Microevolution and taxonomy of European reptiles with particular reference to the grass snake *Natrix natrix* and the wall lizards *Podarcis sicula* and *P. melisellensis*

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The grass snake *Natrix natrix* and the wall lizards *Podarcis sicula* and *P. melisellensis* are used as examples to compare the procedure and achievements of the conventional approach to naming subspecies with the use of multivariate morphometrics to investigate racial differentiation.

The conventional procedure, which has changed little over the last 50 years, fails to take into account the appropriate evolutionary facts or refer to any abstracted levels of divergence necessary for subspecific recognition. Consequently, the patterns of population differentiation are obscured by the recognition of a large number of rather meaningless subspecies. There is a tendency to section clines into artificial categories and arbitrarily delimit subspecies by physiographic features.

On the other hand, the use of multivariate morphometrics reveals the patterns of population differentiation which can be related to geological events and patterns of differentiation in other species and species groups. The nature of 'hybrid' zones and population differentiation enables the relative importance of evolutionary forces such as gene flow, selection and genetic drift to be discussed and provides evidence concerning speciation mechanisms. These techniques also contribute to the discussion regarding the nature of species and provide abstracted and operational criteria for taxonomic decisions.

The difference between the results of multivariate analysis and the conventional approach cannot be explained solely on the basis of choice of characters. Some of the advantages and disadvantages of using multivariate morphometrics, as opposed to other modern techniques, for investigating racial affinities are discussed.

KEY WORDS: – multivariate morphometrics – subspecies – microevolution – taxonomy – population differentiation – *Natrix natrix* – *Podarcis*.

CONTENTS

8

INTRODUCTION

Advances in the methods and theory of evolution and taxonomy have made little impression on the practice of intraspecific taxonomy of European reptiles over the last half a century (compare Hecht, 1930 with Gruber & Fuchs, 1977). Whilst many workers nowadays may be more careful about basing their classification on a reasonable sample from a population and may even employ descriptive univariate statistics the basic procedure tends to continue unabated.

This procedure consists primarily of subjectively discriminating between populations on the basis of one or a few characters, usually from the hue or pattern of the colour markings. If any population or set of populations is capable of being distinguished it is given a subspecific name. Once the taxa have been intuitively decided other characters, such as the scalation or body proportions, may be described for the taxa without critically contributing to their delimitation.

The question as to what level of differentiation is sufficient/necessary for subspecific recognition is generally not considered as an abstracted or generalized problem and is usually not even asked at all. Consequently it cannot be tested or repeated or even seriously discussed. The discussion over the 75% rule (Pimentel, 1959; Sokal, 1965; see also Thorpe, 1979) for the recognition of subspecies has made little impact on European herpetological taxonomists since they have not yet started to use it.

The European herpetologists who base their subspecies on single characters have shown little consideration of the evolutionary fact that different characters show different patterns of geographic variation. Consequently, the selection of different characters could result in the recognition of different subspecies. Similarly there is little recognition of the fact that all demes and populations may differ from one another (given that they are investigated with sufficient assiduity) and so to simply establish that a population differs is not a sufficient criterion to recognize it as a subspecies.

The more recent methodological advances such as the investigation of isozymes (by electrophoresis), cytotaxonomy and multivariate analysis of morphological characters have not been applied to a wide range of European reptiles. Two exceptions to this rule are the grass snake (or ringed snake) *Natrix natrix* (Thorpe, 1973, 1975a, b, 1979, 1980a), the wall lizards *Podarcis* species (Clover, 1979; Gorman, Soute, Yang & Nevo, 1975).

This paper takes one of these methods, the multivariate analysis of morphological characters, and compares its contribution to that of the above 'conventional procedure' of naming subspecies.

This will be based on my analysis of the population systematics of the *N. natrix* species complex and my reanalysis of Clover's (1979) data on the wall lizards *Podarcis sicula* and *P. melisellensis*.

THE GRASS SNAKE *NATRIX NATRIX*

From a conventional viewpoint this 'species' appears as a typical polytypic biological species. The earlier attempts at describing the geographic variation have centred around naming subspecies in the 'conventional' way described above.

Hecht (1930) recognized 21 subspecies (Fig. 1) from five subspecies groups. He used several colour pattern and scalation characters but not consistently
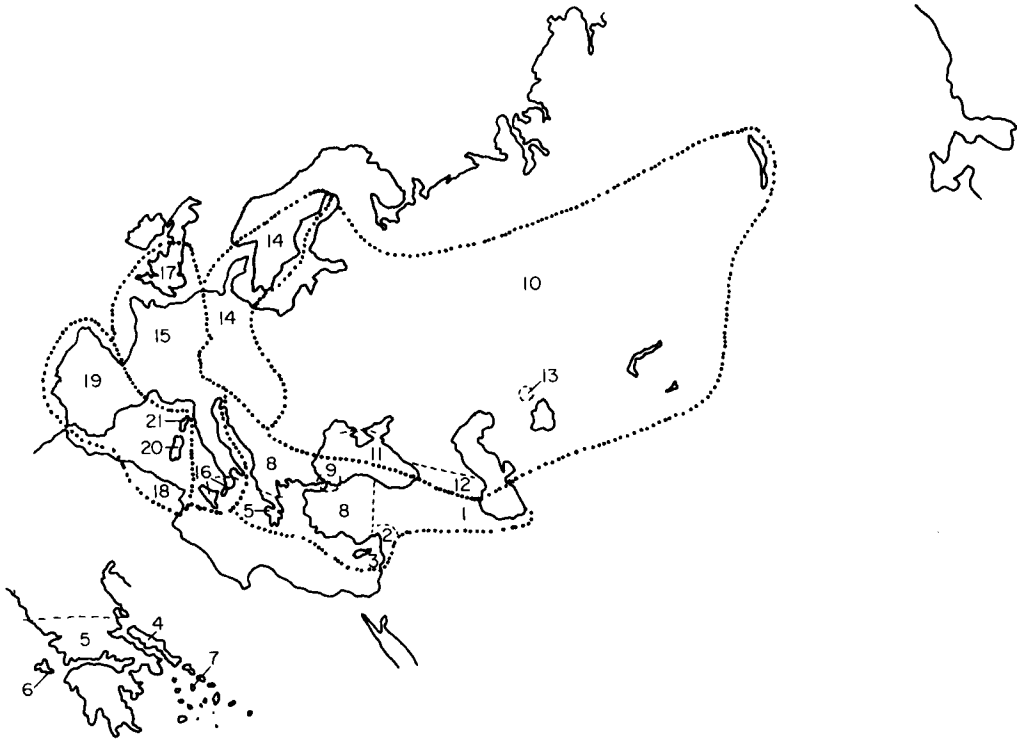
Figure 1. Hecht (1930) recognized 21 subspecies of *N. natrix* from five groups. In the *persa* group there is (1) *persa*, (2) *syriacus*, (3) *cypriacus*, (4) *dystiensis*, (5) *moreoticus*, (6) *cephallonicus* (Cephalonia), (7) *Syrae* (Syros), (8) *dalmatinus*, (9) *bithynius*. In the *scutatus* group there is (10) *scutatus*, (11) *picturatus*, (12) *schirvanae*, (13) *bucharensis*. In the *natrix* group just (14) *natrix*. In the *gronovianus* group there is (15) *gronovianus*, (16) *siculus* (Sicily), (17) *britannicus*. In the *cetti* group there is (18) *algericus*, (19) *astreptophorus*, (20) *cetti* (Sardinia), (21) *corsus* (Corsica).

throughout the species range. Hecht failed to appreciate the importance of non-geographic intraspecific variation (Thorpe, 1976), i.e. sexual dimorphism, local variation and ontogenetic variation, and consequently two of the subspecies he named were individual variants and not geographic races.

