

Quantitative handling of characters useful in snake systematics with particular reference to intraspecific variation in the Ringed Snake *Natrix natrix* (L.)

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This paper is based on the numerous characters used in a biometric study of the intraspecific variation of *Natrix natrix* (L.). These characters are drawn from the internal morphology, scalation, colour pattern, body proportions, dentition and dermal sense organs. The criteria involved in selecting these characters for taxonomic work are considered.

The alternative methods for quantifying the above features are discussed and so are the theoretical problems involved in coding the continuous characters.

The value of the characters in studying the geographic variation, ontogenetic variation and sexual dimorphism in *N. natrix* is indicated.

The use of a wider range of characters than just the scalation and colour pattern is urged when diagnosing the lower taxonomic levels of ophidians. The neglected internal morphology may well be able to supply characters to this end.

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INTRODUCTION

Relatively few features (mainly scalation and colour pattern) are usually employed when investigating the relationships of snakes at the lower taxonomic levels even though there are good theoretical grounds for using a wide range of characters (see Underwood, 1967, for a review of the characters useful when dealing with the higher taxonomic categories of snakes).

In the course of an investigation into the intraspecific variation in *Natrix natrix* (Thorpe, 1975) it became apparent that there is, in fact no lack of suitable characters that can easily be recorded. The external features can usually be recorded without prior preparation and many internal features can be exposed by a simple midventral incision which does not mutilate the specimen.

The characters used and the methods of recording and quantifying them are described because some of them could undoubtedly be used to effect by more herpetologists whilst the coding of the continuous characters may be of more general interest.

No physiological, biochemical, cytological or behavioural characters were included in the study of variation in *N. natrix* because they require living specimens which were not available from the entire species range.

SELECTION OF CHARACTERS

For the biometric analysis of *N. natrix* variation several hundred features were superficially investigated on a small sample of specimens selected from representative regions of the species range. These features were recorded from the following:

- most of the elements of the colour pattern;
- the proportions of the head, trunk and tail;
- the size and position of all the major visceral organs including the presence of a tracheal lung;
- the relative position and size of the jaw muscles and supralabial salivary glands;
- the size and position of the hemipenes, and their spines and retractor muscles;
- most of the features of the scalation;
- the scale sculpture (investigated by scanning electron microscopy) of the labial scales, dorsal body scales and spectacle;
- the number, size and arrangement of the dermal sense organs, i.e., pits and tubercles;
- and the number and comparative sizes of the palatine, pterygoid, dentary and maxillary teeth.

If any of these features could not be recorded with a reasonable expenditure of effort or be defined as precise characters or were invariable then they were excluded from further consideration. There were, however, still too many characters to be able to record them from all the 750 specimens used in the study. Therefore, because the primary aim of the study was to analyse geographic variation, the characters that showed no indication of geographic variation were also discarded.

METHOD

The range of the species was divided into forty-nine geographical units so that the variation within and between these units could be analysed. These geographic units were chosen as objectively as possible on the basis of collecting gaps and geographical isolation (e.g. islands). Where neither of these criteria was applicable the overall similarity of the individual specimens was assessed by cluster analyses so that the resultant geographic units would be as homogeneous as possible.

Ontogenetic variations within the geographical units was detected by plotting the character states against the snout to cloaca length. For all further analyses the allometric character states (Fig. 1A) were adjusted to the values

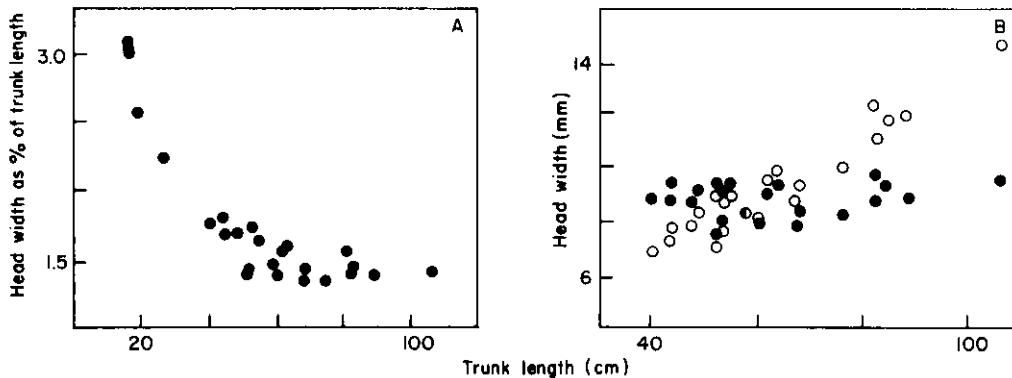


Figure 1. Allometric growth and its correction as exhibited by Scandinavian specimens. A. Allometric growth. B. Adjustment for size independence. \circ , Unadjusted values; \bullet , adjusted values.

they would assume if the specimens were of mean body size (Fig. 1B) by the usual allometric formulae

$$\hat{Y}_i = 10^{\hat{y}_i}$$

where

$$\hat{y}_i = \log_{10} Y_i - b(\log_{10} X_i - \log_{10} \bar{X})$$

where b is the pooled regression coefficient of $\log_{10} Y$ against $\log_{10} X$ (computed from the well represented geographic units); \hat{Y}_i is the adjusted character value of the i th specimen; \hat{y}_i is the logarithm of the adjusted character value of the i th specimen; Y_i is the unadjusted character value of the i th specimen; X_i is the body length of the i th specimen; \bar{X} is the grand mean of the body lengths.

