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Evolution, Vol. 38, No. 2 (Mar., 1984), 244-255.

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CODING MORPHOMETRIC CHARACTERS FOR CONSTRUCTING DISTANCE WAGNER NETWORKS

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Received October 14, 1982. Revised April 25, 1983

Distance Wagner networks are unrooted trees which can be used to indicate the relationships between taxa. They are converted into trees or cladograms by being given a root and thus provide one of the techniques of numerical cladistics (Farris, 1972). These networks not only enable one to hypothesize the branching sequence but also the relative extent of anagenesis.

These networks can be constructed from continuous and meristic morphometric characters. When morphometric data are used there is disagreement as to the appropriate coding procedure. There has been insufficient analysis of the influence of character coding on these networks and Colless (1980) considers "This whole area has been poorly investigated." Johnson and Mickevich (1977) used gap-coding on their six morphometric characters to convert them to ordinal multistate characters. These were then transformed to binary variables by additive coding. Riska (1979) points out some potential difficulties in comparing evolutionary rates of gap-coded characters, while Colless (1980) regards gap-coding as arbitrary and suggests range coding as an alternative. In reply, Mickevich and Farris (1981) have criticized range coding because it treats all characters as if they have evolved the same amount. However, some overt decision about coding is necessary if the characters have been recorded in different or arbitrary units.

This paper attempts to indicate the influence of different coding methods on Distance Wagner networks. The data set is based on a large number of morphometric variables recorded from populations of the western grass snake, *Natrix*

helvetica (Lacepede). This is one of the four semispecies of the grass snake species complex. The systematics of this species complex have been the subject to a series of investigations based on multivariate morphometry (references in Thorpe, 1980).

The causative factor for the main phenetic pattern of geographical variation is thought to be historical (microphylogenesis) rather than adaptation to current ecological conditions (Thorpe, 1979) and subsequently Distance Wagner networks have proved extremely useful in understanding the phylogeny and range expansion of the species complex (Thorpe, 1982, 1983, 1984). This has enabled a decision to be made between a primary or secondary origin for the transition (hybrid) zones within the species. Numerical cladistics have also proved useful for investigating variation in other species where the OTUs may be smaller units, i.e., demes (Johnson and Mickevich, 1977) or larger units, i.e., subspecies (Loudenslager and Gall, 1980) than the compound localities used in this study.

It is not only the network configuration that is of interest at this level but also the relative extent of anagenesis (Thorpe, 1982, 1983, 1984). The ability of the coding procedure to differentiate between the populations is also pertinent because if one cannot differentiate between populations some critical phylogenetic information can be lost, as for example, in the study of range expansion in the eastern grass snake (Thorpe, 1984).

METHODS

Characters

Over 160 phenotypic characters were recorded. Initially some of these were ex-

TABLE 1. Character set.

Reference no.	
3	No. of ventral scales
4	No. of pairs of subcaudal scales
7	Longitudinal level of the reduction from 21 to 19 dorsal scale rows
24	Contact between the temporal and upper postocular scales
27	No. of sublabial scales
33	No. of dark supralabial streaks
36	Extent of light edges on dorsal scales
37	No. of lateral blotches
38	Size of lateral blotch
40	Lower dorso-ventral position of lateral blotch
41	Upper dorso-ventral position of lateral blotch
42	Size of dorsal blotch
44	Lower dorso-ventral position of dorsal blotch
45	Upper dorso-ventral position of dorsal blotch
48	Extent of the occipital line
49	Extent of the parietal occipital marking
50	Extent of the temporal-labial marking
53	Extent of lunar markings
56	Size of the nuchal markings
57	Degree of separation of the nuchal markings
60	Degree of upper-curvature of the nuchal markings
61	Degree of lower-curvature of the nuchal markings
64	Degree of separation of the parietal scales and nuchal markings
86	Length of the cloacal gland
89	No. of maxillary teeth
90	No. of palatine teeth
92	No. of dentary teeth
108	Proportion of tail in % CS units with 10 dorsal scale rows
111	Proportion of the tail in % CS units with 8 dorsal scale rows
120	Proportion of the tail in % CS units with 2 dorsal scale rows
123	% of ventro-lateral blotches
124	Proportion of nuchal markings with streaks
135	% VS position of the pancreas
136	% VS position of the posterior tip of right lung
142	% VS position of the middle of the liver
165	% VS degree of separation between the right and left kidneys
17	Longitudinal level of the reduction from 8 to 6 dorsal scale rows

Reference no. from Thorpe (1979), full description of characters in Thorpe (1975).

cluded because they were logically dependent on other characters while others were excluded because they have a high pooled within-population correlation with other included characters (Thorpe, 1976, 1979). Characters were also excluded if they did not exhibit significant geographic variation in both sexes (AN-OVA), were unrecordable from a sufficient number of populations due to damage, etc., or were influenced by ontogenetic variation. This reduction resulted in a set of 37 characters (Table 1) representing scalation, color pattern, internal morphology and dentition. Having a low within-group correlation, these characters represent a considerable amount of information.

