



## Review

# Geographic variation: a synthesis of cause, data, pattern and congruence in relation to subspecies, multivariate analysis and phylogenesis

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### ABSTRACT

Morphological features are similar to most other types of features insofar as their patterns of geographic variation can be caused by both current ecological conditions and historical factors i.e. phylogenesis. Geographic variation in morphology is almost universal and often complex. Morphological and other features show a wide range of patterns of geographic variation i.e. clinal, categorical, and mosaic etc. The extent of pattern congruence between characters is to some extent predicted by both the extent of genetic independence and the cause of the geographic variation. The existing «conventional» procedure of naming subspecies typically fails to take into account the facts of intraspecific variation and consequently does not elucidate the patterns of geographic variation or their cause. Multivariate character analysis, based on ordination analysis and assisted by mapping techniques, can elucidate the range of patterns of geographic variation and may indicate their congruence, predictivity and cause. A more directly hypothesized intraspecific phylogeny can be obtained from qualitative karyotypic information or numerical phylogenetic analysis of quantitative morphological (and other) data. When the pattern of anagenesis is considered numerical phylogenetic analysis of morphological data indicates the primary or secondary origin of some transition (hybrid) zones. It is evident from the morphological and other studies that intraspecific lineages and their reticulation can be defined and that their ability to reticulate is not necessarily related to rank. Conventional subspecies are found not to relate to multivariate patterns or hypothesized phylogeny. If subspecific nomenclature is to be used then consideration should be given to the nature of the geographic variation, its cause and its rank.

**KEY WORDS:** Geographic variation; Multivariate analysis; Phylogenetic analysis; Subspecies.

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### 1. INTRODUCTION

The interrelationships between the cause of geographic variation, the type of data, the resultant patterns and character congruence is synthesized in relation to the various systematic approaches to studying geographic variation, i.e. naming conventional subspecies, multivariate analysis of phenetic patterns and direct phylogenetic reconstruction. These approaches to studying geographic variation are compared once the groundwork has been laid by considering cause, data, pattern and congruence. Particular reference is made to morphological studies of vertebrates.

### 2. CAUSE OF GEOGRAPHIC VARIATION

One can loosely divide the causes of geographic variation into two classes (Endler, 1983; Thorpe, 1984a), i.e. current ecology and historical processes or phylogenesis. Current ecology consists of the balance between gene flow and natural selection for current conditions. The current ecological conditions can be biotic, e.g. mimicry (Greene & McDiarmid, 1981), character displacement and interspecific competition etc. or physical such as substrate adaptation or adaptation for climatic conditions such as Bergmann's and Allen's rule (Johnston & Selander, 1973; Fleischer & Johnston, 1982).

The relative importance between gene flow and selection was discussed largely in the seventies (Ehrlich & Raven, 1969; Endler, 1977; Jackson & Pounds, 1979). There has been a shift of opinion away from the view typified by Mayr (1970), that gene flow is a powerful cohesive force, to the view that it is of far less significance. Some recent papers (Macauley, 1983; Handel, 1983; Handel & Le Vie Mishkin, 1984) have tended to support the view that gene flow is rather limited.

The most convincing cases of patterns of geographic variation being caused by adaptation to current ecological conditions come from studies of birds recently introduced into the new world (Baker, 1980; Baker & Mooed, 1979; Fleischer & Johnston, 1982; Johnston & Selander, 1973). Being recently introduced and assuming no multiple colonization from divergent stocks, the influence of past events and conditions can be discounted and the patterns can be ascribed to «current ecology». Baker's (1980) study of the house sparrow introduced into New Zealand 80 years previously, indicates that there is a north-south cline in general size. Whilst there is no clear functional explanation this pattern must be due to «current ecology».