Sexual dimorphism was detected by noting the tendency for the male group means to be consistently different from the female group means and whether or not these sexual differences are statistically significant at $P < 0.5$ (as assessed by a Student t test). The sexual dimorphism is prevented from confusing the results by keeping the male and female specimens separate and running every analysis twice, once for the males and once for the females.

Geographic variation in a character is established by using a one-way analysis of variance to verify that the between groups variation of the geographic units is significantly greater than the within group variation at $P < 0.01$.

CHARACTERS

The characters recorded fall into the following categories:

- (1) internal morphology,
- (2) scalation,
- (3) colour pattern,
- (4) dentition,
- (5) body proportions,
- (6) dermal sense organs.

A list of the recorded characters can be seen in the Appendices.

Internal morphology

The size and position of many internal organs was investigated. These characters are very easy to observe since all that is required to expose the visceral organs is a mid-ventral incision. Consequently they could be used in ophidian systematics to a far greater extent than they are at present.

The position, size and separation of the heart, thyroid, lungs, liver, gonads, kidneys and pancreas etc. as well as the number of renal arteries and length of the cystic duct can be recorded from the viscera. Also the length of the hemipenes, cloacal gland and hemipenial retractor muscles can be recorded from the base of the tail. A list of the internal morphological characters recorded for the biometric analysis of variation in *N. natrix* is in Appendix A.

Since the posterior visceral organs may be distorted in gravid females with well developed eggs the characters that appear to have been affected by this should not be recorded from these specimens. Similarly the length of the hemipenes should not be recorded from the specimens which have the organs distorted by partial eversion.

The usual method of recording the position and size of organs is by linear measurements. This however has a serious disadvantage because it is particularly difficult, if not impossible, to record with accuracy the length of the specimen or its organs if it is preserved in a coiled or twisted condition, as are many museum specimens. Furthermore, if the position and size of many of the internal organs are to be measured by this method it is extremely time consuming.

Alternatively, if one numbers the ventral scales posterior to the neck (Dowling, 1951) and the pairs of subcaudal scales posterior to the cloaca, the size and positions of the internal organs can be defined by the number of the adjacent ventral or subcaudal scales. This enables the ventral scale (*VS*) position or subcaudal scale (*CS*) position and size of an organ to be recorded with accuracy to the nearest 0.5 of a ventral or subcaudal scale even with severely distorted specimens. This method also had the advantage of being quick, which is an important consideration when there are a large number of characters to be recorded.

However using ventral scales and subcaudal scales as units of measurement does have its problems because their numbers may vary from specimen to specimen and exhibit sexual dimorphism and geographic variation. Therefore to overcome this problem the ventral or subcaudal measurements may alterna-

tively be expressed as a percentage of the total number of ventral scales (in %*VS* units) or subcaudal scales (in %*CS* units). However, one should always be extremely cautious when using these ratios because a change in the percentage may be caused by variation in either the numerator or the denominator. This should also be borne in mind when considering the ratios used in the scalation and colour pattern.

Apart from the choice of expressing the position of an organ in *VS* or %*VS* units the arrangement of some characters may be alternatively expressed as the degree of their separation from other characters (once again in either *VS* or %*VS* units). Also with single organs, the liver for example, the positions of the anterior and posterior tips of the organs can be replaced by the alternative measurements of the organ length together with the position of one point on the organ, e.g. the middle (mid position) of the organ.

With paired organs, the testes or kidneys for example, the number of alternative ways of expressing their position, size and separation is even greater. The length of the paired organs can be expressed as either the separate lengths of the right and left organs or alternatively as the average of their lengths as well as the difference in their lengths. Furthermore the position of paired organs can be expressed as either the position of the anterior and posterior edge

