

**Primary and Secondary Transition Zones in Speciation and Population Differentiation: A Phylogenetic Analysis of Range Expansion**



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## PRIMARY AND SECONDARY TRANSITION ZONES IN SPECIATION AND POPULATION DIFFERENTIATION: A PHYLOGENETIC ANALYSIS OF RANGE EXPANSION

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Transition (hybrid, tension, intergradation and contact) zones are the focus of attention of many evolutionary studies. Concepts of speciation and population evolution are dependent on whether the zone is thought to be due to the differentiation of the populations in situ (i.e., primary zones) as in area effect, clinal and stasipatric speciation (Endler, 1977; White, 1978) or due to secondary contact of populations (i.e., secondary zones) as in allopatric speciation or differentiation. It has been pointed out (Endler, 1977) that a major logical flaw in many such studies is that one cannot distinguish between a primary and secondary original event by the nature of the zone. Irrespective of the truth of this it is obviously logically desirable to hypothesize the origin of a zone independent of its nature. Using grass snake populations as an example, this paper describes some ideas

concerning a procedure for independently hypothesizing the range expansion of a species (by phylogenetic analysis) and the existence of transition zones (by multivariate ordination analysis). One can then directly deduce whether a zone is primary or secondary in origin by comparing its geographical position with the hypothesized range expansion.

### MICROPHYLOGENESIS AND DIRECTION OF EVOLUTION

The relative similarity of a series of populations, i.e., OTUs (operational taxonomic units), can be represented in an OTU  $\times$  OTU distance matrix. The phylogenetic relationships of these OTUs can be hypothesized by computing a distance Wagner tree from this matrix (Farris, 1972). The "minimum length"\* tree connects the terminal OTUs by branches, the length of which is measured in units of patristic distance. The patristic distance between OTUs is equal to, or greater than, the distance in the original matrix. The patristic distance is taken as a measure of anagenesis in a lineage.

This tree is originally undirected and can be rooted in two ways. The root of

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\* It is now appreciated that the distance Wagner trees are less appropriate than actual minimum length Wagner trees derived from a character  $\times$  OTU matrix. Nevertheless the two procedures gave substantially similar or identical results when tested on some *Natrix* data.

the tree can be taken as the mid-point between the two most patristically dissimilar OTUs. Alternatively it may be rooted by an outgroup. The outgroup is a taxon external to the holophyletic group under consideration (Farris, 1972), and the outgroup root is the point at which this taxon joins the tree. The interstitial nodes on the tree (i.e., junctions between branches) may be considered as representing ancestral populations or HTUs (hypothetical taxonomic units).

In low vagility species such as the grass snake (*Natrix natrix*) one would expect the ancestral populations to be geographically adjacent. Consequently in recently evolved, low-vagility forms the distance Wagner tree should be congruent with the geographic position of the populations. This would not necessarily be so in animals that are transported by man (e.g., mice) or in highly mobile species (e.g., birds) that can leapfrog over pre-existing populations.

Even if a tree is congruent with the geographic position of the populations this does not necessarily indicate that the pattern of geographic variation is due to phylogenesis rather than current ecology, i.e., gene flow and selection. For example, if the racial affinities were dominated by a cline in response to a current selection gradient a distance Wagner tree would connect the populations in a sequence that reflected their geographic position.

However, in this situation one would not expect the extent of anagenesis (see

below) to be progressively greater nearer the out-group root of the tree since there is no reason why current ecology should generally produce such a pattern. If no clear pattern of anagenesis is found in a distance Wagner tree then the pattern of racial affinities might be caused by phylogenesis but current ecology could also be responsible. On the other hand if there is a positive (but not necessarily perfect) relationship between the time of divergence and extent of divergence so that there is greater anagenetic divergence nearer the outgroup root, then the pattern is most likely due to phylogenesis (Thorpe, 1982, 1983).

