

Centro de Ciencias Medioambientales, CSIC, Serrano 115 Dupdo, Madrid 28005, Spain ¹.

Department of Nematology, University of California, Riverside, CA, USA ².

Centro Técnico de Informática CSIC, Pinar 19, Madrid 28006, Spain ³.

PHYLOGENY AND BIOGEOGRAPHY OF *LONGIDORUS* (NEMATODA: LONGIDORIDAE) IN EUROMEDITERRANEA

by

A. NAVAS ¹, J. G. BALDWIN ², L. BARRIOS ³, and G. NOMBELA ¹

Summary. Patterns of distribution of a monophyletic branch of *Longidorus* species in previously established chorological units (CUs) of Euromediterranea, provide a basis for historical biogeography and a phylogenetic hypothesis of the species. The centre of distribution of each *Longidorus* species within each CU was estimated by statistical methods to correct the apochoric component of the species due to expansion. CUs are compared geographically and faunistically (with respect to *Longidorus* composition). Distribution graph matrix analysis, applied to define the direction of the connections between CUs, did not establish which endemic species is most ancestral; rather, hypotheses of ancestry and polarity of multistate characters were tested by a morphologically-based cladogram congruent with the distribution graph. *Longidorus carpelanensis* is supported as an outgroup of all the other species. The results suggest that vicariant biogeography can resolve some aspects of the current pattern of *Longidorus* distribution and speciation origin, but that a dispersalist model is a primary explanation for large groups of *Longidorus* species in Euromediterranea.

The distribution of species of *Longidorus* (Nematoda) in Europe has been intensively studied as a result of its role as a plant pathogen and vector of viruses infecting several kinds of crops. These studies suggest that a monophyletic branch of *Longidorus* originated in Euromediterranea, which is a centre of dispersion and speciation of this branch (Coomans, 1985). Biogeographic patterns of distribution of *Longidorus* species in Euromediterranea could be used to test phylogenetic hypotheses at lower taxonomic categories of the group (Blondel, 1987). Insight into phylogeny of *Longidorus* species may provide hypotheses of geophytopathology and coevolution of specifically-transmitted plant viruses (Weltzien, 1972, Rodriguez-Cerezo, *et al.*, 1989; Fraile and Garcia-Arenal, 1990). In this paper we use data on distribution (Alphey and Taylor, 1986; Navas *et al.*, 1990) to elucidate phylogenetic relationships among *Longidorus* species. We also use historical and ecological biogeography to help identify factors determining the present distribution in Euromediterranea.

Although nematodes constitute a high percentage of the earth's biota (Procter, 1984), there is a paucity of historical biogeographical studies on soil and plant parasitic nematodes (Ferris *et al.*, 1976). Most phylogenetic classifications of nematodes are based on morphology and address supraspecific categories (Lorenzen, 1981; Ferris, 1983; Baldwin and Shouest Jr., 1990; Vinciguerra, 1987). The present taxonomy of *Longidorus*, is primarily based

on morphometric characters. We propose, as a testable alternative, a parsimonious phylogenetic hypothesis of *Longidorus* based on biogeographic data and classical characters. The proposed approach is particularly relevant in the elucidation of the primary mode of speciation and patterns which govern species diversity. In addition, a morphologically-based phylogeny is strengthened by biogeographic insight into outgroups, the most ancient species of ingroups, and character polarity for rooting the phylogenetic trees.

Although there is general agreement that species distribution is relevant to interpreting speciation (Hennig, 1966; Platnik and Nelson, 1978; Sanchiz, 1981; Doadrio, 1988) there are contrary opinions as to how to interpret widespread taxa for analysis of speciation patterns. Speciation can be considered to be the result of the appearance of barriers that fragment the broad ranges of ancestral species (vicariant model), or it can be considered to be the result of evolution from the introduction of a species where a barrier is already in place (dispersalist model). In cladistic analysis, Platnik and Nelson (1978) considered a widespread taxon as a carrier of plesiomorphic states of most of the characters. That is, a taxon is widespread because it is relatively ancestral. Conversely, others treat a widespread taxon as a carrier of synapomorphic states of most characters (Wiley, 1987; Zandee and Roos, 1987). Patterns of distribution frequently are represented by drawing dispersal routes connecting relevant localities (e.g. Rapoport, 1982). In the

present investigation we follow the methods of Page (1987) and Craw (1988), using graph analysis (minimum spanning trees) to recognize the geographically primitive (= plesiochoric) areas as associated with relatively primitive species. Humphries and Seberg (1989) note that "... the most striking aspect of Page's paper is the idea that his application of the graph-theoretic method is somehow more general than vicariance biogeography and component analysis in particular because it can detect a wider range of patterns even when in conflict with one another". Approaches proposed by Page (1987) and Craw (1988) are herein considered for their potential in the reconstruction of the evolutionary patterns of *Longidorus* in Euromediterranea. Evidence for both vicariance and dispersalist speciation in *Longidorus* is evaluated. Morphologically-based hypotheses utilize PAUP parsimony algorithms.

Materials and methods

Our approach to analysis of biogeographical data was to identify distinctive geographical regions (chorological

units, CUs), and recognize the centre of distribution of each *Longidorus* species within each CU. To detect evidence of dispersion, we then compared the CUs' patterns of similarity with respect to nematode species, with the CUs' geographic proximity (Castillo, 1988). To localize the plesiochoric area of the genus, centres of distribution were connected by minimum spanning tree techniques. Finally, to identify evolutionary tracks we connected centres of distribution in a pattern congruent with phylogenetic "connections" of species in morphology-based parsimonious analysis (Liebher, 1988).

Previous appraisals of Euromediterranea indicate fourteen CUs with internally distinctive geography and biota (La Greca, 1964; Navas *et al.*, 1990; Figure 1). Thirty two *Longidorus* species, widely accepted taxonomically and of known distribution in Euromediterranea, were considered (Brown and Taylor, 1987, Table D). A few other species (*L. alvegus*, *L. dunensis*, *L. closelongatus*, *L. kuiperi*, *L. major*, *L. juvenilis*, and *L. pinii*) included in Brown *et al.*, (1990) were omitted in our phylogenetic analysis because they shared the same character codification with another species, or the

TABLE I - *Longidorus* species included in this study which are reported to occur in Euromediterranea.

1. <i>L. aetnaeus</i>	Roca, Lamberti, Agostinelli <i>et</i> Vinciguerra, 1986
2. <i>L. africanus</i>	Merny, 1966
3. <i>L. apulus</i>	Lamberti <i>et</i> Bleve-Zacheo, 1977
4. <i>L. attenuatus</i>	Hooper, 1961
5. <i>L. belloi</i>	Andres <i>et</i> Arias, 1988
6. <i>L. caespiticola</i>	Hooper, 1961
7. <i>L. carpetanensis</i>	Arias, Andres <i>et</i> Navas, 1986
8. <i>L. cobni</i>	Heyns, 1969
9. <i>L. congoensis</i>	Aboul-Eid, 1970
10. <i>L. cylindricaudatus</i>	Kozłowska <i>et</i> Seinhorst, 1979
11. <i>L. distinctus</i>	Lamberti, Choleva <i>et</i> Agostinelli, 1983
12. <i>L. elongatus</i>	(de Man, 1876) Thorne <i>et</i> Swanger, 1936
13. <i>L. eridanicus</i>	Roca, Lamberti <i>et</i> Agostinelli, 1984
14. <i>L. euonymus</i>	Mali <i>et</i> Hooper, 1974
15. <i>L. fasciatus</i>	Roca <i>et</i> Lamberti, 1982
16. <i>L. globulicauda</i>	Dalmasso, 1969
17. <i>L. goodeyi</i>	Hooper, 1961
18. <i>L. intermedius</i>	Kozłowska <i>et</i> Seinhorst, 1979
19. <i>L. iuglandis</i>	Roca, Lamberti <i>et</i> Agostinelli, 1984
20. <i>L. latocephalus</i>	Lamberti, Choleva <i>et</i> Agostinelli, 1983
21. <i>L. leptcephalus</i>	Hooper, 1961
22. <i>L. lusitanicus</i>	Macara, 1986
23. <i>L. macrosoma</i>	Hooper, 1961
24. <i>L. magnus</i>	Lamberti, Bleve-Zacheo <i>et</i> Arias, 1982
25. <i>L. moesicus</i>	Lamberti, Choleva <i>et</i> Agostinelli, 1983
26. <i>L. nevesi</i>	Macara, 1986
27. <i>L. picenus</i>	Roca, Lamberti <i>et</i> Agostinelli, 1984
28. <i>L. profundorum</i>	Hooper, 1986
29. <i>L. protae</i>	Lamberti <i>et</i> Zacheo, 1977
30. <i>L. proximus</i>	Sturhan <i>et</i> Argo, 1983
31. <i>L. unedoi</i>	Arias, Andres <i>et</i> Navas, 1986
32. <i>L. vineacola</i>	Sturhan <i>et</i> Weischer, 1964