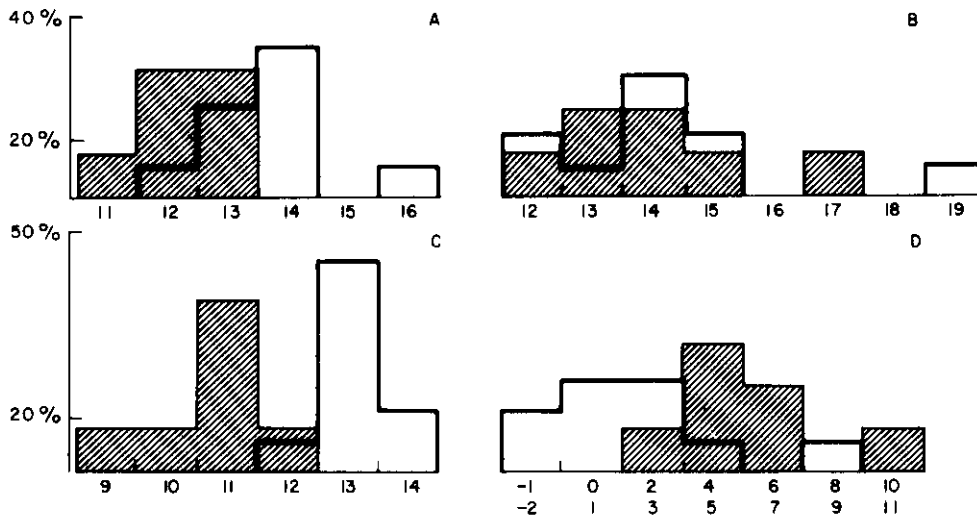


Figure 2. Percentage frequency distributions of kidney size measurements as exhibited by Yugoslavian specimens. Shading, females; bold outline, males. A. Average of right plus left %*VS* kidney length. Significant difference between sexes at $P < 0.05$. B. Right kidney %*VS* length. No significant difference between sexes. C. Left kidney %*VS* length. Significant difference between sexes at $P < 0.05$. D. Right kidney %*VS* length minus left kidney %*VS* length. Significant difference between sexes at $P < 0.05$.

of each organ or else as the mid position of each organ. A third alternative is to express the position of paired organs as the average of their mid-positions together with the degree of their separation.

It can therefore be seen that there are several alternative ways of expressing the information conveyed by the data. As a general rule it is best to keep the character as simple and underived as possible, although expressing the

information in different ways may enable certain trends to be shown that would otherwise be more cryptic. Take for example the sexual dimorphism in the kidney size. One can see that the %VS kidney length is significantly greater in males (Fig. 2A) when the average of the right and left kidney lengths is used. However, Fig. 2B and C show that this sexual dimorphism is restricted (at least in this sample) to the left kidney, the right kidney not being significantly longer in males than females. Furthermore, using yet another character (the difference in size between the right and left kidneys) demonstrates another result of this variation in kidney size; that is the tendency for females to have a greater discrepancy between the size of the right and left kidneys than males (Fig. 2D).

Statistical analysis of the variation in the recorded internal morphological characters of *N. natrix* shows that there is no detectable ontogenetic variation although there is a considerable amount of geographic variation and some sexual dimorphism and they are therefore well worth studying.

Although I could not detect any ontogenetic variation in the internal organs (except the gonads of course) of *N. natrix*, Bergman (1951, 1952, 1953, etc.) indicates differences in the size and position of these organs between the juveniles and adults of other species. However, since Bergman used linear measurements these differences are probably the result of allometric growth in the different regions of the trunk. This appears to be yet another reason for measuring the characters in ventral or subcaudal scale units rather than using linear measurements.

Apart from the previously mentioned sexual dimorphism in the kidney size there is also sexual dimorphism in the position of the kidneys and in the size of the cloacal glands.

All of the internal morphological characters recorded show geographic

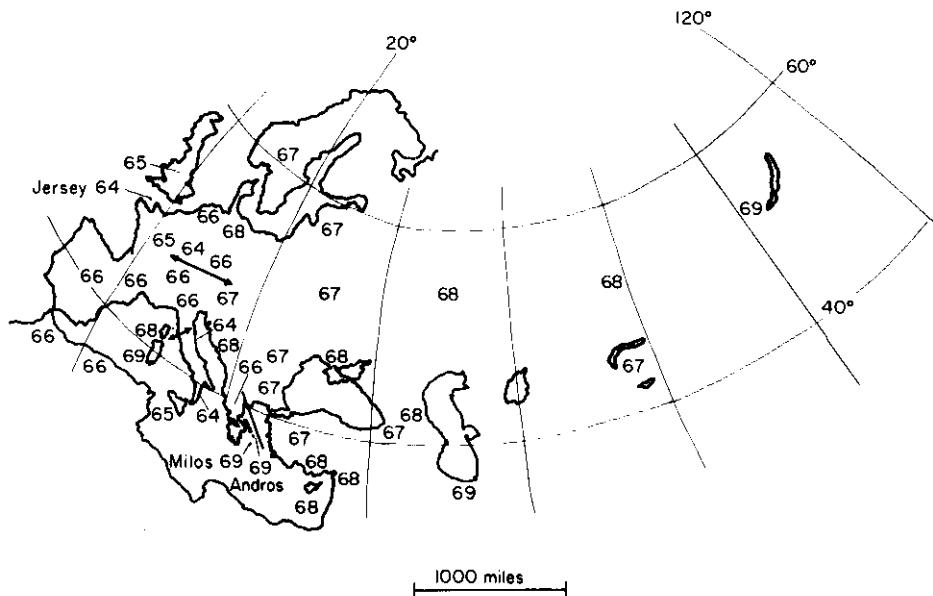


Figure 3. Male group means, indicating geographic variation in the %VS position of the testes. This is independent of the geographic variation in the ventral scales.

variation (when expressed either *VS* or %*VS* units) except the length of the left lung, the liver length and the separation of the heart from the left lung (see Figs 3 and 4A, B and C for examples of infrequently used characters that show geographic variation).

