

Morphological Resemblance and its Relationship to Genetic Distance Measures¹

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ABSTRACT: The advent of a number of genetic and cytogenetic approaches to the measurement of the distance between populations and species has radically changed the study of the relationships between groups of animals. Morphological resemblance, as a measure of divergence, can now be compared with results obtained using these new techniques. This contribution is an attempt to consider the degree of concordance of these different approaches. Particular attention is paid to species of the genus Drosophila; however, a broad range of groups is discussed as well. It is argued that it is not meaningful to relate any genetic divergence measure to the taxonomic categories, subspecies, "sibling" species and "non-sibling" species. With genetical species no relationship exists between morphological divergence and the two most common forms of genetic distance, chromosomal and electromorphic distance. If speciation is thought of in terms of a change from one Specific-Mate Recognition System (Paterson, 1976, 1978, 1980, 1981) to another, one would not expect any consistent relationship to exist.

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There has been a great deal of discussion in recent times regarding the genetic divergence which is to be expected between groups of organisms whether these groups be species, sub-species, etc. The question is an important one since these genetic distances between groups have been used to construct dendrograms of relatedness. Inherent in many discussions is a belief that speciation events are accompanied by a set amount of genetic change (e.g. Avise, 1976; Ayala, 1975). This assumption is vital if degrees of relatedness are to be assessed using the genetic distance method. If speciation events are not accompanied by a set amount of divergence, as measured by the two most common estimates of genetic distance, chromosomal and electromorphic distance, then the method must be treated with extreme caution.

Any discussion of speciation should be based on a firm understanding of the nature of species. This must surely be the logical beginning (Paterson, 1981).

Species Concepts

The most commonly accepted species definition is one based on reproductive isolation. Species are, according to this view, "groups of organisms which are reproductively isolated from other groups" (Mayr, 1963). In keeping with this viewpoint, Dobzhansky (1970) commented "Species are ... systems of populations; the gene exchange between systems is limited or prevented in nature by a reproductive isolating mechanism or perhaps by a combination of several such mechanisms" (Dobzhansky, 1970, p.357). This has been called the Isolation Concept (Paterson, 1978). Isolating Mechanisms are generally regarded as comprising two broad classes: premating and postmating mechanisms (Mayr, 1963; Dobzhansky, 1970; White, 1978; Stebbins, 1950; Grant, 1971).

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Since, however, postmating isolating mechanisms cannot be directly selected for, as realized originally by Darwin (1859), then these are surely not mechanisms which evolved for the function of isolation (*sensu*, Williams, 1966). Similarly, as Paterson (1981) has emphasized, many authors such as White (1978), Dobzhansky (1970) and Mayr (1963) have argued that there is indisputable evidence that species arise in allopatry. Clearly then, species that arise in such a way should not be described as having acquired "Isolating Mechanisms" since these have evolved in geographic separation from the parental population.

Dobzhansky (1951, 1970) maintained logical consistency by advocating a model of speciation which allowed a direct role for natural selection in the origin of species. This is the model of speciation by reinforcement. However Paterson (1978) and Moore (1957) have raised difficulties with the theoretical basis of this model. An increasing number of authors have also commented on the lack of convincing cases in the literature (Mayr, 1963; Loftus-Hills, 1975; Jackson, 1973; Futuyma and Mayer, 1980).

The Recognition Concept defines species purely in relation to conspecifics. According to this view species are groups of organisms which are tied together by a common communication system. This has been called the Specific-Mate Recognition System. Mayr (1963) views species in both negative ('isolation') and positive ('recognition') terms, e.g. "The ethological isolating mechanisms then, are barriers to mating due to incompatibilities in behaviour {negative isolation aspect}. The males of every species have specific courtships or displays to which, on the whole, only females of the same species are receptive. {Positive or recognition aspect}". (Mayr, 1963, p.95). The Recognition Concept views "postmating isolating mechanisms" as unsatisfactory criteria for delineating species (Paterson, 1981). Postmating effects are instead considered as intraspecific phenomena. This is reasonable since in angiosperms incompatibility genes are easily accommodated in this way. Similarly in some animals such as the mosquito species Culex molestus sterility is a within species phenomena (see Paterson, 1981 for an extensive discussion of these points).

If the SMRS of individuals of a daughter population changes such that they no longer recognise as mates members of the parental population, then a speciation event has occurred. This incidentally also results in the origin of a new and distinct gene pool.