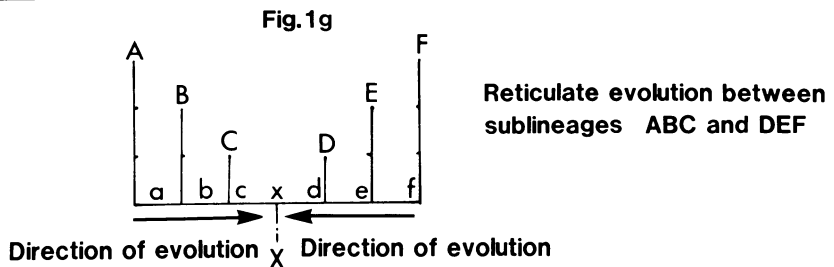
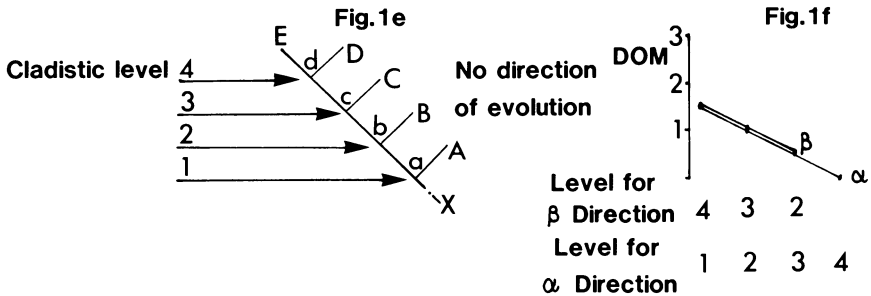
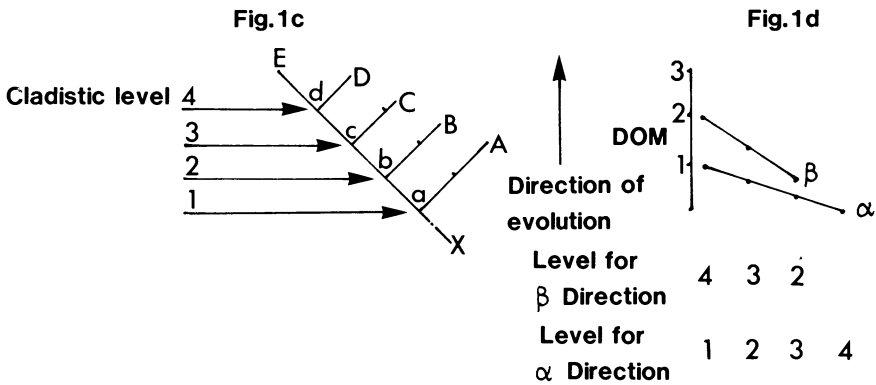
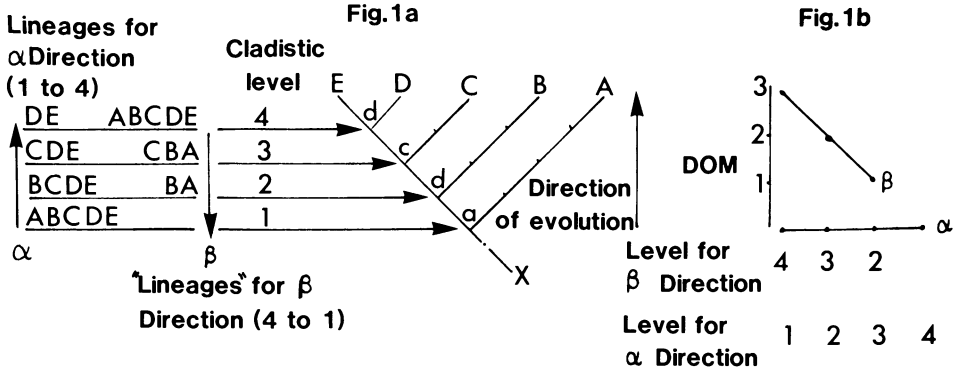
For the purpose of further explanation consider a tree in the form of a pectinate comb marked in units of patristic distance (Fig. 1a). The OTUs are A, B, C, D and E and the nodes (HTUs) are a, b, c and d. This tree has four levels, from the most ancient (level 1) to the most recent (level 4). At level 1 this entire lineage (A, B, C, D, E) is rooted at position a by outgroup x. At level 2 the lineage B, C, D, E is rooted at position b by outgroup A. At level 3 the lineage C, D, E is rooted at position c by outgroup B and at level 4 the lineage D, E is rooted at position d by outgroup C.

For the purposes of this paper the anagenesis of a specific OTU refers to the patristic distance between that OTU and the node joining it to the spine of the comb; i.e., in Figure 1a the anagenesis of A is the length from a to A (4 units), the

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FIG. 1. Types of "phylogenetic" trees and the existence of a clear direction of evolution. See Text for explanation. Fig. 1a. The pattern of anagenesis in this tree is such that there is a clear direction of evolution away from the outgroup root (x) in  $\alpha$  direction, i.e., from level 1 to level 4. Fig. 1b. When the distance between the outgroup root and midpoint root ( $D_{OM}$ ) is plotted against cladistic level there is no correlation (zero slope) for  $\alpha$  direction and a clear correlation and steep slope for  $\beta$  direction in the tree of Fig. 1a. Fig. 1c. The pattern of anagenesis in this tree is such that there is a clear direction of evolution away from the outgroup root x. Fig. 1d. When the distance between the outgroup root and midpoint root is plotted against cladistic level the slope for  $\alpha$  direction is less than the slope for  $\beta$  direction in the tree of Fig. 1c. Fig. 1e. The pattern of anagenesis in this tree is such that there is no direction of evolution in this tree and phylogenesis need not be responsible for the racial affinities between OTUs. Fig. 1f. When the distance between the outgroup root and midpoint root is plotted against cladistic level the slope is the same irrespective of whether one is moving toward ( $\beta$ ) or away from ( $\alpha$ ) outgroup x in the tree of Fig. 1e. Fig. 1g. The pattern of anagenesis in this tree is such that reticulate evolution between sublineage A, B, C and sublineage D, E, F is indicated. Each sublineage resembles the tree of Fig. 1a in that the pattern



