fathers and non-B mothers— 55.4 ± 2.9 as against 47.5 ± 2.7 . Whether this is due to differential fertilisation by X- and Y-bearing sperms or to differential mortality of male conceptions *in utero*, we do not yet know. The latter would *a priori* be more likely,

but is difficult to reconcile with the higher fertility of B mothers as established by Allan. In any event, the effects of the two differentials approximately cancel out, so that there is no progressive alteration, either of sex-ratios or of B-frequency, in the population.

Johnstone failed to confirm the results of Sanghvi (1951), who claimed that the ♂ sex-ratio of O offspring of O mothers was higher than that of A offspring of A mothers (60.5 as against 49.8); possibly this may be due to the fact that Johnstone's sample was British, from London, Sanghvi's Indian, from Bombay. Sanghvi also cites data from New York which show the same trend (56.3 as against 45.7).

For toxæmia of pregnancy, O mothers are at a relative disadvantage, toxæmic patients being 53.6 per cent. O, as against 45.5 per cent. in controls; A and B mothers on the other hand are at a relative advantage, the incidence of A and B and AB in toxæmic patients being markedly lower than in the general population (Pike and Dickins, 1954).

General viability, of course, includes components relative to susceptibility to various specific diseases; and here our knowledge of the differential selective values of the ABO morphs has been much enlarged. Thus Struthers (1951) has shown that a significantly larger proportion of A than of O babies die of broncho-pneumonia during the first two years of life. Aird and Bentall (1953) have shown a similar result for incidence of stomach cancer, a higher percentage of A's being found in cancer patients than in the general population, a lower percentage of O's. The figures are as follows (per cent.):

A		O	
Stomach Cancer	Control	Stomach Cancer	Control
44.8	> 39.8	44.5	< 48.6

Later work shows that B's also are less prone to stomach cancer. There is also an environmental correlation, the incidence of stomach cancer increasing from south to north in Britain; this, however, must depend on some quite other factor than blood-grouping, since in fact the frequency of A in the British population *falls* as we pass northward (see Roberts, 1953, 1954*b*).

Sheppard (1953) has suggested that further analysis might show that susceptibility to stomach cancer was associated with a combination of A with the secretor gene, which would lead to large quantities of the A substance being swallowed. I understand from Professor Aird that this suggestion is now being followed up, and that data are also being collected on the relation of blood-group morphism to cancer of the colon and breast, to brain tumours and to pernicious anæmia

and the leukæmias. The results already show the same differential between A and O as regards cancer of the colon.

Meanwhile, Aird and his team have established an even more striking differential effect in peptic (gastric and duodenal) ulcers (Aird, Bentall and Mehigan, 1954). Here the selective differential between O and A is reversed, O's being much more prone to ulcer than the average of the general population, A's and B's much less so: "persons of group O are almost 35 per cent. more likely to develop peptic ulceration than are persons of the other groups". This has been confirmed by Wallace (1954). It is interesting and curious that B's are at a selective advantage both in regard to stomach cancer and peptic ulcers. Aird suggests that the mucopolysaccharide antigenic blood-group substances may be concerned in these results, perhaps by some kind of protective action against carcinogens and against factors such as hyperacidity which promote ulceration.

This 35 per cent. excess proneness of O's to peptic ulceration is a very large differential, and must have considerable selective effect on viability and general fitness in the biological sense.

To sum up from the genetic angle, we find that the alleles of the ABO morphic system are all ambivalent in respect of one or other character, conferring selective advantage in some respects, selective disadvantages in others; and very curiously, the ambivalence is often in the opposite sense in the two sexes. As previously indicated, such selective ambivalence will lead to the establishment of a morphic balance. Furthermore, the selective advantages and disadvantages of the various morphs tend to cancel each other, so that the morph-ratios in any given population are more or less stabilised.

I now come to perhaps the most striking example of morphic balance in man, and the only one in which an extrinsic selective advantage as well as an intrinsic disadvantage of the morphic system have been clearly established. Sick-cell anæmia is a hæmolytic blood-disease, often fatal and almost always resulting in reproductive failure, characterised by shrunken erythrocytes in which the hæmoglobin is chemically different from normal, being relatively insoluble when reduced. In single dose, the sickling gene produces no visible effect on the blood corpuscles *in vivo*, but causes sickling in blood reduced by being incubated anaerobically: this condition has been called "sickleemia" and those possessing it "sicklers". Further, it is not only not fatal, but possesses the advantage of conferring protection against subtertian malaria (Allison, 1954; Anon., 1954*b*). This, of course, will only be of selective value in strongly malarious districts. In such districts, sicklers show a significantly lower incidence of malaria than non-sicklers and are less easily infected artificially; the frequency of sicklers also increases with age, showing a differential death-rate of non-sicklers.