Scalation

The scalation is usually given a disproportionate importance in ophidian taxonomy but even so the investigation is often restricted to a few features. The scalation is however taxonomically useful since it can provide many readily recordable characters; a few of which are so frequently used that there are standard methods of recording them (Dowling, 1951).

Recording the scalation characters is usually fairly simple but there can be several alternative ways of expressing the data. As with the internal morphology some of the characters may be expressed in ventral scale (*VS*) or subcaudal scale (*CS*) units, or alternatively as a percentage of the total number of ventral scales (%*VS*) or subcaudal scales (%*CS*). Also bilateral characters may be recorded either from just one side of the specimen or as the average of the right and left-hand character states.

The number of dorsal scale rows is reduced in stages from the neck to the tip of the tail in *N. natrix* and these reductions have two levels, a longitudinal level (*VS* or *CS* position or alternatively a %*VS* or %*CS* position) and a dorso-ventral level. The longitudinal level of the reduction is taken as the number of the first ventral scale or subcaudal scale at which the reduced number of rows is found, whilst the dorso-ventral level is taken as the lowest row of the two merging rows.

The longitudinal level of a dorsal scale reduction is recorded as zero if the dorsal scale row starts at a lower number than the pertinent reduction. For example, if the number of dorsal scale rows at the base of the tail stabilizes at twelve rows the longitudinal level of the reduction from fourteen to twelve rows is recorded as zero.

Whilst some scalation features are very frequently used, the dorsal scale reductions on the tail are less frequently employed. These reductions in the number of dorsal scale rows on the tail may also be usefully expressed as the number of tail somites with a fixed number of dorsal scale rows, i.e. 12, 10, 8, 6, 4 or 2 rows. Hence the number of tail somites with 12, 10, 8, 6, 4 and 2 dorsal scale rows may be used as characters and these characters may also be alternatively expressed as a percentage of the total number of tail somites (%*CS* units).

Other scalation features can also be expressed in alternative forms. The number of ventral scales and subcaudal scales for example may be alternatively expressed as the total number of somites (ventral scales plus pairs of subcaudal scales) together with the number of either ventral or subcaudal scales expressed as a percentage of the entire somite number (i.e. the % position of the cloaca).

Apart from the ventral scales, subcaudal scales and dorsal scale row reductions the number and arrangement of some of the head scales etc. were also recorded. Appendix B holds the list of scalation features recorded for the biometric study of *N. natrix*.

The scalation shows a considerable amount of sexual dimorphism and geographic variation but little ontogenetic variation, although the neck scales do exhibit allometric growth.

There is sexual dimorphism in the number of ventral scales and pairs of subcaudal scales as well as the position of the cloaca expressed as a percentage of the total somite number. Furthermore there is sexual dimorphism in the longitudinal level of the dorsal scale row reduction on the tail and of the twenty one to nineteen row reduction on the trunk. Moreover the number of tail somites with a given number of dorsal scale rows (except those with two rows) show pronounced sexual dimorphism when expressed as a proportion of the entire tail (%CS units). The dorso-ventral level of the reduction from ten to eight dorsal scale rows also shows sexual dimorphism as does the size of the dorsal neck scales.

All the scalation characters studied show geographic variation except the number of sublabial and postocular scales, and a few of the longitudinal levels together with most of the dorso-ventral levels of the dorsal scale row reductions.

Colour pattern

The colour pattern, like the scalation, is frequently used in systematic studies on ophidian species and subspecies as it provides many easily recorded characters.

The colour pattern of *N. natrix* supplies many useful characters, some of which are only valuable when studying this particular species, although it is hoped that the methods of quantification will be of wider interest. Only the actual pattern of the markings is used, not the hue, because it is affected by preservation. Also, if it appears likely that ontogenetic fading has altered the state of a character then that particular character is not recorded from the specimens. Bilateral characters, unless otherwise stated, are always recorded as the average of the left and right character states.

N. natrix usually has three pairs of rows of blotches down the body; a ventro-lateral row in contact with the ventral scales; a lateral row; and a dorsal row which may fuse in the vertebral region with its counterpart. *N. natrix* also usually has three paired markings on the neck and posterior region of the head. There are a posterior pair of dark regularly shaped nuchal markings on the dorsal neck scales; an anterior pair of dark irregular-shaped occipital markings on the posterior of the head; and a pair of light lunar markings between these nuchal and occipital markings.

The occipital markings can be further subdivided into four separate components; an occipital line on the dorsal scales and posterior margin of the head scales; a parietal entity on the parietal scales; a temporo-labial entity on the temporal scales and posterior supralabial scales; and a single diamond shaped entity on the dorsal body scales.

