BIOGEOGRAPHY OF LONGIDORIDAE IN THE EUROMEDITERRANEAN AREA

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Summary. Distribution of the family Longidoridae and its component species is defined in the Euromediterranean Region according to the chorological patterns of the Occidental Holopaleartic Region. As an initial descriptive step, the direct analysis of distribution areas is used to define the faunistic elements with geographical affinity. In this way the phytonematological problems of the Euromediterranean area may be characterized from a biogeographical point of view.

A fundamental objective of biogeography is to establish scientific hypothesis which explains distribution organisms based on chronological (historical biogeography) or ecological factors (ecological biogeography).

In plant pathologhy it is accepted as a central process in plant-parasitic epidemiology that ecological and biological behavior of a parasite can be conditioned by its geographical distribution (Minogue and Fry, 1983). Nevertheless, the integration of the spatial model within the temporal one is difficult (Van der Plank, 1975). It is necessary to understand the factors and interactions which affect the spatial distribution of pests and parasites and this led (Weltzein, 1972) to define the concept of geophytopatholoy.

Probably because of the relatively recent development of nematology, there is paucity of biogeographical studies on soil and plant parasitic nematodes. However, opportunities exist for nematologists to recognize many of the mechanisms which govern species diversity (Procter, 1984), host parasite interaction and speciation processes (Coomans, 1979) including speciation by vicariance and dispersion. Vicariance perhaps better explains the higher taxa (i.e. Families, Genera) by means of phylogenetic systematic (Ferris, 1983; Lorenzen, 1983), whereas dispersion which involves species evolution in relatively less time and geographical area than vicariance, is more appropriate for biogeographical regions where the processes for faunistic diversification at lower taxonomic levels are studied (Blondel, 1987).

The basic aspects required to explain nematode distributions are the delimitation of species distribution areas (chorology) and the establishment of biogeographical units (chorologic synthesis) with operational values on which an explicative science may subsequently by founded. That so little attention has been devoted to this subject is surprising in Nematology and specially in so general biogeography (Ball, 1975 and Keast, 1977 or Blondel, 1979 and Rapoport, 1982).

Important evolutionary developments in Longidorus speciation occurred in Europe (Coomans, 1984/85). The distribution of these, and species in related genera in the Longidoridae, have been intensively studied in Europe as a result of their pathogenicity in crops and as several species are vectors of plant viruses. In our study we analysed the distributions of members of the Longidoridae as an initial descriptive stage (Birks, 1987) to define their biogeographical patterns within the Euromediterranean area. Also, examination of the distribution of the most evolved members in the genera may help to elucidate the polarity of the most developed taxonomic characters, mainly supported by morphometry and correction of the apochoric component of their present distributions, which will correspond to the least pleisochoric zones or take these corrections as assistant criteria of their geographic limitation (Henning, 1968).

Materials and methods

In quantitative biology, R-Mode and-Q-Mode are the two logical methods of analysis (Page, 1987). The first was chosen, because it classifies the biotic component according the geographical affinities of species in order to define the faunistic elements. Our selection and scaling of the geographical units were the least arbitrary possible, which allowed the known species distributions to be adjusted to the established chorologic categories in the Euromediterranean Region (La Greca, 1964). The adjustment was made maximizing the geographical component, by using the relative index between the surface and density of species register according to EPPNS atlas (Alphey and Taylor, 1986), with the aim of maximizing the geographical component. The divisive method of information index (Wishart, 1982) was used as a classification algorithm, for its simplicity and as it directly reflects geographical areas having most similarity.

Although the inference of faunistic elements has the objective of identifying the distribution of the species more than the reconstruction of the processes which cause them. The mapping of these elements and the overlapping of their distribution areas indicate which areas (biogeographical units) represent a maximum of pleisochories which may assist to explaining the biogeographical nature of the biotic similarities.

The list sf species and their distribution were obtained from the EPPNS atlas (Alphey and Taylor, 1986 and from Brown and Taylor, 1987). The ecosystems of the Mediterranean basin countries were those from Di Castri (1973) (Albania) Greece, Bulgaria, Rumania, Turkey, Syria, Lebanon, Jordan, Israel, Egypt, Libya, Tunisia, Algeria and Morocco).