Historical factors, i.e. phylogenesis, can leave deep-seated, distinct patterns of geographic variation such as the parapatric forms associated with incipient allopatric speciation (Thorpe, 1975, 1979). When an historical process results in the isolation of populations (e.g. colonization of an island or segmentation of a species

range by geological events) divergent lineages can be caused by founder effects, genetic drift and presumably by past ecological conditions. Subsequent changes in the range of the populations can result in further vicariance, or secondary contact of the populations resulting in either overlap, sharp transition zones or introgression (i.e. reticulation of the lineages).

An example of a historical factor causing a pattern of geographic variation is given by the influence of the Pleistocene ice caps on the vertebrate fauna of Europe. The «hybrid» zones in the grass snake *Natrix natrix* and other vertebrate species (mapped in Thorpe, 1979) have similar, (but not identical) north-south orientation in central Europe, and are not related to abrupt changes in ecological conditions or physiographic features. Consequently, they may have been caused by the Pleistocene ice caps splitting a species into separate south-east and south-west refugia, which diverged in allopatry, and met along the narrow transition («hybrid») zones in central Europe due to post-Pleistocene range expansion.

Workers interested in one of these factors, i.e. ecology or phylogeny, often ignore the importance of the other factor, for example, Endler (1983) has pointed out that workers (Prance, 1982) who interpret the transition zones in the Amazon forest as solely due to the historical effects of Pleistocene forest refugia ignore the equally probable explanation due to current ecological conditions. Similarly, Fleischer & Johnston (1982) in their exemplary study of the effects of current ecology open their paper by the misleading statement that the «variation in morphology across a species range is largely a function of climatic conditions». This ignores the considerable importance of phylogenesis in causing patterns of geographic variation in morphology of many species (Thorpe, 1979, 1984a and references therein).

In reality, most species in natural (not recently introduced) circumstances will have patterns of geographic variation that are influenced by both main factors to a greater or lesser degree.

### 3. DATA TYPES

Whilst this paper is primarily concerned with morphology it is as well to compare it to other types of character so that a sense of proportion can be established as to the utility of the various character types when studying certain facets of geographic variation. Various sets of people may assume that certain types of character are influenced by particular causes of geographic variation but such absolute claims are not supported by close examination. Morphology in particular can be influenced by both sets of factors (see Thorpe, 1984a) for phylogenetic causation and Johnston & Selandier, 1973 for ecological causation) in spite of the above quote from Fleischer & Johnston (1982). As for

biochemical data revealing «genetic» information, i.e. electrophoretic and blood type frequencies, neutralists may assume the absence of selection effects but studies on the geographic variation of gene frequencies in lizards (Nevo, 1981), humans (Piazza *et al.*) and other organisms can be convincingly interpreted in terms of the effects of natural selection for current ecological conditions. Similarly the karyotype may supply excellent information for the reconstruction of intraspecific phylogenies (Corti *et al.*, in press; Thorpe *et al.*, 1982; Searle, 1984) but selection for current ecological conditions is implicated in Berry & Baker's (1971) study of acrocentric number in pocket gophers and in other cases of chromosomal variation (p. 50, White, 1988). Recently mitochondrial DNA sequencing has been used to study geographic variation in small north American mammals etc. with the assumption that it reveals the maternal phylogeny independent of selection effects (Lansman *et al.*, 1983). The mt DNA may be a useful data source for phylogenetic reconstruction but perhaps it is too early to assume selective neutrality without coherent evidence to this end. Pertinent evidence is difficult to obtain but the material inheritance of some human diseases and the maternal inheritance of the age of onset of other human diseases (Merril & Harrington, 1985 and references therein) implicate mtDNA genes. In these cases any deleterious effects before or during reproductive age could hardly be selectively neutral. Some of the mtDNA phylogenies are admittedly incongruent with those indicated by the other available data. This, together with the difference in mode of inheritance between nuclear genotype and mtDNA may mean that phylogenies based on the latter may not necessarily be of predictive value regarding the genotype. See also Wilson *et al.* (1985) and references therein.