of anagenesis indicates a clear direction of evolution. However in this tree the direction of evolution in the two sublineages is toward (rather than away from) the outgroup "root" x. Consequently, x cannot be taken as the root of these sublineages and the midpoint roots a (for sublineage A, B, C) and f (for sublineage D, E, F) are appropriate.

anagenesis of B is b to B (3 units), the anagenesis of C is c to C (2 units) and the anagenesis of D and E is d to D and e to E, respectively (1 unit).

In the tree of Figure 1a the extent of divergence is completely related to time of divergence. Hence there is a clear pattern of anagenesis such that the extent of anagenesis of the OTUs decreases with time and therefore decreases with distance from the outgroup root of the entire tree (i.e., x). Phylogeny is likely to cause this pattern of anagenesis but there are no reasons why adaptation to current ecological conditions should cause it.

This tree (Fig. 1a) can be said to show a clear direction of evolution from level 1 to level 4. The existence of a clear direction of evolution, i.e., a pattern of anagenesis such as exhibited by Figure 1a (or Fig. 1c) can be illustrated and tested in two ways.

First, if there are sufficient OTUs their cladistic order from the outgroup root of the entire lineage (i.e., [E, D], C, B, A) can be rank correlated with their order based on the magnitude of their anagenesis (i.e., A, B, C, [D, E] in this example). A significant negative correlation confirms the existence of a clear direction of evolution and hence a "phylogenetic" rather than "ecological" causation.

Second, the alternative test is more involved and is based on the distance between the outgroup root and mid-point root ( $D_{OM}$ ) at any given level on the tree. As mentioned above, at level 1 the outgroup is x and the outgroup root is a (Fig. 1a). The mid-point root is also at a because this is the midpoint between the two most patristically dissimilar OTUs (i.e., A and B or C or D or E). Hence the distance between the midpoint root and outgroup root at level 1 is zero ( $D_{OM} = 0$ ). This is repeated for each level (1 to 4) going in  $\alpha$  direction away from the outgroup root of the entire lineage (x). The  $D_{OM}$  for a given level is then plotted against the level as in Figure 1b and a horizontal line ( $\alpha$ ) results. In other words with this shape of tree the outgroup root and midpoint root coincide irrespective

of cladistic level when going away from the outgroup root of the entire lineage.

If we repeat this operation going in the opposite direction to evolution, i.e., from level 4 to 1, then the distance between the outgroup root and midpoint root is plotted as line  $\beta$  (Fig. 1b). Taking level 3 as an example, C is the putative outgroup root for "lineage" C, B, A. The midpoint of this "lineage" is a as it is halfway between the two most dissimilar OTUs A and C. Since the midpoint root a, and the out-group root c, are two units apart  $D_{OM}$  equals 2 at level 3. When this is repeated for each level one can see that  $D_{OM}$  decreases from levels 4 to 1 for direction  $\beta$  (Fig. 1b).

The existence of a clear direction of evolution can therefore be demonstrated by showing that the scatter along line  $\alpha$  (direction of evolution) has no significant correlation while the scatter along line  $\beta$  (opposite to the direction of evolution) has a significant correlation. When the extent of divergence is not so directly related to time of divergence as in Figure 1c then a clear direction of evolution can be demonstrated by showing that the slope of line  $\alpha$  is shallower than the slope of line  $\beta$  (Fig. 1d).

If a tree such as Figure 1e is found then no clear direction of evolution can be demonstrated by these tests (Fig. 1f) and the pattern of racial affinities could be due to either "current ecology" or microphylogenesis.