These and other colour-pattern characters have to be precisely defined and quantified for any objective or statistical research. The problems of quantification and definition tend to fall into three categories; how to quantify and define the size, position and dimensions of the markings on the dorsal scales;

how to define serially homologous characters; and how to code the character states of the continuously variable cephalocervical characters, e.g. occipital markings.

Firstly, the size of a marking located on the dorsal scales (e.g. nuchal markings) can be defined as the number of scales partially or completely covered by the marking (Fig. 6A) and the dimensions can be defined by the number of dorsal scale rows spanned in any particular direction (Fig. 5).

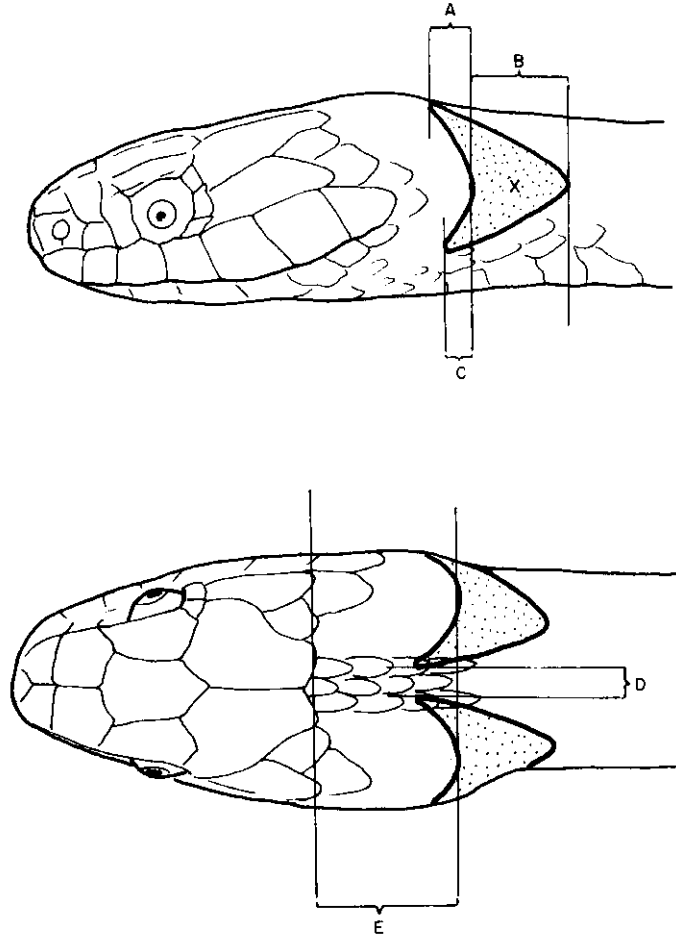


Figure 5. The use of dorsal scales to define the dimensions and positioning of the nuchal markings. A, Upper curvature; B, length; C, lower curvature; D, separation; E, distance from parietals; X, nuchal markings.

Furthermore the separation of paired markings can also be defined by the number of dorsal scale rows spanned and the dorso-ventral level of other blotches (e.g. lateral blotches) can be defined by the dorsal scale rows on which they are found (recorded from a region with a constant number of dorsal scale rows).

Secondly, there is the problem of defining serially repeated but variable features (e.g. lateral blotches). This can be objectively overcome by defining the character state as the mode of twenty recordings taken from ten blotches (a

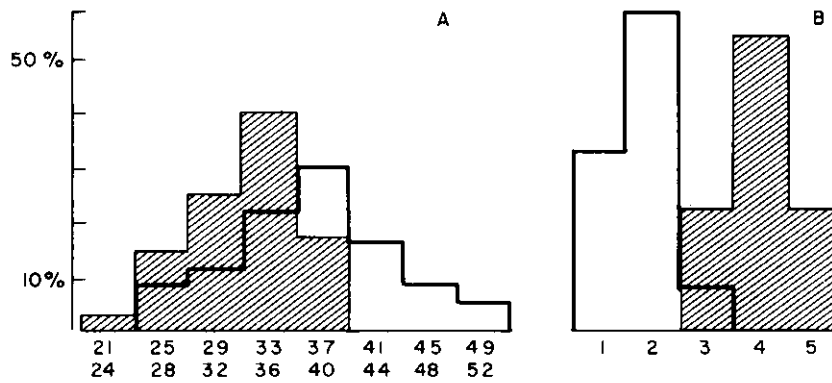


Figure 6. Quantification of colour pattern characters. Shading, eastern central European specimens; bold outline, western central European specimens. A. The use of dorsal scales to quantify blotch size. Percentage frequency distribution of the number of dorsal scales covered by a nuchal blotch. B. The use of ratio scales to quantify continuous colour pattern characters. Percentage frequency distributions of the coded character states of the temporal occipital marking.

third of the way down the body where the number of dorsal scale rows is stable) on each side of the specimen.

Thirdly, there is the problem of coding the character states of continuous, cephalocervical characters such as the occipital markings (Fig. 6B). This can be difficult and the exact method used depends on the particular marking being coded.