Mertens (1947, 1957, 1966) recognized 10 subspecies to which Kramer (1970) added an eleventh (Fig. 2). These subspecies are currently in use (Gruber & Fuchs, 1977) by some herpetologists.

In Merten's surveys the body proportions and scalation are described for the subspecies which are delimited (as far as one can tell) on the basis of colour pattern differences. Whilst Mertens based his descriptions on a greater number of specimens he, like Hecht, failed to fully appreciate the extent of sexual dimorphism and allometry and was also inconsistent in his choice of characters used to describe the various subspecies.

There is a tendency to use physiographic features such as rivers, sea channels and mountains to delimit the range of the subspecies (perhaps, partly because this is convenient in written descriptions of the subspecies distribution). Any island populations that are investigated also tend to be given subspecific status and the delimitation of mainland subspecies often involves sectioning a cline. For example, the river Dnepr separating the intergrading forms *N. n. natrix* and *N. n.*

Figure 2. Mertens (see text) recognized ten subspecies of *Natrix natrix*: (1) natrix, (2) persa, (3) scutata, (4) syriaca, (5) schweizeri (Milos), (6) helvetica, (7) astreptophora, (8) cetti, (9) corsa, (10) sicula. Kramer later recognized one further subspecies, (11) lanzai.

scutata and the *helvetica-lanzai-sicula* series on mainland Italy are examples of arbitrarily sectioned clines.

From 1973 onwards (Thorpe, 1973, 1975a, b, 1979, 1980a) I have used multivariate analysis of morphological characters to elucidate the patterns of race formation and geographic variation within the entire range fo this species. The localities are usually grouped into compound samples depicted in Fig. 3 on the basis of the affinity of the individual specimens (Thorpe, 1973, 1979). The racial similarity between these samples are then assessed using a large number of characters from a range of different systems (scalation, internal morphology, colour pattern, dentition, body proportions and dermal sense organs). Initially 160 characters were recorded from each specimen and from this set 54 (females) and 56 (males) characters were selected on the basis that they contributed information independent of other included characters (a low pooled within-group correlation), that showed significant geographic variation and were recordable from all included samples (Thorpe, 1979).

Once the appropriate statistical methods had been used to overcome the problem of non-geographic variation the affinity between the samples was assessed using a wide range of multivariate methods (Thorpe, 1979, 1980a). These were robust between sexes, methods and character sets in showing the basic pattern of intraspecific differentiation and so just one method is selected to illustrate the results.

The method (chosen for consistency with the later analysis of wall lizards) is the principal coordinate analyses of 44 male samples based on 56 characters
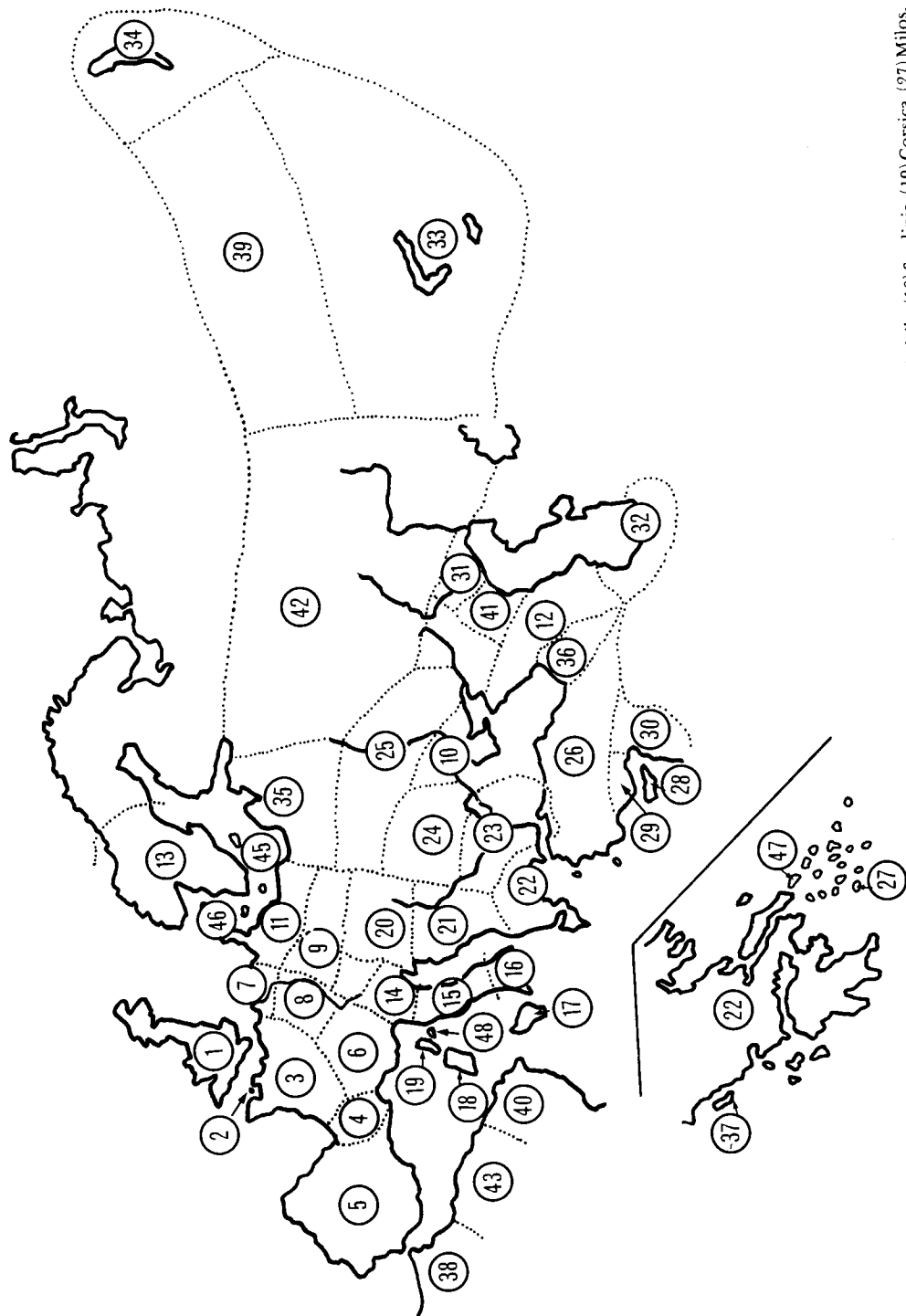
Figure 3. The range of *Natrix natrix* divided into numbered (compound localities). The island samples are: (2) Jersey, (17) Sicily, (18) Sardinia, (19) Corsica, (27) Milos, (28) Cyprus, (37) Corfu, (45) Bornholm, (46) Zeeland, (47) Andros, (48) Elba. Adapted from Thorpe, 1979 (reproduced with the permission of the Royal Society of Edinburgh).
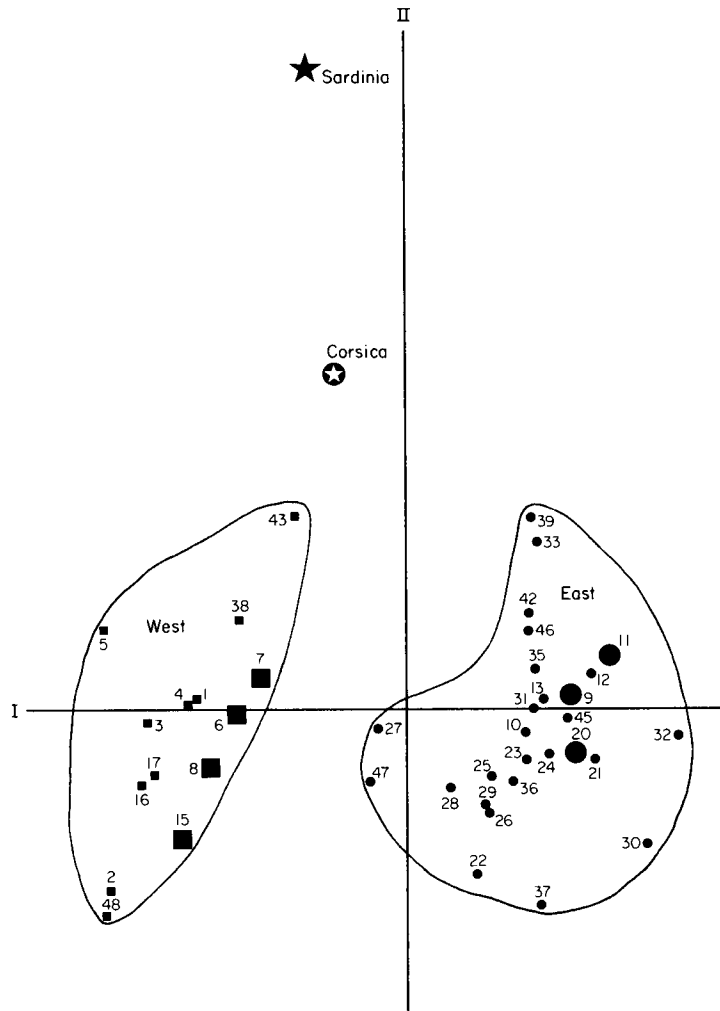
Figure 4. Principal coordinate analysis. Scatter diagram of the male samples of *N. natrix* on the first two coordinates show the eastern (circles) and western (squares) populations as distinct groups. The populations where the two forms meet in central Europe are shown with enlarged symbols. The Corsican and Sardinian populations are divergent. See Thorpe (1979) for further details.