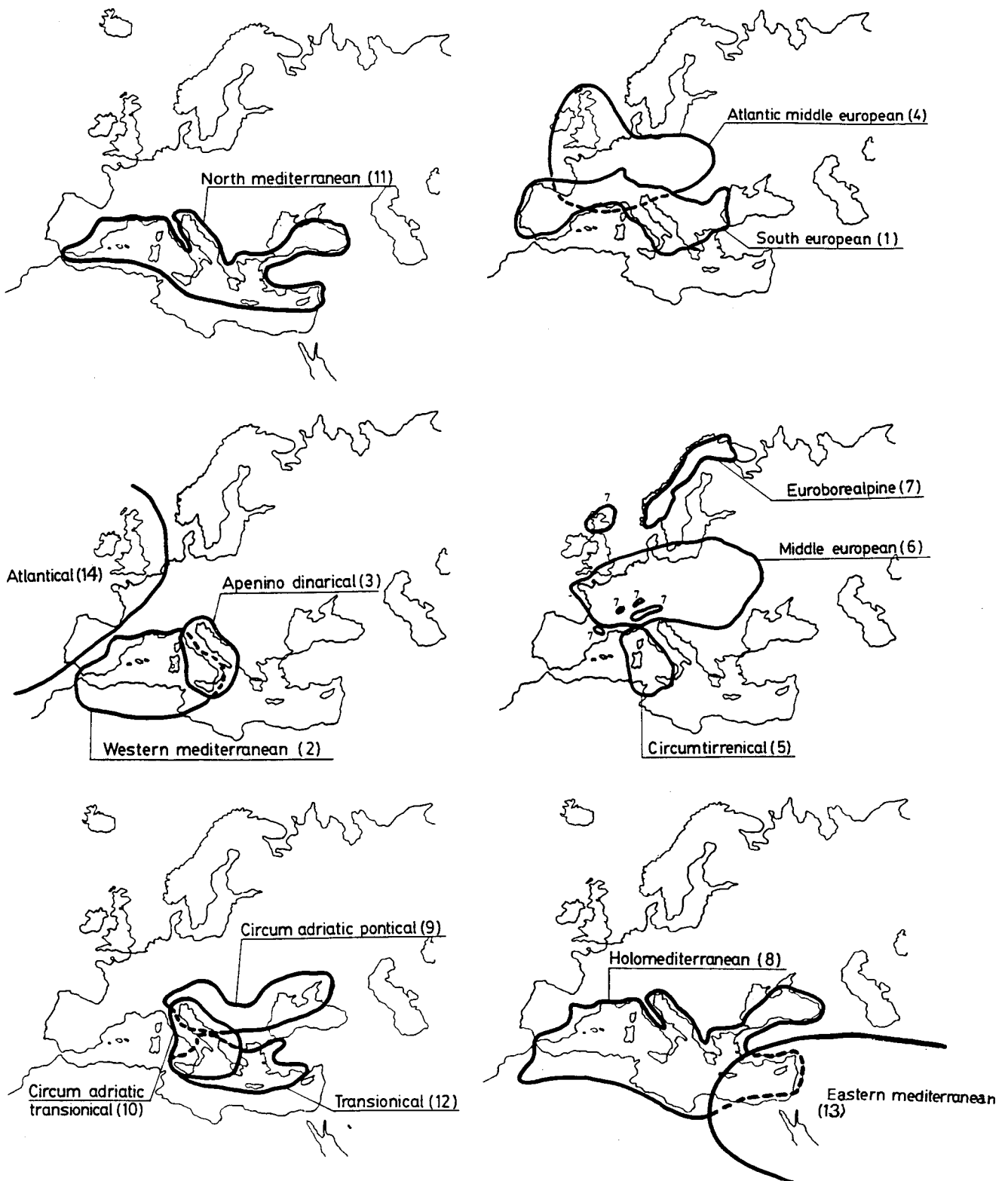


Fig. 1 - Chorological units in Euromediterranea.



Fig. 2 - Centres of species distribution in Europe and the Mediterranean (numbers represent species from Table I).

interpretation of morphological differences is particularly questionable pending further examination (see note on Table IV). We do not accept that *L. latocephalus* and *L. pisi* are synonym species (Choleva *et al.*, 1991). Reasons for rejecting their proposed synonymy are addressed in a separate paper (Navas *et al.*, 1993). Preliminary phylogenetic analyses of *Longidorus* support these 32 species as a monophyletic group (Navas, unpublished). Collection sites for each species in native and agricultural areas provided an estimate of overall dispersal. Estimation of the centre or original point of the dispersal was desirable because it could correspond to the origin of a species. Selecting the midpoint of current distribution was an impractical approach to estimating the centre, because the distribution of a given species is frequently discontinuous. Two alternate comparative methods were used to estimate the centre of distribution, and both involved reducing the component due to expansion (apochoric component *sensu* Hennig, 1966) or dispersal, such as that recently influenced by man.

The first method was based on a proportionality index for each species in each CU. The proportionality index is represented as $I_{ij} = X_{ij}(100)/X_i(S_j)$ where X_{ij} is the number of recordings of each species in each CU, X_i is the total number of recordings of each species and S_j is the area of each CU. The proportionality indices (I_{ij}) for each CU region were calculated, I_{ij} 's were averaged for Euromediterranea, and values of I_{ij} that exceeded the Euromediterranean average were treated as significant centres for inclusion in biogeographical analysis. The second method selects values of I_{ij} that exceed the average of the proportionality index quartiles $(Q_3 - Q_1)/2$ where Q_3 is the value exceeded by 25% of the sample, and Q_1 is the value exceeding 25% of the sample.

It is hypothesized that the CU regions reflect historical patterns of geographic convergence and divergence which impacted distribution and evolution of a wide range of plant and animal species. The convergence-divergence between CUs and *Longidorus* species was demonstrated

TABLE II - Number of records of each species when present in more than one CU as well as total of records fitting species to the CU.

	So. Eur.	We. Med.	Ap. Di.	At. MEu	Ci. T.	M. Eur.	Eurb.	Holom	Ci.A.P.	Ci.A.T.	No. Med.	Trans.	Ea. Med.	Atl.	Total
1. <i>L. aetnaeus</i>					×										
2. <i>L. africanus</i>													×		
3. <i>L. apulus</i>		1	13												14
4. <i>L. attenuatus</i>	20			52	3	45		8			8				72
5. <i>L. belloii</i>															
6. <i>L. caespiticola</i>	(15)	10		73	2	28		4			4			53	89
7. <i>L. carpetanensis</i>														×	
8. <i>L. cohni</i>													×		
9. <i>L. congoensis</i>		×													
10. <i>L. cylindricaudatus</i>				5		5									5
11. <i>L. distinctus</i>	16					1		6	16		6				16
12. <i>L. elongatus</i>	(35)		7	215		109	78	7	9	7	7				277
13. <i>L. eridanicus</i>	(5)	(5)	5							5		5			5
14. <i>L. euonymus</i>	59		46	3	(11)	13		(56)		46	(34)	(20)			72
15. <i>L. fasciatus</i>		(1)	1		1					(1)		(1)			1
16. <i>L. globulicauda</i>														×	
17. <i>L. goodeyi</i>	(4)	1	(1)	93	(1)	22		1		(1)	1				97
18. <i>L. intermedius</i>	(15)	7	15	(14)		(14)		15		15		4			29
19. <i>L. iuglandis</i>	(1)		1					1		1	1	1			1
20. <i>L. latocephalus</i>									×						
21. <i>L. leptoccephalus</i>	3			89		49			2					79	96
22. <i>L. lusitanicus</i>														×	
23. <i>L. macrosoma</i>	38	(10)	1	70	1			9		1	13				75
24. <i>L. magnus</i>	(13)	(5)	13		(3)			12		13	(9)	1	1		13
25. <i>L. moesicus</i>	(48)	(32)	45		(13)				6	45	(45)	49	12		56
26. <i>L. nevesi</i>														×	
27. <i>L. picenus</i>	(9)		9					3		6	3				9
28. <i>L. protundorum</i>	35	5		35		21	1	2			1			(15)	53
29. <i>L. protae</i>	(2)	(2)			2			1			(2)	2			2
30. <i>L. proximus</i>						×									
31. <i>L. unedoi</i>		×													
32. <i>L. vineacola</i>	(6)			19		16			(3)		1			(6)	20

- × Species only present in one area
 Coincidence of significant values of two fitting criteria
 Significant values of $\frac{Q3 - Q1}{2}$

by the numerical approach (Castillo, 1988). The UPGMA clustering analysis algorithm, CLUSTAN package (1982), was applied to the *Longidorus* distribution matrix (Table II) as well as to the geographical overlap of CUs to produce comparable clustering patterns. Geographical overlap

was detected using the index of Margalef (1974; Table III). The biogeographical connections between the hypothesized centres of origin of each species were estimated by a graph executed by minimum spanning tree techniques (CLUSTAN package, 1982). Connective lines extending to

the tree root provide a testable hypothesis of phylogenetic patterns of speciation of *Longidorus* in Euromediterranea.

A phylogenetic hypothesis based on a matrix of classical quantitative and qualitative morphological characters of *Longidorus* was generated using parsimony as the optimizing criterion (PAUP program, version 2.4, Swofford, 1986). To tentatively infer character polarity, character states were compared with *Xiphinema*, a plausible outgroup of *Longidorus* (Coomans, 1985).

Traditional qualitative characters included were those of Hooper (1980) and Rey *et al.* (1988). Several multistate morphometric characters with wide ranges for each species was adapted from original descriptions for inclusion in the matrix. Interspecific differences among states of each morphometric character were statistically confirmed by discriminant analysis using SPSS statistical package (1975) to avoid inappropriate coding of continuous morphometric characters.

Results

Distribution and Geographic Matrices

Data were compiled for biogeographical analyses on two matrices. The first (Table II), showed the number of

recorded collection records of each species in each CU as well as the sum of recorded collections across all sites. This matrix was the basis for estimating the origin of each species. Ten species were recorded at only a single CU. The proportionality $Q_3-Q_1/2$ estimate of the origin generally was less restrictive than the first method of estimate based on the values of I_{ij} that exceeded the Euromediterranean average. Identity of the most reliable centre of origin was based on coincidence of results of the two methods. Each species associated with more than one area was graphically positioned at an equidistant geometric point. Species distribution centres were represented on a map (Fig. 2). Three fundamental distribution nuclei of species groups were resolved as Atlantic-Centroeuropean, Mediterranean, and primarily Iberian. Only three African or Southern Mediterranean species (*L. africanus*, *L. congoensis* and *L. cobnii*), are not clearly associated with these three nuclei.