Species and their characteristic stability

Since the Recognition Concept solves many of conceptual difficulties inherent in an isolationist approach to the study of species, this discussion will be framed in terms of species as a group of individuals which share a common SMRS. This is a genetically programmed system which has been acted upon by natural selection to function efficiently in the preferred habitat of a species and results in conspecific syngamy. Paterson (1976) has discussed details of the system and pointed out that it is under stabilizing selection. This is because individuals which are deviant in one or more of the steps comprising the SMRS are less likely to be recognized as mates by conspecifics. The more deviant an individual is, the lower is its selective advantage. We would then expect that the SMRS will show a stability within a species that is not shown by most other characters, as was realized by Walker (1964, pp. 351-353).

Recent studies on Drosophila melanogaster provide evidence in support of this expectation. Teissier (1958) and Takanashi and Kitagawa (1977) have shown that French and Japanese populations of this species differ considerably as reflected by biometric techniques. Kojima *et al.* (1970) and Girard and Palabost (1976) show that significant differences in the frequencies of electromorphs exist between the two populations. However, choice experiments between these two populations, reported by Petit *et al.* (1976) reveal that the SMRS's of the two populations have not diverged,

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and that individuals of either population do not distinguish between Japanese and French mates. David and Bocquet (1975) and David *et al.* (1977) have compared biometrically African and French strains of Drosophila melanogaster and found them to be very divergent. In fact the populations have non-overlapping distributions in a bivariate plot of characters such as female ovariole number and female abdominal chaetae length. Tests in progress, designed to compare the degree of divergence of the SMRS's of the populations have not revealed any divergence (David, personal communication). A similar case illustrating a lack of variation in the SMRS is that of Anderson and Ehrman (1967). These authors demonstrated random mating between widespread populations of Drosophila pseudoobscura from North America.

These studies provide evidence for the geographic stability of the SMRS. This is vital so that individuals of any sexually reproducing species can recognize conspecific mates for the purpose of sexual reproduction. Although other coadapted characters exist, many which are not involved in mate recognition are not subject to these same constraints, and hence are more likely to respond to local selective pressures and show greater variation.

If each biparental species has its own SMRS and hybrids are rare in nature, then speciation occurs when a daughter population moves from the SMRS of a parental population to another quite distinct and effectively non-overlapping system. This involves a change in the male-female communication system of the original population from which the founder came and the restabilization of the new system in the daughter species. When the population increases to a large size, the SMRS becomes stabilized, and hence is buffered from further change. Only under conditions of small population size is it likely that the SMRS can change and again become fixed. Sometimes in small peripheral isolates natural selection can directly cause a change in the SMRS resulting in an increase in its efficiency in the new environment. The alternative, and other likely outcome of such a situation, is that the population will become extinct. Another possible process that can lead to a new SMRS is that in a small isolate the SMRS of one sex could be pleiotropically affected by another gene. If this gene confers a selective advantage upon individuals carrying it, and the population is small, it may become fixed. Under this no-choice situation through many generations, the SMRS of the unaffected sex will be selected to recognize once again the signals of the other sex. A good model for such a process is the yellow allele in Drosophila melanogaster (Bastock, 1956). Yellow males have a deviant courtship pattern while yellow females are normal. Since the gene also confers on its carrier a resistance to starvation (Kalmus, 1941) this could, in a certain new environment, lead to its fixation in a small isolate. Females would then be selected for improvement in recognition of the mutant male SMRS.

The work of David, Teissier and Petit *et al.* presented earlier, shows that morphologically and electromorphically populations of a species can diverge, while the system of mate recognition remains stable. In a large population the recognition system should be resistant to change owing to the difficulty in fixing genes in anything but small populations.

Evolutionary Biology's "Cardinal Problem"

A genetic consequence of this concept of a species is that after any particular speciation event the degree of divergence in genes controlling external morphological characters is not necessarily representative of the total of all the genetic changes that have occurred. If a speciation event is the change from one stabilized SMRS to another reconstructed and restabilized SMRS, then this will sometimes be accompanied by very small changes in the total genome and sometimes by larger changes. Ayala (1975) has described the question of the amount of genetic change that occurs at speciation as "... the cardinal problem of evolutionary biology". Nevo and Cleve (1978) have recently said "How many and what kind of genes are implicated in speciation

is a central unresolved problem of evolutionary biology. Does speciation require major genomic changes or may minor ones suffice? Lewontin in his influential book (1974, p.186) has suggested that the genetic differences between sibling species will always be greater than 10% of the total genome as reflected by electrophoresis studies.