Figure 5. A transect across the transition zone of *N. natrix* in northern Switzerland shows the sharp change in eastern to western morphology (solid circles) based o a 'hybrid index' (discriminant function) of 26 characters in females. Since the intermediate population (Turbenthal) does not have the full range of eastern and western forms these intermediates cannot be the direct F1 hybrid product of a parent from each of the incipient species. This is, strictly speaking, not a hybrid zone but is most probably a very sharp secondary integradation zone.

Note the increase in variability (2 standard deviations either side of mean are given) in the intermediate population of Turbenthal (T) and the proportional decrease through Hutwilen (H) and Constance (c) to the eastern populations (9 and 20). Note also that the shoulders of this sharp step are 'rounded' off. This is probably due to gene flow spreading genes (and consequent variability) from the opposing coadapted 'gene pool' several kilometres into th eastern range. However gene flow has not been influential enough to smooth this sharp step into a gradual line. Taken from Thorpe (1979: diag. 8, appendix) (erroneously referred to as male). (Reproduced with permission of the Royal Society of Edinburgh.)
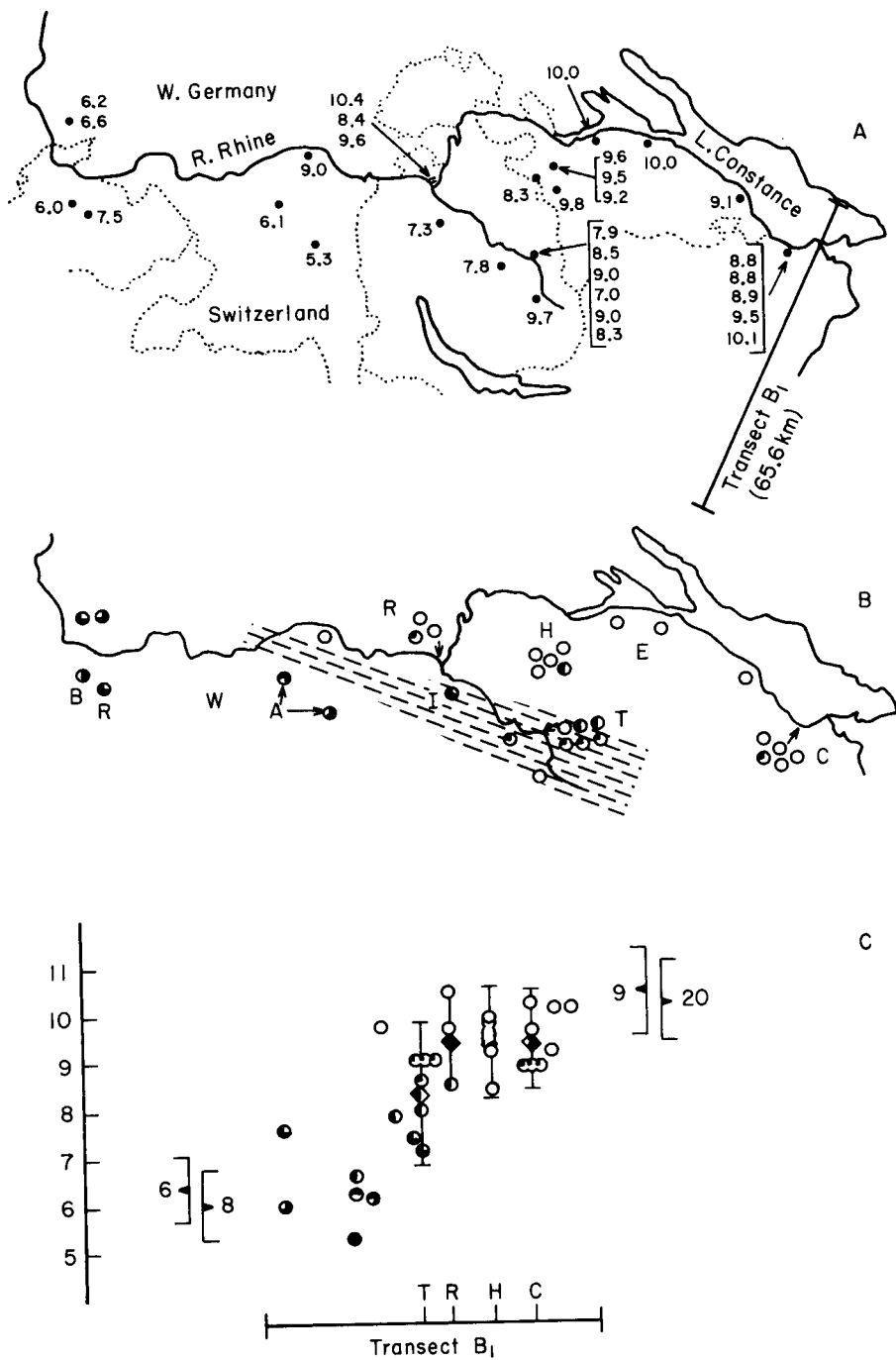
Figure 5.

