Instituto de Edafologia y Biologia Vegetal, C.S.I.C.
Madrid, Spain
and
Scottish Crop Research Institute, Invergowrie,
Dundee, Scotland

BIOGEOGRAPHICAL CLASSIFICATION OF SOME PLANT-PARASITIC NEMATODE SPECIES GROUPS IN SPAIN

by
A. Bello, P. B. Topham, T. J. W. Alphey and A. Dale[1]

The aims of this study were to determine whether faunistic groups could be recognised within the nematofauna of the Iberian peninsula using two groups of plant-parasitic nematodes (Criconematidae and Longidoridae) and to classify them by their geographic distribution. Soil nematode species are biogeographically interesting since their long range distribution, like that of plants, is passive. The Iberian peninsula has frequently attracted the attention of biogeographers since it is transitional between Europe and Africa in one direction and between the Atlantic and Mediterranean regions in another, whilst also having links with the American continent.

Ecological and geographical data collected from studies of the nematofauna of a single crop or region are usually interpreted empirically to form the basis of further experimental work on the biology and control of economically important species. However, such studies are not usually designed for biogeographic purposes and the data are difficult to integrate in the wider ecological context. On the other hand, nematode surveys are time-consuming, involving collection and analysis of soil samples

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[1] *Present address: Ministry of Agriculture and Food, Horticultural Experiment Station, Box 587. Simcoe, Ontario N3Y 4N5, Canada.*

and the extraction, identification and counting of their nematode contents. Therefore, despite the value of distributional data, a nematologist who undertakes much survey work risks becoming a mere collector of data. As a result, few nematological biogeographic studies have been undertaken (Ferris *et al.*, 1976, 1981; Procter, 1984; Topham and Alphey, 1985).

The use of numerical techniques of data analysis offers great advantages in biogeographic studies, in both botany (Birk, 1976) and zoology (Kikkawa and Pearse, 1969; Ezcurro *et al.*, 1978; Hengeveld and Hogeweg, 1979; and Hodkinson, 1980). Such techniques facilitate speedy and effective identification and display of relationships between regions and between taxa. In this study several techniques of analysis were used to classify members of two groups of plant parasitic nematodes in continental Spain (Arias, 1979; Bello, 1979) and to interpret the results in ecologic, geographic and historical terms.

Materials and Methods

The data were derived from almost 6000 samples collected in various surveys in Spain and collated for distributional mapping (Alphey, 1979). The presence/absence of 31 species of Criconematidae and 18 species of Longidoridae in 100 km Universal Transverse Mercator (UTM) squares (Bello, 1979; Arias, 1979) (Table I) were the basis. Additional data on *Xenocriconemella macrodora* (Ibanez, 1979), and on *Macroposthonia xenoplax* and *Crossonema menzeli* from UTM grid squares XL and UK have been included. Unconfirmed records of *Lobocriconema neoaxestum*, *Macroposthonia peruensis*, *Nothocriconema lamellatus* and *Variasquamata rhombosquamatum* were excluded as were records not identified beyond the generic level. Five species were excluded because each occurred in a single 100 km UTM square only: *Macroposthonia crenata*, *M. maritima*, *Nothocriconema princeps*, *Xiphinema coxi* and *X. pyrenaicum*.

The incomplete UTM squares adjacent to zones-of-compensation or abutting on the coast or frontiers were grouped into pairs to give units approximately equal in area (Fig. 1).

Area classification. Three methods were used to group the 100 km squares: two hierarchical, Information Analysis (Lance and Williams, 1966) and Ward's clustering method (Ward, 1963) and one using monothetic division, Association Analysis (Williams and Lambert, 1959). These methods were

Table 1 - *Species used to group 100 km squares and the order in which they were used to divide the two hierarchical analyses.*

| SPECIES	METHOD			
	All species		Criconematidae only	
	Information Statistic	Association Analysis	Information Statistic	Association Analysis
Crossonema multisquamatum (Kirjanova, 1948) Khan, Chawla *et* Saha, 1975	1	1	1	1
Criconemoides informis (Micoletzky, 1922) Taylor, 1936	2	4	3	4
Xiphinema turcicum Luc *et* Dalmasso, 1964	3	—	X	X
Macroposthonia solivaga (Andrássy, 1962) De Grisse *et* Loof, 1965	4	—	2	—
Hemicycliophora thornei Goodey, 1963	—	2	X	X
Nothocriconema annuliferum (De Man, 1921) De Grisse *et* Loof, 1965	—	3	4	—
Macroposthonia vadensis (Loof, 1964) De Grisse *et* Loof, 1965	—	—	—	2
Macroposthonia pseudosolivaga (De Grisse, 1964) De Grisse *et* Loof, 1965	—	—	—	3