The sickling gene only occurs in populations from areas where malaria is endemic; it is found among African negroes (in decreasing frequency from east to west), in the Veddoids of South India, the

probable Veddooids of South Arabia, and in Greece and southern Italy (Lehmann, 1954). The quantitative correspondence between sickle-gene frequency and degree of endemicity of malaria is not accurate (Moore *et al.*, 1954; Roberts and Lehmann, *Brit. Med. J.*, 1955, p. 519); this may be due to recent migration or to modifiers, but does not affect the general correlation.

Pauling and his associates (1949) have provided the biochemical and genetic clue to the ambivalence of the sickling gene. It determines a chemical alteration of the hæmoglobin (probably in its globin) which apparently alters the surface properties of the molecule in such a way as to lead to birefringence and to crumpling at low oxygen-tensions. In homozygous sicklers, there is no normal hæmoglobin, and the erythrocytes are destroyed, leading to severe and often fatal anæmia. The sickling gene is often described as dominant, but it is actually what I have called a *diversifier* (p. 26). Both it and its normal allele produce their characteristic effects when co-present; the heterozygous sicklemic thus has erythrocytes containing both normal and abnormal hæmoglobin. We may presume that the normal hæmoglobin is sufficient to prevent serious anæmia, while the abnormal is sufficient to render the blood-corpuscles "unpalatable" —unutilisable or uninfected by the malaria parasite.

In North American negroes sickle-gene frequency is much lower than in Africa. This is presumably in part due to the fact that "negroes" in the U.S. are largely hybrids with whites, but also, as Allison suggests, to the fact that most of the area is non-malarious, which will reduce the selective advantage of the sickling gene and lead to a reduction in its frequency.

It was at one time thought that the mortality of homozygotes was higher in American than in African negroes, which could be explained on the assumption that in its original home the deleterious effects of the sickling gene had been buffered by protective modifiers, and that the buffering system had been largely destroyed by race-crossing in the U.S. (*cf.* the "de-buffering" of the deleterious hyperpituitarism of St Bernard dogs on crossing with Great Danes (Stockard, 1941) and the deleterious effects of *Platylocilus* macromelanophore genes in species-crosses, mentioned on p. 18. However, Dr Allison tells me that the difference is in all probability apparent only, due to inadequate medical statistics in Africa. Neal *et al.* (1951) have shown that heterozygotes enjoy higher biological fitness.

The position is further complicated by the existence of other alleles causing less extreme symptoms (hæmoglobin C; Edington and Lehmann, 1954), and probably of modifiers affecting the proportion of abnormal hæmoglobin in heterozygotes (Allison, *in litt.*). Lehmann and Edington (1954) suggest that even homozygotes enjoy some advantage in protecting against malarial symptoms. Roberts and Lehmann (*op. cit.*) give data on the distribution of four hæmoglobin morphs in Africa.

In any case, sickling provides an outstanding example of how a

mutant which might be regarded *a priori* as essentially deleterious, may in certain circumstances possess a selective advantage, become ambivalent, and so form the basis for a balanced morphism.

Thalassemia is another genetic blood-disease which gives a rather similar picture. It depends on a single, partly dominant gene, which inhibits the formation of adult hæmoglobin. In double dose it causes Cooley's disease and is lethal before reproductive age is reached, and in single dose produces symptoms ranging from clinically healthy microcythæmia, through mild to severe but not lethal microcytic anæmia. It occurs in morphic balance, with frequencies up to 10 per cent., in malarious areas of Italy and Greece, and also (Allison *in litt.*) in Thailand, where it presumably arose independently. Allison suggests that the heterozygotes may prove to have a greater resistance to malaria, as with the sickle-cell gene: and Bianco, Montalenti *et al.* (1952) have shown that they show a higher fertility than the homozygous normals, even though the mortality of their children is higher. The total number of conceptions per family, including abortions and stillbirths, is 5.89 for heterozygotes as against 3.60 for normals; and the total number of living children found was 3.26 as against 3.14. Further statistics on this interesting phenomenon would be of great interest.