(Thorpe, 1979, 1980a). Other methods, i.e. canonical analysis, showed an even more clearly defined pattern (see Thorpe, 1976, 1979, 1980a for a discussion on, and references to, this method).

The plot of the samples on the first two principal coordinates (Fig. 4) shows that the majority of samples fall into two distinct aggregations which occupy the west and east of the species range respectively. The samples where the two racial groups meet geographically (6, 7, 8 and 15 in the west and 9, 11 and 20 in the east) are well separated by the principal coordinate analysis.

The Sardinian population is extremely divergent and the Corsican population is equidistantly intermediate between the Sardinian and mainland populations.

The two major groups (east and west) are probably evolved from separate eastern and western glacial refugia. The differentiation between these refuge populations was probably due to natural selection rather than genetic drift since there are parallel patterns of character variation in the related *Natrix maura/tessellata* complex. Post glacial range expansion has produced the pattern of east-west differentiation which can be seen in so many other palearctic vertebrates which have presumably undergone the same events (Thorpe, 1979). This pattern of differentiation in *Natrix natrix* and the other species supplies some of the soundest evidence in support of allopatric speciation (White, 1978) at a time when the omnipotence of allopatric speciation is under attack (Endler, 1977).

The relationship between the eastern and western forms borders on the species level (Thorpe, 1975a). Other cases with similar levels of divergence have been considered as either races or species. I consider that the two forms are best regarded as conspecific since a transect across the region where they make contact (Fig. 5) shows that they completely, albeit very sharply, integrade and cannot therefore be considered as reproductively isolated (Thorpe, 1979). Closer study of the nature of this secondary intergraduation zone by multivariate methods enables discussion on the relative influence of gene flow and selection (Thorpe, 1979).

There is considerable racial differentiation within the eastern and western mainland forms but the 'races' can always be shown to gradually intergrade and there is always less differentiation between adjacent populations than there is across the contact zone (Thorpe, 1979). Nevertheless, these small increments of differentiation between adjacent populations sum up so that the difference between terminal populations in these conspecific series (whether including or excluding allopatric populations) is greater than the difference across the contact zone. In other words the difference within (incipient) species is greater than the difference between (incipient) species.

It is possible that the Corsican population was the product of a preglacial migration from the mainland by a few 'founders' and that the Sardinian population was in turn founded from the Corsican population.

Deciding which of these allopatric populations can be regarded as being conspecific with the mainland is more of a problem since the 'interbreeding' criterion of the biological species concept cannot be tested (see Sokal, 1973 for discussion and references).

White (1978) has claimed that this limitation of biospecies is superficial but the situation in the *Natrix natrix* complex shows this is not the case. Moreover, it is not a problem that is likely to be limited to this 'species' since an investigation

of the distribution of European reptiles as reported in Arnold & Burton (1978) shows that of the 82 species* only four have no obvious allopatric populations.

What is needed then is a biologically meaningful level of phenetic divergence below which an allopatric population is regarded as conspecific and above which it can be regarded as a separate species. There are several relevant phenetic levels. One is the level of phenetic divergence associated with incipient speciation, i.e. the divergence between adjacent populations across the zone where the two incipient species make contact (Fig. 6). This has limitations: it deals with incipient speciation and not full speciation, the level of divergence differs along the length of the zone, and there are some small differences between sexes and methods.

It can be seen that both the Sardinian and Corsican populations are more divergent than this 'incipient speciation' level (Fig. 6) but it should be noted that since the Corsican population is intermediate between that of Sardinia and the mainland populations the phenetic gap between Sardinian populations and the mainland populations (via Corsica) is reduced (to $d = 1.9$).

As well as the divergence between incipient species the divergence within the eastern and western forms and within the species as a whole can be considered.

Since the phenetic gaps between Sardinia and Corsica and their most similar populations is below that found between contiguous series of conspecific populations or between conspecific populations from the species as a whole I consider that it is best to regard the Sardinian and Corsican populations as being conspecific with *Natrix natrix* (Fig. 6).

Nevertheless the arbitrary nature of this species is evident and it is difficult to see how it can be regarded as having genetic cohesion between its constituent populations and consequently be a natural genetic and evolutionary unit (except like a genus it is the product of evolution) or be an ecological unit as conceived by Mayr (1970). It is also impossible to see how it could be divided to produce taxonomic species which have the attribute of 'biological' species (*sensu* Mayr, 1970; White, 1978).

The four main forms, eastern, western Sardinian and Corsican, although treated as conspecific are obviously not far below the level of species. The application of trinomials can be useful in these circumstances, i.e. to indicate taxa just below the species level, and these four forms were named as subspecies (Thorpe, 1979).

There is considerable differentiation within the eastern and western forms, particularly some allopatric populations (e.g. Milos), but these are not recognized as subspecies because the phenetic gap between them and the other populations is below any critical level (e.g. level associated with incipient speciation). The local forms are best referred to using an informal nomenclature based on geographic position, e.g. Milos form, Iberian form and so on.

The four subspecies, *sensu* author, reflect the main pattern of population differentiation whilst the conventional subspecies strongly contradict these new subspecies and obscure this pattern.

THE ADRIATIC WALL LIZARDS *PODARCIS SICULA* AND *P. MELISELLENSIS*

To show that the situation in *N. natrix* is not an isolated example the situation in *Podarcis sicula* and *P. melisellensis* can be considered.