With infraspecific data there will not be any absolute reproductive isolation between lineages and so reticulate evolution can occur if they come into secondary contact and introgress. The direction of evolution will in normal circumstances be away from the outgroup root of a lineage. However, if there is reticulate evolution between two sublineages (as in Fig. 1g) then the above tests may still show a clear direction of evolution in each sublineage but the direction will converge on (rather than diverge from), the outgroup root of the entire lineage (i.e., x in Fig. 1a). In the example of Figure 1g, each sublineage,

i.e., A, B, C and D, E, F resembles the tree in Figure 1a in that it has a clear direction of evolution. Since the pattern of anagenesis in sublineages A, B, C and D, E, F shows the direction of evolution to be towards the outgroup root, x, instead of away from it, then x has to be rejected as the root of these sublineages. Instead when confronted with reticulate evolution such as in Figure 1g one should choose the midpoint root of the sublineages, this is a for sublineage A, B, C and f for sublineage D, E, F. This is explained further with calculated examples in Thorpe (1982).

It is apparent that when working at the intraspecific level these "direction of evolution" tests may not only enable one to confirm that phylogenesis rather than "current ecology" is the causative factor, but may also enable one to detect reticulate evolution (Thorpe, 1982).

#### *The Basic Pattern of Geographic Variation and Transition Zones*

A series of multivariate studies (Thorpe, 1975, 1979, 1980) based on large numbers of independent morphometric characters reveals that the mainland populations of the grass snake (*Natrix natrix*) belong to either an eastern or western group. Numerical cladistic analysis also shows these eastern and western mainland groups to be separate monophyletic clades.

I have previously suggested (Thorpe, 1975, 1979, 1980) on the basis of similar patterns of differentiation in other sympatric species, that the eastern and western forms are the consequence of south-east and south-west Pleistocene refugia which expanded northwards in post Pleistocene times to meet along a sharp secondary transition zone in central Europe. Apart from this major transition zone, which has previously been described (Thorpe, 1979, 1980) (Fig. 5) there are several other transition zones associated with the minor racial categories revealed by canonical analysis. One is related to the Pyrenees, a physiographic 'barrier' (Fig. 2a), while another, in the

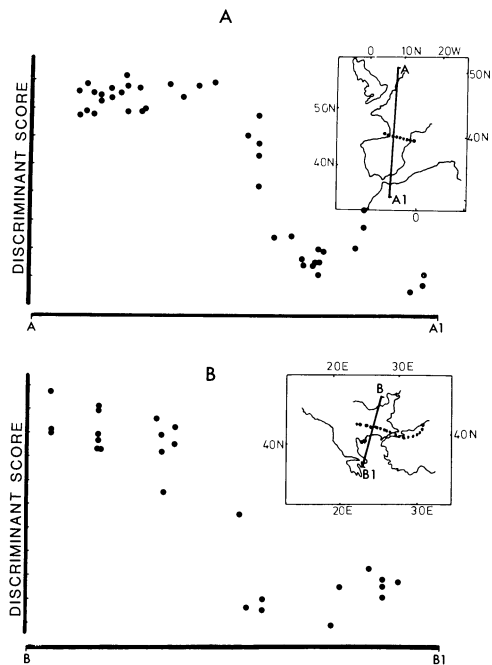


FIG. 2. Transition zones indicated by geographical transects of mapped canonical variate (discriminant function) scores. Vertical axis indicates canonical variate scores of individual specimens and is marked in units of within-group standard deviations. Horizontal axis is the geographical transect indicated in the inset map. The dotted lines indicate the transition between phenetic (racial) categories. Fig. 2a. Western Europe. The transition between Britain/north France/Holland and Iberia/Morocco/Algeria, with the Pyrenees phenetically and geographically intermediate. Based on canonical analysis of the western form using 37 characters as listed in Thorpe (1984). Fig. 2b. Balkans. The transition zone between the north Balkans and Greece/Turkey is illustrated. This is based on canonical analysis of eastern populations using 50 characters (list C1a in Thorpe, 1979).

Balkans and Turkey (Fig. 2b) is clearly unrelated to physiographic features. Neither, as far as one can tell, is the Balkan zone related to population differentiation in other species.

#### *Eastern Grass Snake: Microphylogenesis and Range Expansion*

If the above hypothesis of post-Pleistocene expansion is correct then a cladistic analysis of the eastern form should

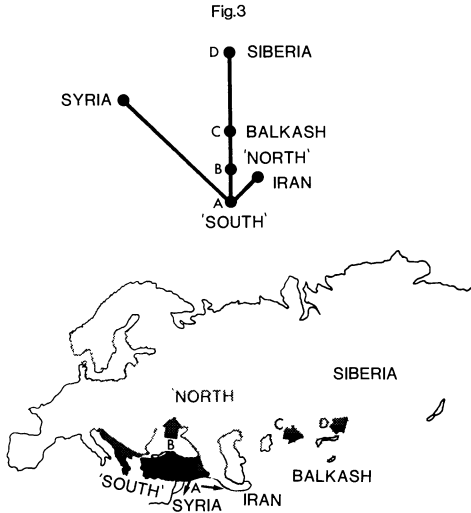


FIG. 3. Phylogeny and range expansion in the east. The midpoint rooted distance Wagner tree (2a) was derived from nine gap-coded characters (4, 35, 41, 45, 51, 89, 90, 91, 92, Thorpe, 1979). The divergence (2b) of Syria and Iran at level 'A' is followed by northward expansion from 'south' to 'north' (level B) and north-east expansion to Balkhash (level C) and Siberia (level D).

result in a southern root and subsequent differentiation of more northerly groups.