I now pass to cases, some of them very curious, where no selective effects have yet been discovered. Some of these involve visible differences, either structural, *e.g.* lobed versus non-lobed ears; or behavioural *e.g.* position of the crossed hands, whether with right or left thumb uppermost, etc.; tongue-rolling, or the ability versus inability to roll the protruded tongue into a trough (Sturtevant, 1940; Komai, 1951). Komai (*op. cit.*) has found a gene in Japan which may be quite widespread and prevents full extension of the tongue, and also renders difficult the playing of wind-instruments and the pronunciation of the letters r and l. These last cases are of wide interest, since ability to control tongue-movements might well be correlated with ability to pronounce certain sounds. Darlington (1947, and see Darlington and Mather, 1949, p. 361 ff.) has already demonstrated a correlation between another human morphism, in this case high frequency of the O blood-group allele, and the existence of fricative dental (th and dh) sounds in the language spoken. Much interesting research obviously remains to be done on the differential ability of individuals of different genetic, and especially different morphic constitution, to pronounce various sounds.

Perhaps the most interesting human morphisms concern sensory capacity. Thus Muller has pointed out that the widespread existence of myopia in so many human societies, which is usually ascribed to the absence of counter-selection and the consequent accumulation of the loss-mutants determining it, could be, in part at least, explained as the result of positive selection, myopic individuals being at an advantage in the performance of fine work demanding close vision. This selective advantage would only begin to operate at a certain stage in human cultural evolution, and would cease with the widespread use of

spectacles ; but selection over this period of 6000 or 7000 years would be long enough to effect a considerable increase in myopic frequency. (See Sorsby, 1951, for facts concerning variations in the frequency of myopia.)

The most familiar human sensory morphism is red-green colour-blindness, whose frequency is far too high to be due solely to recurrent mutation. The commonest gene concerned is a sex-linked recessive, and the frequency of affected males (and therefore also of carrier females) varies between 3 and 8 per cent. in most races, though it is only 1 per cent. or lower in Eskimos and Navaho Indians. Other minor defects of colour-vision appear also to depend on sex-linked genes (Pickford, 1953), which suggests the existence of a morphic system of linked genes all concerned with this character. However, we know nothing as yet of the selective advantage of the mutant morph, which must be operative. In insectivorous birds, Ford (*in verbis*) has suggested to me that red-green colour-blindness might be of marked advantage in detecting insects which have evolved cryptic colouration in relation to predators possessing normal colour-vision. Thus normal human beings find great difficulty in detecting the larvæ of the Emperor Moth (*Saturnia pavo*) against their normal background of blossoming Ling (*Calluna*) ; but red-green colour-blind persons readily pick them out, even at a considerable distance, by their shade-differences.

Another sex-linked sensory morphism has recently been discovered—the ability to smell solutions of KCN. Eighteen per cent. of white Australian males are “non-smellers” for this substance (Kirk and Stanhouse, 1953). Dr Courtney-Pratt (*in litt.*) writes that marked variation in threshold exists for the “vile smell” of phenyl isocyanate. Hunt (1953) showed that weak kerosene increased the olfactory sensitivity of blowfly larvæ to NH_3 .

The best-analysed sensory threshold morphism is that for tasting phenylthiocarbamide (PTC). “Tasters”, with low threshold, include a majority from about two-thirds to nearly 100 per cent. of human populations, but the frequency varies somewhat with sex and ethnic composition (see Boyd, 1950). In some ethnic groups, *e.g.* North American Indians and Mongoloids, the non-tasting allele is absent except as a rare mutant. In the Vietnamese the frequency of non-tasters is distinctly lower than in whites (10-20 per cent.), though higher than in Chinese (6 per cent.) and Koreans (3 per cent.), and slightly higher than in Japanese (9-14 per cent.) (Huard *et al.*, 1953).

Non-tasting depends on a recessive allele, but modifiers exist which affect the threshold. There are also aberrant tasters, commoner in Far Eastern peoples, to whom the normally bitter PTC tastes acid, salty, sweet, like orange-peel, etc. (Huard *et al.*, *op. cit.*). Barrows (1947) found about 5 per cent. non-tasters of brucine, with a threshold 4000 times as high as that of tasters. Non-tasting is probably recessive.