X: not present in data set.
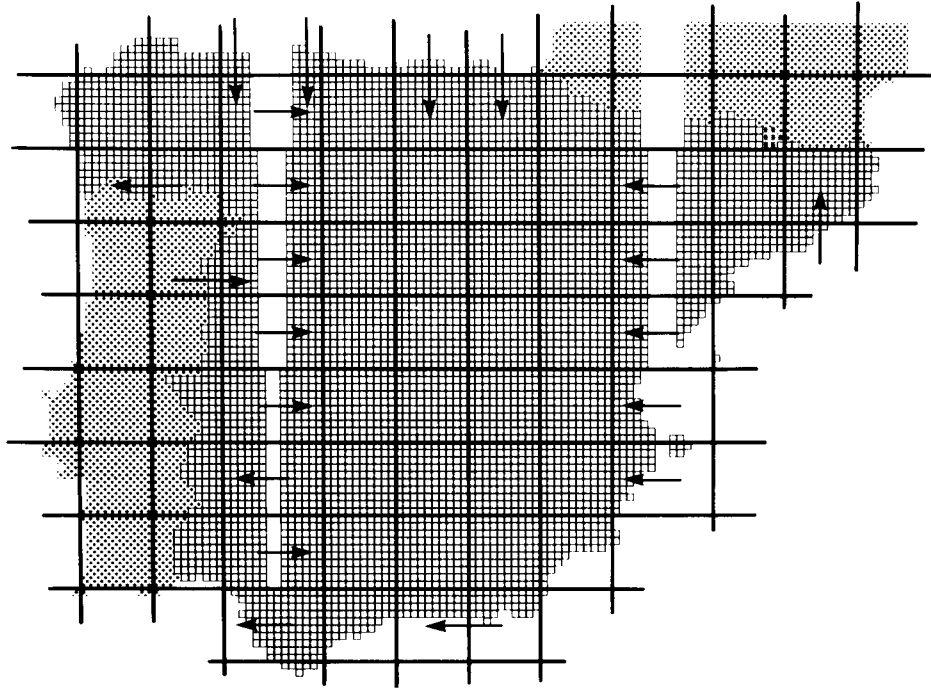
Fig. 1 - Map of Spain showing the 100 km squares of the UTM system and the grouping of incomplete squares along zones-of-compensation, the coast and frontiers.

applied to the following sub-divisions of the data: the complete data; the Longidoridae; the Criconematidae; the Criconematidae omitting the sub-family Hemicycliophorinae, which has a very localised distribution in Spain. No geographic or proximity constraints were placed on the grouping procedures which were carried out using the CLUSTAN computer package (Wishart, 1978). In each case, division into five groups of 100 km UTM grid squares appeared meaningful and these were mapped to examine and evaluate the distribution patterns.

Species classification. The 44 species were clustered using their presence/absence in the 100 km UTM squares; the analyses agreed in dividing the species into a series of chained groups which depended entirely on the number of 100 km UTM squares in which they were present.

The centre of distribution for each species was calculated from the co-ordinates of each 10 km UTM square for every record of that species. These co-ordinates were averaged in both north/south and east/west directions to give centres and a Euclidean distance matrix was calculated between these positions (Phipps, 1975). This matrix then formed the basis of a furthest-neighbour single linkage cluster analysis, carried out using the GENSTAT computer package (Alvey *et al.*, 1982). These clusters were used to define faunistic groups.

Results

Classification of squares into geographic patterns. The limits of the five groupings of squares produced by the different methods and data sets varied slightly and it was considered that this variation was due to the co-existence in certain areas of species characteristic of different distributional classes; areas of high faunistic diversity tended to be grouped together.