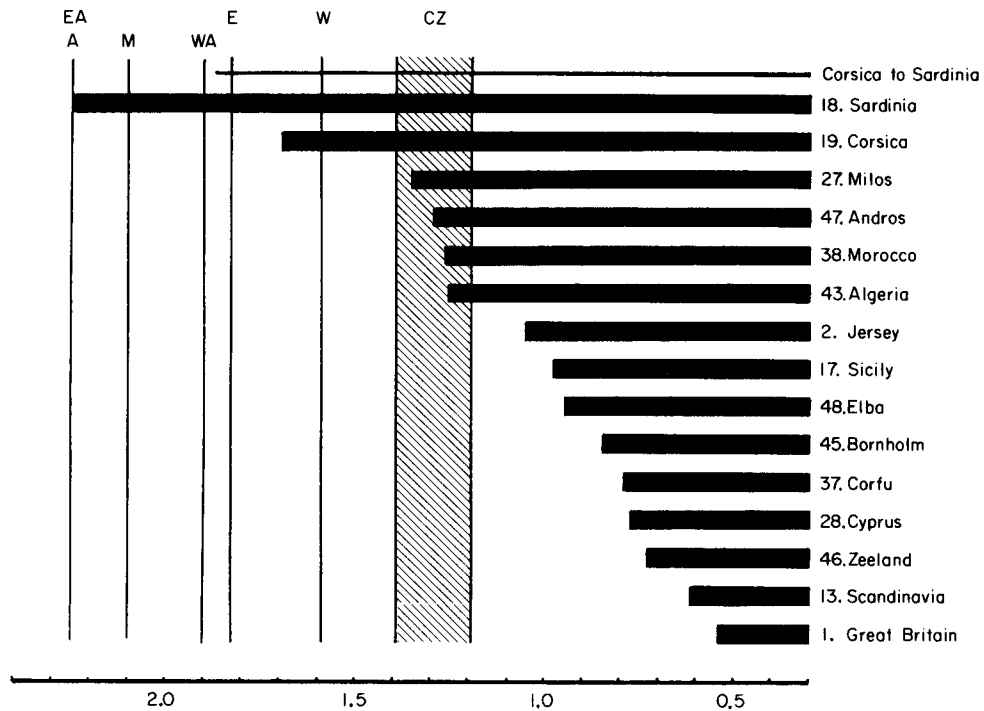* The largely Asian species *Eremias arguta* is excluded.

Figure 6. The divergence of the allopatric male populations of *N. natrix* from their most similar adjacent mainland population based on taxonomic distance (56 characters). CZ indicates the taxonomic distance between pairs of well represented samples across the contact zone. E and W indicate the taxonomic distance between dissimilar pairs of mainland populations within the eastern and western subspecies, respectively. M represents the highest taxonomic distance between any pair of mainland populations and A represents the distance between any pair of populations excluding Corsica and Sardinia (this is the same as the highest taxonomic distance between any pair of populations in the eastern subspecies, EA). WA is the highest taxonomic distance between any pair of populations in the western subspecies. Adapted from Thorpe (1979: fig. 11), (Reproduced with the permission of the Royal Society of Edinburgh.)

Conventional subspecies are as popular for wall lizards as they are for grass snakes, there being over 172 recognized for the 13 species of *Podarcis* (*P. melisellensis* has 18). In the study area there are three subspecies of *sicula* (plus one undescribed population) and ten subspecies of *melisellensis* (plus six undescribed populations).

Clover (1979) recorded ten meristic scalation characters and five linear dimensions from six Adriatic island populations of *P. sicula* and 24 Adriatic island populations of *P. melisellensis* (Fig. 7, Table 1).

These are continuously growing species and I considered it advisable to adjust the linear dimensions for size independence. This was done by extracting the five principal components from the covariance matrix between the linear dimensions based on all 31 population means. The first component had the same sign for all characters and was discarded as it is taken as being the size component. The remaining four components described various aspects of the shape and were retained as four shape 'characters'. This is far from being the best way to adjust for size independence (Thorpe, 1976) but was permissible with the given data.

The population means (male) of the ten scalation and four shape characters
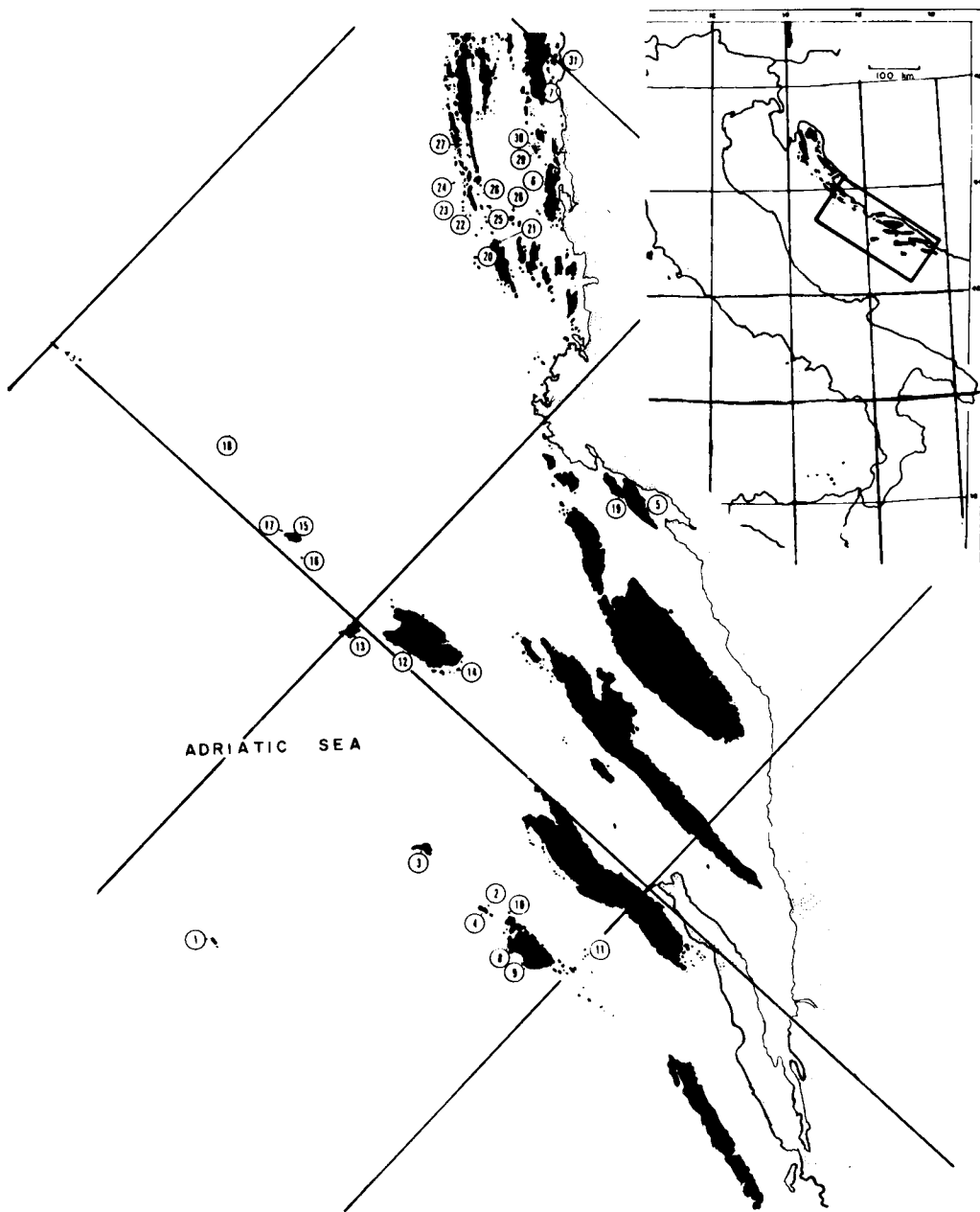
Figure 7. A map of Clover's samples of *Podarcis sicula* and *melisellensis* in the Adriatic (Clover, 1979: fig. 1).

were then adjusted to zero mean and unit standard deviation and subjected to principal coordinates analysis keeping the species separate.