Results

Figures 1 to 7 represent the generalized chorological distribution areas in the Euromediterranean Region, used here to define the plant-parasitic nematofauna (Bello *et al.*, 1986) and are a subdivision of the categories described by La Greca (1964). Also an East-Mediterranean area is delimited taking into consideration the recorded species from Saudi Arabia, Egypt, Iraq, Israel and Syria.

The revision of the family Longidoridae in Europe by Brown and Taylor (1987) has been followed. According to these authors, X. basilgoodeyi Coomans, 1964, X. ensiculiferum (Cobb, 1893) Thorne, 1937 and X. rotundatum Schuurmans Stekhoven et Teunissen, 1938 are tropical species and rarely present in this Region. Also L. macroteromucronatus Altherr, 1974; L. paraelongatus Altherr, 1974, L. poessneckensis Altherr, 1974 and L. pseudoelongatus Altherr, 1976 are regarded as doubtful and have been omitted.

Nematode identification in Spain regarded as doubtful by Arias et al. (1985) (X. krugi Lordello, 1955; X. radicicola Goodey, 1936; X. surinamense Loof et Maas, 1972 and X. vulgare Tarjan, 1964) have been excluded. L. pisi Edward, Misra et Singh, 1964 is conspecific with L. latocephalus Lamberti, Choleva et Agostinelli, 1983 (B. Choleva and D. Brown pers. comm.) and X. phoenicis Loof, 1983 and L. orientalis Loof, 1982 reported from Saudi Arabia have been included for geographical reasons.

Table I shows the number of 50 km2 quadrangle from the chorological units, used for computer analysis to obtain the relative density of the species. The non-limited, extreme areas, Atlantic, East-Mediterranean and Turanian are excluded. In table II the occurrence of nematode species, following the appropriate adjustments as described, are given for each of the Euromediterranean chorological regions.

Chorological patterns

From our examination of the recorded species the regions with endemisms present are:

Apenino-Dinerical: X. porosum Roca et Agostinelli, 1986; L. apulus Lamberti et Bleve-Zacheo, 1977; L. eridanicus Roca, Lamberti et Agostinelli, 1984; L. magnus Lamberti, Bleve-Zacheo et Arias, 1982; L. major Roca et D'Errico, 1987.

- South-European: L. picenus Roca, Lamberti et Agostinelli, 1984.

— Western Mediterranean: X. algeriense Luc, 1983; X. conurum Siddiqi, 1964; X. sahelense Dalmasso, 1969; L. congoensis Aboul-Eid, 1970; L. tarjani Siddiqi, 1962 and L. unedoi Arias, Andres et Navas, 1986.

- Middle European: X. dentatum Sturhan, 1978 and L. cylindricaudatus Kozlowska et Seinhorst, 1979.

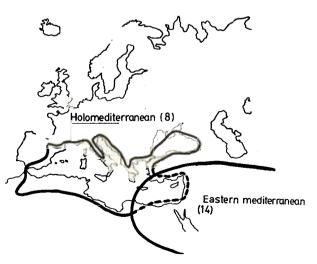
- Atlantic Middle European: X. coxi Tarjan, 1964; X. pseudocoxi Sturhan, 1984; L. leptocephalus Hooper, 1961 and L. profundorum Hooper, 1966.

— Circumtirrenical: X. melitense Lamberti, Bleve-Zacheo et Arias, 1982; L. aetnaeus Roca, Lamberti, Agostinelli et Vinciguerra, 1986 and L. protae Lamberti et Bleve-Zacheo, 1977.

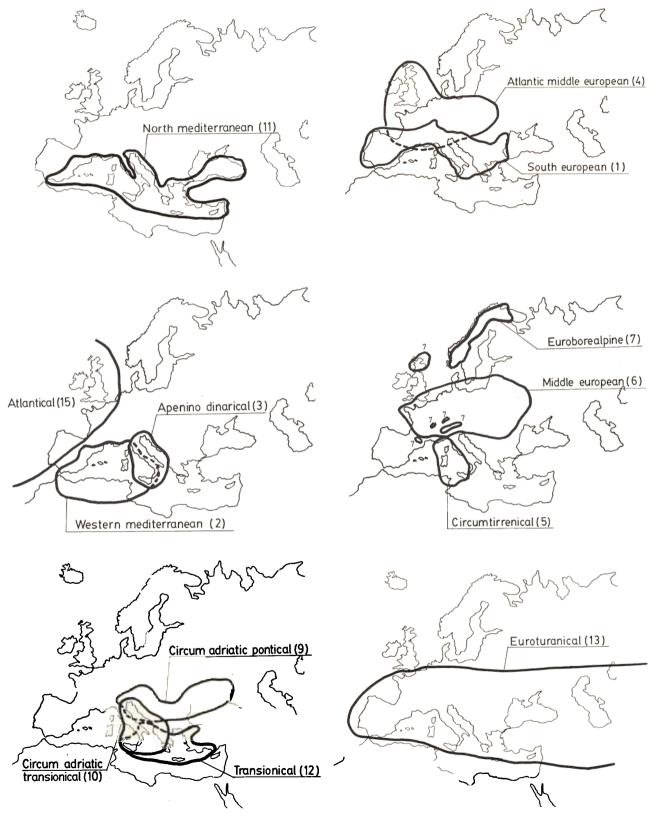
- Euroborealpine: X. pyrenaicum Dalmasso, 1969.