A distance Wagner tree can be obtained from morphometric characters converted to discretely coded variables by gap-coding (Thorpe, 1984) where a gap between population means is recognized if it is over one within-population standard deviation. With eastern females nine of the original 160 plus characters (i.e., characters 4, 35, 41, 45, 51, 89, 90, 91, 92, Thorpe, 1979) were so coded. Since the gaps in these characters are eradicated by outgroups the resultant distance Wagner tree (Fig. 3a) was mid-point rooted. This tree shows a southern root and sequential expansion away from this root in the 'south' to 'north' then to Balkhash and finally to Siberia (Fig. 3b).

While this enables one to hypothesize a southern refugium and expansion from this to northern and northeastern populations, the gap-coding results in large numbers of populations being grouped into large geographical units. This does not enable one to investigate the details

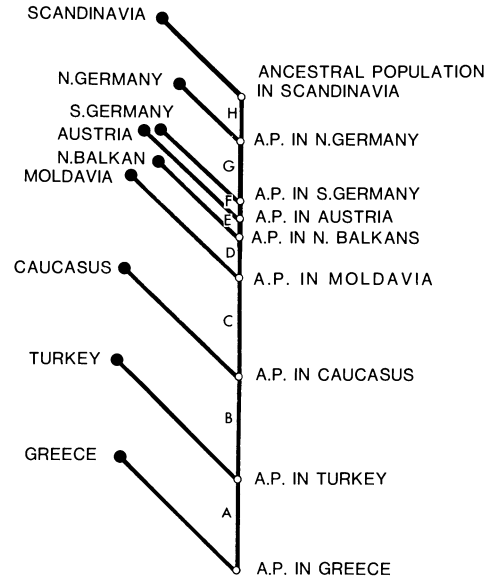


FIG. 4. Phylogeny of the central European lineage (eastern grass snake). A distance Wagner tree of populations from the entire species complex was derived from 51 normalized morphometric characters (list Clb plus 22 in Thorpe, 1979). The out-group-rooted central European lineage is illustrated and converted to a phylogeny as explained in the text. The southern root and direction of evolution can be confirmed by the statistical tests explained in the text. The northward range expansion involved in the phylogenetic steps A to H are plotted in Fig. 5.

of range expansion. For example, one cannot tell whether the route of northward expansion was to the west of the Black Sea (making the Balkan zone primary) or to the east of the Black Sea (making the Balkan zone secondary).

To obtain a more detailed picture than provided by gap-coding the data were normalized (Thorpe, 1980). That is, the characters, which were originally recorded on different scales, are recorded so that they are assigned equal rates of evolution. For a discussion of coding procedures in relation to these *Natrix* data see Thorpe (1984).

A cladistic analysis of the species complex based on 51 normalized characters yields a distance Wagner tree that shows a southern mid-point and out-group root