A second matrix was compiled to show the area of each CU and the portion of the area that overlapped with each other CU (Table III). Sampling records of species were occasionally found in highly overlapping CUs such as 3 (Ap Di), 5 (Ci T), and 10 (Ci A. T.). In these cases the logical criteria for assignment was to record them in the single area in which they were most nearly central.

TABLE III - Total and overlapping surfaces of Chorological Units*.

CU's	Total surface	Chorological Units (CU's)**													
		So. Eur.	We. Med.	Ap. Di.	At. M. Eur.	Ci.T.	M. Eur.	Eurb.	Holom.	Ci.A.P.	Ci.A.T.	No.Me.	Trans	Ea. Med.	Atl.
So. Eur.	12.42	—	6.42	4.17	7.77	3.31	5.70	3.50	11.08	6.01	4.52	11.79	2.61	0.00	3.52
We. Med.	7.67		—	4.15	1.73	4.25	0.00	0.00	7.32	0.00	3.77	6.47	1.69	0.00	0.00
Ap. Di.	4.66			—	1.20	3.70	0.00	0.00	3.91	2.17	4.75	4.69	2.56	0.00	0.00
At. M. Eur.	9.48				—	1.29	6.21	4.02	3.60	3.61	1.25	5.07	0.00	0.00	7.08
Ci. T.	4.39					—	0.00	0.00	4.01	0.00	3.02	3.94	1.33	0.00	0.00
M. Eur.	12.26						—	2.93	0.00	6.18	0.00	0.00	0.00	0.00	3.95
Eurb.	11.14							—	0.00	0.00	0.00	0.00	0.00	0.00	1.37
Holom.	15.18								—	2.55	5.30	14.87	6.38	4.56	0.00
Ci.A.P.	7.85									—	3.69	0.06	0.00	0.00	0.00
Ci.A.T.	5.29										—	5.10	3.90	0.00	0.00
No. Med.	14.87											—	6.40	3.59	0.00
Trans.	8.03												—	2.26	0.00
*** Ea. Med.	37.80													—	0.00
Atl.	13.72														—

* Index of Margalef: $S_m = \frac{I^2}{A \times B}$ where I = surface area shared by A and B, A = surface area of A, B = surface area of B.

** See Figure 1 for location and corresponding numbers of CU's.

*** As there is no limit in the East, its surface is considered as an ellipsoid to be able to do the Cluster Analysis.

Cluster Analysis From Distribution and Geographic Matrices

The clustering patterns generated by UPGMA (Fig. 3) are useful to test the hypothesis of a major dispersal or expansion process in *Longidorus*, because if dispersal was not important there would be great similarity between the geographic and nematode-based cluster patterns. Results indicate great disparity between the two cluster patterns. Only CUs 1 (South Europe) and 8 (Holomediterranea) are concordant between the two clustering patterns. Comparisons between the clustering patterns of the two data sets indicate a relatively high level of geographic continuity and a relatively low level of similarity of *Longidorus* species distribution among CUs.

Distribution matrix graph analysis

Distribution matrix graph analyses were conducted with three data sets to assist in identifying species with the most plesiomorphic character states and sister groups based on geographic distribution. The data sets for comparisons included origins estimated by Iij that exceeded the Euromediterranean average (Fig. 4A), by $Q_3 - Q_1/2$ (Fig. 4B), and by estimates coincident with the two approaches (Fig. 4C). CUs 8 (Fig. 4A), as well as 7 and 11 (Fig. 4B) are transitional areas with diverse species whose origins generally do not fit to these areas by the proportionality indices indicated above. Consequently, dendrograms based on coincidence of origin data compare elimination of transitional CUs 8 and 11, with elimination of CUs 7, 8, and 11. When transitional areas are removed, the dendrograms are essentially identical. The dendrogram developed from the simplified matrix is thereby primarily controlled by endemic species, and indicates orientation toward the Atlantic where there is the greatest concentration of such endemic species (i.e. *L. carpetanensis*, *L. globulicauda*, *L. lusitanicus* and *L. nevesi*). The distribution graph does not establish which endemic species is most ancestral; rather, hypotheses of ancestry are tested by a morphologically-based cladogram congruent with the distribution graph.

Morphological data matrix

A matrix for cladistic analysis was developed from morphological data extracted from original descriptions of *Longidorus* (Table IV). *Xiphinema* outgroups were also included to infer polarity. Quantitative characters considered were female body length (L; 1), odontostyle length (7), odontophore length (8), and classical ratios a (2), b (3), c (4), c' (5), V (6), as well as distance of the oral aperture from the guide ring/width of lip region (11). Qualitative characters were the shape of the anterior region (9), the amphid pouch in lateral view (10), and the female tail (12).

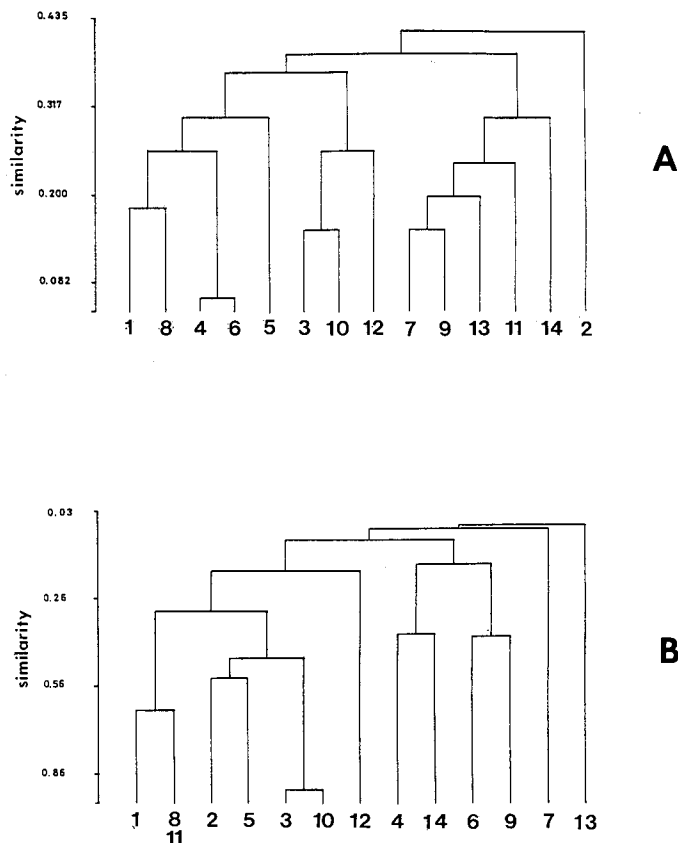


Fig. 3 - Comparison of faunistic and geographical similarity of the chorological units (CUs). A: Faunistic similarities among CUs based on presence or absence of *Longidorus* species (Table II). B: Geographical similarities among CUs based on the index of Margalef (1974) (Table III). Numbers represent CUs from Fig. 1.

Distinct character states of qualitative characters were entered into the matrix as described in the literature (Hooper, 1980; Rey *et al.*, 1988). Plotting maximum against minimum values of the 64 species accepted by Rey *et al.*, 1988, indicated continuous values for quantitative characters except for the most extreme values of V. Discriminant analysis was used to recognize greatest significant differences for coding character states of quantitative characters for the matrix (Table IV). Character states of distance of the oral aperture from the guide ring/width of the lip region follow Hooper (1980).

Several criteria were used to develop initial hypotheses of polarity for qualitative characters (Table IV). Polarity of lip region shape, amphid pouch shape, and oral aperture to guide ring distance/lip region width, in the absence of other criteria, were initially coded by the argument that widely distributed states are most often plesiomorphic

TABLE IV - Matrix of multistates characters. (See Table V for corresponding characters).

	Characters											
	1	2	3	4	5	6	7	8	9	10	11	12
1. <i>L. aetnaeus</i>	0	0	0	0	0	0	0	2	2	3	3	0
2. <i>L. africanus</i>	0	1	0	0	1	0	0	2	3	1	3	0
3. <i>L. apulus</i>	2	3	0	2	1	0	0	0	1	2	2	0
4. <i>L. attenuatus</i>	2	3	1	0	0	1	0	2	1	2	2	0
5. <i>L. belloi</i>	2	1	1	3	1	2	0	1	4	3	2	1
6. <i>L. caespiticola</i>	2	0	0	0	1	1	0	1	3	1	2	1
7. <i>L. carpetanensis</i>	0	1	0	0	0	0	0	2	1	2	1	0
8. <i>L. cobni</i>	2	3	1	2	1	0	0	0	2	1	2	0
9. <i>L. congoensis</i>	0	0	0	0	1	0	0	1	3	2	2	1
10. <i>L. cylindricaudatus</i>	1	1	0	1	1	0	2	0	3	2	3	0
11. <i>L. distinctus</i>	1	1	0	0	0	0	0	2	1	3	2	0
12. <i>L. elongatus</i>	1	1	0	0	1	1	0	1	2	1	2	0
13. <i>L. eridanicus</i>	1	1	0	2	1	0	3	0	2	1	3	1
14. <i>L. euonymus</i>	2	3	2	1	1	0	0	2	1	1	2	0
15. <i>L. fasciatus</i>	2	3	2	2	1	0	0	0	3	3	2	1
16. <i>L. globulicauda</i>	1	1	0	0	1	0	0	2	2	1	3	0
17. <i>L. goodeyi</i>	2	1	1	1	1	0	0	1	3	3	2	1
18. <i>L. intermedius</i>	0	0	0	0	1	0	0	2	2	2	3	0
19. <i>L. iuglandis</i>	2	0	0	2	1	2	0	0	3	2	2	1
20. <i>L. latocephalus</i>	1	3	0	0	0	0	0	2	1	1	3	0
21. <i>L. leptocephalus</i>	1	1	1	0	1	1	0	2	2	1	3	0
22. <i>L. lusitanicus</i>	2	1	1	3	1	1	0	2	1	3	2	0
23. <i>L. macrosoma</i>	3	2	1	2	1	1	2	1	4	1	2	1
24. <i>L. magnus</i>	3	0	1	2	1	0	0	1	3	3	2	1
25. <i>L. moesicus</i>	2	2	1	2	1	0	0	0	3	2	3	1
26. <i>L. nevesi</i>	2	1	1	3	1	1	2	0	3	2	2	0
27. <i>L. picenus</i>	2	0	0	2	1	0	2	0	3	2	2	1
28. <i>L. profundorum</i>	2	1	1	2	1	2	0	0	4	2	3	1
29. <i>L. protae</i>	2	3	1	2	1	0	0	2	1	2	2	0
30. <i>L. proximus</i>	2	2	1	2	1	0	0	2	2	1	2	1
31. <i>L. unedoi</i>	1	3	1	1	0	2	0	2	1	3	2	0
32. <i>L. vineacola</i>	2	3	1	2	1	0	0	2	1	2	2	1
Hypothetical Ancestor	0	0	0	0	0	0	0	0	1	1	2	0