The Information Analysis and the Association Analysis had the advantage over Ward's method of emphasizing the species which had most influence on sub-division into like areas (Table I). The Information Analysis used species of higher biogeographical importance to sub-divide the squares. It also defined the most meaningful sub-division into areas, based on empirical knowledge, especially when only the criconematid data were used; when the data for the Longidoridae were also included, certain widespread longidorid species tended to dominate the analysis.

The Information Analysis grouping of squares (Fig. 2) based on the complete data set gave five clusters at the similarity coefficient level of 0.75, and these clusters were accepted as geographic patterns and will be discussed as such in the rest of the paper. The geographic distribution of these patterns (Fig. 3) showed a reasonable degree of geographic segregation, allowing for the coarse scale, and this could be related to altitudinal variations (Fig. 4). The squares of group C contain much land over 1000 m, groups A and D between 500 and 1000 m and squares of groups B and E tend to be below 500 m, that of B occurring along the Mediterranean coast.

The species and their frequency in these five patterns established by Information Analysis are listed in Table II. Pattern A contained the greatest number of species, 36, followed by C with 33, B with 32, whilst D and E each contained 23 species, many of which are common in the Iberian peninsula.
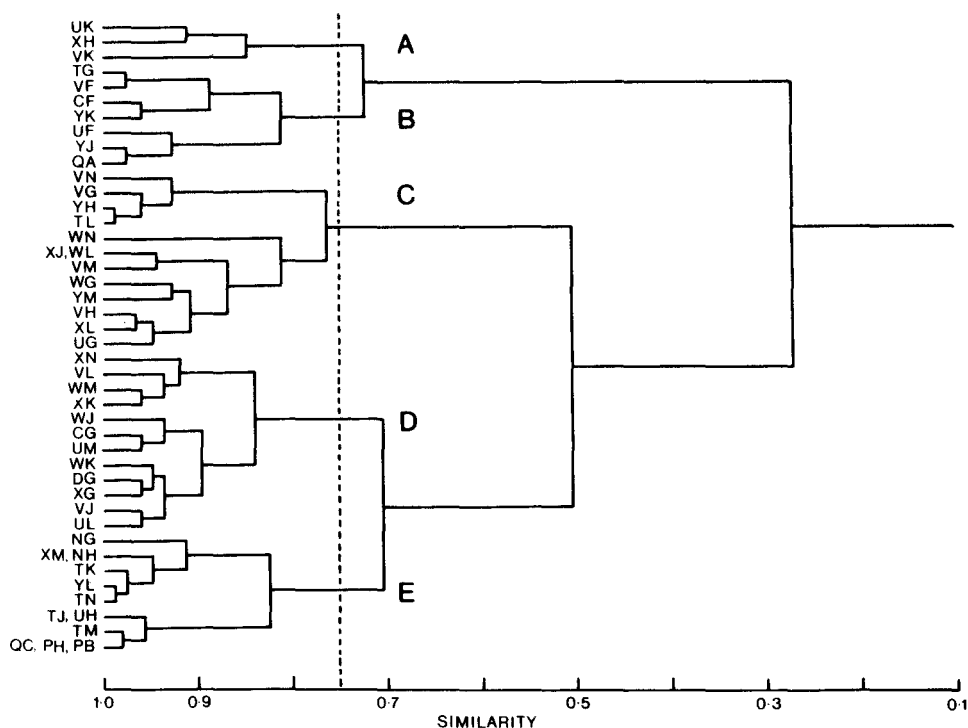
Fig. 2 - Dendrogram of the Information Analysis grouping of UTM 100 km squares, showing geographic patterns.