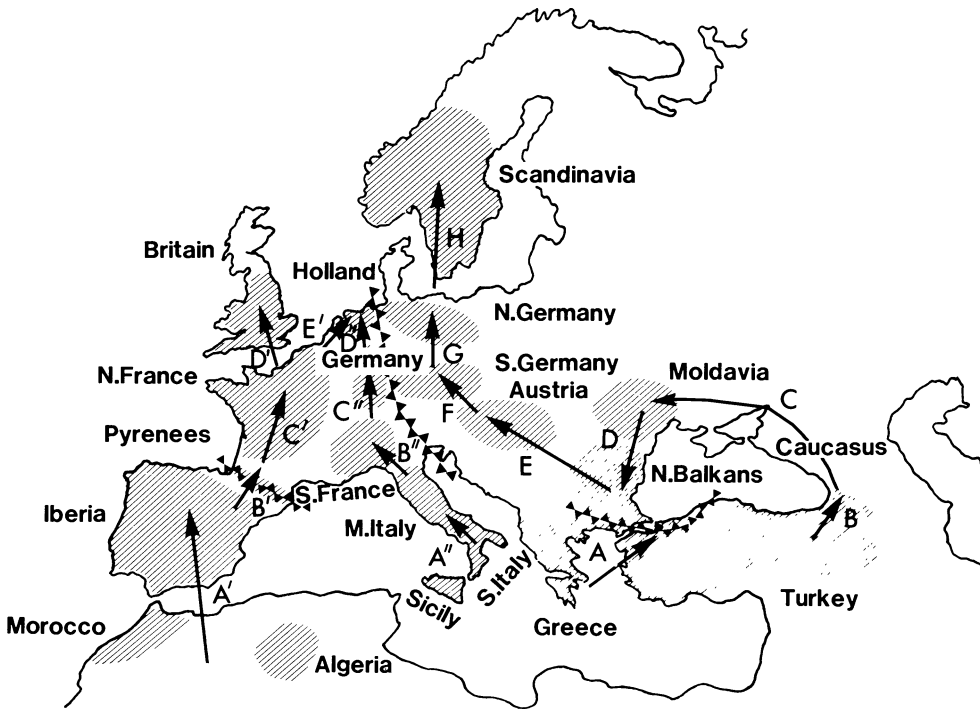


FIG. 5. Range expansion from southern to northern areas as hypothesized by numerical phyletics (Figs. 4, 6). Transition zones between phenetic categories are indicated by a double series of triangles for central Europe (Thorpe, 1979), Pyrenees (Fig. 2a) and the Balkans (Fig. 2b). Arrows indicate phylogenetic steps between hypothesized ancestors (Figs. 4, 6). Note that there is secondary meeting of populations at the central European and Balkan transition zones but not in the Pyrenean zone (localities in Thorpe, 1973, 1979).

for the eastern mainland form. When the relevant outgroup-rooted 'central European' lineage is extracted from this cladogram one can see (Fig. 4) that it is largely consistent with the geographic location of the populations (i.e., they are in geographic sequence). This lineage is similar to the tree in Figure 1c and tests for a direction of evolution in this lineage, based on the distance between outgroup and midpoint roots show a significant (northwards) direction of evolution ( $P < .001$ ) using slope angles (as described above and in Thorpe, 1982, 1983). Moreover, there is a Kendall's rank correlation of  $-0.7$  ( $P < .05$ ) between extent of anagenesis (OTU to HTU patristic distance) and rank order from the outgroup root. This pattern of significantly greater ana-

genesis near the outgroup root confirms the north to south direction of evolution implied by the outgroup root and indicates that the pattern of racial variation is more likely due to phylogeny than current ecology.

One can simply convert the cladogram to a phylogenetic tree by naming the nodes as the ancestors of the mainland populations to which they give rise, where the immediate ancestor of an extant mainland population is in the same geographical locality as that population (as in Fig. 4). Since the phylogenetic tree is consistent with the geographic location of the populations, the range expansion can be plotted by joining the populations on a map in the same sequence that the ancestral populations are joined in the phy-

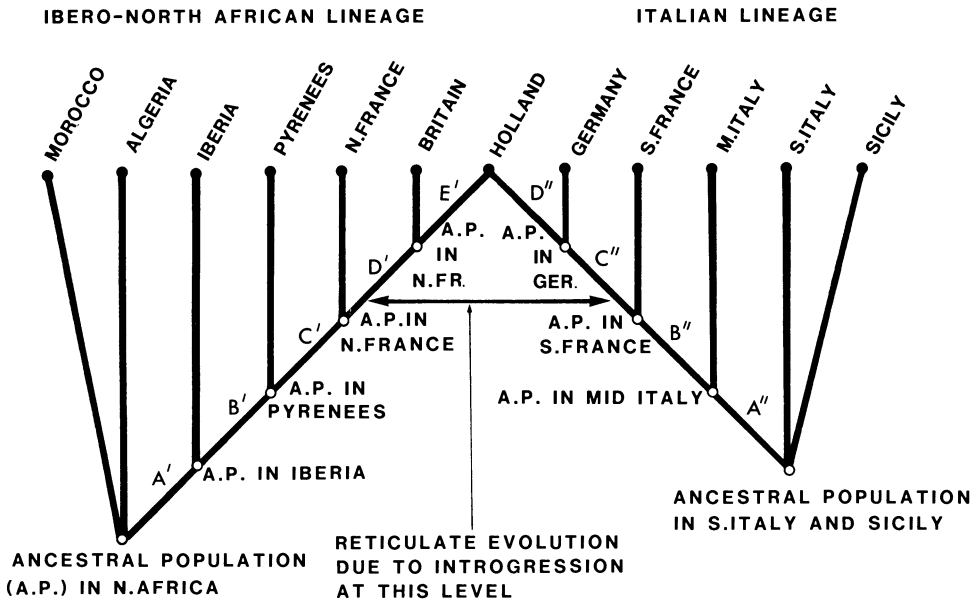


FIG. 6. Phylogeny of the western grass snake. Derived from a distance Wagner tree of populations from the entire species complex derived from 53 normalized characters (Thorpe, 1982). The reticulate evolution between the Ibero-African and Italian sublineages and consequent southern roots of these sublineages is tested in Thorpe (1982). The expansion northward from the main north African root (through stages A' to E') and from the secondary Sicilian/southern Italian root through stages A'' to D'' is mapped in Fig. 5. The hypothesized location of ancestral populations is indicated. Reticulate evolution occurs between the northern European populations in France, Holland and Germany. Note that the transition zone in the Pyrenees (Fig. 5) is hypothesized as being due to differentiation in situ and not due to the secondary meeting of separate lineages.