The principal coordinate analysis of the seven populations of *P. sicula* shows (Fig. 8) that they segregate into two groups, one from northern islands and one from the southern islands.

Similarly the principal coordinate analysis of the 24 populations of *P. melisellensis* shows (Fig. 9) that these also tend to segregate into northern and

R. S. THORPE

Table 1. Island populations of *Podarcis sicula* and *P.
melisellensis* in the Adriatic (from Table 1, Clover
1979)

Island	OTU	Subspecies	Region
Palagruza	1	*P. s. pelagosae*	S
Pod Kopiste	2	*P. s. cazzae*	S
Susac	3	*P. s. cazzae*	S
Kopiste	4	*P. s. cazzae*	S
Ciovo	5	*P. s. campestris*	N
Murter	6	*P. s.* (undescribed)	N
Sveta Katarina	7	*P. s. campestris*	N
Lastovo	8	*P. m. lissana*	S
Lastovo	9	*P. m. lissana*	S
Pod Mrcaru	10	*P. m. lissana*	S
Tajan	11	*P. m.* (undescribed)	S
Vis	12	*P. m. lissana*	S
Bisevo	13	*P. m. lissana*	S
Greben	14	*P. m. lissana*	S
Svetac	15	*P. m.* (undescribed)	S
Brusnik	16	*P. m. melisellensis*	S
Kamik	17	*P. m. galvagnii*	S
Jabuka	18	*P. m. pomoensis*	S
Ciovo	19	*P. m. traguriana*	N
Zirje	20	*P. m.* (undescribed)	N
Mikavica	21	*P. m. mikavicae*	N
Veli Puh	22	*P. m. thetidis*	N
Vodeni Puh	23	*P. m.* (undescribed)	N
Purara	24	*P. m. kornatica*	N
Mrtovenjak	25	*P. m. kornatica*	N
Babina Guzica	26	*P. m. kornatica*	N
Krpeljina	27	*P. m.* (undescribed)	N
Calvin	28	*P. m. kornatica*	N
Vrtlic	29	*P. m. kornatica*	N
Mrvenjak	30	*P. m.* (undescribed)	N
Planac	31	*P. m. var. imitans*	N

southern groups. These aggregations are not compact and widely separated from one another but they are clearer than both Clovers (1979)* cluster analysis and non-metric multidimensional scaling analysis.

Wagner networks (Farris, 1972) may also be computed from the same taxonomic distance matrix as used for the principal coordinate analyses. Instead of emphasizing the relative similarity of the populations these aim to represent the most parsimonious evolutionary network connecting the populations and may be useful in revealing the colonization pathways involved.

The Wagner network joining the populations of *P. sicula* shows, in agreement with the principal coordinate analysis, that they clearly segregate into northern and southern groups (Fig, 10). With *P. melisellensis* there are two main and one subsidiary branches to the network (Fig. 11). The subsidiary branch is a heterogeneous assemblage of two northern and one southern populations. However the two main branches segregate the remaining northern and southern populations completely.

The more terminal branches of the network did not reveal a geographically meaningful pattern. This may be due to (1) parallelism due to geographically separate islands having similar ecological conditions and consequently similar

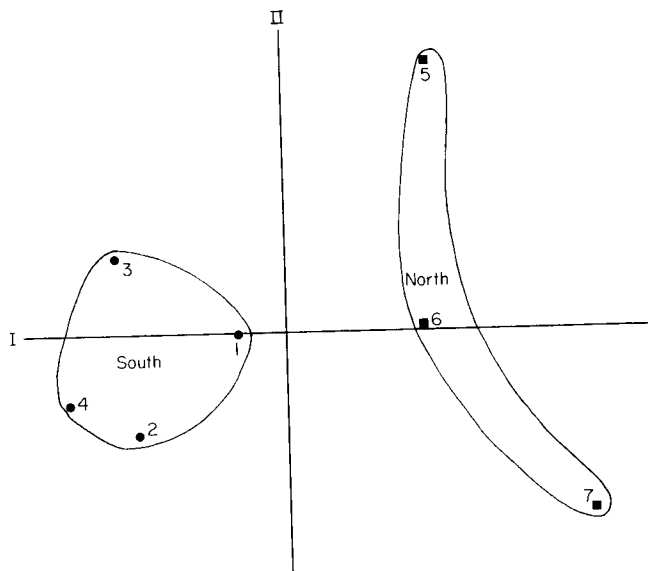* Population 19 is mislabelled in Clover, 1979:fig. 3.

Figure 8. Principal coordinate analysis. Scatter of male samples of *P. sicula* on the first (43%) and second (23%) principal coordinates. Southern samples (circles) are distinct from the northern samples (squares).
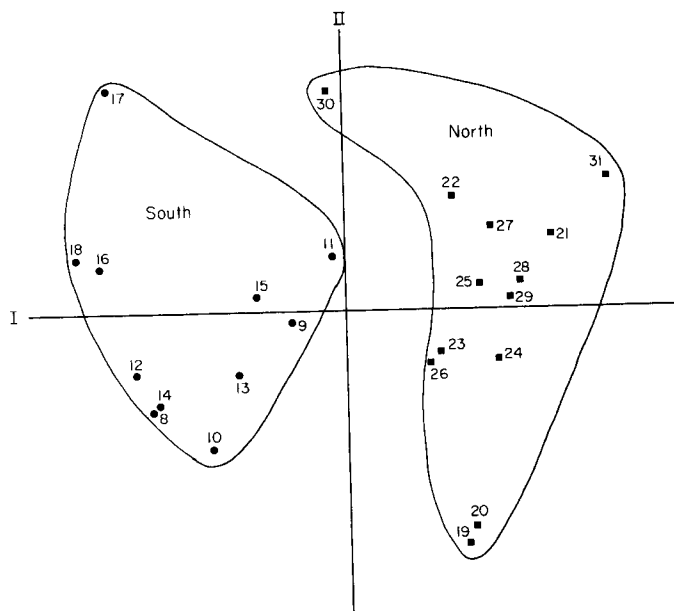

Figure 9. Principal coordinate analysis. Scatter of male samples of *P. melisellensis* on the first (30%) and second (14%) principal coordinates. Symbols as for Fig. 8.
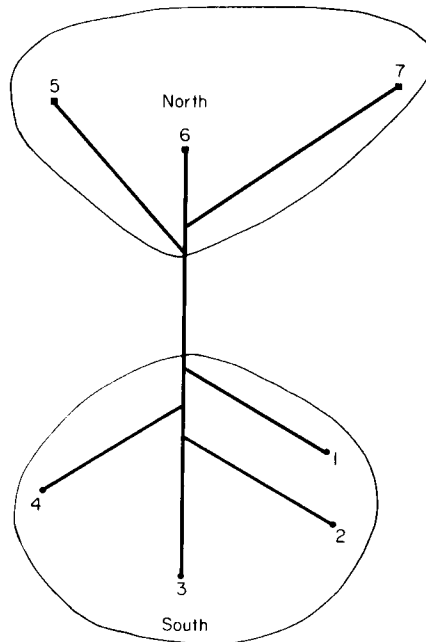
Figure 10. Wagner network (% S.D. 11.5, length 4.6) based on taxonomic distance between male populations of *P. sicula*. Note the separation of northern and southern populations. Symbols as for Fig. 8.

selection pressures, (2) the inappropriate use of euclidian rather than manhattan distances*, (3) an inadequate sample of characters, or (4) the use of a distance matrix rather than the original characters to deduce the network.