A second set of characters was also considered for the gap coding (A15) analysis. This set included characters with a high within-group correlation and characters that did not exhibit significant geographic variation when tested by analysis of variance. The five additional characters from this set that could be gap-coded for both sexes were the dorso-ventral position of the reduction from 19 to 17 dorsal scale rows (10), the sub-caudal position of the reduction from 6 to 4 (19) and from 4 to 2 (21) dorsal scales, the length of the nuchal markings (58), and the number of pits on the temporal scales (99). These and the initial 37 characters are described in Thorpe (1975).

Populations

There are 15 compound localities based on distribution, potential barriers and collecting gaps. They are tested multivariately to show that further subdivision will not significantly increase their homogeneity. The 15 populations (OTUs) are as follows: Britain (BRI), Jersey (JER), northern France (NFR), Pyrenees (PYR), Iberia (IBE), Holland (HOL), southern France and western Switzerland (SFR), western Germany (GER), mid Italy (MIT), southern Italy (SIT), Sicily (SIC), Morocco (MOR), Tunisia and eastern Algeria (TUN, females only), Algeria (ALG), and Elba (ELB, males only). The

approximate distribution of these populations is mapped in Thorpe (1979).

Distance Wagner Networks

The Distance Wagner networks were computed from Manhattan distance matrices following Farris (1972). The algorithm (Dr. Friday, Department of Zoology, Cambridge) seeks to minimize the underestimation of tree length which can occur with type V sites (Farris, 1972). An algorithm will not necessarily find the most parsimonious network, only an approximation to it. Since different algorithms give different 'minimum' networks (Colless, 1980) the same algorithm was used for all analyses. In retrospect it would have been preferable to use networks derived directly from the characters rather than from a distance matrix. However, on comparing some networks derived by these two procedures it was evident that only minor differences occurred. Consequently, the use of networks derived directly from the characters may be more appropriate but would be unlikely to lead to substantially different conclusions with regard to coding effects.

For ease of comparison the networks are displayed with the two most dissimilar nodes as opposite poles on a horizontal axis, only the 13 populations common to both sexes are illustrated, and the branch lengths are not shown. Since unrooted trees (networks) are used there are no assumptions regarding the direction of evolution. The congruence between a pair of networks is assessed by the contraction metric of Robinson and Foulds (1981) and is expressed as the distance between trees divided by the number of distinguishable OTUs. The minimum number of nearest neighbor interchanges required to convert one network to the other (Waterman and Smith, 1978) was also computed and indicates exactly the same pattern of intersexual congruence as the above contraction metric.

Coding Procedure

1) *Normalization*.—This is a standard procedure when using morphometric data

to assess population affinities (Thorpe, 1976). The characters are transformed to zero means and unit variance by subtracting the mean and dividing by the standard deviation. A continuous variable results.

2) *Range Coding*.—The character states are divided by the range for that character (Colless, 1980). Given that Manhattan distances remain invariant when a constant is subtracted from the mean, range coding is very similar to normalization. This is because under both the above coding procedures the spread of the character states is rendered constant for all characters. In normalization the standard deviation estimates the spread while in range coding the range estimates the spread. A continuous variable results from range coding.

3) *Segment Coding*.—The range of the character states is divided into equal size segments and then given an ordinal code i.e., 0, 1, 2 etc. depending on the number of segments.

The number of segments should be a function of the number of populations and general level of divergence. A highly divergent set of taxa containing large numbers of OTUs will need more segments than a few, slightly divergent OTUs. In this study two segments were used giving a binary coding.

4) *Gap Coding, A*.—The population means are ranked and gaps in this series of means are recognized on the basis of their magnitude being greater than a given critical level, i.e., one pooled within-population standard deviation. The groups of means between gaps are given the same ordinal code, while means separated by gaps are given different ordinal codes (Table 2). The number of codes is dependent on the number of recognized gaps.

