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Delimitation of areas in the Iberian Peninsula on the basis of freshwater fishes

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Abstract. In the present study a regionalitation of the Iberian Peninsula has been done on the basis of freshwater fish distributions. Their dispersion is evaluated and several methods, till now only used in taxonomy, are employed. Two main regions are defined: the northern Iberian region, constituted by the basins of the Ebro river, Cantabrian watershed, Catalonia and the Cenia; and the southern Iberian region that includes the other hydrographic basins in the Iberian Peninsula. Other subregions inside these main regions are defined. This hypothesis has been contrasted with freshwater fish phylogeny and paleogeographic knowledge of the Iberian Peninsula.

Key words. Biogeography, Iberian Peninsula, freshwater fishes, Cyprinidae, Cobitidae, Homalopteridae, chorology.

Introduction

Delimitation of areas is considered important for scientific historical biogeography because it facilitates comparison of relationships between areas using paleogeographic and evolutionary data, such as phylogeny of the organisms that inhabit them.

An attempt has been made to study and define areas in the Iberian Peninsula on the basis of freshwater fish distributions. Most authors (Arevalo, 1929; Lozano, 1952; Illies, 1978) have not considered the different types of dispersion of the fish groups constituting the Iberian ichthyofauna.

Method

A two-part method was employed: descriptive (chorology) and interpretative biogeography.

Descriptive method

The distribution of the 25 Cyprinidae, Cobitidae and Homalopteridae family taxa known in the Iberian Peninsula was analyzed (Doadrio, 1981; Doadrio et al., 1980; personal unpublished data) (see table 1). The *Cyprinus*, *Carassius*, *Tinca* and *Gobio* genera were excluded because they are assumed to have been artificially introduced.

The present distribution of *Phoxinus phoxinus* L. was included, except for the Duero river basin where the species has been recently introduced.

59 hydrographic basins were studied, but only 44 figure in the results because 15 had identical fauna to basins already included. They are Deva = Lastras; Miera = Pas, Nansa, Cares, Sella, Narcea and Navia; Eo = Masma, Oro, Sor, Eume, and Donas; Limia = Cave and Ave; Barbate = Guadalete. In the absence of precise theoretical criteria, the hydrographic basins Blondel (1979) describes by region, were used to define operative biogeographic units (OBU sensu Sanchiz, 1981). The use of hydrographic basins is fairly objective since they have welldefined geographical limits which fluvial fish rarely leave under natural circumstances. Moreover, this type of geographic entity has a historical basis; in the Iberian Peninsula, the hydrographic basins remained separated because no canals connected them, as occurs in other European countries.

Two of the largest basins in the Iberian Peninsula were divided into sections on the basis of faunistic differences, corroborating to a certain degree the identity of the fluvial basins as OBUS. The Tajo River was divided into two sections corresponding to the tributaries on its right and left banks. Three sections were established in the Duero river: the Duero in Portugal, from the mouth to the Spanish border; south-east of the Duero, between the Spanish border and the City of Zamora; and the rest of the fluvial basin.

True distribution of the organisms was modified by maximally reducing apochories. The use whenever possible, of the species areas of origin was considered appropriate. Likewise, plesiochories were sought using the methods proposed by Sanchiz (1981).

Interpretative methodology

The areas were phenetically delimited by faunistic similarities and their connections were evaluated by applying the vicariate method first proposed by Croizat (1958) and Croizat et al. (1974) and later used by Platnick (1976) and Rosen (1975, 1978). Cladograms were made to facilitate calculation of relations between zones. This calculation was done by applying methods usually used for phylogenetic evaluation, such as the Camin-Sokal parsimony method and the Dollo and Wagner methods.