In keeping with this inherent supposition that a speciation event is marked by a set amount of genetic divergence Ayala (1975) and Avise (1976) have maintained that a certain degree of genetic change can be equated to various taxonomic categories, e.g. subspecies, "sibling" species, etc. If speciation is thought of in terms of a change in SMRS then one would not expect any consistent relationship to exist. It is argued here that a thorough search of the literature reveals that this expectation is verified.

A consistent relationship? - Evidence from the literature

The important Hawaiian *Drosophila* project (see Carson et al. 1970 for review) has provided a number of evolutionary examples which have a bearing on this general question. Firstly, *D. heteroneura* and *D. silvestris* (of the *plantibia* subgroup) are two closely related species which are sympatric at many localities on the island of Hawaii. These species are homosequential for the banding pattern on larval polytene chromosomes and have a genetic similarity coefficient of 0.95. On the scale provided by Ayala (1975) this is similar to the level of subpopulations of one species. However, morphologically, males of these species are very distinct (see Val, 1977 for details) and were originally (i.e. before the use of these genetic techniques) considered by systematists not to be closely related.

Another two Hawaiian *Drosophila* species, *D. setosimentum* and *D. ochrobasis*, members of the *adiastola* subgroup, are two closely related species and chromosomally divergent to the extent that they have a chromosomal similarity coefficient of 0.66 - 0.68 (Carson et al. 1975). The species have an electromorphic similarity coefficient, in some areas of 0.98 (Carson et al. 1975). Again this falls within the range of populations of the one species according to Ayala (1975). Also within the *plantibia* subgroup *D. cyrtoloma*, *D. ingens* and *D. melanocephala* have similarity coefficients from 0.99 - 0.96 (Johnson et al. 1975). These examples alone demonstrate the lack of utility in Ayala and co-workers' proposal.

Cases such as these are readily understood when speciation is thought of in terms of changes in the SMRS. Many Hawaiian *Drosophila* perform lek mating behaviour. Males attract females to a courtship site away from the feeding area. They display to females and these males signals, such as the waving of patterned wings and the presence of elaborate head characteristics, are certainly involved in the SMRS (Spieth, 1974). These species use optical signals in mate recognition and hence we can also use them in order to recognize these discrete units in nature.

A number of the species of the *Anopheles gambiae* complex of mosquitoes are morphologically identical despite many attempts to distinguish them. (Coluzzi, 1964; Green, 1972). These species have diverged enzymatically, to the extent that Mahon et al. (1976) and Miles (1978) have used electrophoresis as a reliable method of identification of these cryptic species. Presumably males and females of these species use non-morphological cues in their recognition of conspecific mates, i.e. in the SMRS, and the degree of morphological change associated with a change in the SMRS in this group in no way reflects the degree of total genetic change that has occurred.

Indeed the mere existence of cryptic species, with varying degrees of genetic similarity, argue against any consistent relationship between morphological and genetic change at speciation. It might be suggested that these varying degrees of genetic change are the result of different types of speciation. However we regard non-allopatric models of speciation as unconvincing (as do Futuyma and Mayer (1981)).

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Chromosomal changes have not been shown to cause speciation, for example, they have only been shown to be correlated with it. If speciation occurs via small isolated populations, this would be expected. Paterson (1981) has discussed a number of these models and concluded that convincing evidence is available for speciation of allopatric populations only. Speciation via founder populations would indeed predict varying degrees of genetic change at speciation.

Lambert (1979, 1981a) has presented cytogenetic evidence for the existence of four cryptic species within the African mosquito "Anopheles marshallii". Ovarian polytene chromosome analysis shows a total lack of interbreeding between individuals of these species in the wild, even though they are sympatric over wide areas. This indicates that complete divergence in the SMRS's of these species has occurred. The species are morphologically very alike and adults can only be separated by multivariate analysis of wing and palp characters. These species are electromorphically very similar, having similarity coefficients of from 0.9718 to 0.8027 (Lambert, 1981b).

Although they do not commit themselves with regard to the status of their forms, Carde et al. (1978) have presented very good evidence of the existence of two previously unsuspected cryptic species within the European corn borer (Ostrinia nubilalis). The two species use the same chemical components, Z-11 and E-11 tetradecenyl acetate in their pheromones. These are involved in mate recognition. However they are present in different proportions - one uses a mixture of 97:3, and the other 4:96. The two species are very similar as indicated by electromorph studies, having a similarity coefficient of 0.997. Field trapping experiments by Carde et al. (1978) illustrate the individuals of the two species respond only to the blend characteristic of their own species. In this case a change in the SMRS has been accompanied by very little electromorphic divergence.