Classification into species groups. Five main groups of species were found when the distribution centres were clustered (similarity coefficient = 8.5) (Fig. 5). The central group could be subdivided still further into four sub-groups by relaxing the similarity coefficient criterion to 9.8. The eight resulting groups or faunistic elements (Table II) include several species groups as outliers which are not characteristic of the Iberian peninsula. For example there are two northern groups each of three species, all of which are common in the British Isles (Brown and Taylor, 1979; Boag and Orton Williams, 1979) and rare in Spain (Arias, 1979; Bello, 1979). There are also two southern components, one of seven species, the other of one, which are rare or absent in Britain. The large cluster in the central region contained many widespread species, a high proportion with Mediterranean or Central European affinities. The division here into four sub-groups was more tentative (Fig. 6), but the south east central group contained many of the more abundant and widespread species in this study.
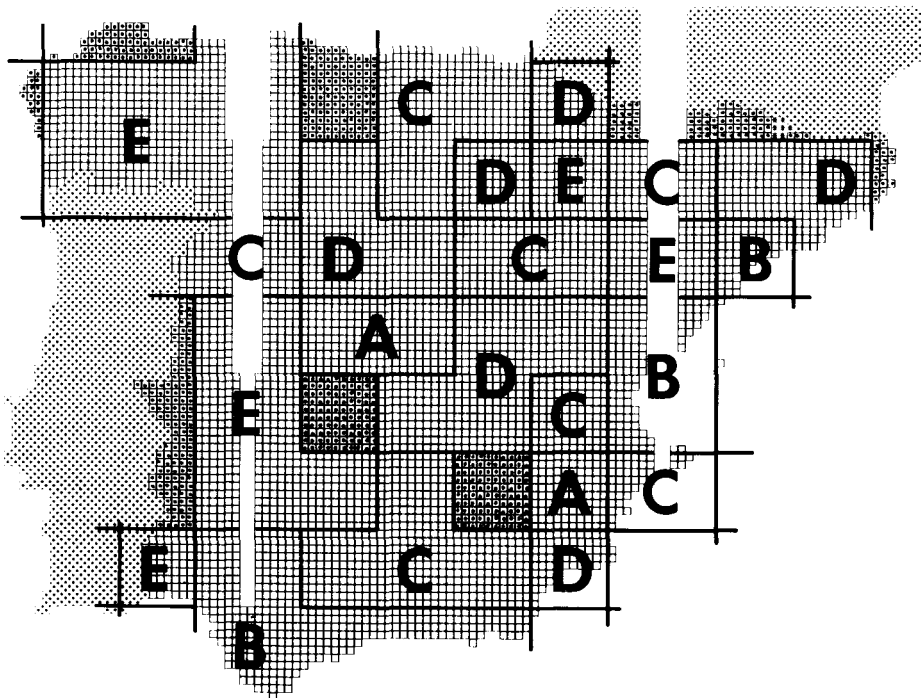
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Fig. 3 - Map of Spain showing the geographic distribution of the five groups of UTM 100 km squares defined by Information Analysis of the complete data. Dotted squares indicate areas without records.

Relationship between areal patterns and species groupings. The geographic patterns established by the Association Analysis of the 100 km squares can be further characterized by the relative frequency of the eight faunistic groups (Table III). In pattern C, which contains areas of high altitude, species with a northern distribution predominate. Pattern B however, with areas of low altitude, contains southern species together with many of the south west central and south east central species; *Longidorus caespiticola* of the northern group seems an exception here.

Patterns D and E share many species with C but the two southern and the south west central groups occur less frequently. The south east central group is fairly well represented in pattern D, largely because both contain some of the widespread and abundant species. Pattern E contains squares with relatively few records and is defined by the absence of *Crossonema multisquamatum*, *Macroposthonia solivaga* and *Criconemoides informis*. This pattern includes Galicia and many of the peripheral areas;

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Table II - *Species in the faunistic groups, showing the number of 10 km squares in each geographic pattern in which each species occurred.*

SPECIES	Geographic Patterns					Total
	A	B	C	D	E	
North-eastern						
1. *Longidorus caespiticola* Hooper, 1961	1	3	5	0	0	9
2. *Macroposthonia rustica* (Micoletzky, 1915) De Grisse *et* Loof, 1965	0	0	9	3	1	13
3. *Seriespinula cobbi* (Micoletzky, 1925) Khan, Chawla *et* Saha, 1975	0	0	1	1	0	2
South-eastern						
4. *Xiphinema neovuittenezi* Dalmasso, 1969	1	1	0	0	0	2
Southern						
5. *Hemicycliophora lutosa* Loof *et* Heyns, 1969	0	6	0	0	0	6
6. *Hemicriconemoides gaddi* (Loos, 1949) Chitwood *et* Birchfield, 1957	1	0	1	0	0	2
7. *Crossonema multisquamatum* (Kirjanova, 1948) Kahn, Chawla *et* Saha, 1975	4	20	0	0	0	24
8. *Macroposthonia sphaerocephala* (Taylor, 1936) De Grisse *et* Loof, 1965	7	27	3	2	1	40
9. *Hemicriconemoides cocophillus* (Loos, 1949) Chitwood *et* Birchfield, 1957	0	9	0	0	0	9
10. *Nothocriconema mutabile* (Taylor, 1936) De Grisse *et* Loof, 1965	12	30	5	4	0	51
11. *Criconemoides morgensis* (Hofmänner *et* Menzel, 1914) Taylor, 1936	0	1	0	1	0	2