Consequently, broadly speaking, morphology appears to be the same as the other types of characters insofar as the patterns of geographic variation can be influenced by both current ecology and phylogenesis.

### 4. PATTERNS OF GEOGRAPHIC VARIATION

Generally speaking, (given some exceptions), the question «is there geographic variation» is trivial. This is because geographic variation is ubiquitous and only in a very restricted number of cases, e.g. minute breeding range as in birds living on single oceanic islands, can vertebrates not show geographic variation. Even in species that were thought not to show geographic variation due to genetic or phenotypic stability (e.g. *Limulus*, Mayr, 1970), geographic variation has been found once the appropriate techniques have been used (Riska, 1981) and cases of within island geographic variation in vertebrates are being documented (Thorpe & Baez, 1987).

To be of much value the above question has to be qualified to «is there detectable geographic variation in a given set of characters in a given segment of the species range». Some characters may not show any geographic variation or enough geographic variation for it to be detectable, whilst some areas may be too uniform or too recently colonized for any detectable spatial variation to be apparent.

In most studies one is interested in the actual pattern of geographic variation rather than simply showing that geographic variation occurs. Morphological studies show a wide range of patterns of geographic variation which can be classified as follows:

#### 4.1. Clinal variation

A gradual, smooth, unidirectional change in the character with space is clinal variation. An example of this is the change in bill length with longitude in the nuthatch *Sitta tephronata* (Fig. 4 in Grant, 1972). The spatial dimensions involved include bathymetric depth as in the clinal variation in trilobite somite number and altitude as in clinal variation in grasshopper morphometrics (Campbell & Dearn, 1980) and lizard scalation (Thorpe & Baez, 1987). Examples of clinal variation in vertebrates are given by Johnston & Selander's (1973) study of clinal variation in general body size of sparrows in North America and Piazza *et al.*'s (1981) and Menozzi *et al.*'s (1978) multivariate study of latitudinal clines of gene frequencies in humans.

Stepped clines can refer to the situation where there is a sharp step in an otherwise gradual cline (Grant, 1972) or it can also refer to the situation where there are two uniform areas separated by a transition zone (Endler, 1977, 1983). I believe (Thorpe, 1985a) that this latter type of variation is more usefully referred to as categorical variation (as below), i.e. two «uniform» categories separated by a sharp transition zone.

#### 4.2. Categorical variation

When distinct geographic categories can be recognised the variation is referred to as categorical geographic variation. Categories of island populations are exemplified by the northern and southern categories of the Adriatic island wall lizards *Podarcis sicula* and *meli-sellensis* (Clover, 1979; Thorpe, 1980), and the geographic categories of green geckos *Phelsuma* in the Seychelles (Thorpe, 1983a; Gardner, 1984).

Allopatric mainland categories are similar to island categories insofar as there is no transition zone between the categories. An example of purported allopatric mainland categories is afforded by eastern and western lowland gorillas (Groves, 1970). When morphology is plotted against a geographical transect then parapatric mainland categorical variation is seen as a flat plateau joined to a flat valley by a transition zone, as in the eastern and western races of *N. natrix*

(Thorpe, 1979, 1980, 1985a). Other examples of this type of geographical variation in the morphology of vertebrates include the variation of the mouse *Mus musculus/domesticus* (Ursin, 1952) and the hooded and carrion crow races, *Corvus corone*, in Europe (Meise, 1928).

#### 4.3. Transition zones

Transition, contact or «hybrid» zones are regions of rapid transition between relatively stable geographic races. They are of considerable interest to population geneticists, evolutionary biologists and systematists (Mayr, 1970; Endler, 1977, 1983; Barton & Hewitt, 1985; Thorpe, 1984a; Woodruff, 1973) and many of the theories of speciation are based on observations on transition zones (White, 1978). They are not fully dealt with here.