It is evident that in both species of wall lizard the primary pattern of differentiation is the existence of two main groups, one from the northern islands and one from the southern islands.

Clover (1979) relates the pattern of phenetic similarity of the northern and southern groups to post-Pleistocene changes in sea level and channel depths. The topography of the Adriatic basin is such that the northern and southern groups of islands would have been isolated from one another and the populations of the northern islands would have been capable of exchanging genes more recently than those of the south. *P. sicula* is readily transported by man and it should be borne in mind that an investigation of the mainland populations may reveal alternative explanations.

Clover discusses the various evolutionary forces in relation to the pattern of population differentiation and concludes that gene flow and selection are most likely to have been responsible for the pattern. Genetic drift, however, is unlikely to have had much influence on the primary pattern of differentiation.

It is apparent from a comparison of Table 1 with Figs 8–11 that the conventional subspecies of these wall lizards obscure this parallel pattern and that, unlike Clover's study, they do not contribute to an understanding of evolutionary processes.

* Further analyses, run on manhattan distances, did not give superior results.
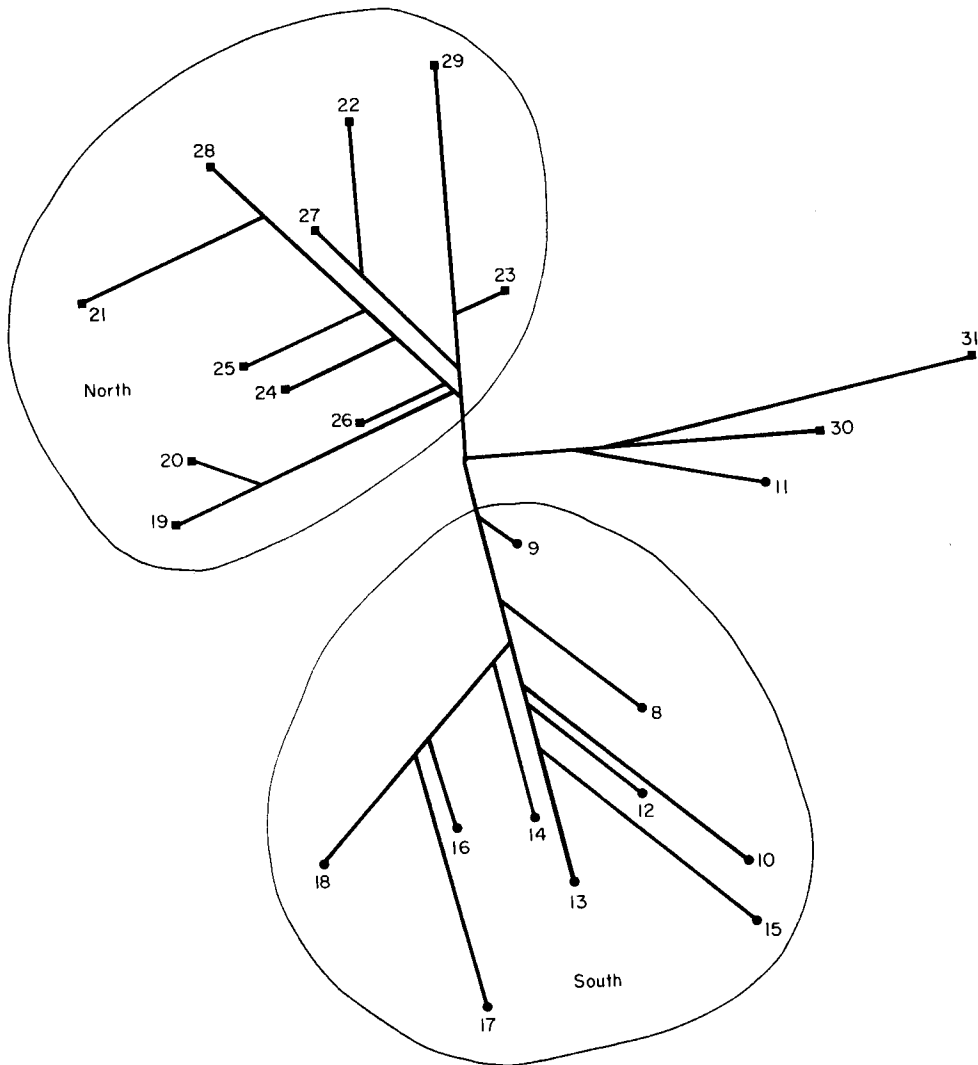
Figure 11. Wagner network (% s.d. 38.6, length 13.8) based on taxonomic distance between male population of *P. melisellensis*. Northern and southern populations tend to segregate. Symbols as for Fig. 8.

TYPES OF CHARACTER

One of the differences between 'conventional' subspecies and the multivariate approach is the selection of characters. Whilst conventional subspecies tend to be based on colour pattern it could be argued that multivariate analyses of population affinities should be based on a range of character types (Thorpe, 1976).