Note: Excluded species are: *L. alveus* that has the same codification of *L. attenuatus*; *L. dunensis* which has the same codification as *L. protae*, except in its value of V which is in the limit between *L. attenuatus* (1) and *L. protae* (0); this species belongs to the *protae-attenuatus* group. *L. closelongatus* which was included by Dalmasso into the complex *elongatus* and has the same codification for ten characters with *L. protae*, for nine characters with *L. vineacola* and ten characters with *L. apulus*; it belongs to the monophyletic group erected from the node J of our cladogram. *L. kuiperi* because it shares codification with *L. cobni*, *L. apulus*, *L. vineacola*, and *L. fasciatus*. *L. major* which shares the same states for all characters with *L. magnus*, except a questionable difference in length of the odontophore. *L. juvenilis* because it shares the same states for all characters with *L. reneyii*, except for possible differences in the amphidial shape; it also shares the same states for all characters except V and amphidial shape with *L. laevicapitatus*; in addition, it would be the only "European" species with a very short odontostyle, it shares a synapomorphy (state 1 of odontostyle) with *L. laevicapitatus*, *L. reneyii*, *L. monile*, *L. paramonile*, *L. moniloides* and all non-Bulgarian populations (except a South African population) recorded as *L. pisi*. *L. pini* described in 1987 by Andres and Arias near the type locality and habitat of *L. carpetanensis*, shares with *L. carpetanensis* the codification for all characters except L and a; even the authors of the species did not consider it a year later in a paper about identification species of *Longidorus* (Rey *et al.*, 1988).

(Hecht and Edwards, 1977). Hypotheses of polarity of quantitative characters were also tested by comparison with outgroup *Xiphinema*. A state of such a character which is shared with the average of the character value for *Xiphinema* initially was treated as plesiomorphic within *Longidorus* (Fig. 5). Initial assignment of polarity of tail shape was problematic because values for this index in outgroup *Xiphinema* are outside the range of *Longidorus*. Similarly, polarity was less clearly established for odontostyle length, shape of anterior region, and shape of the lateral pouch.

Initial hypotheses of polarity (Table IV) suggest *L. aetnaeus*, *L. carpetanensis*, *L. distinctus*, and *L. latocephalus* as the species with the greatest complement of plesiomorphic character states. Hypotheses of the ancestral endemic species in Euromediterranea were tested by preliminary phylogenetic methods.

Phylogenetic inference

To test hypotheses of the *Longidorus* outgroup of all other Euromediterranean *Longidorus* species, tentative cladograms were generated using a hypothetical ancestor with ordered and unordered character options because the evolution of characters was unknown. Resulting consensus of the most parsimonious phylogenetic trees were congruent with graph analysis in supporting *L. carpetanensis* as an outgroup of all the other species. Qualitative characters were considered as unordered character options in two data sets (A and B). Odontostyle length was compared as ordered (data set B) and unordered (data set A) (Fig. 6). Alternately, a phylogenetic tree was generated using only the ordered character option in the matrix for all characters (Fig. 6C). *Longidorus caespiticola* is supported as an outgroup of two large monophyletic groups symbolized

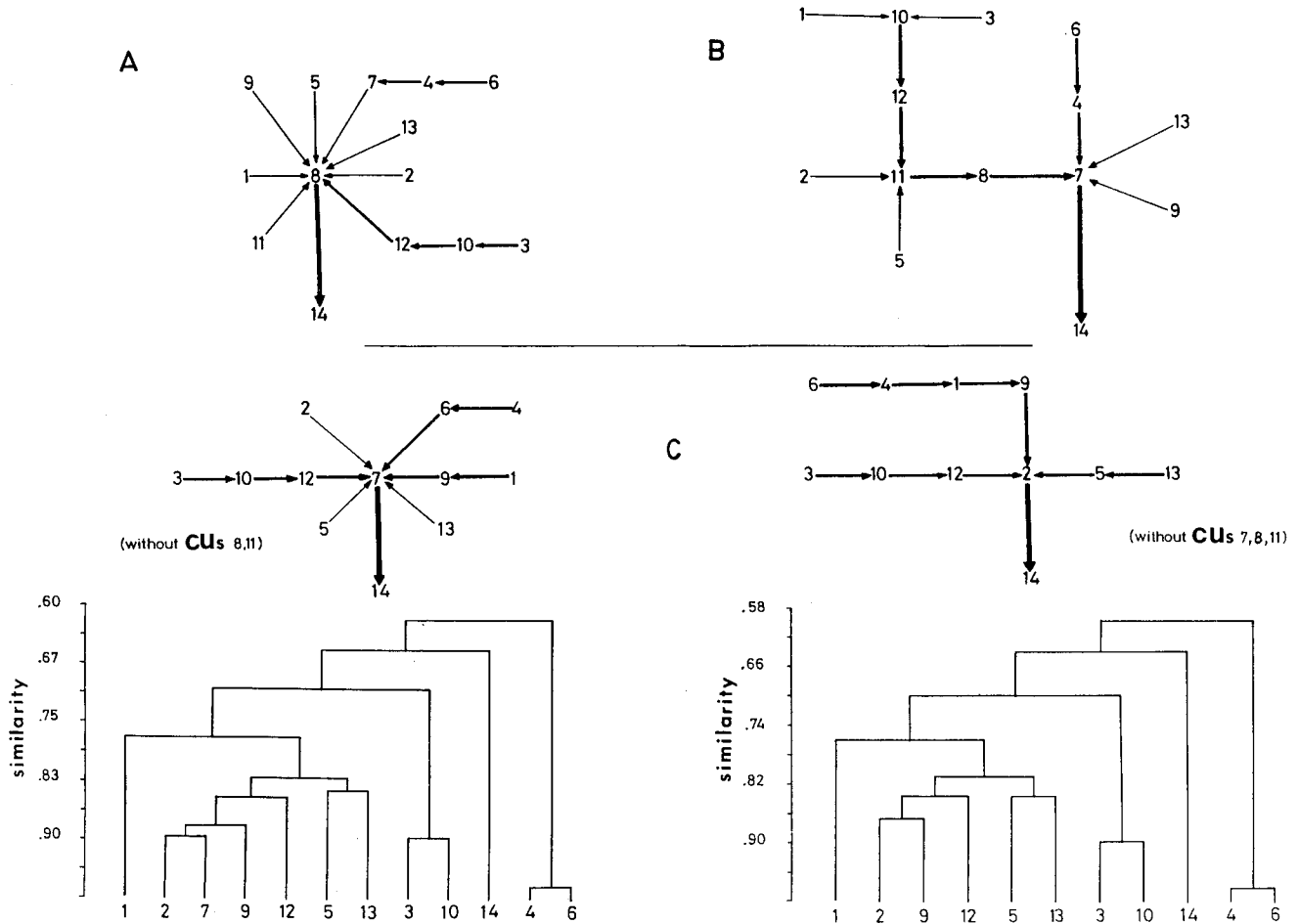


Fig. 4 - Graphs analysis among CUs A: according to the significant average of the Iij index of proportionality. B: according to the average of quartiles of Iij of the index of proportionality. C: graphs according to both criteria and clusters based on each of the graphs. Numbers of CUs are from Fig. 1.

by *X* and *Y* (*X* and *Y* are expanded to show species in Fig. 7A). Monophyly of *L. leptocephalus/L. elongatus/L. globulicauda/L. africanus* is indicated by data sets A and B and consensus AXB but *L. globulicauda* and *L. africanus* are excluded by data set C, and *L. globulicauda* by the consensus of AXBXC. Monophyly of the *L. caespiticola* group is further supported by a subsequent separate analysis of this region apart from all other species. Since this analysis agreed with the configuration of the same species in consensus AXB, this was selected for further testing (Fig. 7). The length of this parsimonious phylogenetic tree is 98 steps. The consistency index (C. I.) of 0.276 suggests a very high degree of homoplasy including a large number of parallelisms and reversals of states in a large number of characters (Table V). Each terminal branch was labeled geographically as an aid to infer the speciation process.

Evolutionary Tracks of Longidorus

The selected cladogram (Fig. 7) indicates main nodes of dichotomies and these are always geographically located between two plesiochoric components, whether considering the species with the largest complement of ancestral characters (nodes B, C, and D) or those with the largest complement of derived characters (nodes located among European, Iberian and Mediterranean species). Tracks always have an opposing orientation following East-West or North-South (Fig. 8).