It is essential when initially recording and coding these continuous characters to appreciate the different kinds of scale and their limitations. One can recognize four basic types of scale (Stevens, 1951), nominal scales, ordinal scales, interval scales and ratio scales.

Nominal scales are no more than arbitrary labelling of different features, such as albinism or melanism. Hence these coded character states cannot be arithmetically manipulated, i.e. added, subtracted, divided or multiplied.

Ordinal scales are scales where the character states are coded in numerical order according to the extent or intensity of a marking etc. Because the intervals between the states are irregular in this type of scale they also cannot be arithmetically manipulated and this is a point of considerable significance.

Interval scales (e.g. thermometers) are similar to ordinal scales except that the intervals between the character states are regular and they may therefore be added or subtracted. They may not however be divided or multiplied because they do not have an absolute zero.

Ratio scales are similar to interval scales but they have an absolute zero and therefore can be added, subtracted, divided and multiplied.

The need for the intervals between the character states to be regular for any of the essential arithmetic manipulations to be valid is of prime importance. This requirement may run contrary to the necessity of defining each character state in a precise manner because the stages at which the continuous character may be able to be precisely defined may not be separated by equal intervals.

The often contrary requirements of equal intervals and character states that are precisely defined by a noticeable point in the character's continuum may be resolvable by only compromise, although the greater emphasis should always be

put on obtaining regular intervals. There is however relatively little difficulty in obtaining an absolute zero with many scaled continuous colour pattern characters.

The single, diamond or triangular shaped marking on the occipital region provides an example of a continuously variable colour pattern character. This marking can be coded into four character states which can be precisely defined by the completeness of the marking, with the intervals between the states being approximately equal. Hence the four character states are (1) a complete marking; (2) one side of the marking incomplete; (3) two sides of the marking incomplete; (4) no recognisable marking. See Fig. 6B for an illustration of how a coded continuous colour pattern character can contribute useful information about the dissimilarity of populations.

Apart from the previously mentioned lateral, ventro-lateral and dorsal blotches on the trunk and the occipital, lunar and nuchal markings on the head and neck several other colour pattern features were recorded. These include the presence or absence of longitudinal stripes (a dimorphic character), dark edges to the labial scales and white streaks on the dorsal scales. A list of the colour pattern characters used in the biometric study of *N. natrix* is in Appendix C.

Unlike the scalation and internal morphological characters there are few alternative methods of expressing the colour pattern characters (other than the different original methods of recording). However, the number of ventro-lateral blotches and dispersed lateral blotches can be alternatively expressed as a percentage of the total number of lateral blotches and the number of streaked nuchal scales can be expressed as a percentage of the total number of scales covered by the nuchal markings.

The colour pattern of *N. natrix* shows little ontogenetic and sexual variation but a considerable amount of geographic variation. Ontogenetic variation in the colour pattern is limited to fading of the colour pattern of the older specimens from the western part of the species range particularly Iberia and northern Africa.

There is little or no sexual dimorphism in the colour patterns of *N. natrix* which possibly indicates that sexual recognition in the species is not based on the colour pattern.

All the recorded colour pattern characters show geographic variation.

Body proportions

The body proportions may supply useful taxonomic characters and can be easily recorded as linear measurements made with graduated calipers. It is important to ensure that the measurements are consistent by clearly defining the reference points between which the measurements are made.

Whenever possible, care should be taken to take the measurements across regions which are not easily deformed in preserved specimens, i.e., where there is underlying skeletal tissue. The body width, of course, cannot be measured in this way, although it may be assessed by dividing the specimen's volume (found by water displacement) by its length. This method has several limitations including the effect on volume of the variable amount of fat reserves and whether or not there is a ventral incision in the trunk. A better method of assessing the body width is to measure the width of the widest ventral scale once it has been detached.

Some of the proportions of the trunk, tail and head (width, depth and length) were recorded; a complete list of the body proportion characters used is in Appendix D. Obviously the length of the trunk and tail depends on the overall size (and hence age) of the specimen although when these lengths are expressed as a proportion of the total length the two resultant (mutually exclusive) proportions are independent of the specimen's overall size.

When using body proportion characters one should always be aware of the possibility of allometric growth, as failure to take this into account properly (e.g. Mertens, 1947) can lead to misleading results (Fig. 1). The body width and the proportions of the head show allometric growth and therefore they have to be statistically adjusted for size independence before the other types of variation (e.g. sexual and geographic) can be analysed.

All the recorded body proportion characters show geographic variation and all but the head width show sexual dimorphism.

Dentition

The dentition is often neglected in studies of the lower taxonomic levels of ophidians and even when it is considered often only the maxillary teeth are used (see Duellman, 1958 for an exception).

The number of maxillary, palatine, pterygoid and dentary teeth can all be counted when the dentigerous bones are exposed by simply separating the mandibles at their symphysis and cutting through the floor of the mouth along a paramedial line. This incision results in the minimum of damage.

All the sets of teeth in *N. natrix* proved useful and contributed additional information to the analysis of the geographic variation and sexual dimorphism. Although the numbers of maxillary, palatine, pterygoid and dentary teeth show geographic variations and sexual dimorphism, no ontogenetic variations could be detected in these characters.