— Holomediterranean: L. laevicapitatus Williams, 1959.

- Circum Adriatic Pontical: X. incertum Lamberti, Choleva et Agostinelli, 1983; X. simile Lamberti, Choleva et Agostinelli, 1983; L. distinctus Lamberti, Choleva et Agostinelli, 1983.



Figgs. to 7 - Chorological areas in Euromediterranean Region.



- Circum Adriatic Transionical: X. barense Lamberti, Roca, Agostinelli et Bleve-Zacheo, 1986; X. globosum Sturhan, 1978; L. edmundsi Hunt et Siddiqi, 1977.

- North-Mediterranean: X. ingens Luc et Dalmasso, 1963.

— Transionical: L. fasciatus Roca et Lamberti, 1981; L. proximus Sturhan et Argo, 1983.

- Eastern Mediterranean: X. insigne Loos, 1949; X. israeliae Luc, Brown et Cohn, 1982; X. phoenicis Loof, 1983; X. pini Heyns, 1965; L. africanus Merny, 1966; L. cohni Heyns, 1969; L. orientalis Loof, 1982; L. pisi Edward, Misra et Singh, 1964; L. sylphus Thorne, 1939; L. taniwha Clark, 1963.

—Atlantic: X. pachydermum Sturhan 1983; L. carpetanensis Arias, Andres et Navas, 1986; L. globulicauda Dalmasso, 1969; L. goodeyi Hooper, 1961; L. lusitanicum Macara, 1985 and L. nevesi Macara, 1985.

Apparently endemisms occur in all the chorological regions with the maximum variation present between the Eastern and North-Western areas. However, the endemisms present in the Middle European and Southern European perhaps are exceptional and result from the sporadic localization of *L. cylindricaudatus*, *X. dentatum* and *L. picenus*. All endemisms in the Atlantic Region are present only in the Atlantic zone of the Iberian Peninsula.

Regions without or with doubtful endemisms (Euroturanical; Middle European and Southern European) are rather large with many shared species. The glaciation boundary (Pomerol, 1973) probably delimits where species have become established. Thus, several chorological regions will require to be modified for the family Longidoridae i.e., suppressing the Southern-European and Euroturanical regions and confining the extension of the Atlantic and Middle European regions.

Twenty nine of the 49 endemisms are in the genus Longidorus with their main predominance in the Apenino-

TABLE I - Relative density of delimited chorologic units.

Chorologic units	Numbers of quadrangles					
Apenino Dinerical (3)	34					
Atlantic Middle European (4)	166					
Circum Adriatic Pontical (9)	63					
Circum Adriatic Transionical (10)	44					
Circumtirrenical (5)	27					
Euroborealpine (7)	35					
Holomediterranean (8)	238					
Middle European (6)	146					
North-Mediterranean (11)	144					
South-European (1)	113					
Transionical (12)	53					
Western Mediterranean (2)	103					

Dinerical, Circumtirrenical, Transionical and Atlantic regions.

Geographical patterns

A quantitative analysis of geographical patterns may be established by grouping the species according to their distribution areas (Fig. 8). The results again suggest that the regions without endemism should be reduced. Otherwise interpretation of the dendrogram may be misleading and does not offer any explanation for the groups. However, it is easy to discern empirically the regions which are grouping in the South-East of the Southern European Region (1), as well as several other regions which group in a more irregular way. Two large groups of faunistic elements can be established from the intermediate South European region which includes nine faunistic groups, and these mainly comprise the chorological categories: Western -Mediterranean (2), Atlantic - Middle - European (4), Circum - Tirrenical (5), Middle - European (6), Circum - Adriatic - Pontical (9), Eastern - Mediterranean (14) and Atlantic (15).