The zone between the hooded and carrion crows in Scotland is moving southwards and so provides an example of a dynamic transition zone changing its position with time (Cook, 1975). The transition zone between the eastern and western races of *N. natrix* is an example of a zone that has different widths along its length (Thorpe 1979) as it is much wider in the Po Valley (northern Italy) than in northern Switzerland. Endler (1983) defines the relative width of a transition zone as the width divided by the gene flow distance and he suggests that this value varies from *ca.* 4 for sharp zones to *ca.* 100 for gradual zones. In northern Switzerland the steepest part of the *N. natrix* zone (Thorpe, 1979) is *ca.* 15 Km wide and with an assumed gene flow distance of 2 this gives a relative width of *ca.* 7 which on Endler's scale is quite steep.

Apart from the width one can also directly observe other phenetic facets of the nature of the zone such as the shape, penetrance of a given character or linear combination of characters and one can even deduce whether the intermediates are FIs from whether the two parental types are in the same locality as the intermediates (Thorpe, 1979). Also the genetic structure of the zone, e.g. the selective disadvantage of intermediates and mate selection, can be studied. However, the most pertinent point is whether the zone is due to secondary contact of previously allopatric populations or if it is due to primary differentiation of the populations in situ, and as Endler (1977) has pointed out this cannot readily, if ever, be deduced directly from the nature of the individual zone. Consequently, the studies of transition zones, upon which speciation mechanisms etc. are proposed, generally assume, rather than deduce, whether the zone is primary (e.g. stasipatric speciation) or secondary (e.g. allopatric speciation) in origin. In fact, it can be possible to directly deduce whether an individual zone is primary or secondary in origin but this may require additional phylogenetic analysis as in Thorpe's (1984) study of transition zones in the grass snake (see below).

#### 4.4. *Mosaic variation*

Mosaic, patchwork or crazy quilt variation is where geographical areas, inhabited by populations with distinct characteristics, are haphazardly distributed across the range of the species. Sokal *et al.*'s (1980) study of the morphology of gall aphids provides an example of this type of geographic variation. Since patch size may be related to dispersal ability, vertebrates, with their tendency for higher vagility, are less likely to provide examples of this type of geographic variation than invertebrates but size variation within the island of Tenerife may provide an example (Thorpe & Baez, 1987).

#### 4.5. *Independent divergence of island populations*

As well as the distinct categories of island populations mentioned above, many island populations diverge from the mainland independently of one another and so show no special affinity to other island populations. Many of the island populations of *N. natrix* show this pattern of divergence (Thorpe, 1979; 1984b, c). As exemplified by *N. natrix*, a species may have a series of populations which show a progressive range of divergence from those that are similar to the mainland populations to those that are very highly divergent from all other populations.

#### 4.6. *Ecotypic variation*

Species with low vagility, that are also subject to strong selection for a particular phenotype in a given habitat, may develop a pattern of geographic variation where spatial patches of a particular habitat type or ecotype are occupied by populations with the appropriate characteristics, e.g. industrial melanism in lepidoptera (Kettlewell, 1961). These characteristics are genetically controlled rather than the product of direct environmental induction.

#### 4.7. *Microgeographic variation*

The house mouse affords some of the best examples of microgeographic variation as its strongly demic population structure and short life cycle allow morphological and biochemical differences to develop over very small distances. Morphological differences between demes of house mice can be found within barns, houses and hayricks (Anderson, 1970; Berry, 1963; Petras, 1967; Thorpe, 1981; Weber, 1950) and this tendency for microgeographic variation is confirmed by electrophoretic studies of differentiation within barns (Selander, 1970).

#### 4.8. *Geographic trends in the extent of inter-locality divergence*

It is apparent that within some species there are regions of high inter-locality divergence (i.e. high geo-

graphic variation) whilst in other regions there tends to be a low level of inter-locality divergence. Both the western grass snake *N. natrix helvetica* (Thorpe, 1984b) and eastern grass snake *N. n. natrix* (Thorpe, 1984c) are an example of this as they tend to show less morphological divergence between adjacent populations in the north of the range than between adjacent populations in the south of the range. A further example of this pattern is provided by sub-Saharan human populations which are reported to show greater divergence in the geographic periphery than in the geographic centre (Rightmire, 1976).