These ordinal codes may be converted to binary variables by additive coding but this was not done in this study since it makes no difference to the resultant Manhattan distance matrix and was not necessary for the algorithm I used.

The population mean rather than median was used in this study because it

TABLE 2. Gap coding (A). Character \times tara matrix for gap-coded (A) data. Females are above the line, males below.

Char. no.	BRI	JER	NFR	PYR	IBE	SFR	HOL	GER	MIT	SIT	SIC	MOR	TUN	ALG	ELB
4	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	1/1	0/	0/0	/0
42	0/1	0/1	0/1	0/1	0/1	0/1	0/0	0/1	0/3	1/3	1/3	0/1	0/	0/1	/2
45	0/1	0/1	0/1	0/1	0/1	0/1	0/1	0/1	0/1	1/1	1/1	0/1	0/	0/0	/1
48	0/1	0/0	0/1	1/1	1/1	0/1	0/1	0/1	0/1	0/1	0/1	1/1	1/	1/1	/0
49	0/1	0/0	0/1	0/1	2/3	0/1	0/1	0/1	0/1	0/1	0/1	2/3	2/	1/2	/1
50	0/0	0/0	0/0	1/0	2/2	0/0	0/0	0/0	0/0	0/0	0/0	2/2	2/	1/1	/0
53	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	0/1	0/1	0/0	1/1	1/	1/1	/0
56	1/1	0/0	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/	1/1	/1
57	0/0	1/2	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/	0/0	/1
124	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/1	1/2	0/0	0/	0/0	/2

gives a better estimate of the centrality of the distribution as it derives its value from the character states of all the samples.

Many characters lack gaps of one standard deviation so only 10 (Table 2) of the initial 37 characters can be gap-coded for both sexes (set Gap A10). When characters from the second set (high within-group correlation or insignificant ANOVA) are considered a further five characters can be gap-coded for both sexes giving a total set of 15 (set Gap A15).

5) *Gap Coding, B.*—Since a character may exhibit statistically significant variation between populations yet not have a gap of one (within population) standard deviation between means, a lower criterion for gap recognition was also used. For those characters without gaps of one standard deviation a single gap was recognized on the basis that it was the largest gap over .5 of a within-population standard deviation. Characters without gaps of over .5 of a standard deviation were excluded. This excluded character 33 for males and characters 36, 41, 86, 90, 108 and 135 for females.

6) *Divergence Coding.*—In this case the divergence level between OTUs that is used is the least significant difference (Snedecor and Cochran, 1967) for 95% confidence. Other levels of divergence, e.g., two standard deviations or 99% LSD, could also be used. “Homogeneous subset coding” is suggested by Simon (1983) and this has some similarities to divergence coding.

The group means are first ranked in order of magnitude. A group mean is taken and coded as zero and those groups along the row with significantly higher means are coded as +1 while those with significantly lower means are coded as -1. This is repeated for each group mean until one obtains an OTU \times OTU matrix with zeros in the diagonals, some positive values above the diagonal and some negative values below the diagonal. The sum of the columns gives the integer code for the group. This is illustrated in Figure 1.

Divergence coding does not standardize the spread for the different characters. Consequently each character can have a different between group standard deviation and the range of codes may vary from zero to $2(N - 1)$, where N is the number of groups. If desired one could add a constant to the integer values to make them all positive and then convert them to additive binary codes (Sokal and Sneath, 1963).

Divergence coding is directly related to standardizing the characters by dividing the group means by the pooled within-group standard deviation because the least significant difference is based on the pooled within-group variance (note also that one could use the pooled within-group standard deviation directly as one’s level of ‘divergence’). While dividing by the pooled within-group standard deviation results in a continuous variable, divergence coding results in a (high magnitude) integer and it therefore has the