The first (most ancestral) evolutionary event (node B) presupposes a West-East direction from an ancestor located in the North of the Mediterranean. This ancestor is supported as giving rise to *L. aetnaeus* and the typically Balkan species, *L. distinctus*, and *L. latocephalus*. There is little distance between node C which gives rise to *L. intermedius* and node D. Node D leads to the monophyletic sister group from node M including *L. globulicauda/L. leptocephalus/L. elongatus/L. africanus*, the first three species being of Atlantic-European distribution. The first species of "African" or Southern Mediterranean distribution arise from nodes E and M (*L. congoensis* and *L. africanus*). The Southern European ancestor at node G gives rise to two lines with a West-East direction involving a second Iberian (node I; ancestor of *L. belloii* and *L. lusitanicus*) and the last Balkan speciation (*L. moesicus*). The ancestor represented at node K defines North-South evolutionary lines including speciation of *L. macrosoma*, *L. goodeyi*, *L. profundorum*, *L. magnus* and *L. iuglandis*. While Iberian speciation occurs both from an ancestor represented at node I, speciation also occurs from the ancestor of *L. fasciatus* in the middle-east region of the Mediterranean basin. Excluding the eastern speciation of *L. cobni*, there is a convergence of two European lines from the ancestor at node 12 as well as that of *L. cobni*.

Discussion

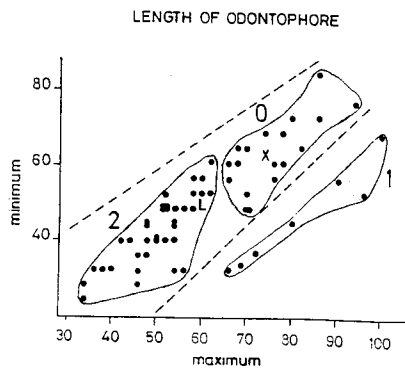
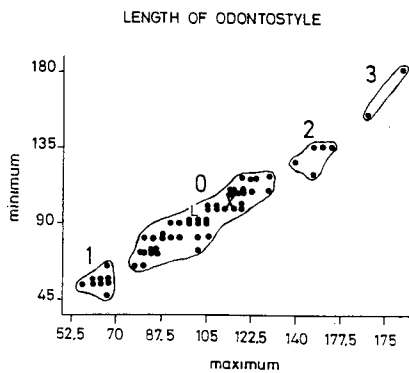
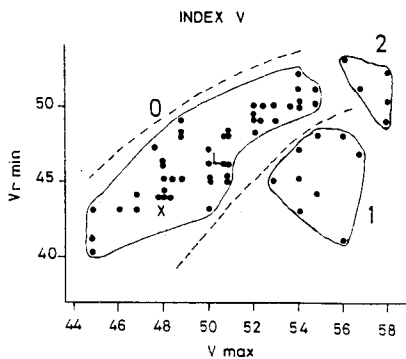
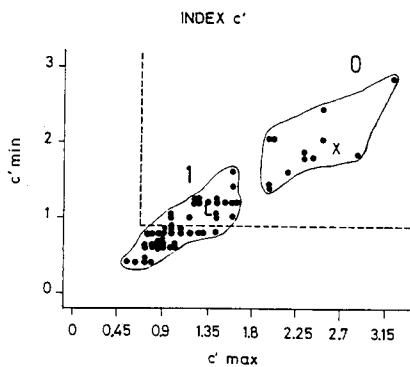
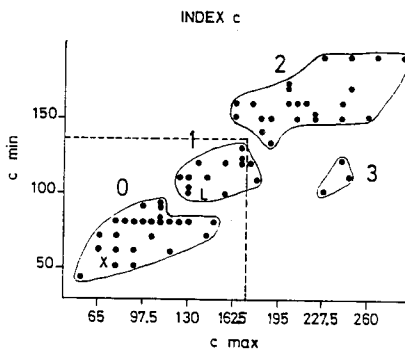
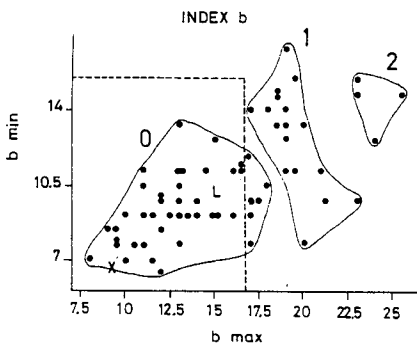
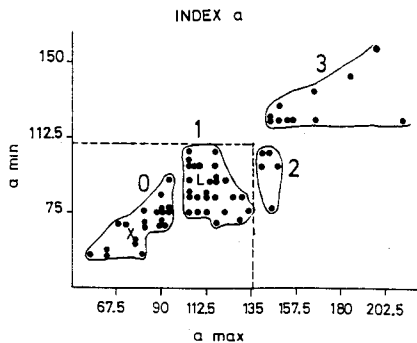
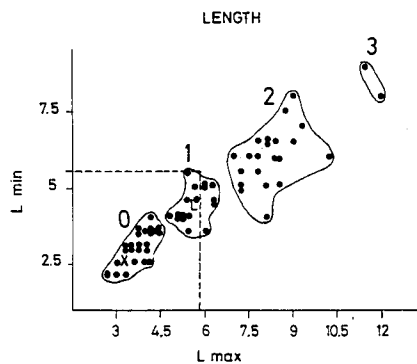
Nematodes, including *Longidorus*, may prove to be well suited for biogeographic investigations, particularly because they are less vagile than most organisms and specific ecological requirements restrict dispersion (Zullini, 1970, Yeates, 1979; Freckman, 1982; Navas *et al.*, 1988). In the light of conservative dispersal mechanisms, explanations for differences in morphology and geography-based patterns of *Longidorus* species must be sought in reconstructing the past. These differences are primarily explained by convergences and divergences of CUs and *Longidorus* species. In addition, we have demonstrated that these differences are affected by factors that may obscure the natural expansion process. Such effects can be minimized by correcting for the apochoric component and fitting the origin by proportionality methods.

Some incongruence in morphology-based and geography-based patterns may also reflect a paucity of reliable morphologic characters for phylogenetic analysis. Many classical diagnostic features are at the limits of LM, so that some coding could be based on misinterpretations; also, characters most informative for phylogenetic analysis may prove to differ from homoplasious classical characters which are nevertheless acceptable for species diagnosis. Furthermore, independence of characters, and particularly ratios, is questionable and may confound phylogenetic analyses. A large suite of reliable characters improves parsimony tests of homoplasy. The *Longidorus* phylogeny herein described, provides a hypothesis which is testable in the future by new species, new collections sites, and particularly by new character data from morphology and biochemistry.

Although inferences of historical biogeography must be based on current distribution of organisms, criteria can nevertheless be selected that favour a historical rather than an ecological interpretation (Kikawa and Pearse, 1969). In historical biogeography it is necessary to look for species-area relationships. Sauer (1990) observed that the same area may be occupied by several closely related species because divergent evolution may occur without geographic isolation. Since specific CUs may therefore not be evident from *Longidorus* distribution alone, we used CUs previously defined by distribution of a broad suite of other organisms (La Greca, 1964). Fitting present distribution with proportionality indices to hypothesize a centre of origin is used analytically (Page, 1987) to infer polarity of morphoclines (Presch, 1989) and outgroups for phylogenetic tree construction. We consider our approach of assigning polarity to morphometric character states acceptable from a Popperian premise, since the hypotheses derived from character analysis is falsifiable by subsequent revision of the original matrix with new characters. In the present proposed phylogeny of Euromediterranean spe-

TABLE V - Evolution of characters of Longidorus and reduced states according to their possible grouping.

<u>Character</u>	<u>Evolution</u>	<u>Parallelism</u>	<u>Possible grouping</u>
1 (L:body length)	$ \begin{array}{c} \overleftarrow{\hspace{1.5cm}} \\ 1 \leftarrow 0 \rightarrow 2 \rightarrow 3 \end{array} $	state 1	0-1
2(a:body length/body width)	$ \begin{array}{c} \overrightarrow{\hspace{1.5cm}} \\ 0 \rightleftarrows 1 \rightarrow 2 \rightleftarrows 3 \end{array} $	state 3	0-1, 2-3
3(b:body length/oesophagus length)	$0 \rightleftarrows 1 \rightarrow 2$	state 2	1-2
4(c:body length/tail length)	$ \begin{array}{c} \overleftarrow{\hspace{1.5cm}} \\ 0 \rightarrow 2 \rightarrow 1 \\ \quad \quad \quad \updownarrow \\ \quad \quad \quad 3 \end{array} $	state 1	0-1
5(c':tail length/tail width)	$0 \rightleftarrows 1$	—	—
6(V: % of vulva position)	$0 \rightleftarrows 1 \rightarrow 2$	state 2	1-2
7(Odontostyle length)	$0 \rightarrow 2 \rightarrow 3$	state 2	0-2
8(Odontophore length)	$ \begin{array}{c} \overrightarrow{\hspace{1.5cm}} \\ 0 \leftarrow 1 \rightleftarrows 2 \end{array} $	state 0	0-2
9(anterior region shape)	$ \begin{array}{c} \overleftarrow{\hspace{1.5cm}} \\ 1 \rightleftarrows 2 \rightleftarrows 3 \rightarrow 4 \end{array} $	states 2, 4	1-2, 3-4
10(Amphid shape)	$ \begin{array}{c} \overleftarrow{\hspace{1.5cm}} \\ 1 \leftarrow 2 \rightarrow 3 \end{array} $	states 1, 3	2-3
11(Oral aperture to guide ring distance/lip region width)	$1 \rightarrow 3 \rightleftarrows 2$	state 2	2-3
12(Tail shape)	$0 \rightleftarrows 1$	—	—



L average of *Longidorus*
 X average of *Xiphinema*
 - - - - limit of *Xiphinema*

Fig. 5 - Division of quantitative characters of *Longidorus* into states. Plotting of maximum versus minimum values of the taxonomically valid species.

cies, graph analysis (Page, 1987) was used to select one of four species as the most likely hypothetical outgroup. Although Page's (1987) graph analysis approach was criticized by Humphries and Seberg (1989), they recognized the value of the method for generating tracks of geographical patterns, particularly when information for alternate approaches to selecting an outgroup is unavailable.