#### 4.9. *Combination of patterns and other factors*

These simple patterns are often obscured in practice because different patterns can be overlaid in the same section of the species range or occur in different sections of the range. Moreover, the geographic variation can be complicated by sexual dimorphism, ontogenetic variation, local variation and seasonal variation. Even more complications arise from the fact that these other sources of variation show geographic variation in their intensity, e.g. sparrows show geographic variation in the intensity of sexual dimorphism (Johnston & Selander, 1973), green geckos (Gardner, 1984) and *N. natrix* show geographic variation in the extent of ontogenetic variation, island lizards (Soule, 1972; Thorpe, 1985b) show geographic variation in the extent of local variation and shrews show seasonal variation in skull shape (Pucek, 1970) which may vary geographically.

### 5. CONGRUENCE

Character congruence is of central importance to the study of geographic variation. Congruence in the patterns of variation shown by different characters in a character set is influenced by both genetic/ontogenetic dependence and also the cause of the geographic variation.

Genetically/ontogenetically independent characters (i.e. with a low within-locality correlation) may or may not show congruence in their patterns of geographic variation (between-locality correlation). However, genetically/ontogenetically dependent characters (with a high within-locality correlation) are bound to have congruent patterns of geographic variation (high between-locality correlation). Generally then, the between-locality correlation (congruence) is equal or higher than the within-locality correlation (dependence) (Thorpe, 1976; Sokal *et al.*, 1980). Consequently, congruence in patterns of geographic variation can only be meaningfully discussed with genetically/ontogenetically independent characters.

The general level of congruence in a set of independent characters may also be influenced by the cause of

the geographic variation. If selection for current ecology is the cause then one does not predict widespread congruence between different types of character. For example, one would not necessarily expect the latitudinal variation in the size of a small endotherm in response to Bergmann's rule to necessarily be reflected in the isozymes.

On the other hand, if a major vicariance event temporarily splits a species into two one would expect a large range of character system to reflect this period of independent phylogenesis, as is the case, for example, in the eastern and western forms of *N. natrix* (refs. Thorpe, 1984a, 1985a). In this situation, where phylogenesis is the cause of geographic variation, one set of characters may predict the geographic variation in another set. This has been found to be the case in *N. natrix* (Thorpe, 1985a). Under these circumstances Wilson & Brown's (1953) assumption, that congruence deteriorates with the addition of characters, can be shown to be incorrect (Thorpe, 1985a, c, d).

## 6. DIFFERENT APPROACHES TO GEOGRAPHIC VARIATION

It is against this background of cause, pattern and congruence (predictivity) that the various approaches to analysing geographic variation can be evaluated. Three main approaches will be considered using *N. natrix* and other species as examples. These three approaches are:

A) naming «conventional subspecies» where the central question is «is the population different»?

B) multivariate analysis (also referred to as character analysis or phenetics) where the question asked is «what is the pattern of variation» or «what is the relative similarity of the populations»?

C) phylogenetic analysis where the question is «what are the ancestral-descendant lineages»?

### 6.1. Conventional subspecies

Studying geographic variation by simply naming subspecies, rather than describing the pattern, is widespread even today. Whilst authors may differ in methodological detail this approach is typified as follows. A single character in selected and is used intuitively to define subspecies i.e. categories. Other characters may be described but are not used for the original delimitation. Little or no account is taken of the non-geographic variation and generally no abstract criteria or minimum level of differentiation is used for subspecies recognition. In practice the 75% rule is not used.