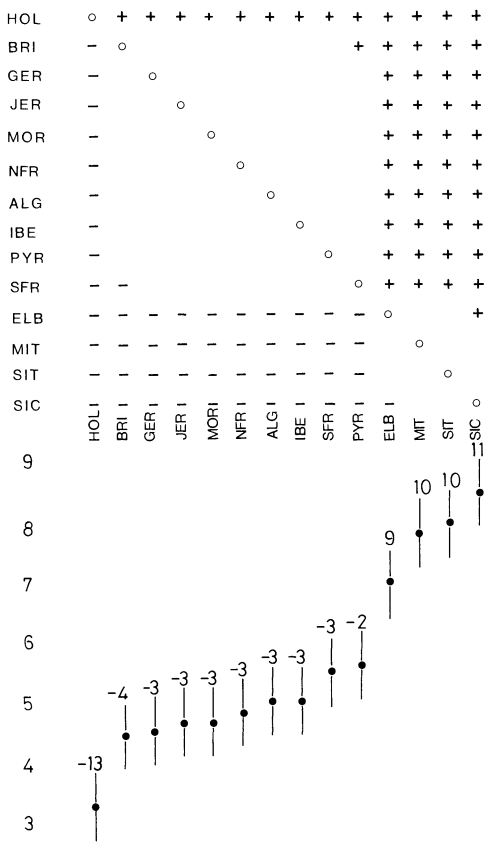


FIG. 1. Divergence (significance) coding for the size of dorsal blotches (42) in males. The group means (circles) are in rank order with one half the LSD value plotted either side. Moving along the rows of the matrix a self-comparison (diagonal) is coded as zero whilst significantly lower means are coded as minus one and significantly higher means are coded as plus one. The final integer code is the sum of the column and this is indicated on the bar diagram. If only the upper diagonal is computed the code is found as -1. (Row - column).

advantage that it can be used with network algorithms that require binary codes.

Some Considerations

There are some a priori considerations regarding coding methods such as the desirability of giving all characters the same amount of evolutionary change, bias in

and extent of character exclusion, loss of resolution, and the reliability of parameters.

Range coding and normalization both result in continuous variables with a standardized spread and are consequently very similar. I have a slight a priori preference for the latter technique because the spread of the raw character is estimated by the standard deviation. This is superior to the range as it is based on all sample values and not just the two extremes. Both range coding and normalization are capable of expressing subtle differences between populations and do not require that significantly varying characters be rejected. However, both normalization and range coding have the undesirable property of treating characters as if they show the same amount of evolutionary change when in fact different characters will have evolved different amounts. It should be noted that in this study characters with little or no 'evolutionary change,' (i.e., no significant difference between populations by ANOVA) are excluded. Consequently, one avoids the extreme case of treating a character with no evolutionary change the same as a character with substantial evolutionary change.

If one is comparing anagenesis in lineages, normalization and range coding should perturb the analysis only if there is a bias such that one lineage is divergent due to a set of characters which tend to show little evolutionary change, while another lineage is divergent due to a set of characters which tend to show substantial evolutionary change. With a small set of characters which include both highly divergent characters and those with insignificant divergence this could be a problem. However, it is less likely to be a problem when a substantial number of characters are used which all show significant divergence, as in this study.

Segment coding does not require significantly varying characters to be rejected but it does result in the loss of slight differences in character states be-

tween populations. For example, the size of lateral blotches (Table 3a) shows clear southeasterly clinal variation from Britain, through France, down the leg of Italy as well as categorical variation between southwest and northern Europe. Segment coding blunts this into a binary character that only differentiates the Italian populations from the others. Segment coding has the disadvantage that it assigns a binary code irrespective of the extent of evolutionary change shown by the character.

Gap coding (A) does not have this disadvantage. Not all characters have the same number of gaps and so they are not assigned the same range of codes. For example, for the size of dorsal blotches (Table 3b) multiple codes are assigned (at least in males) which give a more detailed reflection of the pattern of geographic variation than segment coding and which credits this character with a relatively substantial amount of evolutionary change.

Gap coding (A) does however reject a substantial number of characters (e.g., size of lateral blotches, Table 3a) even though they show a significant, highly interpretable, geographically coherent pattern of variation. Others, even if accepted, are reduced to a binary code. This may be of little significance for indicating the broad pattern of cladogenesis but failure to distinguish between significantly divergent populations can lead to the loss of critical detail, as in Thorpe (1984). Moreover, bias in the selection and weighting of characters may perturb an analysis of anagenesis. Riska (1979) suggests such a bias and claims that "characters that are relatively less variable are more likely to have gaps." He is here referring to within-group variability but there is no reason why this must be so. This suggestion can be rejected for the set of 37 characters (males) even though there is considerable variation in the magnitude of the pooled within-group standard deviation. There is no significant correlation between the number of gaps (meth-

od A) and the magnitude of the pooled within-population standard deviation ($r = .02$, 36 *d.f.*) and no difference in the magnitude of this standard deviation between those characters with one or more gaps and those with none ($t = .003$, 35 *d.f.*). This also holds true when the effect of scale on the variability is removed by regressing the pooled within-group standard deviations against the grand means. The residuals are not correlated with the number of gaps ($r = -.005$, 36 *d.f.*) and there is no significant difference in the residuals between those characters with gaps and those without ($t = .53$, 35 *d.f.*). Is there a bias in favor of selecting characters that, say, exhibit categorical rather than clinal geographic variation? If there is no such bias then the number of gaps recognized should be broadly related to the 'strength' of the pattern of geographic variation. That is, the characters with a high F value (where F equals the between-group variance divided by the within-group variance) should tend to have gaps, and more of them, than characters with a low F value.