The nematode groups are: a) X. diversicaudatum (Micoletzky, 1922 and 1927) Thorne, 1939; X. vuittenezi Luc. Lima, Weischer et Flegg, 1964; L. attenuatus Hooper, 1961; L. elongatus (de Man, 1876) Thorne et Swanger, 1935; L. macrosoma Hooper, 1961; L. profundorum Hooper, 1966 and L. vineacola Sturhan et Weischer, 1964. b) X. ingens Luc et Dalmasso, 1963 and X. opistohysterum Siddiqi, 1961. c) X. brevicolle Lordello et Da Costa, 1961; X. dentatum Sturhan, 1978; L. cylindricaudatus Kozlowska et Seinhorst, 1979 and L. intermedius Kozlowska et Seinhorst, 1978. d) X. index Thorne et Allen, 1950; X. italiae Meyl, 1953; X. pachtaicum (Tulaganov, 1938) Kirjanova, 1951; X. turcicum Luc et Dalmasso, 1963 and L. picenus Roca, Lamberti et Agostinelli, 1984. e) X. elongatus Schuurmans Stekhoven et Teunissen, 1938; X. insigne Loos, 1949; X. israeliae Luc, Brown, et Cohn, 1982; X. phoenicis Loof, 1983; X. pini Heyns, 1965; L. africanus Merny, 1966; L. cohni Heyns, 1969; L. orientalis Loof, 1982; L. pisi Edward, Misra et Singh, 1964; L. sylphus Thorne, 1939 and L. taniwha Clark, 1963. f) X. americanum Cobb, 1913; X. incertum Lamberti, Choleva et Agostinelli, 1983; X. neovuittenezi Dalmasso, 1969; X. simile Lamberti, Choleva et Agostinelli, 1983; L. distinctus Lamberti, Choleva et Agostinelli, 1983; L. closelangatus Stoyanov, 1964; L. euonymus Mali et Hooper, 1974 and L. moesicus Lamberti, Choleva et Agostinelli, 1983. g) X. lusitanicum Sturhan, 1983; L. nevesi Macara, 1985; X. pachidermum Sturhan, 1983; X. rivesi Dalmasso, 1969; L. carpetanensis Arias, Andres et Navas, 1986; L. globulicauda Dalmasso, 1969; L. goodevi Hooper, 1961 and L. lusitanicus Macara, 1985. h) X. algeriense Luc, 1983; X. conurum Siddiqi, 1964; X. sahelense Dalmasso, 1969; L. caespiticola Hooper, 1961; L. congoensis Aboul-Eid, 1970; L. tarjani Siddiqi, 1961 and L. unedoi Arias, Andres et Navas, 1986 and finally a group of relatively rare species which do not have a recognizable distribution pattern comprises the species: X. barense Lamberti, Roca, Agostinelli et Bleve-Zacheo, 1986; X. coxi Tarjan, 1964; X. globosum Sturhan, 1978; X. melitense Lamberti, Bleve-Zacheo et Arias, 1982; X. porosum Roca et Agostinelli, 1986; X. pseudocoxi Sturhan, 1984; X. pyrenaicum Dalmasso, 1969; L. aetnaeus Roca, Lamberti, Agostinelli et Vinciguerra, 1986; L. apulus Lamberti et Bleve-Zacheo, 1977; L. edmundsi Hunt et Siddiqi, 1977; L. eridanicus Roca, Lamberti et Agostinelli, 1984; L. fasciatus Roca et Lamberti 1981; L. iuglandis Roca, Lamberti et Agostinelli, 1984; L. juvenilis Dalmasso, 1969; L. laevicapitatus Williams, 1959; L. leptocephalus Hooper, 1961; L. magnus Lamberti, Bleve-Zacheo et Arias, 1982; L. major Roca et D'Errico, 1987; L. protae Lamberti et Bleve-Zacheo, 1977 and L. proximus Sturhan et Argo, 1983.