Dermal sense organs

Dermal sense organs consist of pits and tubercles which can be prepared for investigation by Underwood's (1967) method or by finally mounting in more polyvinyl alcohol instead of xylene or canada balsam. They may also be investigated with a scanning electron microscope.

The dermal sense organs can be difficult to see in some circumstances (and hence subject to limited recording error) and their preparation prior to recording can be time consuming. Although studying these characters may be laborious the two characters investigated in *N. natrix* (the number of pits on the upper post ocular scale and the number of pits on the temporal scales) were useful as they show sexual dimorphism in a limited geographic region and also more general geographic variation. No ontogenetic variation was detected.

DISCUSSION

There is a tendency for herpetologists working on the lower taxonomic levels of ophidians to rely heavily on the scalation or colour pattern characters for diagnosing the groups such as genera, species and subspecies. Other diagnostic characters that are used occasionally include features such as the proportional

length of the tail, the number of maxillary teeth, the hemipenial structure (Inger & Marx, 1965), the scale pits (Gans, 1959) and some osteological features.

However, the large number of possibly diagnostic features that the visceral anatomy of ophidians may be able to provide are largely ignored in spite of the facility with which they may be recorded. Examples of exceptions to this trend are the use of the respiratory system to diagnose the genus *Gonyosoma* (Thompson, 1914; Brongersma, 1957) and the use of the cloaca to help diagnose species of *Calamaria* (Inger & Marx, 1965).

It is considered theoretically desirable in both phylogenetic (Simpson, 1961; Hennig, 1950) and phenetic (Sneath & Sokal, 1973; Blackith & Reyment, 1971) taxonomy that the classification should be based on a wide range of characters, particularly for the lower taxonomic levels.

This however, is not widely practised by herpetologists working on the lower taxonomic levels of ophidians. Therefore, although collecting enough ecological, behavioural, electrophoretic and ecological data may be prohibitive, and studying the osteology or dermal sense organs may be time consuming, a broader range of characters can be easily obtained by using the internal morphology, the body proportions (other than just the proportional length of the tail) and the dentition (other than just the maxillary teeth) as well as a wide range of characters from the more frequently used colour pattern and scalation.

It would be regrettable if ophidian research entered the era of numerical and multivariate taxonomic studies only to be dominated by the use of one or two character systems, such as is the case with mammalogical multivariate studies, which tend to rely very heavily on skull features.

The taxonomic value of a character is often considered to be determined by its lability but sometimes at subspecific and specific levels this approach may be an oversimplification. The value of a character in differentiating between populations may be better expressed as the statistically assessed (one way ANOVA) relationship between the within-population variation and the between-population variation. Furthermore, when dealing with the dissimilarity of populations one should always be aware of the correlation between the characters (assessed as the correlation within each population) since the taxonomic value of a character is also partly determined by how much original information it contributes towards the assessment of the dissimilarity.

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APPENDIX A

Internal morphological characters

- The VS or %VS position of the anterior edge of the thyroid gland.
- The VS or %VS position of the posterior tip of the heart.
- The VS or %VS position at which the left bronchus enters the trachea.
- The length of the left lung (in VS units).
- The VS or %VS positions at which the right and left systemic arteries join.
- The VS or %VS position of the anterior and posterior tip of the liver.
- The VS or %VS position of the anterior edge of the pancreas.
- The VS or %VS position of the posterior tip of the right lung.
- The VS position of the anterior and posterior tips of both the right and left testes.
- The VS or %VS positions of the anterior and posterior tips of both the right and left kidneys.
- The number of renal arteries going to the right and left kidneys.
- The CS length of the cloacal glands.

The *CS* position of the posterior tips of the hemipenial retractor muscles.
 The *CS* length of the hemipenes measured from the crotch between the lobes.

From the above measurements several other characters (mutually exclusive to the original measurements) can be derived. These are as follows:

The *VS* and %*VS* separation of the anterior tip of the thyroid and posterior tip of the heart.
 The *VS* separation of the posterior tip of the heart and the left bronchus.
 The *VS* and %*VS* separation of the posterior tip of the heart and the junction of the systemic arteries.
 The *VS* and %*VS* length of the liver.
 The *VS* and %*VS* position of the middle of the liver.
 The %*VS* separation of the posterior tip of the liver and the pancreas.
 The %*VS* position of the mid point between the middle of the right and middle of the left testes.
 The %*VS* separation between the middle of the right and middle of the left testes.
 The *VS* and %*VS* lengths of the right and left kidneys.
 The average of the (*VS* and %*VS*) lengths of the right and left kidneys.
 The difference in the *VS* length of the right and left kidneys.
 The *VS* and %*VS* position of the middle of the right and middle of the left kidneys.
 The *VS* and %*VS* position of the midpoint between the middle of the right and middle of the left kidneys.
 The *VS* and %*VS* separation between the middle of the right and the middle of the left kidneys.