Minimum spanning tree graphs consistently orient toward the Atlantic (area 14) where *L. carpetanensis*, the species with a large set of plesiomorphic states, is endemic, as might be predicted by the dispersalist model. Nelson

and Platnick (1981) consider the pleisomorphic condition of a taxon as primitive cosmopolitanism. The dispersalist model of biogeography, predicts that the once primitive cosmopolitanism would become restricted to a small area as a geographical relic (Simpson, 1944). The vicariance model, on the other hand, predicts that the primitive cosmopolitanism would persist as widespread. Both processes produce equal patterns but with different explanations (Briggs, 1992). More generally, it may only be assumed that where geographic areas and species distribution are congruent, they have a common or vicariant history.

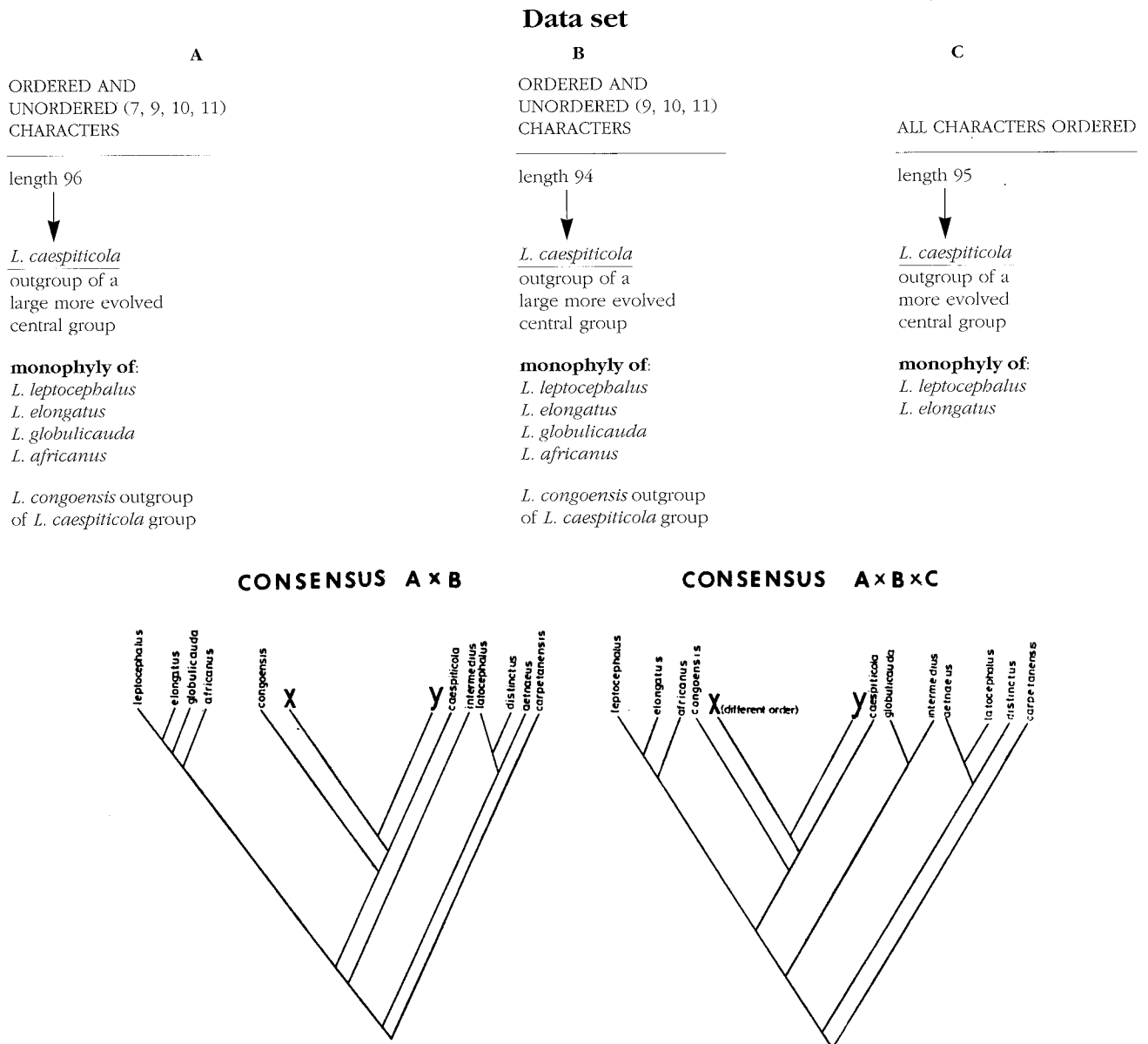


Fig. 6 - Scheme of the phylogenetic inference process.

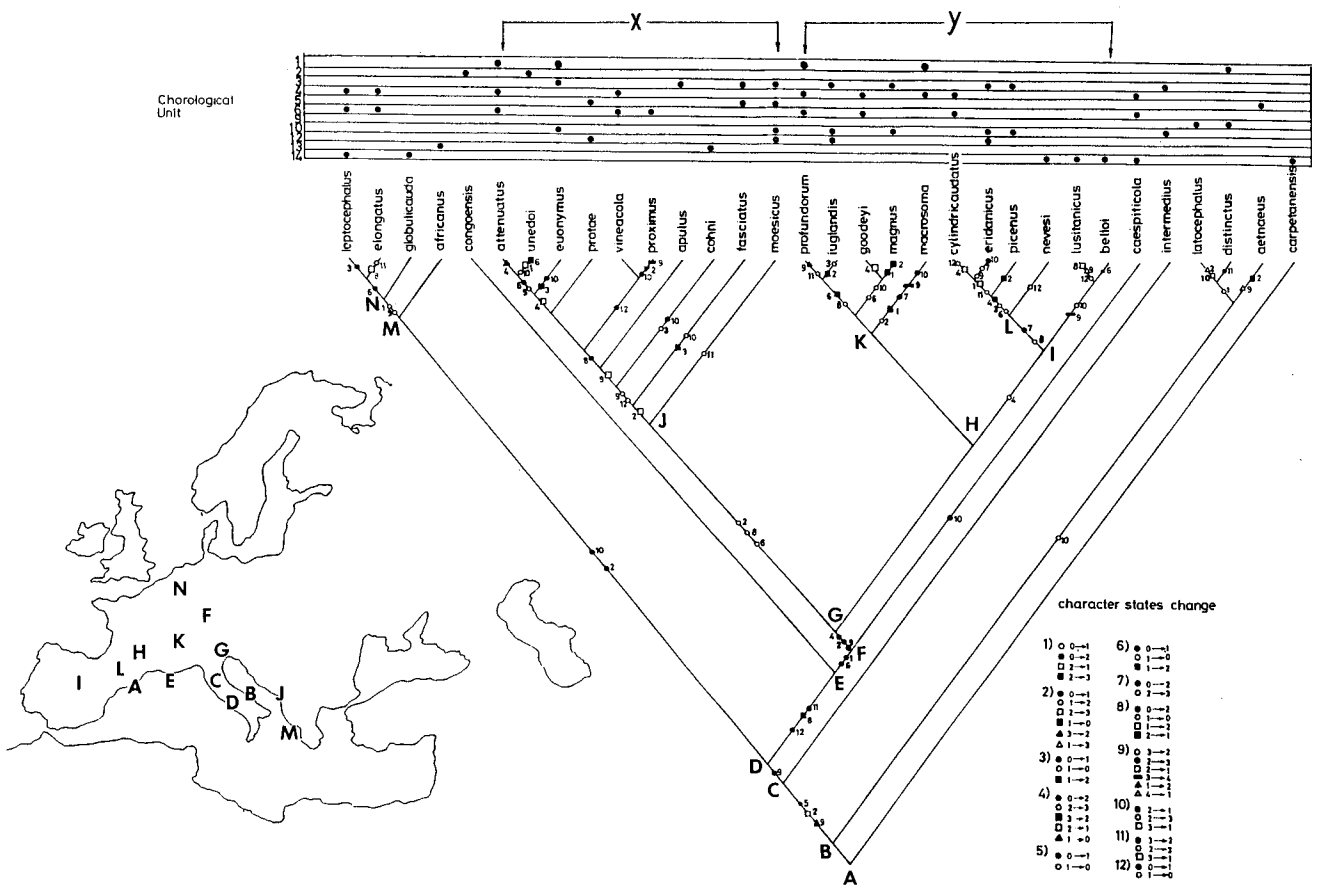


Fig. 7 - Proposal of the phylogenetic relationships in the genus *Longidorus* in Euromediterranea. In the map are located the main nodes of the cladogram according to the criteria of areas shared by sister groups.

Conversely, if congruence is weak, the hypothesis must be considered that the species and areas do not have a common history but only a relatively recent association since species dispersion (Mayden, 1988; Graham, 1990).

The phylogenetic hypothesis generated here by PAUP has a low consistency index (CI) which is predicted where there is a large number of taxa (Archie, 1989a, b). A low CI may also indicate homoplasy, including redundant or parallel evolution and, particularly in the present case, reversal of character states. An alternative explanation that assumptions of homology of extant characters are faulty or based on miscoding, is testable by new investigations of existing characters and discovery of new characters (Kluge, 1989; Baldwin and Schouest, 1990). Of particular interest to *Longidorus* is the concept of nonuniversal derived character states, in which true parallelism is potentially significant for phylogenetic inference (Sluys, 1989) at certain levels within the group under consideration. In fact, the repeated appearance of states in several taxa of an ingroup is used to support the hypotheses of mono-

phyly of the ingroup as suggested by the "underlying synapomorphy" of Saether (1983), the "unique inside parallels" of Brundin (1976) and the "non universal derived character states" of Cantino (1985). Sober (1988) considers dispersion and extinction as the conceptual correspondence to homoplasy: both may confound phylogenetic inference. Parsimony guides us toward preference for hypotheses that minimize such assumptions.