Table II - (continued)

SPECIES	Geographic Patterns					Total
	A	B	C	D	E	

North-western

12. *Hemicriconemoides pseudobrachyurus* De Grisse, 1964	1	0	0	0	1	2
13. *Longidorus macrosoma* Hooper, 1961	1	0	1	0	1	3
14. *Longidorus goodeyi* Hooper, 1961	0	0	1	0	1	2

Southwest central

15. *Hemicycliophora thornei* Goodey, 1963	0	2	2	0	0	4
16. *Hemicycliophora thienemanni* (Schneider, 1925) Loos, 1948	2	0	2	0	1	5
17. *Longidorus elongatus* (De Man, 1876) Thorne *et* Swanger, 1936.	2	1	0	1	0	4
18. *Macroposthonia curvata* (Raski, 1952) De Grisse *et* Loof, 1965	18	15	7	5	7	52
19. *Longidorus attenuatus* Hooper, 1961	2	4	2	3	0	11
20. *Xiphinema turcicum* Luc *et* Dalmasso, 1964	4	3	0	0	1	8
21. *Criconemella parva* (Raski, 1952) De Grisse *et* Loof, 1965	8	2	1	0	0	11
22. *Xiphinema sahelense* Dalmasso, 1969	4	4	1	1	1	11

Table II - (continued)

SPECIES	Geographic Patterns					Total
	A	B	C	D	E	
Northwest central						
23. *Hemicycliophora conida* Thorne, 1955	1	1	0	0	1	3
24. *Nothocriconema crotaloides* (Cobb, 1924) De Grisse *et* Loof, 1965	6	0	2	0	0	8
25. *Xiphinema ingens* Luc *et* Dalmasso, 1964	2	1	1	2	2	8
26. *Macroposthonia pseudosolivaga* (De Grisse, 1964) De Grisse *et* Loof, 1965	4	0	3	0	1	8
27. *Xiphinema diversicaudatum* (Micoletzky, 1927) Thorne, 1939	17	2	3	3	1	26
Northeast central						
28. *Crossonema menzeli* (Stefanski, 1924) Khan, Chawla *et* Saha, 1975	1	0	1	0	0	2
29. *Macroposthonia rotundicauda* (Loof, 1964) De Grisse *et* Loof, 1965	2	1	0	3	0	6
30. *Macroposthonia vadensis* (Loof, 1964) De Grisse *et* Loof, 1965	1	0	5	0	0	6
31. *Criconemoides amorphus* De Grisse, 1967	2	1	0	0	0	3
32. *Xenocriconemella macrodora* (Taylor, 1936) De Grisse *et* Loof, 1965	9	2	4	7	1	23
33. *Longidorus profundorum* Hooper, 1961	4	2	6	3	3	18

Table II - (continued)