logenetetic tree. For the 'central European' lineage this hypothesizes a southern root near Greece and sequential expansion from this root to Turkey, Caucasus, Moldavia, north Balkans, Austria, south Germany, north Germany and Scandinavia (Fig. 5). From this one can deduce that the north Balkan populations and the Greek/Turkish populations met through range expansion and *the transition zone is secondary in origin.*

*Western Grass Snake:  
Microphylogenesis, Reticulate  
Evolution and Range Expansion*

The western grass snake is both a coherent phenetic group and a monophyletic clade. The distance Wagner tree based on 53 normalized characters (Fig. 6) is congruent with the geographic location of the western populations and has

two sublineages, corresponding to the two peninsulas, i.e., an Ibero-African sublineage and an Italian sublineage. These sublineages join at a northern root in Holland. The hypothesis of a northern Pleistocene refugium is not only inconsistent with a southern refugium for the eastern grass snake; it is also ecologically untenable because this area was covered with ice and could not have supported a population.

The pattern of anagenesis in the western lineage is given in Thorpe (1982) and resembles the tree in Figure 1g. That is, each sublineage (i.e., Ibero-African and Italian) resembles Figure 1a and consideration of the direction of evolution using the above tests (calculations in Thorpe, 1982) shows that it is toward (rather than away from) the northern "root" of the entire western lineage. This indicates re-

ticulate evolution between the Ibero-African and Italian sublineages. The mid-point roots of the Ibero-African and Italian sublineages are therefore taken as the correct roots and these are both in the south.

This is consistent with a southern root for the eastern grass snake and also the details of the climatic fluctuations of the time. If the western grass snake populations kept the same distance from the ice caps as they do today, then at the height of the last Pleistocene glaciation the northern limit of the western grass snake refugium would be the southern half of Iberia. As the climate began to get warmer 20,000 years ago the population could have expanded northward out of the Iberian peninsula and colonized the Italian peninsula. Ten thousand years ago in the Late Weichselian the climate deteriorated substantially (West, 1968), depressing the grass snake populations further south and separating the populations of the Iberian and Italian peninsulas. As the climate once again improved the populations would have expanded up out of the two peninsulas simultaneously and introgressed in northern Europe. This has resulted in the current pattern of reticulate evolution between these two lineages.

The western cladogram can be converted to a phylogenetic tree as explained above with the following exception. Where a branch gives rise to an island population, i.e., Britain, the node on the Wagner tree is hypothesized as being the penultimate rather than ultimate ancestor and is consequently in the same geographic position as the previous node, i.e., northern France.

Northward expansion from the mid-point root of the Italian sublineage in southern Italy results in the progressive colonization of mid-Italy, south France, Germany and then Holland (Figs. 5, 6). The central European transition zone is therefore deduced to be due to secondary contact of the populations from the western (Italian, but influenced by reticulate evolution from the Ibero-African lin-

age) lineage and populations from the eastern (central European) lineage. This confirms the previous deductions based on comparison of contact zones in other species (Thorpe, 1975, 1979, 1980).

The northward expansion from north Africa goes into Iberia and then from Iberia to the Pyrenees, to north France, to Britain (Figs. 5, 6). The transition zone in the Pyrenees is therefore not hypothesized as the site of secondary meeting of populations and one can deduce that it is due to differentiation of the populations in situ, i.e., *it is a primary transition zone*. This procedure does not allow us to decide between inhibition of gene flow or different selection regimes as the cause of this primary differentiation.

#### DISCUSSION

The use of numerical cladistic techniques to investigate range expansion and the independent use of 'phenetic' (multivariate ordination) techniques to indicate the existence and position of transition zones enables one to directly hypothesize a primary or secondary origin for such zones. With this procedure it was possible, first, to confirm the previously published view that the transition zone in central Europe, which is found in so many other species, is secondary in origin; second, to hypothesize a primary origin for the Pyrenean transition zone; and third, to hypothesize a secondary origin for the Balkan transition zone. This procedure is particularly useful when no parallel differentiation in other species is apparent, as for example in the Balkan zone. Once the origin of a zone can be hypothesized independent of its nature it is then possible to investigate whether certain facets of transition zones, i.e., increased variability, sharpness of transition, etc., are specifically related to a primary or secondary origin.