When this is tested on males it can be seen that characters without gaps have significantly lower F values than those with gaps ($t = 3.8$, 35 *d.f.*, $P < .001$). Moreover, there is a significant correlation between the number of gaps and the magnitude of F ($r = .68$, 36 *d.f.*, $P < .001$).

Investigation of the exceptions, i.e., characters with a high F value and no gaps and characters with a low F value and gaps reveals that there is a very slight tendency for gap coding to favor categorical variation. However, the extent of this is trivial.

The recognition of gaps therefore appears to be largely unbiased but since a slight shift in a mean could eradicate or erect a gap, is it so fortuitous as to render the extent of anagenesis unreliable? The fact that gap recognition can be fortuitous is illustrated by the occipital line marking (character 48, Table 2). The geographic variation in this character is highly con-

TABLE 3. Population means for males for two characters and the influence of coding procedures. Character 38 has a pooled within-population standard deviation of 1.41 while the largest gap between means is 1.24. Character 42 has a pooled within-population standard deviation of .86. The divergence codes are given a positive value by the addition of a constant.

Table 3a. Character 38. Size of lateral blotches														
	BRI	JER	NFR	PYR	IBE	SFR	HOL	GER	MIT	SIT	SIC	MOR	ALG	ELB
RAW	6.46	6.00	6.67	5.60	5.00	7.33	5.00	6.00	8.57	10.20	8.83	5.67	6.00	9.00
Normalized	-.24	-.53	-.11	-.78	-1.15	.30	-1.15	-.53	1.08	2.09	1.24	-.73	-.53	1.34
Range coded	1.24	1.15	1.28	1.08	.96	1.41	.96	1.15	1.65	1.96	1.70	1.09	1.15	1.73
Segment coded	0	0	0	0	0	0	0	0	1	1	1	0	0	1
Gap-coded (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gap-coded (B)	0	0	0	0	0	0	0	0	1	1	1	0	0	1
Divergence coded	1	1	1	1	0	6	0	1	14	15	14	1	1	14

Table 3b. Character 42. Size of dorsal blotches														
	BRI	JER	NFR	PYR	IBE	SFR	HOL	GER	MIT	SIT	SIC	MOR	ALG	ELB
RAW	4.42	4.67	4.83	5.60	5.00	5.50	3.25	4.50	7.86	8.00	8.50	4.67	5.00	7.00
Normalized	-.77	-.61	.51	-.02	-.40	-.09	-1.51	-.71	1.41	1.50	1.82	-.61	-.40	.87
Range coded	.84	.89	.92	1.07	.95	1.05	.62	.86	1.50	1.52	1.62	.89	.95	1.33
Segment coded	0	0	0	0	0	0	0	0	1	1	1	0	0	1
Gap-coded (A)	1	1	1	1	1	1	0	1	3	3	3	1	1	2
Divergence coded	9	10	10	11	10	10	0	10	23	23	24	10	10	22

gruent between sexes, the population means of raw data being correlated at $r = .9$. Even so, the gap coding is entirely different for the two sexes ($r = .2$). In females the North African/Iberian populations are coded as different from the other populations while in males the Jersey and Elba populations are (convergently) similar and coded as different from the remaining populations.

This is unlikely to be a problem where there is a large number of characters with a substantial number of gaps. In this study, in which only a few of the characters can be gap coded, there are a priori grounds for being concerned about the reliability of the extent of anagenesis. Character gaps in geographic variation studies are likely to reflect gaps in the sampling of localities as well as evolutionary steps. The deletion or inclusion of a population could alter the gap coding scheme. Moreover, an excellent sample of localities will insure that intermediate populations will be found so that all gaps are eradicated. It is my experience that more populations result in fewer recognizable gaps when dealing with intraspecific data.