Although the segregation of the populations of *P. melisellensis* into northern and southern groups is rather less than it could be it does contradict the conventional subspecies. It could be argued that since these conventional subspecies are largely based on the colour pattern that the inclusion of these
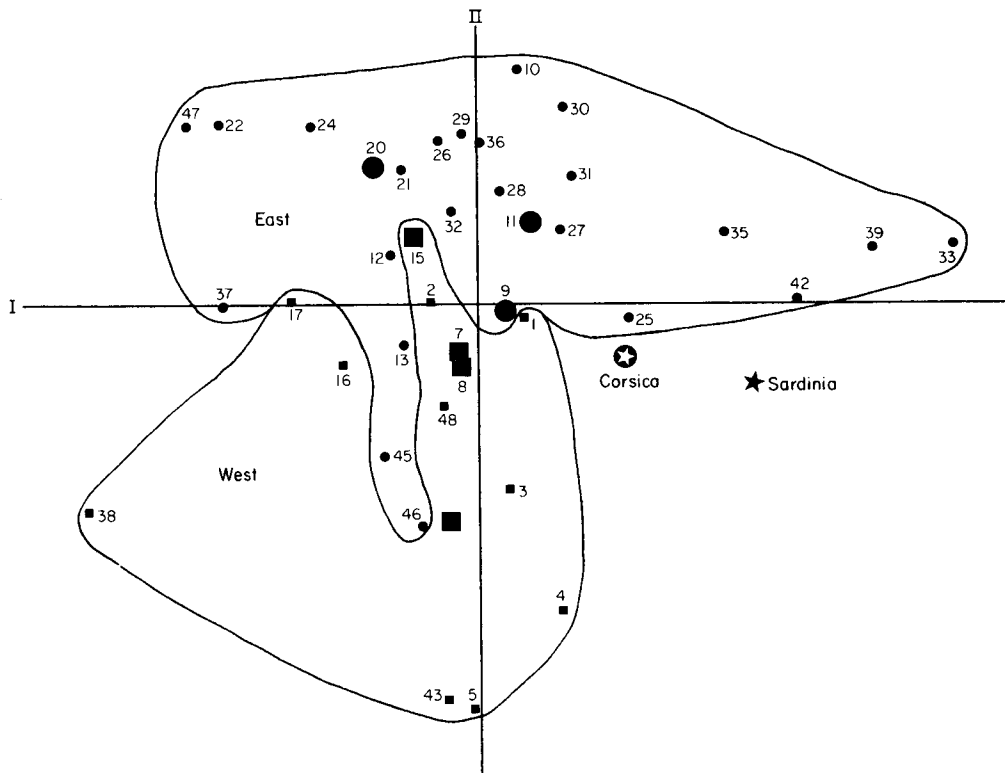
Figure 12. Principal coordinate analysis. Scatter of male samples of *N. natrix* on first (19%) and second (17%) principal coordinates. Symbols as for Fig. 4. The four taxa are not represented as distinct aggregations although consideration of the third coordinate (14%) does show the eastern and western samples as abutting rather than interlocking groups.

characters in the multivariate analysis would render the two patterns more congruent.*

This is unlikely for several reasons. Firstly, independent multivariate analyses of the scalation and shape (and size for *P. sicula*) show that both these character systems differentiate between northern and southern populations. Why then should a third system (colour pattern) disagree with these two systems and agree with the conventional subspecies? Secondly, in the comparable situation in the grass snake the colour pattern characters, if subjected to multivariate analysis, do not support the conventional subspecies that were based on colour patterns but reflect the four main taxa as indicated by analyses of all the character systems.

I consider that the inclusion of other character systems (such as colour pattern) in Clover's study rather than supporting the conventional subspecies would be more likely to result in a clearer separation of northern and southern groups. Evidence in support of this comes from analysing the comparable situation in the grass snake. As well as the points above it can be seen that multivariate analysis of just the 13 scalation characters in *N. natrix* (Fig. 12) results in the same situation as in *P. melisellensis*, i.e. a poor segregation of the major groups. Whereas, the inclusion of other character systems, (including colour pattern) shows these primary groups clearly (Fig. 4).

* Clover excluded the colour pattern characters because of difficulties in encoding them. However, these difficulties can often be overcome (Thorpe, 1975b).

The difference between conventional subspecies and the patterns indicated by multivariate analysis is therefore not simply a question of character choice.

CONCLUSIONS AND DISCUSSION

It is apparent that the conventional procedure of naming subspecies does not take into account the appropriate evolutionary facts and in practice does not refer to any abstracted levels of divergence necessary for subspecific recognition. Consequently, a large number of meaningless subspecies are erected which obscure the patterns of population differentiation and which do not contribute much to our understanding of evolutionary processes. Moreover, the naming of island populations and the 'convenient' use of physiographic barriers to delimit the boundary between clinally intergrading subspecies may circularly and erroneously reinforce the view, typified by Mayr (1970), that gene flow is the primary force influencing population differentiation. There has been a general trend away from this view over the last decade although it is still a contentious area (Jackson & Pounds, 1979).

Conversely, the appropriate use of multivariate morphometrics can reveal the patterns of population differentiation and the nature of 'hybrid' zones. These patterns can be related to geological events and patterns involving other species and species groups. This approach contributes to our knowledge of speciation processes and evolutionary forces such as gene flow, selection and genetic drift. This approach can also provide abstracted and operational criteria for taxonomic decisions. Subspecies, based on multivariate morphometric analysis, and used to represent categories at just below the species level, can reflect the major patterns of population differentiation.

The use of multivariate morphometrics can also contribute to the polemic regarding the nature of species. White (1978) insists "that every species is at the same time a reproductive community, a gene pool and a genetic system". Whilst this may be true of some species it is difficult, if not impossible, to see how this can be true of "every species", particularly when there are allopatric populations (i.e. the majority of cases).

The high levels of differentiation within *Natrix natrix,* or the two main subspecies (even when allopatric populations are not considered) is so great that one cannot conceive of the terminal populations of a series as belonging to the same reproductive community. It is patently meaningless to consider a population of *N. natrix* in Eastern Siberia as belonging to the same reproductive community or sharing a gene pool with a population in say Sardinia or even north Africa, Cyclades or Scandinavia etc. when the animal has such low vagility and when the levels of differentiation between extreme populations exceeds that associated with incipient speciation. Similarly one cannot conceive of this 'species' as evolving as a unit (even though it may, like a genus, be a monophyletic product of evolution).

The advantage of using multivariate analysis of morphological characters to investigate species structure is that one can use preserved specimens. This means that it is feasible to investigate the total species range. Techniques such as electrophoresis generally need the collection of live specimens which is expensive and logistically difficult with widely distributed species. Consequently these latter techniques generally mean that only a small section of the species

range is investigated. This in turn means that these techniques are less likely to be used to provide evidence concerning the reality of species.

It could be argued that one of the disadvantages of using morphometric characters is that they will be influenced by environmental as well as genetic factors. Moreover, with reptiles, we are unlikely to be able to accurately estimate the heritability of a range of characters. This is because the procedures of biometrical genetics are not commensurate with the long breeding cycles, multiple insemination and sperm storage often found in reptiles.

Nevertheless, it is apparent from multivariate work on inbred strains and sublines of laboratory mice (Thorpe, 1980b) that even when morphometric characters are known to be influenced by environmental factors (c. 50–60% heritability) they give a better discrimination of genetic stocks than using an equal number of electrophoretically characterized isozymes from known loci. This is because morphometric characters are generally polygenically controlled and each character reflects the variation in a large number of loci. This argues that multivariate morphometrics is very suitable for analysing even slight racial differences (Thorpe, 1976, 1980b).

Whilst this paper is concerned with European reptiles the comments concerning the inadequacy of dealing with geographic variation by the conventional approach to naming subspecies is relevant to any geographic area and taxonomic group. In fact other regions may suffer even more from the inadequate or amateur studies, particularly where there are large numbers of allopatric populations.

For example, Indian Ocean islands are inhabited by large numbers of allopatric populations of green-geckos (*Phelsuma*). The island forms are named as subspecies and even as species without any scientific or comprehensive comparison of populations and without any reference to abstracted or generalized criteria for deciding the level of divergence necessary for recognition at a particular taxonomic rank. This out-dated and unacceptably shallow approach contributes little to our understanding of evolution and can only act as a source of confusion for ecological studies (Thorpe & Crawford, 1979).

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