Any estimation of the degree of genetic divergence which accompanies a change in the SMRS must be complicated by the factor of postspeciation change. However data such as that discussed for Hawaiian Drosophila, "Anopheles marshallii" and the European corn borer indicate that some speciation events, at least, are accompanied by very little detectable change. It is certainly at least possible that regulatory genes are involved in the genetic changes associated with speciation (Wilson, 1975). This would then account for the low levels of divergence as reflected in electromorph studies. At this stage however, we consider that the evidence for this is suggestive but certainly not conclusive.

In animals which use non-morphological cues in the recognition of conspecific mates, speciation can occur without any accompanying divergence in morphology. If the divergence in genes controlling external morphology is no reflection of the total genetic changes that have occurred in the speciation events, then we should not be surprised to find two such strikingly different degrees of electromorphic divergence as that found in the corn borer and the A. gambiae group of species. It is conceivable that very small changes might accompany the change in pheromone components in the two species of corn borers, for example, and perhaps much more considerable changes in the case of some of the A. gambiae species. This may well be related to the rapidity with which each individual speciation event occurs. If it happens quickly, and the population size increases quickly, few genetic differences may result. However, if it takes a longer period, more changes are likely to accumulate. A flush-crash cycle such as detailed by Hampton Carson (1975) could conceivably result in an altered SMRS becoming fixed in an allopatric isolate of a parental species while resulting in only minor electromorphic divergence. See Powell (1978) for some experimental support for Carson's theory. Similarly the degree of genetic change may be dependent upon the characteristics of the environment in which the small population is restricted. Drastic changes in characteristics of the available habitat may, for example, result in substantial genetic change accompanying speciation.

Maxson and Wilson (1974) have presented a case of the two North American tree frogs (Hyla eximia and Hyla regilla) which are morphologically almost identical and yet vary considerably on proteins; so much so that the species differ as much from each other as they do from species outside the genus Hyla. Perhaps the best example of small genetic divergence accompanied by very considerable morphological changes is the case of man and chimpanzees (King and Wilson, 1975). These species have a similarity coefficient which is equal to that found for many cryptic species and yet are morphologically quite distinct. Recently Bruce and Ayala (1978) have reported the results of electromorphoresis studies which show that human proteins are very similar to the proteins of seven species of apes studied.

Lyons et al. (1977, 1981) have recently shown the existence of two biologically distinct species with different chromosome numbers, $2n=32$ and $2n=36$, within the taxonomic species Mastomys natalensis. This "species" has been implicated as a carrier of Lassa virus and Plague bacilli in Africa. These studies have shown that there is little homology between the G-banding patterns of the species. Further studies (Green et al. 1978) have revealed a divergence in haemoglobin patterns of the two species as shown by gel electrophoresis. Consequent attempts to distinguish the two species using discriminant function analysis on morphological characters have yielded only limited results (Gordon, personal communication), indicating the high degree of morphological similarity of the species. Mate recognition in these species is achieved at least partly by ultrasonic communication, and the two species have diverged considerably in this regard (Gordon, personal communication).

Since haemoglobins are such evolutionarily stable molecules (Dickerson and Geis, 1969) and considering the results of the G-banding studies, these species appear to have been separate for a considerable period of time yet morphologically they are extremely similar. Obviously a phenetic approach to such a problem is completely inappropriate as Green et al. (1978) have stressed. Only a genetical or behavioural approach to such a situation could have revealed the existence of these two cryptic species.

A number of cases which have been proposed as examples of divergence with little protein differentiation have appeared in the literature (Avisé et al. 1975; Gartside et al. 1977; Nevo and Cleve, 1978; Nevo and Shaw, 1972; Prakash, 1972, 1977; Turner, 1974; Brown, 1981). The degrees of morphological divergence which have accompanied these changes vary from quite considerable, in the case of the Californian minnows, to almost none in the case of the species of the complex of mole rats and the ribbon snakes.

Conclusion

At the level of closely related species the argument presented here is that there is no consistent correlation between morphological resemblance and genetic distance, because no set amount of genetic divergence can be found to accompany speciation events. Similarly, depending upon the predominant communication channel, e.g. visual, chemical, auditory, etc. that the species use in mate recognition, there will be varying degrees of morphological divergence associated with a change in the SMRS. It should be pointed out that, in the long term, the longer the time since the divergence of two species from a common ancestral population, the greater the genetic distance can be expected to be.

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