| SPECIES	Geographic Patterns					Total
	A	B	C	D	E	
Southeast central						
34. *Xiphinema vuittenezi* Luc, Lima, Weischer *et* Flegg, 1964	4	1	1	1	0	7
35. *Criconema palmatum* (Siddiqi *et* Southey, 1962) Khan, Chawla *et* Saha, 1975	1	2	1	0	0	4
36. *Xiphinema index* Thorne *et* Allen, 1950	16	12	5	9	3	45
37. *Nothocriconema annuliferum* (De Man, 1921) De Grisse *et* Loof, 1965	3	0	4	4	2	13
38. *Macroposthonia xenoplax* (Raski, 1952) De Grisse *et* Loof, 1965	37	26	27	15	10	115
39. *Macroposthonia antipolitana* (De Grisse, 1963) De Grisse *et* Loof, 1965	0	2	9	6	2	19
40. *Criconemoides informis* (Micoletzky, 1922) Taylor, 1936	22	22	34	27	0	105
41. *Xiphinema italiae* Mevl, 1953	13	11	4	10	3	41
42. *Xiphinema brevicolle* Lordello *et* da Costa, 1961	18	16	5	3	1	43
43. *Macroposthonia solivaga* (Andrássy, 1962) De Grisse *et* Loof, 1965	4	6	21	0	0	31
44. *Xiphinema pachtaicum* (Tulaganov, 1938) Kirjanova, 1951	84	83	75	59	27	328
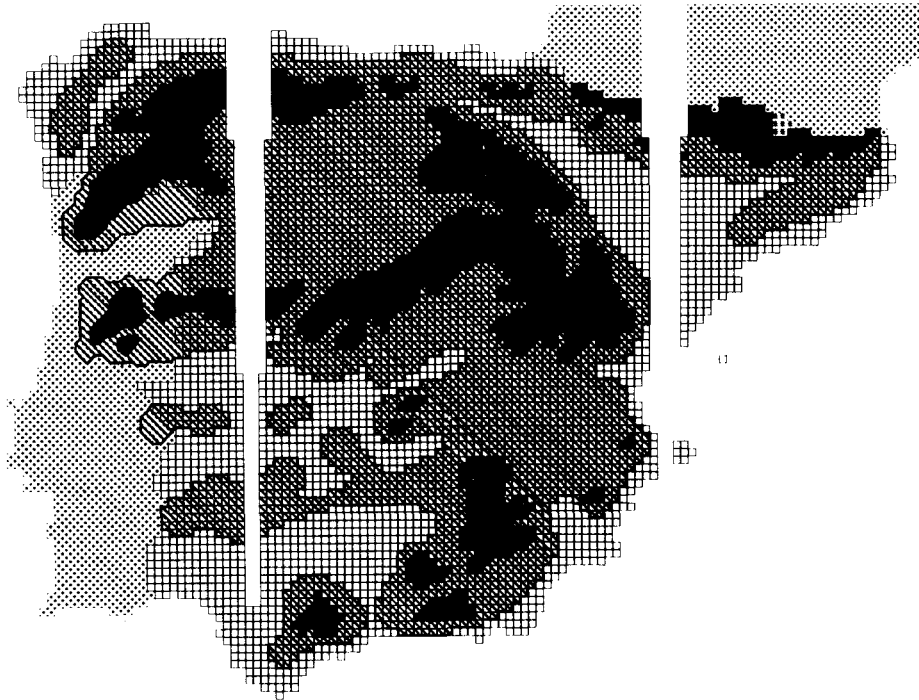
Fig. 4 - Map of Spain showing generalised distribution of altitude. Empty squares: be-
low 500 m; black squares: above 1000 m.

whilst some parts of it are probably under-recorded, it is also character-
ized by a loss of distinctively southern species without any compensatory
gain of the rarer northern species.

Pattern A contains the greatest diversity of faunistic elements and the
largest number of species, including not only the common species from
other patterns but also many less common and less widely distributed
species. It contains two disjunct areas, both of which are varied topograph-
ically and ecologically; the one region including Madrid is noteworthy for
its natural diversity and is transitional between the north and south of
Spain.