From these results it is possible to establish regions (Figs 9 to 11) which, according to the predominance of species, clearly distinguish groups a, g, and f as European-Atlantic and groups b, d, e and b as Mediterranean. Our results combined with the chorological and structural cat-

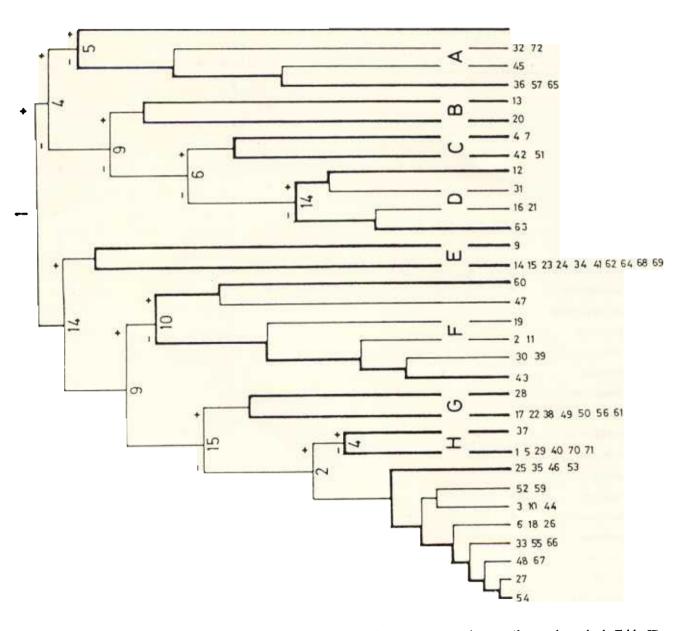


Fig. 8 Classification of species according to their geographical distribution. Faunistic elements (for numbers check Table II).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 - X. algeriense		•													
2 - X. americanum									٠				٠		
3 - X. barense										•					
4 - X. brevicolle	•					•		•							
5 - X. conurum		•													
6 - X. coxi				٠											
7 - X. dentatum						٠									
8 - X. diversicaudatum	٠			•	•	٠							•		
9 - X. elongatum		٠												•	
10 - X. globosum										•					
11 - X. incertum									•						
12 - X. index	٠							•						•	
13 - X. ingens	٠								•	•	•				
14 - X. insigne														•	
15 - X. israeliae														•	
16 - X. italiae	•							•							
17 - X. lusitanicus															•
18 - X. melitense					•										
19 - X. neovuittenezi		•							•						
20 - X. opistohysterum	•								•						
21 - X. pachtaicum	•							•							
22 - X. pachydermum															•
23 - X. phoenicis														•	
24 - X. pini														•	
25 - X. porosum			•												
26 - X. pseudocoxi				•											
27 - X. pyrenaicum							•								
28 - X. rivesi		•													•
29 - X. sahelense		٠													
30 - X. simile									•						
31 - X. turcicum	٠													•	
32 - X. vuittenezi	•			•										•	
33 - L. aetnaeus					•										
34 - L. africanus														•	
35 - L. apulus			٠												
36 - L. attenuatus	•			•											

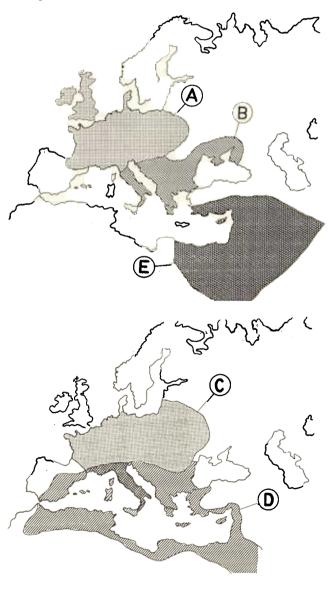
TABLE II - Adjusted of real distribution to chorologic units.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
37 - L. caespiticola		٠		٠											
38 - L. carpetanensis															٠
39 - L. closelongatus					٠				٠						
40 - L. congoensis		٠													
41 - L. cohni														•	
42 - L. cylindricaudatus						•									
43 - L. distinctus									٠						
44 - L. edmundsi										٠					
45 - L. elongatus	٠			٠			٠								
46 - L. eridanicus			٠												
47 - L. euonymus						٠			•	٠					
48 - L. fasciatus												•			
49 - L. globulicauda															•
50 - L. goodeyi															•
51 - L. intermedius	٠					•									
52 - L. iuglandis										•		•			
53 - L. juvenilis			٠												
54 - L. laevicapitatus								٠							
55 - L. leptocephalus				٠											
56 - L. lusitanicus															٠
57 - L. macrosoma	•			•											
58 - L. magnus			٠												
59 - L. major			٠												
60 - L. moesicus					•				٠	٠					
61 - L. nevesi															•
62 - L. orientalis														٠	
63 - L. picenus		٠													
64 - L. pisi *														•	
65 - L. profundorum	٠			•											
66 - L. protae					٠										
67 - L. proximus												٠			
68 - L. sylphus														٠	
69 - L. taniwha														٠	
70 - L. tarjani		٠													
71 - L. unedoi		٠													
72 - L. vineacola	•			٠										٠	