APPENDIX B

Scalation characters

The number of ventral scales, pairs of subcaudal scales, postocular scales, sublabial scales, supralabial scales, posterior temporal scales.
 The number of sublabial scales in contact with the anterior chin shield.
 The number of rows of gular scales.
 Whether or not the anterior temporal scale is in contact with the upper postocular scale (when there are three postoculars).
 Whether or not the anterior temporal scale is in contact with the lower postocular scale (when there are three postoculars).
 The length of the largest dorsal neck scale (to the nearest 0.1 mm) that is in contact with a parietal or upper posterior temporal scale but not in contact with a lower posterior temporal scale.
 The dorso-ventral level and the longitudinal level of the series of reductions from 23 to 17 dorsal scale rows on the trunk and of the series of reductions from 14 to 2 dorsal scale rows on the tail.

From the basic measurements several other characters (mutually exclusive to the original measurements) can be derived. These are as follows:

The %*VS* level of the series of reductions from 23 to 17 dorsal scale rows and of the %*CS* level of the series of reductions from 14 to 2 dorsal scale rows.
 The proportions of the tail (in %*CS* units) with 12, 10, 8, 6, 4 and 2 dorsal scale rows.
 The total number of somites (ventral scales plus pairs of subcaudal scales).
 The positions of the cloaca expressed as a percentage of the total number of somites.

APPENDIX C

Colour pattern characters

The presence or absence of two longitudinal light stripes.
 The number of supralabial scales with dark posterior borders.
 The number of sublabial scales with dark posterior borders.
 The presence of light antero-dorsal and antero-ventral edges on some dorsal scales (divided into three semi-arbitrary states, clear light edges – paler edges – absence of lighter edges).
 The number of lateral blotches.
 The size of the lateral blotches (in numbers of scales).
 The number of dispersed lateral blotches with indistinct borders (as opposed to compact blotches with well developed borders), which can also be expressed as a percentage of the total number of lateral blotches.
 The dorsal scale row on which the lower edge of the lateral blotches is located.
 The dorsal scale row on which the upper edge of the lateral blotches is found.
 The size of the dorsal blotches (in numbers of scales).

- The dorsal scale row on which the lower edge of the dorsal blotches is found.
 The dorsal scale row on which the upper edge of the dorsal blotches is found.
 The presence or absence of at least three round dorsal blotches (as opposed to quadrilateral blotches).
 The number of ventro-lateral blotches which can also be expressed as a percentage of the number of lateral blotches.
 The size of the ventro-lateral blotches (in numbers of dorsal scales).
 The size of the nuchal markings (in numbers of dorsal scales).
 The length of the nuchal markings (in rows of dorsal scales spanned (Fig. 5)).
 The degree of curvature of the upper arm of the nuchal markings (Fig. 5).
 The degree of curvature of the lower arm of the nuchal markings (Fig. 5).
 The separation of the nuchal markings (in rows of dorsal scales spanned (Fig. 5)).
 The distance of the nuchal markings from the parietal scales (in rows of dorsal scales spanned (Fig. 5)).
 The number of scales covered by the nuchal markings which have a thin light longitudinal streak along the scale centres, which can also be expressed as a percentage of the total number of scales covered by the nuchal markings.
 The presence of light centres to the nuchal markings on both sides, one side or neither side of the head.
 The presence or absence of lunar markings; the degree of separation of the lunar markings (in numbers of dorsal scale rows spanned).
 Whether or not the lunar markings encroach on the posterior temporal scales on both sides, one side or neither side of the head.
 Whether or not the lunar markings encroach on the posterior supralabial scales on both sides, one side or neither side of the head.
 The extent of the occipital line (divided into five semi-arbitrary character states; a complete thick line – a complete thin line – a discontinuous line – a minute marking – no marking).
 The extent of the parietal occipital marking (divided into five semi-arbitrary character states; no marking – minute marking – thin dark edges to the parietal scales – thick dark edges – totally covered parietal scales).
 The extent of the temporal labial occipital marking (recorded as five semi-arbitrary character states similar to the parietal occipital marking).
 The presence of dorsal diamond occipital marking (divided into four character states, a complete marking – one discontinuous side – two discontinuous sides – no marking).

APPENDIX D

Body proportion characters

- The trunk length measured from the tip of the snout to the cloaca.
 The tail length measured from the cloaca to the undamaged tip of the tail.
 The head width measured as the distance across the skull in the region of the postorbital bones.
 The head length measured as the distance between the snout and posterior edge of the lower jaw.
 The head depth measured at the deepest point anterior to the posterior edge of the parietal scales.
 The body width measured as the width of a ventral scale detached from the widest part of the body.

APPENDIX E

Dentition characters

- The number of maxillary, palatine, pterygoid and dentary teeth.

APPENDIX F

Dermal sense organ characters

- The number of pits on the upper post ocular scale (when there are three postoculars), usually measured from the right hand side of the specimen.
 The number of pits on the anterior plus posterior temporal scales, usually measured from the right hand side of the specimen.