PTC morphism also must be very ancient, since it occurs also in chimpanzees and other anthropoids, and with a similar minority

of non-tasters (Fisher, Ford and Huxley, 1939). A minority of non-tasters also exists in rats (see Boyd, 1950, p. 282), who suggests that "tasting" here was originally correlated with ability to taste the chemically related but physiologically important substance, thiouracil.

Blakeslee (1935*a* and *b*) has discovered a number of other sensory threshold morphisms, both for smell and taste. Thus over 25 per cent. of people can taste benzoate of soda, advertised as a tasteless food-preservative! I have already mentioned that in about 20 per cent. of tasters, PTC has other tastes than the normal. In some cases, there are two components in the taste of one substance (*e.g.* mannose), or in the smell of one strain of flowers, *e.g.* Freesias. In such cases some people can smell or taste both, some the first only, some the second only, and some neither. This clearly implies the involvement of two independent morphic genes. We may expect sensory threshold morphism to be widespread in higher animals: the devising of suitable methods for their detection in other groups than mammals will open up an interesting field of research.

Since sensory threshold and blood-group morphisms can be readily investigated on a large scale in man, we may expect that their study will help materially in the mapping of the human gene-complex and the elucidation of ethnic relationships. In any event, morphism in man is likely to prove the most fruitful area of human genetics. It has disclosed new and surprising phenomena, and will undoubtedly lead to new approaches in general genetics. It is making it possible for man to repay his genetic debt to other organisms. Animals like *Drosophila* and fowls, plants like *Primula* and maize, have enabled us to lay the foundations of human genetics. Now man is beginning to shed new light on the genetics of the rest of the organic world.

7. CONCLUSION

It will now be apparent that morphism (balanced genetic polymorphism) constitutes an important mode of intraspecific differentiation in many groups of animals and plants. In certain cases it may give rise to secondarily monomorphic populations, which, if isolated, may then evolve into distinct species or subspecies. It may involve a great variety of characters, both extrinsically adaptive (such as mimetic or cryptic resemblance, disease-resistance, temperature-tolerance, clutch-size and migratory habit in birds, germination-time in plants, caste in social insects) and non-adaptive (such as demonstrably non-aesthetic characters of colour or pattern). Its genetic basis may be genic (one or more single genes or groups of closely linked genes); or chromosegmental (inversions or translocations); or chromosomal (one or more extra chromosomes); or a high degree of continuous variance affecting meristic characters or stages (number of eggs in birds or moults in arthropods).

But we still do not know the details of its distribution in any given phylum or class; why some sub-groups (*e.g.* in birds and mammals) show frequent visible non-adaptive morphism and others show none;

why some groups (*e.g.* in Diptera) show abundant inversion-morphism but few or no phaneromorphic characters; why other groups show mainly or only genic morphism; or why (and where) morphic differentiation sometimes gives rise to secondary monomorphic differentiation. We are lamentably ignorant of the nature of the selective forces involved in most morphisms, and of the genetic stability-mechanisms underlying them. And in many cases we do not know whether polymorphic variation in a species is due to true morphism or to recombination after crossing of geographically differentiated monomorphic types, or even to geographical differentiation alone.

I have the feeling that Bateson would have enjoyed both our knowledge and our ignorance concerning morphism and would have found satisfying occupation in the study of the many problems which it poses.

Every clear case of true morphism challenges the general biologist to discover the ecological influences, the selective forces, and the genetic mechanisms at work. And the realisation of the widespread significance of morphism as the basis for a special type of intraspecific adaptive differentiation points to the need for a concerted and comprehensive survey of its distribution and role in all groups of animals and plants.

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ADDENDA

The page-references refer to the relevant pages of the main paper

Page 5. Jamieson (unpub.) suggests that there may be genetic differences in responsiveness to the stimuli inducing the two "phases" of *Locusta migratoria*. If so, the dimorphism would be partly genetic though mainly environmental.

Page 7. For further theoretical discussions bearing on "heterosis" as a basis for morphism, see Buzzati-Traverso, Dobzhansky, and other articles in Gowen (1952); Tebb and Thoday (1954); Burdick, 1954; Mather (1955), and especially Stone, Alexander and Clayton (1954), with its interesting discussion in biochemical and developmental terms. Sang (1955) has demonstrated the greater biochemical and metabolic efficiency of heterozygotes between two highly inbred lines of *Drosophila*, but this particular form of heterosis could probably not be utilised as a genetic basis for balanced morphism, as it presumably depends on a number of freely segregating genes.