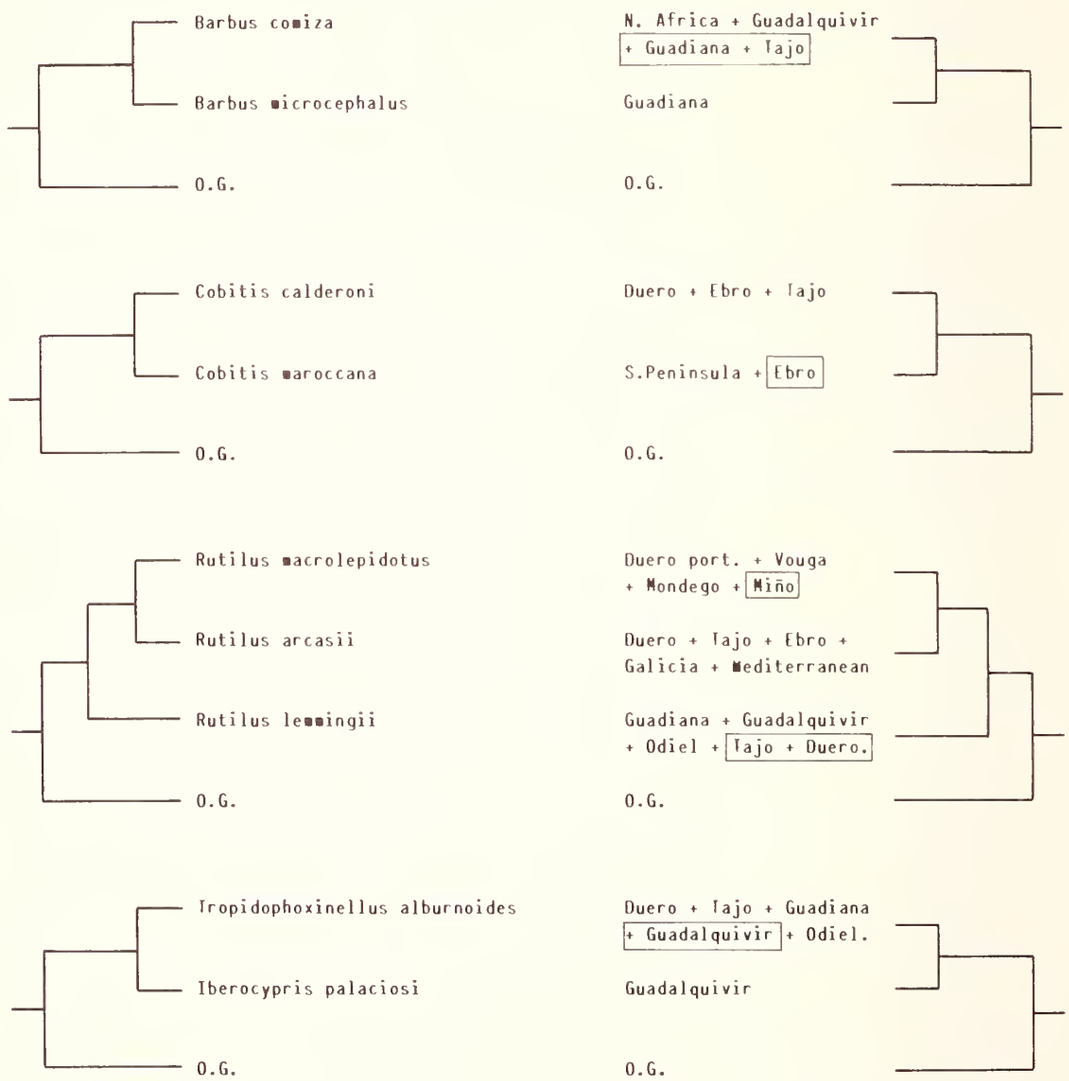

Fig. 1: Reduction of apochories after Sanchiz (1981). A = Hypothesis of relationships between the different taxa. B = Real distributions. Encircled areas have been dropped by apochoric reduction. O. G. = Outgroup.

Results

Descriptive biogeography

The real areas occupied by the freshwater fish taxa studied can be seen in table 1.

These areas were modified following the criteria of Sanchiz (1981): Sympatry with the sister group (see figure 1).

The transformed distributions of the 25 taxa studied are shown in table 2.