* Also present in Bulgaria (Choleva, Brown, pers. comm.) but we fit mainly to a Eastern-European distribution.

egories of Bello *et al.* (1986), are in general agreement with a study in which the faunistic distances of these species in Europe were examined (Topham and Alphey, 1985). Also, our biogeographical study support the hypothesis that phytonematological problems in the Mediterranean area are due to the pathogenic and virus vector species from areas b, d, e, and b (X. index, X. italiae, X. pachtaicum, X. elongatus, L. africanus, L. cohni and L. caespiticola).

Further, our results agree with those of Reichert and Palti (1966) who described the pathogeography of plant diseases in the Mediterranean region and Lamberti (1981) who listed the longidorid nematodes pathogenic in the Mediterranean region. These species X. diversicaudatum, X. vuittenezi, L. attenuatus, L. elongatus, L. macrosoma and L. vineacola and the undefined X. coxi, X. pseudocoxi, and L. apulus are similar tho those listed by Lamberti (1981).



Discussion

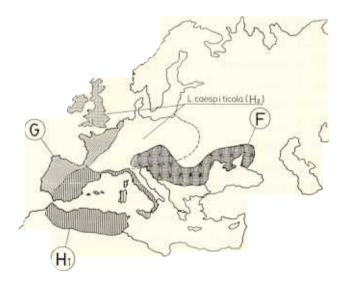
According to our results, including corrections to the Southern European, middle European and Atlantic areas, the distribution patterns of longidorid nematodes in Europe broadly follow the two basic models, allopatry (general) and sympatry (species).

According to the allopatric model the presence of Xiphinema species in Europe can be considered to be a very recent dispersion process, with the pleisochoric limits of the genus being in the Southern Mediterranean region, where endemisms of the genus occur. Similarly the pleisochoric limit of Longidorus is in the Northern Mediterranean and Southern European countries which suggests an early dispersal process.

The sympatric distribution pattern is exemplified by the presence of two or more species belonging to the same genera being present in the same region. The presence of these species, probably results from normal evolutionary process (Bush, 1981), may be the result of more recent dispersion (McNamara and Flegg, 1981) influenced by ecological factors where they survive in different niches in a common distribution (Navas and Arias, 1986).

Adjacent chorological regions with similar faunas may each have affinities lead to a similar range of nematodes present. However, differences may exist in the pathogenicity and associated diseases caused in crops by the nematodes present in these areas.

Specificity of virus transmissions and variability in transmission of viruses and virus strains by virus vector nematode species and populations (Brown, 1986, Brown *et al.*, 1989) support such a hypothesis. However, whilst identifying areas with similar nematofauna and flora compositions is useful for defining the faunistic groups with similar distribution areas, it must be taken into account



that few species have identical distributions or regions have identical compositions. Much variation exists in the distribution of species in the family Longidoridae in the Euromediterranean Region. The proposed Euromediterranean chorological regions may subsequently be used to help to identify the factors that determine the present distribution of the nematodes.

Craw (1982, 1983) criticed biogeographical studies which defined areas by political or geographical boundaries. At the continental level (Topham and Alphey, 1985) such studies may include species in regions where the species have allopatric distributions restricted to local areas as endemisms which may be explained by geological isolation from other organisms (Barbieri et al., 1974). Study of such Nematodes endemisms by the use of cladogrames erected from species data may help to identify distribution regions without geographic boundaries (Platnick and Nelson, 1984). Alternatively, the cladogram erected from the regional data may help to identify species phylogeny and the polarity of taxonomic character of Xiphinema and Longidorus nematodes. However, as explained in the introduction to this study we do not ascribe fully to either of the two schools of historical biogeographers as the cladistic information is relevant for both (Platnick and Nelson, 1978).

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