Biogeographic and phylogenetic data suggest both vicariant and dispersalist speciation of European species of *Longidorus*. The mosaic pattern of distribution of the two largest monophyletic groups (X and Y) as well as the *L. leptocephalus/L. elongatus/L. globulicauda* group suggest major dispersalist speciation events originating from the same evolutionary level at nodes F and N of the cladogram (Fig. 7 and 8). This conclusion is supported by geographic distribution which suggests a convergence of species at these nodes. In addition to dispersalist speciation, some evolutionary tracks may indicate a vicariant process at origins more ancient than nodes F and N (Fig. 9),

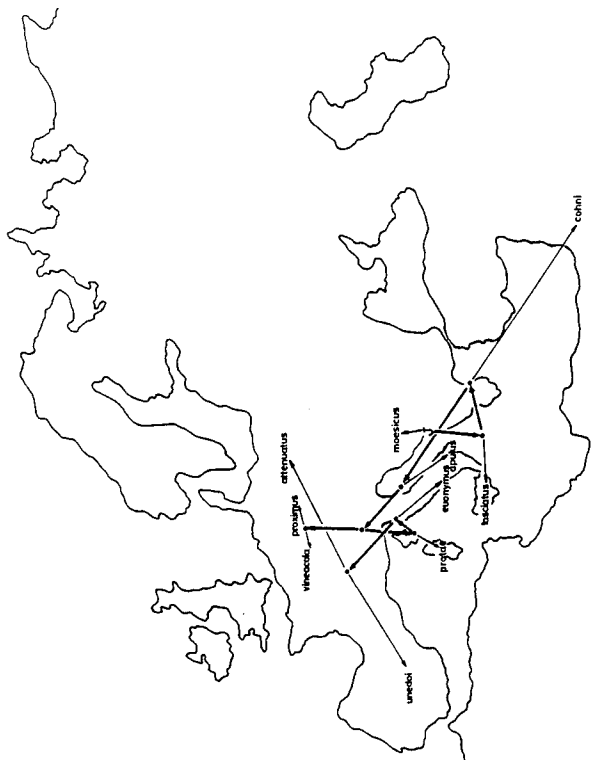
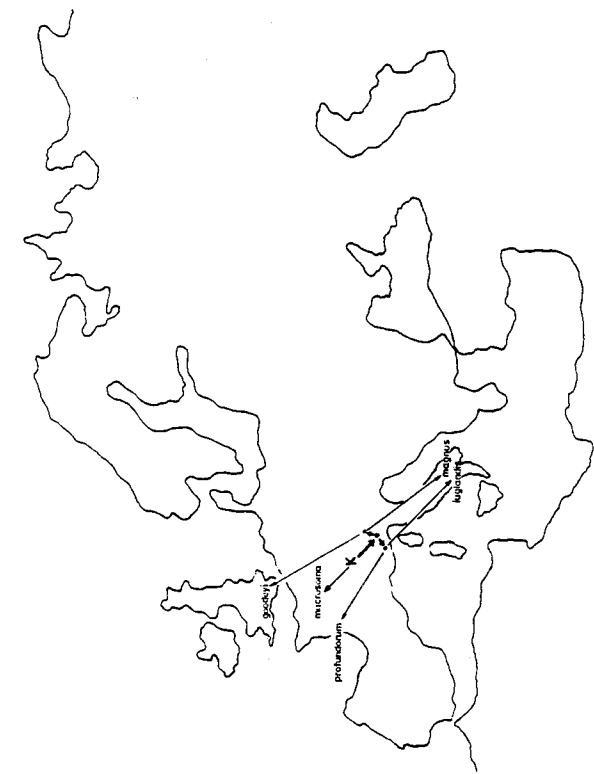
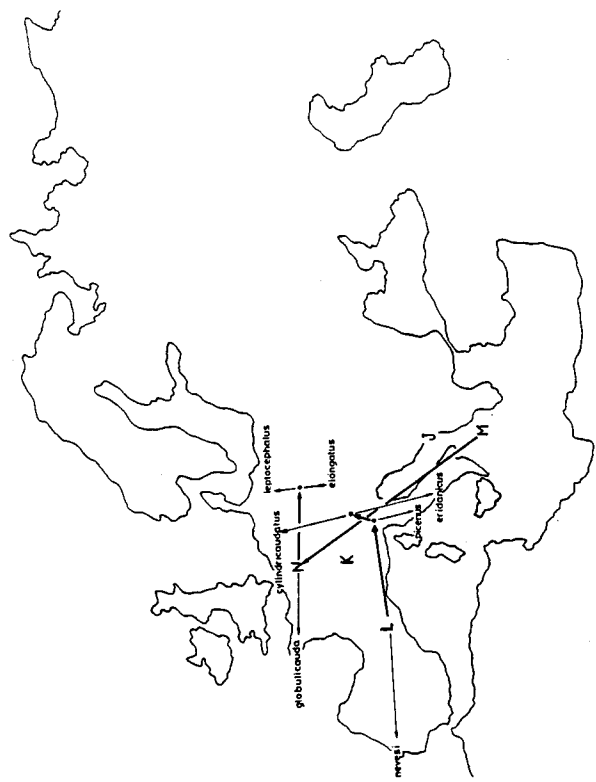


Fig. 8 - Evolutionary tracks of *Longidorus* in the Euromediterranea. Letters are the main nodes of cladogram of Fig. 7.



Fig. 9 - Evolutionary lines which connect areas in the first speciation event based on shared areas of the cladogram. Letters are the main nodes of cladogram of Fig. 7.

including separation at nodes B, C, D, E, and M. In *Longidorus* vicariant species are those primarily characterized by sets of pleisomorphic states, including *L. latocephalus*, *L. distinctus*, and *L. aetnaeus*. These species are clearly geographically separated by their presence or absence in CUs 5 or 9 (Figs. 9). This orientation of the evolutionary tracks is predicted by the complex geological history of central Mediterranean (Rögl and Steiniger, 1983). The West-East orientation of tracks from nodes M and the location of nodes F from E (Figs. 8 and 9), approximates to the southern boundary of glaciation (Pomerol, 1973). After glaciation a plausible hypothesis is that founder species *L. intermedius* (C), *L. africanus* (M) and *L. congoensis* (E) were the origin of dispersive speciation throughout much of Euromediterranea (Fig. 8). Initial vicariant speciation, followed by subsequent evolutionary hybridization, is

common in other edaphic groups (Coates, 1989a, b; Stace, 1989) and may result in a high degree of dispersal speciation as observed in *Longidorus*. This pattern of speciation could explain the high degree of homoplasy. It could also explain the observation that the majority of *Longidorus* species are polyphyletic *sensu* Farris (1974) and Platnick (1977).

Our results show that vicariant biogeography can resolve some aspects of the current pattern of *Longidorus* distribution and speciation origin, but that present data suggest a dispersalist model as a primary explanation for large groups of *Longidorus* species in Euromediterranea. Oosterbroek and Arntzen (1992) reinforces our views on first Iberian speciation, central Mediterranean nodes (lineages), Balkan speciation and vicariant and dispersalist models. Biogeographic studies on insects of the Neartic

Region led to similar conclusions that vicariance alone cannot explain current patterns of species (Noonan, 1988).

The authors appreciate the critical review of the manuscript by Dr. S. A. Gardner, and the valuable suggestions on an earlier draft by Professor A. V. Coomans. This work received financial support from the DGICYT (Ministerio de Educación y Ciencia, Spain).