Gap coding (B) allows characters such as the size of lateral blotches (Table 3a) to be used and only requires a few significant characters to be rejected. Characters with gaps over 1 standard deviation are coded as for method A but characters with gaps between .5 and 1.0 standard deviations are given the same binary code irrespective of the amount of evolution they exhibit. Consequently, the range of codes does not reflect the amount of evolution in this character set except in a very crude manner.

Divergence coding can yield a high range of integer values which can reflect relatively slight differences between populations. It does not require significantly varying characters to be rejected. Moreover, the range of codes (and consequently the character weight) is directly related to the extent of evolution in the character. Characters with little evolution, i.e.,

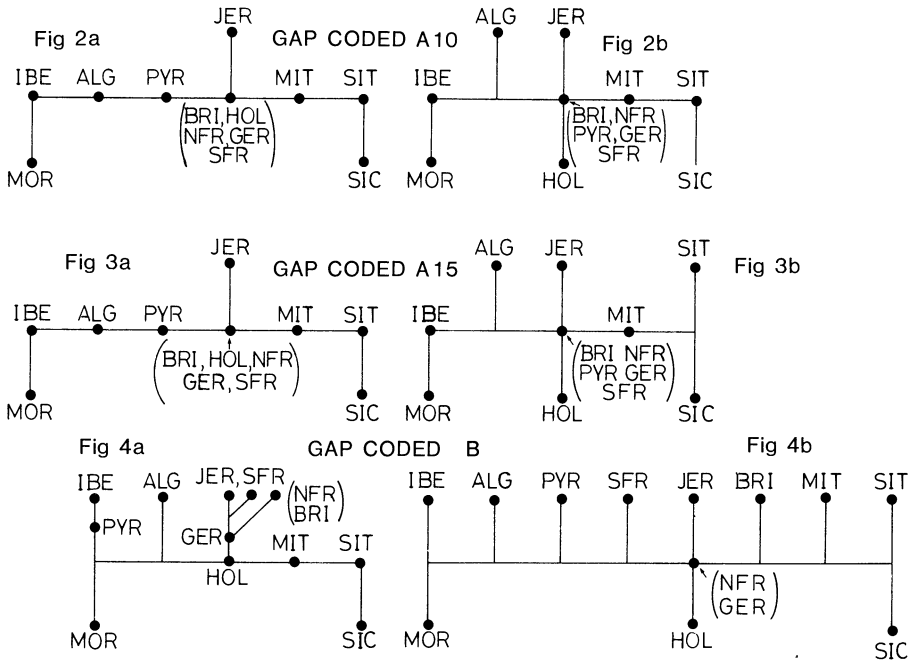
high within group variation in relation to between group variation, have only a narrow range of codes while highly divergent characters have a higher range of codes (e.g., size of dorsal blotches, Fig. 1). On a priori grounds this method should be suitable for indicating anagenesis.

RESULTS

In a broad sense all of the networks tend to show a relationship with the geographic location of the populations with the Ibero/North African populations and Italian populations at the ends of the networks and the northern European populations in between. In many networks, particularly the males, there is a very close relationship with the geographic location of the populations. Many of the male networks (i.e., normalized, range, divergence and segment coded) are very congruent even though derived from fundamentally dissimilar coding procedures. This set of networks has a close agreement with the geographic location of the populations. It is the female networks that tend to vary and become less consistent with the geographic location of the populations.

Intersexual congruence varies from very good (.33) to poor/medium (1.23). The coding method with the best intersexual congruence is gap coding (A10) (Fig. 2). There is a distance of 3 for the nine OTUs giving a congruence of .33; the constellations of indistinguishable populations differ between the sexes, in males the constellation includes the Pyrenees while in females it includes Holland.

This high intersexual congruence is in part due to the more labile northern populations being aggregated into one OTU. As well as not differentiating between the northern populations gap coding shows no anagenetic divergence between the OTU and its nearest HTU in a large proportion of cases. Including the additional set of characters (Gap coding A15, Fig. 3) makes no difference to the indistin-



FIGS. 2-4. Distance Wagner networks derived from gap-coded characters. (a) and (b) are for females and males, respectively. Fig. 2: Distance Wagner networks derived from 10 gap-coded (method A) characters. Fig. 3: Networks derived from 15 gap-coded (method A) characters. Fig. 4: Networks derived from 31 and 36 characters respectively. Gap-coded by method B.

guishable sets of populations but the intersexual congruence is slightly lower at .44.