This procedure has not changed for many years and ignores many of the facts of geographic variation including the following:

a) all populations differ in some respects so that simply finding a difference is not a meaningful criteria;

b) subspecies are categories but not every geographic variation is categorical;

c) different characters may have different patterns of geographic variation (especially if «ecology» is the cause) so single characters should not be used to delimit subspecies. In fact it has been shown (Thorpe, 1985a) that even when phylogenesis causes distinct races (categorical variation) which are reflected in numerous characters, it is most improbable that a single character can adequately represent the simple geographic variation.

The use of this approach to studying geographic variation has had the following consequences:

a) All types of geographic variation are forced into a categorical mould irrespective of whether categories exist naturally. For example, clines are arbitrarily sectioned into subspecies (Thorpe, 1984b).

b) Since these subspecies are not natural categories they have to be artificially delimited in geographic space by inappropriate physiographic features such as rivers (e.g. Danube, Rhine and Dnepr for *N. natrix* subspecies in Thorpe, 1979, 1980). This has led to the circular argument that gene flow is important *sensu* Mayr (1970).

c) Numerous subspecies tend to be erected and they obscure the major patterns of geographic variation (Thorpe, 1980; Clover, 1979).

d) Subspecies erected in this way generally tend to be highly author-dependent and do not relate to external factors such as geological events or patterns of geographic variation in other species. They generally offer little or no clue to the cause of the variation other than a false and circular assumption that physiographic features are the cause (Thorpe, 1980).

### 6.2. Multivariate character analysis

This is essentially a phenetic approach where the data analysed may be biochemical (Piazza *et al.*, 1981; Menozzi *et al.*, 1978) or morphological (Thorpe, 1976, 1983b) etc. The main questions that this approach attempts to answer relate to describing generalized patterns of geographic variation and the actual or implied relative similarity of the populations. Since these techniques can describe the patterns, without any prejudice as to its cause, they are often useful techniques to employ irrespective of ones final aim.

Numerous illustrative and numerical techniques are used in this area (Sokal, 1983; Thorpe, 1976, 1983b). Those that relate the population differentiation to the geographic position of the populations include geographic networks (Thorpe, 1984b); contouring and isometric plots with all their various forms of presentation (Sokal, 1983; Thorpe, 1976 and references therein); colour mapping to overcome the problem of mapping more than one factor (Piazza *et al.*, 1981); transects (Thorpe, 1984b); autocorrelations (Sokal, 1983) etc.

Other techniques, e.g. ordination analysis and cluster analysis (Thorpe, 1976, 1983b) can directly summarise the affinities of the populations without reference to their geographic origin although they interact with those procedures that do (e.g. ordination scores can be contoured or colour mapped etc).

Ordination is suitable for analysing all the types of pattern of geographic variation described above but cluster analysis is essentially categorical in nature and is often unsuitable for analysing other types of variation (see Thorpe, 1983b on Smith, 1979).

In general, these techniques have been useful in indicating how much variation occurs within a species compared to between species (Thorpe, 1979, Lessios, 1981); in revealing population structure and patch size (Sokal, 1983); in revealing the evolutionary potential of central versus peripheral populations and isolated versus contiguous populations etc; in summarising and describing patterns of geographic variation and in describing the exact position and nature of transition zones (Thorpe, 1979, 1980). More specifically, when current ecology is the cause of the variation they can define morphological factors like size and shape and relate them to geographic and temporal variation in selection pressures due to climatic changes via Bergmann's and Allen's rules (Johnston & Selander, 1971; Fleischer & Johnston, 1982). They can also generalise gene frequency changes in relation to climatic conditions (Piazza *et al.*, 1981).

When phylogenesis is the cause of the geographic variation then these techniques enable the major patterns to be established with considerable reliability (Thorpe, 1979, 1985a, c, d); they enable these patterns to be related to geological events and the patterns of variation within other species e.g. *Natrix* (Thorpe, 1979), *Podarcis* (Clover, 1979; Thorpe, 1980) and *Phelsuma* (Gardner, 1984) and they indicate cases of incipient speciation and causes of speciation (Thorpe, 1975; White, 1978). Whilst naming subspecies is not the aim of this approach these techniques can be used to give consistent phenetic criteria for their recognition (Thorpe, 1979).