Page 14. Interesting symmetry morphisms are found in Flatfish (Norman, 1934; Hubbs and Hubbs, 1945; Ginsburg, 1952). Most groups are essentially monomorphic dextral or sinistral, but some species are dimorphic for asymmetry. The normally dextral European Flounder, *Platichthys flesus*, has 5-36 per cent. sinistrals, the ratio varying geographically. The American *P. stellatus* is about 50 per cent. sinistral in California, 75 per cent. in Alaska, and 100 per cent. (monomorphic) in Japan. Most species of *Paralichthys* are 100 per cent. sinistral, but *P. californicus* and *P. aestuarius* are nearly 40 per cent. dextral. Some species of *Hippoglossina* and *Xistreuis* are "indifferently" dextral or sinistral, as in the primitive genus *Psettodes*. *Psettodes* is also dimorphic for the asymmetry of its optic chiasma; but higher forms are monomorphic (either dextral or sinistral) for this character, even in specimens with reversed symmetry of body-form. Reversed individuals, e.g. in *P. flesus*, appear to be at a selective disadvantage, as their frequency decreases

with age. A further analysis, aimed at discovering the counterbalancing advantage of reversal, would be of interest.

In the worm, *Spirorbis*, and the mollusc, *Ancylus*, monomorphic, sinistral and dextral species occur, but no species dimorphic for asymmetry (Caullery and Mesnil, 1897; Holmes, 1899).

Page 13. Some Deermice (*Peromyscus*) show colour-morphism. *P. maniculatus* is dimorphic buff or grey in at least 4 subspecies, buff being dominant (Clark, 1938). In *P. m. blandus*, buffs vary from 24 to 57 per cent., apparently in relation to their cryptic value on soils of different tint (Blair, 1947).

The common Water-vole of Britain, *Arvicola amphibius*, has a melanic morph whose frequency increases to the north (the "normal" grey-brown morph of the northern subspecies *A. a. reta* is also darker). In addition, all-black colonies of *A. a. amphibius* occur in the Fen district of E. Anglia (Matthews, 1952, p. 158).

The Stoat, *Mustela erminea*, is well-known for its seasonal dimorphism, turning white in winter. However, the capacity for this seasonal colour-change exhibits a marked ratio-cline, with more winter-whites to the north and east, and hardly any in the Irish sub-species *M. e. hibernica*. While temperature and possibly day-length affect the process, genetic capacity is also clearly involved, and exhibits a geographically-graded true morphism. The British Weasel, *M. nivalis*, never whitens in Britain but does so in northern and mountainous regions in Europe (Matthews, 1952, pp. 225-7, 251-2).

The Brown Rat, *Rattus norvegicus*, has a melanic morph sporadically all over its range, while the Black Rat, *R. rattus*, shows geographical colour-variation which has led to hybrid recombinational variation in certain areas (Matthews, 1952, p. 169).

The White-throated Packrat, *Neotoma albigula*, is dimorphic, with melanics outnumbering "normal" greys in areas of dark lava (Blair, W. F., 1954, *J. Mammal.*, 35, 239). The advantage of the melanic is cryptic; the presence of about 33 per cent. greys is due to gene-flow and immigration from non-dark areas.

The mongoose, *Herpestes brachyurus*, is dimorphic (reddish and blackish) in several subspecies (Schwartz, 1947). Stullken and Hiestand (1953) show that pigmentation may be of general (metabolic) advantage in relation to heat-conservation.

Page 16. Melanics occur in the introduced *Trichosurus vulpecula* population of New Zealand (Wodzicki, 1950), but whether they were part of the original introduction or due to the spread of later mutants is uncertain; nor are any data as to morph-ratios available. Wodzicki does not record any colour-variants in the introduced Rabbits in New Zealand, and mentions the extreme rarity of winter-whites in introduced Stoats in New Zealand. It would be interesting to determine the incidence of morphism in introduced species, and the residual polymorphism (if any) in feral populations of variable domestic species such as cats and pigs.

Page 18. Bateson (1913) gives various examples of sharp coloration-morphism in insects. *E.g.* the yellow-spotted butterfly, *Thais rumina*, has a red-spotted morph in one area (p. 27); the moth, *Noctua castanea*, is dimorphic for red and grey forewings, with geographical variation in morph-ratio: in one British locality, a rare yellow-winged morph occurs (p. 122). The high polymorphism of the Potato-beetle, *Leptinotarsa*, later described by Tower (1918), appears to be largely geographical, but with true morphism also involved: it might well be re-investigated by modern methods. The Lesser Underwing Moth, *Tryphaena comus*, has a dark morph (*curtisii*) in the northern parts of its range. Ford (1952) has shown that the *curtisii* morphs in Orkney and in the Hebrides, though indistinguishable by inspection, have had their dominance independently established by the incorporation of different modifiers.