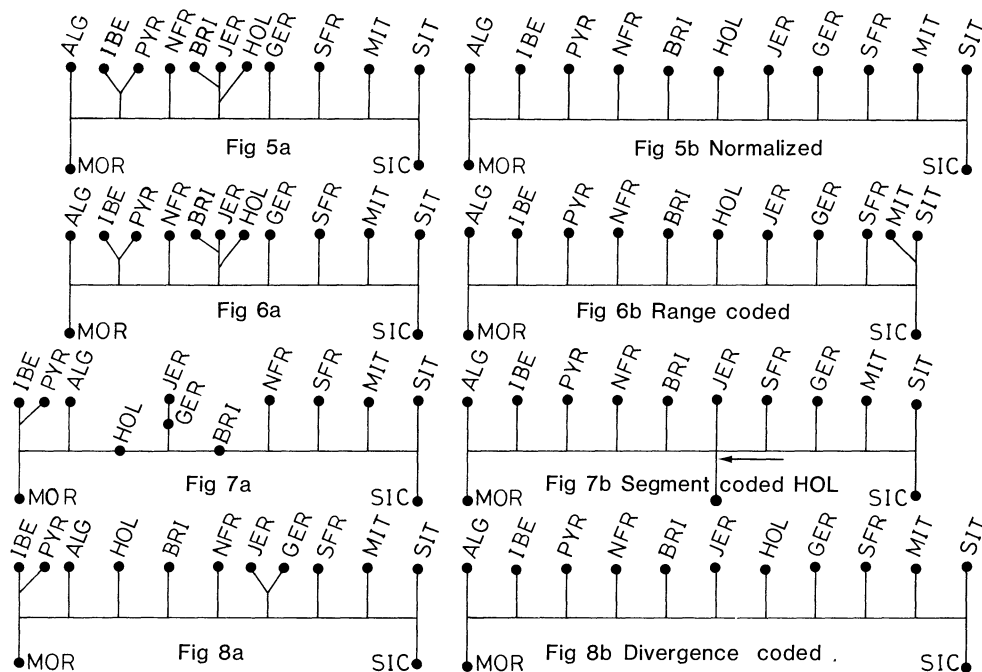
Including gaps of between .5 and 1.0 standard deviations (Gap coding B, Fig. 4) results in a considerable deterioration in intersexual congruence (a distance of 14 with 12 OTUs giving a congruence coefficient of 1.17) without the ability to distinguish between all populations or indicate anagenetic divergence between OTU and nearest HTU in several cases. Once again the constellations of indistinguishable populations differ between sexes.

After gap coding (A) the coding method with the best intersexual congruence is normalization (Fig. 5). A distance of 6 with 13 OTUs give a congruence coefficient of .46 which is very close to that of gap coding A15. Range coding, as ex-

pected, is very similar to normalization. The female networks are identical and the males have only one difference. The intersexual congruence is slightly poorer at .62 (Fig. 6).

Divergence coding (Fig. 8), although attractive on a priori grounds gives poorer intersexual congruence than normalization. There is a distance of 12 with 13 OTUs giving a congruence of .92. The males have a network very similar to normalization (only 1 difference) which is consistent with geographic location of the populations but the female divergence coded network is dissimilar to normalized network and inconsistent with the geographic location of the populations (particularly Algeria and Holland).

A similar situation occurs with segment coding. Although a fundamentally different coding procedure from normal-



FIGS. 5-8. Distance Wagner networks derived from several coding methods. (a) and (b) are for females and males respectively. Fig. 5: Distance Wagner networks derived from normalized data. Fig. 6: Networks derived from range-coded data. Fig. 7: Networks derived from segment-coded data. Fig. 8: Networks derived from divergence (significance)-coded data.

ization and divergence coding, the male network has only two differences from the networks derived from these procedures. However, the female segment coded network has some inconsistencies with the geographic location of the populations and is 16 units distant to the male network giving the poorest congruence coefficient of all (1.23) (Fig. 7).

Choice of Coding Procedure

The choice of coding procedure will be influenced by the aims of the study and the nature of the data as well as observations on the performance of the coding procedure.

In the present study, gap coding (A) has the highest intersexual congruence and can be recommended as a suitable procedure particularly if one's data have

a lot of gaps or if one is not interested in either cladogenesis of the 'indistinguishable' populations or the pattern of anagenesis. Gap coding is susceptible to bias in geographical sampling. Moreover, one's data set may contain only a few characters suitable for gap coding and several populations that cannot be distinguished by this procedure. If this is the case and one is interested in the cladogenesis of the 'indistinguishable' populations or the pattern of anagenesis then gap coding may not be suitable in spite of its reliability.