Comparing the pattern of geographic variation to that in other species and geological events may enable one to propose the main phylogenetic processes but it does not enable one to directly hypothesise a complete phylogenetic tree. For example, multivariate analysis shows clearly eastern and western forms of *N. natrix* with a distinct transition zone between them. The position of the transition zone, its relationship with other zones, the maximum extent of the Pleistocene ice caps and other factors enable one to hypothesise a secondary origin for the transition zone due to the ice caps splitting the progenitor population into separate south-west and south-east refugia which expanded and met with the retreat of the ice. Multivariate analysis also enables one to characterise the Balkan and Pyrenean transition zones but in these cases it is not

clear whether they have a primary or secondary origin. This indicates one of the limitations of this approach.

### 6.3. Phylogenetic analysis

Phylogenetic analysis may, in some circumstances, overcome the above limitation of multivariate analysis and allow one to directly hypothesize a primary or secondary origin of the zone by an analysis of the range expansion (Thorpe, 1983c, 1984a). Whether a zone is primary or secondary in origin is of central importance to speciation theory but it is generally not possible to deduce this from the nature of the zone (Endler, 1977).

Wagner trees and a range of other procedures are available to give a tree from numerically coded morphological data (see papers in Felsenstein, 1983). The following example of intraspecific phylogenetics is based on Wagner trees derived from morphological data of *N. natrix*.

Previous work, based on multivariate analysis, suggests a phylogenetic origin for the east-west differentiation in *N. natrix* due to ice-cap induced vicariance, and if this is correct one expects a phylogenetic analysis to show (1) populations arranged on the tree in some geographic sequence; (2) a root among the origin of the southerly populations; (3) an eastern and western lineage; that time of divergence is related to the extent of divergence (anagenesis) giving a significant «direction of evolution» within the lineages and hence showing a «phylogenetic» rather than «ecological» cause for the geographic variation (Thorpe, 1984a).

A phylogenetic analysis of the species complex shows separate eastern and western lineages. The appropriate eastern lineage fulfills the above expectations. There is a root in the south with populations arranged in a south to north sequence and a pattern of anagenesis giving a clear (N-S) direction of evolution (Thorpe, 1984a). An interpretation of the tree in terms of range expansion (Thorpe, 1983c, 1984a) shows a south-eastern refugium and subsequent expansion north through the Caucasus, west around the Black Sea to the Balkans (where there is a secondary meeting with the south-Balkan population making the Balkan transition zone «secondary» in origin) and north to Austria, Germany and finally Scandinavia.

The western lineage fulfills some of the above expectations. There are distinct «Iberian» and «Italian» lineages with the populations arranged in strict geographic sequence and there is a clear pattern of anagenesis (greater in the south) with a «significant direction of evolution» (Thorpe, 1984a). However the direction of evolution in the Iberian and Italian lineages converges indicating reticulate evolution due to the two lineages meeting and introgressing in northwest Europe (Thorpe, 1982, 1984a). An analysis of the range expansion can be interpreted in light of the climatic changes since the last glacial maxima.

When the climate ameliorated after the last glaciation (ca. 20000 years ago) the populations expanded out of N. Africa and Iberia into France and Italy. However, with the temporary return of cold conditions in the Weichselian the populations were depressed into Iberian and Italian refugia. Expansion out of these refugia, as indicated by an interpretation of the phylogenetic tree (Thorpe, 1984a), shows the Italian lineage expanding northwards out of southern Italy into mid-Italy, north-Italy, Germany and Holland; whilst the Iberian lineage expands northwards around the Pyrenees into France (indicating no secondary meeting of the populations in the Pyrenees therefore hypothesising it to be a «primary» transition zone), Britain and Holland. Where these two lineages meet in northwest Europe they introgress giving reticulate evolution.