The procedure outlined in this paper should not be perturbed by intense selection causing sharp transitions (i.e., 'pseudosecondary' zones), or by extensive introgression after secondary contact

producing gradual clines (i.e., 'pseudo-primary' zones). This is because the nature of the zone is hypothesized by the phylogenetic relationships of all the populations and not just those involved in the transition. Indeed, the situation in *Natrix* appears to cover both contingencies. The Pyrenean zone is very sharp yet is hypothesized by these analyses to be a primary zone. On the other hand the differences between the northern population of the Ibero-African sublineage and the northern population of the Italian sublineage are so slight that they had not previously been recognized as a contact zone, let alone a secondary contact zone. Nevertheless, these procedures hypothesize a secondary contact and introgression in this region.

The recognition of such reticulate evolution is dependent on one's being able to detect a direction of evolution in the tree independent of rooting. Similarly, the ability to detect a clear direction of evolution in a tree based on the pattern of anagenesis allows us to deduce that the geographic variation reflects phylogenetic relationships rather than adaptation to current environmental gradients. Endler's (1982) computer simulation of cladograms has drawn attention to the difficulty of distinguishing between the influence of current ecology and phylogeny in biogeography. However, the extent of anagenesis was not taken into account and I suggest that considering the pattern of anagenesis may contribute to a solution of this problem.

The observed close relationship between the geographic position of the populations and their position along the phylogenetic tree is to be expected when recent phylogenesis is responsible for the geographic variation within low-vagility species. However, this is based on the assumption of recent phylogenetic change since even in low-vagility species this pattern may be obscured given sufficient time. One might, therefore, expect greater agreement between geographic position of populations and their order on the tree in more recent lineages compared

to those near the root. With *Natrix* it is not possible to go further than this and to quantify the relationship between time and vagility, because the dispersal rate per generation in extant populations is unknown. Moreover, dispersal rate per generation is likely to vary considerably in time as ecological conditions change. In a refugium with high population density the dispersal rate may be substantially lower than in a post-Pleistocene population that is expanding into uninhabited territory. It is evident that even though cladistic and phenetic classifications may be mutually exclusive the techniques upon which these approaches are based can be complementary in the investigation of geographic variation.

#### SUMMARY

Concepts of speciation and microevolutionary theories are frequently based on interpretations of transition (hybrid) zones even though the authors have been unable to deduce directly from the nature of the zone whether it is due to parapatric differentiation or secondary contact. However, one can analyze the range expansion of a species by phylogenetic interpretation of a numerical cladogram depicting population affinities. Complementary use of techniques from the opposing schools of "cladistics" and "phenetics" then enables one to detect transition zones and directly deduce a primary or secondary origin. These techniques are illustrated in this paper by analysis of geographic variation in the grass snake *Natrix natrix*, in which both primary and secondary contact zones are revealed.

#### ACKNOWLEDGMENTS

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#### LITERATURE CITED

- ENDLER, J. A. 1977. *Geographic Variation, Speciation and Clines*. Princeton University Press, Princeton.
- . 1982. Problems in distinguishing histor-

- ical from ecological factors in biogeography. *Amer. Zool.* 22:441-452.
- FARRIS, J. S. 1972. Estimating phylogenetic trees from distance matrices. *Amer. Natur.* 106:645-668.
- THORPE, R. S. 1973. Intraspecific variation of the ringed snake, *Natrix natrix* (L.). Ph.D. Thesis, Council for National Academic Awards.
- . 1975. Biometric analysis of incipient speciation in the ringed snake *Natrix natrix* (L.). *Experientia* 31:180-182.
- . 1979. Multivariate analysis of the population systematics of the ringed snake *N. natrix* (L.). *Proc. R. Soc. Edinburgh* 78B:1-62.
- . 1980. Microevolution and taxonomy of European reptiles with particular reference to the grass snake *Natrix natrix* and the wall lizards *Podarcis sicula* and *P. melisellensis*. *Biol. J. Linn. Soc.* 14:215-233.
- . 1982. Reticulate evolution and cladism: tests for the direction of evolution. *Experientia* 38:1242-1244.
- . 1983. Phylogenetic analysis of range expansion in the grass snake: reticulate evolution: primary and secondary contact zones. p. 464-468. *In* J. Felsenstein (ed.), 1983, *Numerical Taxonomy*. N.Y.
- . 1984. Coding morphometric characters for constructing distance Wagner networks. *Evolution* 38:244-255.
- WEST, R. G. 1968. *Pleistocene Geology and Biology*. Longmans, London.
- WHITE, M. J. D. 1978. *Modes of speciation*. W. H. Freeman and Co, San Francisco.

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