In this latter situation the next most congruent technique, normalization, is recommended, particularly if the character set is composed of a large number of characters with a relatively similar degree of evolutionary change. Character normalization credits each character with

the same amount of evolutionary change but in this situation one is not unduly concerned about the possible chance effects of this on the relative extent of anagenesis in different lineages (see above). When normalization is used one would generally wish to exclude characters with insignificant between group variation rather than credit them with the same amount of evolutionary change as a significantly varying character.

Range coding is similar to normalization but is marginally less suitable because of its slightly lower intersexual congruence and because the range is a less reliable parameter than standard deviation for measuring character spread.

Divergence coding has a priori advantages for indicating relative anagenesis but has poor intersexual congruence with this data set. Since the male divergence-coded network is highly congruent with a large set of other networks its measures of anagenesis may still be useful. Segment coding and gap coding (B) have little to recommend them.

SUMMARY

Various methods of coding morphometric characters, including normalization, range coding, segment coding, gap coding and divergence (significance) coding, were investigated. The intersexual congruence of the resultant Distance Wagner networks was found using data from the western grass snake, *Natrix natrix helvetica*. Gap coding has the highest intersexual congruence and normalization the next highest. Depending on the nature of the data and the aims of the study gap coding or normalization are recommended. A set of highly congruent male networks included some networks derived from fundamentally dissimilar coding procedures.

ACKNOWLEDGMENTS

I would like to thank Don Colless (CSIRO, Canberra), Chris Simon (Hawaii) and Bob Sokal (SUNY) for their comments on an earlier draft of this paper. I would also like to thank Bruce Riska, Joe Fel-

senstein and an anonymous reviewer for their comments. I am grateful to Don Colless for computing some networks from my data; Chris Simon for raising the question of coding characters to take into account the significant differences between populations; and Michael Waterman (USC) for checking some of my calculations and for discussing network congruence with me.

LITERATURE CITED

- COLLESS, D. H. 1980. Congruence between morphometric and allozyme data for *Menidia* species: a reappraisal. *Syst. Zool.* 29:288-299.
- FARRIS, J. S. 1972. Estimating phylogenetic trees from distance matrices. *Amer. Natur.* 106:645-688.
- JOHNSON, M. S., AND M. F. MICEVICH. 1977. Variability and evolutionary rates of characters. *Evolution* 31:642-648.
- LOUDENSLAGER, E. J., AND G. A. E. GALL. 1980. Geographic patterns of protein variation and subspeciation in cut-throat trout, *Salmo clarki*. *Syst. Zool.* 29:27-42.
- MICEVICH, M. F., AND J. S. FARRIS. 1981. The implications of congruence in *Menidia*. *Syst. Zool.* 30:351-370.
- RISKA, B. 1979. Character variability and evolutionary rate in *Menidia*. *Evolution* 33:1001-1004.
- ROBINSON, D. F., AND L. R. FOULDS. 1981. Comparison of phylogenetic trees. *Math. Biosci.* 51:131-147.
- SIMON, C. M. 1983. A new coding procedure for morphometric data with an example from periodical cicada wing veins, p. 378-382. *In* J. Felsenstein (ed.), 1983 *Numerical Taxonomy*. Springer, N.Y.
- SOKAL, R. R., AND P. H. A. SNEATH. 1963. *Principles of Numerical Taxonomy*. W. H. Freeman and Co., San Francisco.
- THORPE, R. S. 1975. Quantitative handling of characters useful in snake systematics with particular reference to intraspecific variation in the ringed snake *Natrix natrix* (L.). *Biol. J. Linn. Soc.* 7:24-43.
- . 1976. Biometric analysis of geographic variation and population affinities. *Biol. Rev.* 51:407-452.
- . 1979. Multivariate analysis of the population affinities of the ringed snake *Natrix natrix* (L.). *Proc. Roy. 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. Felstenstein (ed.), 1983 Numerical Taxonomy. Springer, N.Y.
- . 1984. Primary and secondary transition zones in speciation and population differentiation: a phylogenetic analysis of range expansion. *Evolution* 38:233–243.
- WATERMAN, M. S., AND T. F. SMITH. 1978. On the similarity of dendrograms. *J. Theoret. Biol.* 73:789–800.

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