These studies of *N. natrix* (Thorpe, 1982, 1983b, 1984a, b, c) and other species (Baum, 1983; Corti *et al.*, in press; Loudenslager & Gall, 1980; Searle, 1984; Thorpe *et al.*, 1982) show that ancestral-descendant intraspecific lineages can be characterised by both numerical and non-numerical procedures; that the pattern of anagenesis can be used to decide evolutionary direction and cause (i.e. phylogenetic versus ecological); that reticulation between lineages can be shown; that branching sequence (cladistic level) is not necessarily related to reproductive isolation and that the phylogenetic tree can be interpreted in terms of range expansion thereby allowing one to hypothesise a primary or secondary origin for a transition zone.

Irrespective of the above advantage of phylogenetic analysis it does not indicate the pattern of geographic variation (e.g. the position of primary transition zones) and it presumes a phylogenetic rather than ecological causation. Given an ecologically caused cline, a cladogram based on a Wagner tree may link the populations in geographic sequence. Of course this does not mean that the geographic variation can be interpreted phylogenetically and this has been pointed out for intraspecific studies (Thorpe, 1982, 1983c, 1984a) and for the parallel situation in cladistic biogeography (Endler, 1982).

Consequently, when only cladogenesis, and not anagenesis, is considered one cannot differentiate between historical and ecological factors. Since the realization of this limitation it has subsequently been shown (Thorpe, 1982, 1983c, 1984a) that the pattern of anagenesis can be statistically tested to differentiate between ecologically and phylogenetically caused differentiation and define a direction of evolution along a putative lineage, so that the range expansion can be plotted, thereby allowing one to distinguish between primary and secondary transition («hybrid») zones.

Unfortunately some authors (Barton & Hewitt, 1985) have failed to understand the relevance of considering the pattern of anagenesis and misinterpret the applicability and direction of previous studies (Endler, 1982) which pertained only to the cladogenic pattern.

Consequently, they have been unable to appreciate how infraspecific phylogenesis, which considers both anagenesis and cladogenesis, can, with the support of statistical tests, lead to hypothesise a primary or secondary origin for a transition zone. Moreover, some phylogenetic trees can be subject to other statistical tests, i.e. treeness tests, pertinent to understanding the cause of the geographic differentiation (Astolfi & Zonta-Sgaramella, 1984; and references therein).

## 7. CONCLUSIONS

In conclusion, the use of trinomials can be assessed in light of the cause, pattern and congruence of the geographic variation and, where appropriate, the intraspecific lineages.

Few species have been studied in relation to all the above factors so *N. natrix* provides a useful example. The eleven conventional subspecies of *N. natrix* do not relate to either the actual phenetic patterns of geographic variation or to the intraspecific lineages, even though the latter two are complimentary (Thorpe, 1979, 1980, 1982, 1984a, b, c). The use of conventional subspecies, as exemplified by the *N. natrix* case, is inadvisable. They give a misleading portrayal of the geographic variation because the procedure upon which they are based is inadequate.

This does not mean that subspecies should be completely abandoned as they may be appropriate in a restricted set of circumstances. (1) The pattern of variation should give distinct races, i.e. categorical variation or very divergent isolates, so they can be objectively delimited in geographic space by their characteristics. If substantial introgression occurs between lineages resulting in reticulation and loss of the categorical pattern then, I believe, that is inappropriate for subspecific recognition. (2) In addition, the subspecies should be predictive. That is, the variation in one set of characters, upon which the subspecies are based, should predict the variation in other sets of independent characters (as in Thorpe, 1985a). This requires a high level of congruence between independent sets of characters which may be likely to occur when a past «phylogenetic» event has caused the differentiation rather than when the variation is caused by a small set of dependent characters varying in relation to a particular, current, selection pressure (i.e. current ecology). (3) Lastly, one must consider the rank, or level, at which subspecies are used. I believe their use should be restricted to just below the species level, i.e. the main categories or lineages within a species rather than the subsidiary categories or lineages.

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