Literature cited

- ALPHEY T. J. W. and TAYLOR C. E., (eds.), 1986. European Atlas of the *Longidoridae* and *Trichodoridae*, Invergowrie, Dundee: EPPNS, 123 pp.
- ARCHIE J. W., 1989a. Homoplasmy excess ratios: New indices for measuring homoplasmy in phylogenetic studies and a critique of the consistency index. *Syst. Zool.*, 38: 253-269.
- ARCHIE J. W., 1989b. A randomization test for phylogenetic information in systematic data. *Syst. Zool.*, 38: 239-252.
- BALDWIN J. G. and SCHOUEST L. P. Jr., 1990. Comparative detailed morphology of the *Heteroderinae* Filip-ev and Schuurmans Stekhoven, *sensu* Luc *et al.* (1988): Phylogenetic systematics and revised classification. *Syst. Parasitol.*, 15: 81-106.
- BLONDEL J., 1987. From biogeography to life history theory: A multithematic approach illustrated by the biogeography of vertebrates. *J. Biogeography*, 14: 404-422.
- BRIGGS J. C., 1991. Historical biogeography: The pedagogical problem. *J. Biogeography*: 18: 3-6.
- BROWN D. J. F. and TAYLOR C. E., 1987. Comments on the occurrence and geographical distribution of Longidorid nematodes in Europe and Mediterranean Region. *Nematol. mediterr.*, 15: 333-373.
- BROWN D. J. F., TAYLOR C. E., CHOLEVA B. and ROMANENKO N. D., 1990. The occurrence of *Longidoridae* (Nematoda: Dorylaimida) in Western USSR with further comments on Longidorid nematodes in Europe and the Mediterranean Basin. *Nematol. mediterr.*, 18: 199-207.
- BRUNDIN L., 1976. A neocomian chironomid and *Podominae-Aphroentinae* (Diptera) in the light of phylogenetics and biogeography. *Zool. Scr.*, 5: 139-160.
- CANTINO P. D., 1985. Phylogenetic inference from non-universal derived character states. *Syst. Bot.*, 10: 119-122.
- CASTILLO M., 1988. Another approach to the world biogeography of the families of inland fishes. *Syst. Zool.*, 37: 34-46.
- CHOLEVA B., PENEVA V. and BROWN D. J. F., 1991. *Longidorus latocephalus* Lamberti; Choleva & Agostinelli, 1983 a junior synonym of *L. pisi* Edward, Misra & Singh, 1964 (Nematoda: Dorylaimida). *Revue Nematol.*, 14: 505-509.
- CLUSTAN (Third Edition), 1982. (Wishart D., Editor) Program Library Unit, Edinburg University, 177 pp.
- COATES K. A., 1989a. Phylogeny and Origins of Enchytraeidae. *Hydrobiologia*, 180: 17-33.
- COATES K. A., 1989b. Preliminary investigation of hybridation/reticulate evolution in *Guaranidrilus* (Enchytraeidae: Oligochaeta). *Hydrobiologia*, 180: 35-45.
- COOMANS A., 1985. A phylogenetics approach to the classification of the Longidoridae (Nematoda: Dorylaimida). *Ag. Ecosys. and Environn.*, 12: 335-354.
- CRAW R., 1988. Continuing the synthesis between panbiogeography, phylogenetic systematics and geology as illustrated by empirical studies on the biogeography of New Zealand and Chatham islands. *Syst. Zool.*, 33: 291-310.
- DOADRIO I., 1988. Delimitation of areas in the Iberian Peninsula on the basis of freshwater fishes. *Bon. Zool. Beitr.*, 39: 115-118.
- FARRIS J. S., 1974. Formal definitions of paraphyly and polyphyly. *Syst. Zool.*, 23: 548-554.
- FERRIS V. R., 1983. Phylogeny, historical biogeography and the species concept in soil nematodes. *In: Concepts in Nematode Systematics*. Ed. by A. R. Stone, H. M. Platt and L. F. Khalil: 143-161. Academic Press. London, New York.
- FERRIS V. R., GOSECO C. G. and FERRIS J. M., 1976. Biogeography of freeliving soil nematodes from the perspective of plate tectonics. *Science*, 193: 508-510.
- FRAILE A. and GARCIA-ARENAL F., 1990. A classification of Tobamoviruses based on comparisons among their 126K proteins. *J. Gen. Virology*, 71: 2223-2228.
- FRECKMAN D. W. (editor), 1982. *Nematodes in Soil Ecosystems*. University of Texas Press. Austin. 206 pp.
- GREHAM J., 1990. Panbiogeography: Beyond dispersal versus vicariance. *J. Biogeography*, 17: 99-101.
- HECHT M. K. and EDWARDS J. L., 1977. The methodology of phylogenetic inference above the species level. *In: Major Patterns in Vertebrate Evolution*. Ed. by M. K. Hecht, P. C. Goodey, and B. M. Hecht: 3-51. Plenum Press. New York, London.
- HENNIG W., 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana. Chicago. London. 263 pp.
- HOOPER D. J., 1980; "Lattice" for identification of *Longidorus* species. Rothamsted Experimental Station, 5 pp.
- HUMPHRIES C. J. and SEBERG O., 1989. Graphics and generalized tracks: Some comments on methods. *Syst. Zool.*, 38: 69-76.
- KLUGE A., 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Syst. Zool.*, 38: 7-25.
- KIKKAWA J. and PEARSE J., 1969. Geographical distribution of land birds in Australia: A numerical analysis. *Australian J. of Zool.*, 17: 821-840.
- LA GRECA M., 1964. La categoria corologica degli elementi faunistici italiani. *Mem. Soc. Ent. Ital.*, 43: 147-165.
- LIEBHERR J. K., 1988. General patterns in West Indian insects, and a graphical biogeographic analysis of some circum-Caribbean *Platynus* beetles (Carabidae). *Syst. Zool.*, 37: 385-409.
- LORENZEN S., 1981. Entwurf eines phylogenetischen System der freilebenden Nematoden. Ed. by S. A. Gerlach and A. Gaertner. *Veröff. Inst. Meeresforsch. Bremerh. suppl.* 7, Bremen, 472 pp.
- MARGALEF R., 1974. *Ecologia*. Barcelona: Editorial Omega, 951 pp.
- MAYDEN R. L., 1988. Vicariance biogeography, parsimony and evolution in North American freshwater fishes. *Syst. Zool.*, 37: 329-355.
- NAVAS A., BELLO A. and ARIAS M., 1988. Ecology and potential distribution of *Xiphinema diversicaudatum* and *X. pachtaicum* (Nematoda: Longidoridae) in continental Spain. *Nematologica*, 38: 314-334.
- NAVAS A., ANDRES M. F. and ARIAS M., 1990. Biogeography of *Longidoridae* in the EuroMediterranean area. *Nematol. mediterr.*, 18: 103-112.
- NAVAS A., BALDWIN J. and LAMBERTI F., 1993. Contributions to the taxonomy status of *Longidorus latocephalus* Lamberti, Choleva & Agostinelli, 1983 and *Longidorus pisi* Edward, Misra & Singh, 1964 (Nematoda: Longidoridae) *Nematol. mediterr.*, 21: 117-122.
- NELSON G. and PLATNIK N. I., 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press. New York. 567 pp.
- NOONAN G. R., 1988. Biogeography of North American and Mexican insects: A critique of vicariance biogeography. *Syst. Zool.*, 36: 366-384.

- OOSTERBROEK P. and ARNTZEN J. W., 1992. Area-cladograms of circum-mediterranean taxa in relation to Mediterranean palaeogeography. *J. Biogeography*, 19: 3-20.
- PAGE R. D. M., 1987. Graphs and generalized tracks: Quantifying Croizat's panbiogeography. *Syst. Zool.*, 36: 1-17.
- PLATNIK N. I., 1977. Paraphyletic and polyphyletic groups. *Syst. Zool.*, 26: 195-200.
- PLATNIK N. I. and NELSON G., 1978. A method of analysis for historical biogeography. *Syst. Zool.*, 27: 1-16.
- POMEROL CH., 1973. *Stratigraphie et Paleogeographie: Ere Cenozoique (Tertiaria et Quaternarie)*. Doin Editeurs, Paris, 269 pp.
- PRESCH W., 1989. Systematics and Science: A Comment. *Syst. Zool.*, 38: 181-189.
- PROCTER D. L. C., 1984. Towards a biogeography of free-living soil nematodes. I. Changing species richness, diversity and densities with changing latitude. *J. Biogeography*, 11: 103-117.
- RAPOPORT E. H., 1982. *Aerography: Geographical strategies of species*. Pergamon Press., London, 269 pp.
- REY J. M., ANDRES M. F. and ARIAS M., 1988. A computer method for identifying nematode species. 1. Genus *Longidorus* (Nematoda: Longidoridae). *Revue Nematol.*, 11: 129-135.
- RODRIGUEZ-CEREZO E., MOYA A. and GARCIA-ARENAL F., 1989. Variability and evolution of the plant RNA virus pepper mild mottle virus. *J. Virology*, 63: 2198-2203.
- RÖGL VON F. and STEINIGER F. F., 1983. Vom Zerfall der Tethys zu Mediterran und Paratethys. Die neogene Palaogeographie und palinspastic des Zirkm-mediterranen Raumes. *Ann. Naturhist. Mus. Wien*, 85 A: 135-163.
- SAETHER O. A., 1983. The canalized evolutionary potential: Inconsistencies in phylogenetic reasoning. *Syst. Zool.*, 32: 343-359.
- SANCHIZ B., 1981. Aportes al método de delimitación de regiones en biogeografía histórica. *In: Colquio sobre Ecología y Biogeografía*. Ed. by SEEB: 224-243. Guadalajara, Spain.
- SAUER J. D., 1990. Allopatric speciation: Deduced but not detected. *J. Biogeography*, 17: 1-3.
- SIMPSON G. G., 1944. *Tempo and Mode in Evolution*. Columbia University Press. New York. Reprint (1984), 237 pp.
- SLUYS R., 1989. Rampant parallelism: An appraisal of the use of non-universal character states in phylogenetic reconstruction. *Syst. Zool.*, 38: 350-370.
- SOBER E., 1988. The conceptual relationship of cladistic phylogenetics and vicariance biogeography. *Syst. Zool.*, 37: 245-253.
- SPSS: Statistical Package for the Social Sciences (Nie N. H. and others). 2d ed., 1975. McGraw Hill. New York. 675 pp.
- STACE C. A., 1989. Dispersal versus vicariance - no contest. *J. Biogeography*, 16: 201-202.
- SWOFFORD D. L., 1986. Phylogenetic Analysis Using Parsimony. (User Manual. Version 2.4). Illinois Natural History Survey, 87 pp.
- VINGIGUERRA M. T., 1987. A new classification of *Actinolaimoidea* Thorne, 1939, using a cladistic approach. *Nematologica*, 33: 251-277.
- WELTZIEN H. G., 1972. Geophytopathology. *Ann. Rev. Phytopathol.*, 10: 277-298.
- WILEY E. O., 1987. Methods in vicariance biogeography. *In: Systematics and Evolution: A Matter of Diversity*. Ed. by P. Hovenkamp: 283-306. Institute of Systematic Botany, Utrecht.
- YEATES G. W., 1979. Soil nematodes in terrestrial ecosystems. *J. Nematol.*, 11: 213-229.
- ZANDEE M. and ROOS M. C., 1987. Component-compatibility in historical biogeography. *Cladistics*, 3: 305-332.
- ZULLINI A., 1970. *Ecologia dei nematodi del suolo*. *Ist. Lomb. Accad. Sci. Lett. Rendic. i Sci. Biolog. Med. B.*, 26: 289-380.