Discussion

Using 44 species of plant-parasitic nematodes of the Criconematidae, and
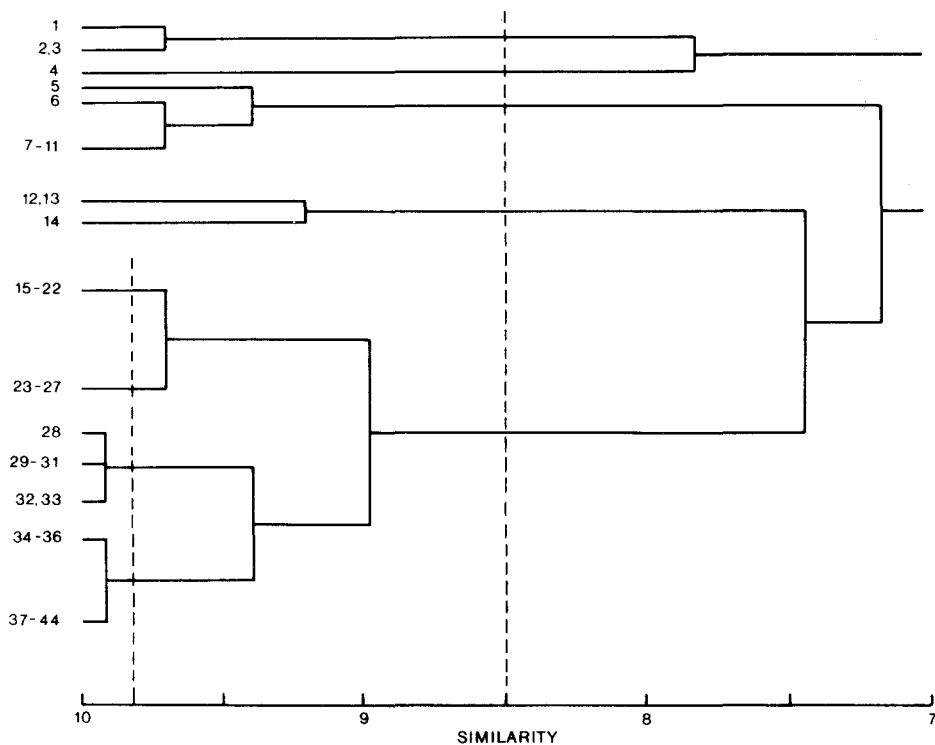the Longidoridae and multivariate analysis techniques we have defined

Fig. 5 - Dendrogram of the furthest neighbour clustering of the species centres of distribution. Numbers as in Table I.

faunistic groups and regional patterns and examined the relationships between them. The numerical techniques, grouped together as pattern analysis by Australian workers (Williams, 1976), have been used to identify structures within the data which seem in broad agreement with our knowledge of the distribution and ecology of this group both in Spain and Europe generally. Although the data are limited compared to those which are available for some other groups of animals, the attempt has been worthwhile since so little was previously known of nematode biogeography at this scale.

Of the two familes studied, the Criconematidae showed a higher diversity both in faunistic groups and in the geographic patterns in which its species occur; several of its species were important in defining geographic patterns by their presence. In contrast, the Longidoridae, with the exception of a group of northern species in the genus *Longidorus*, is
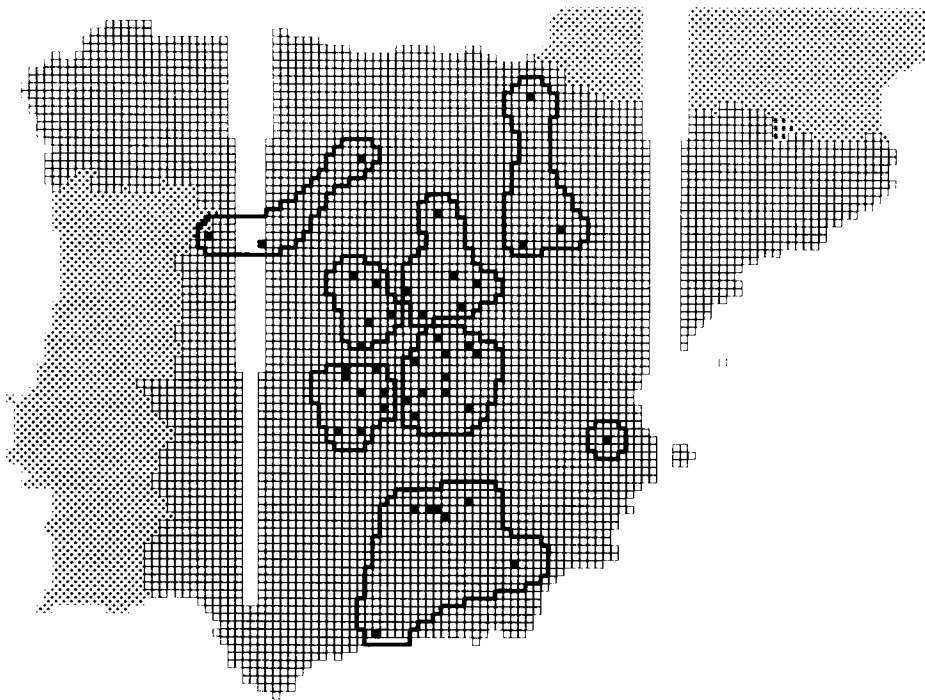
Fig. 6 - Map of Spain showing centres of distribution of individual species (black squares); the eight groups (Table I) are enclosed.

mainly represented by widespread species with Mediterranean and central European tendencies.