Page 19. *Lebistes* is much more ecologically versatile than the related (and often sympatric) *Poecilia vivipara* and *Micropoecilia parae*, which are monomorphic

in both sexes (*cf. Drosophila*, p. 12). *Platypoecilus* (now *Xiphophorus*) *maculatus* has numerous morphic patterns in both sexes. These are controlled by two sets of multiple alleles (or semi-alleles), one (autosomal) of 7, the other (sex-linked) of 5, for micro- and macro-melanophore pattern respectively. The morph-ratios differ considerably in different isolated populations, and some alleles are absent in most. One population has had a roughly constant morph-ratio since 1867. The related monomorphic *P. (X.) couchianus* and *P. (X.) xiphidium* are more restricted in range (Gordon, 1947; Gordon and Gordon, 1950, 1954; Clark, Aronson and Gordon, 1954). Myers (1925, 1931) states that *Mollenesia*, *Gambusia* and *Fundulus* may show "melanodimorphism".

In the Bluehead Wrasse, *Thalassoma bifasciatum*, Tee-Van (1932) showed that most of the striking variation is physiologically determined, but some seems to have a genetic (morphic) basis. Pomini (1940) claims that in trout (*Salmo trutta*), in addition to marked geographical polymorphism, some populations show true morphism. Hardy (1955, *The Open Sea*, Collins) states that the marine catfish, *Anarrichas lupus*, has a spotted morph in addition to the usual banded form.

Page 20. In *Primula sinensis* short-style homostyly depends on a gene which enlarges the "eye" of the corolla as well as reducing style-length in genetically long-styled plants—an excellent example of a "correlated character" (p. 13). For references and other examples, see Huxley, 1942, p. 189.

Page 21. Excessive variability, presumably implying continuous morphism, occurs in many other animals: *e.g.* in the moths, *Dianthoecia carpophaga* (as against the "monomorphic" *D. capsincola*), *Agrotis segetum* and *A. tritici* (as against *A. suffusa* (*ypsilon*)), *Noctua festiva* (as against *N. triangulum* and *N. umbrosa*), *Taeniocampa instabilis* (as against *T. cruda* (*pulvurulenta*)), *Plusia interrogationis* (as against most other species), or *Peronea cristata* (as against *P. schalleriana*); see Bateson, 1913, ch. 1.

Page 23. Hoestland (1955, *C. R. Acad. Sci.*, 240, 916) gives further data on *Sphaeroma*. In Britain, as in Brittany, it has five "structural" and two coloration morphs. The frequency of most morphs is correlated (to varying degrees) with temperature; but of one, with sheltered habitat. Morph-ratios differ in the various islands of the Scillies.

Page 25. Callan (1941) discovered a sex-chromosome morphism in the earwig, *Forficula auricularia*, males being either X_1Y or X_1X_2Y , those of the latter type producing fewer male than female offspring. Callan suggests that this may be an advantage where population is dense, and one male can accordingly fertilise several females. In any event, the male sex-ratio does vary markedly in *Forficula*, and is lowest (16 per cent.) in the very dense populations of the Scilly Islands (Brindley, 1912), where the greatest proportion of "high" (long forceps) males also occurs (p. 25). Further research on this association of two morphic characters would be of great interest.

Page 34. Grüneberg (1947) refers to various blood-group systems in other mammals. Thus, in domestic rabbits, there are several, including one whose genetic basis (3 multiple alleles or semi-alleles) is similar to that of the human ABO system. In rats there are 4 blood-groups; and in wild *Peromyscus* there are specific and subspecific antigenic differences. The high correlation (0.7) found between leucocyte-level and longevity in rats and mice shows how blood-characters may have selective correlates. He also mentions genetic differences in disease-resistance in various animals, in resistance to various drugs in mice, and in metabolic capacity in rabbits and sheep, which presumably might in certain circumstances become established as morphisms.

Haldane (1954, ch. 2) gives examples of genetic biochemical differences in blood and other characters which may prove to be morphic.