As is usual in these studies neither the faunal groups nor the regional patterns fall into discrete categories. Differences in the dominance and overlaps of the faunistic groups explain the variations in regional grouping using different methods. However, the structure that emerges is one of differentiation into regional patterns, controlled by altitude and geographic diversity rather than geographic subdivisions. It must be remembered too that the UTM grid squares cut across many natural boundaries and will blur some of the distinctions. Boag (Pers. comm.) has indicated that the British Isles are dominated by north-south distribution gradients and Topham and Alphey (1985) attributed many differences between European countries in their nematofauna to the influences of glaciation - an influence which would play a very minor role in the Spanish nematofauna.

Table III - *The characteristics of the geographic patterns.*

Geographic Pattern	Altitude	No. of 100 km UTM Square	10 km records/ 100 km square	% distribution of records in Faunistic elements							
				S	SE	NE	NW	SW cent.	NW cent.	NE cent.	SE cent.
A	Medium	3	106	18	50	4	29	38	57	33	27
B	Low	7	46	69	50	13	0	30	8	10	24
C	High	13	19	7	0	63	29	14	17	28	25
D	Medium	12	14	5	0	17	0	10	9	22	18
E	Medium	13	6	1	0	4	43	10	9	7	6

Differences in altitude are accompanied by climatic and vegetational changes which in turn are related to edaphic characteristics, all of which undoubtably influence the soil-inhabiting plant-parasitic nematofauna. The dynamics of spatial structure in this group depend partly on historical factors determining the presence of species of different faunistic elements in any given area and partly on the adaptive capacity of the various species. Comparison of populations of individual species from different countries may indicate differences in behaviour, morphology and adaptation which reflect its origin in a particular faunistic group; for example *Xenocriconemella macrodora* occurs at low altitudes in Scotland (Boag, Pers. comm.) and in northern Spain, but in southern Spain it is found only at elevations over 800 m. The important factor in such distributions is not the species itself but the variation with latitude of the occurrence of the ecosystem or the potential climax vegetation.

There are limitations as a result of incomplete data, a coarse scale and the subjective choice of techniques. However, the approach adopted here has enabled the information contained in the Atlas of Plant Parasitic Nematodes of Spain (Alphey, 1979) to be summarized in a meaningful way. The conclusions drawn and the groupings made may now be evaluated by further study of the biology, taxonomy and ecology of this group. For instance, problems in taxonomic interpretation can arise when populations of a single species are described as a new species because they originate from different geographic areas (de Grisse and Loof, 1970) or when they differ in their biological response in different parts of their range (Dalmasso, 1970; Brown and Trudgill, 1983). The terms biotype and pathotype are well established in nematology to cover variations in host range and damage; Rivoal (1977) found that different biotypes occurred in different areas within a species' range. Nematodes are frequently described as morphospecies, and only rarely are behavioural or ecological considerations taken into account. It is not usually possible to know whether certain taxa are widespread polytypic species or clusters of phenotypically similar but geographically differentiated species. Furthermore for many parthenogenetic species hybridization cannot be used to check for biospecies. Classification on a biogeographic basis would help to distinguish between interspecific and intraspecific geographic and ecotypic variation.

SUMMARY

Distribution data for the Criconematid and Longidorid nematofauna in Spain were analysed to identify both species groups with similar distribution patterns and areas typified by a distinct fauna. Nematode presence/absence data in 100 km squares of the Universal Transverse Mercator (UTM) grid were usefully grouped into areas by Information Analysis whilst the faunistic elements were best differentiated by Cluster analysis of the mean co-ordinate position of all records for each species within 10 km UTM squares. Eight main faunistic groups were distinguished: north-eastern, north-western, southern, south-eastern and four central groups; and five areal groupings which were related to altitude within Spain. The varying frequency of nematodes from the different faunistic groups within areal groupings was used to define four distinct distribution patterns in which (i) northern species were predominant, (ii) southern species were predominant, (iii) mediterranean and central-European species were predominant and (iv) areas of high faunistic diversity, characterised by a wide range of environmental factors.

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