Interpretative biogeography

Camin-Sokal Method

For modern taxa distributions (fig. 2)

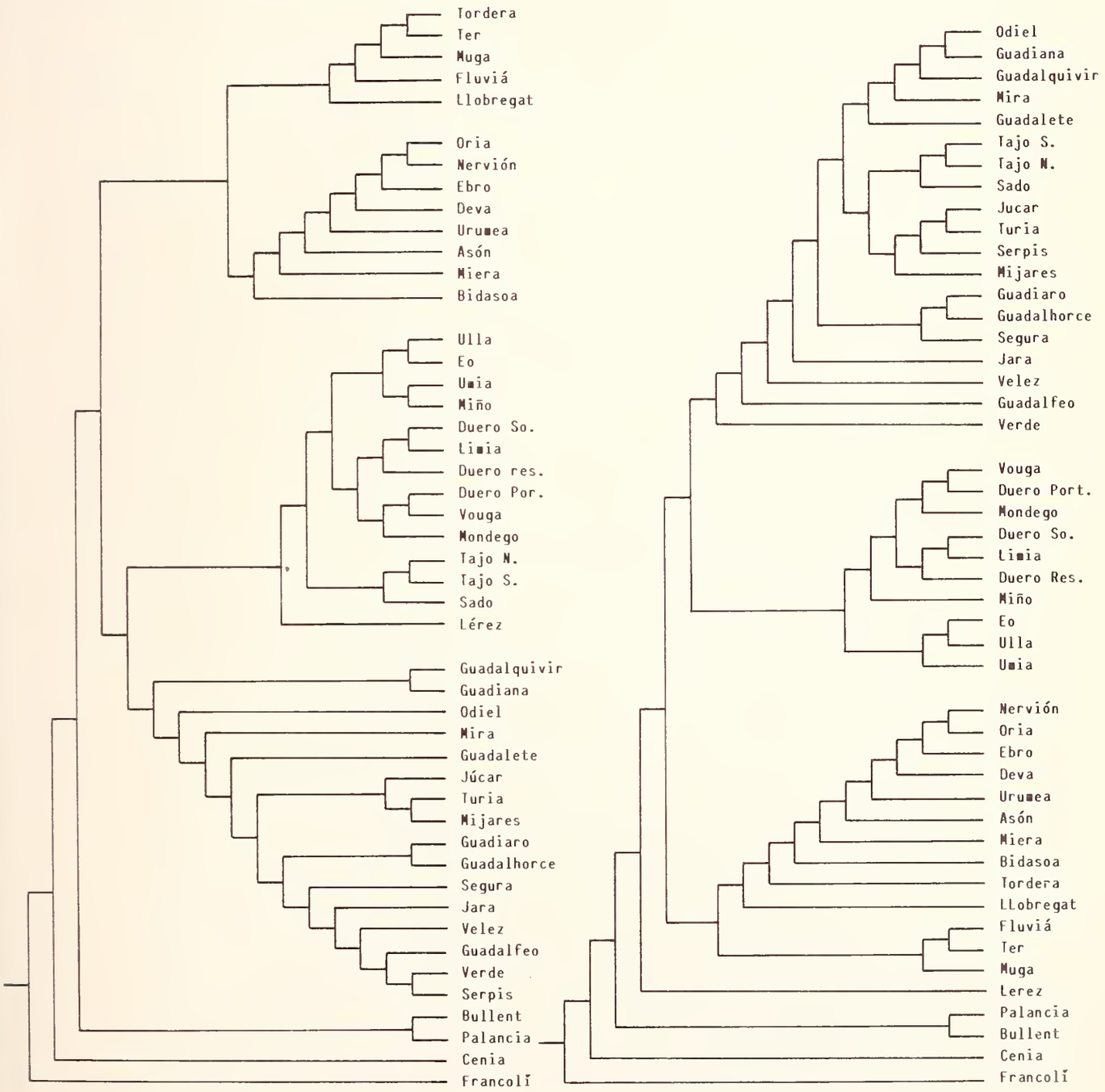

Fig. 2 (left side): Camin-Sokal clustering for real distributions.

Fig. 3: Camin-Sokal clustering for distributions modified by apochoric reduction.

Three large regions were defined:

1. Fluvial basins of Catalonia, Cantabrian watershed and the Ebro.
2. Galician fluvial basins, Duero, Tajo, Sado and Portuguese basins.
3. Fluvial basins of the southern Iberian Peninsula.

In the first region, two large groups should be differentiated: the Catalonian basins, and the Ebro and Cantabrian watershed basins.

In the second region, three subregions or sectors were separated:

a) The basins of Galicia.
b) Duero and Portuguese basins.
c) Tajo and Sado basins.

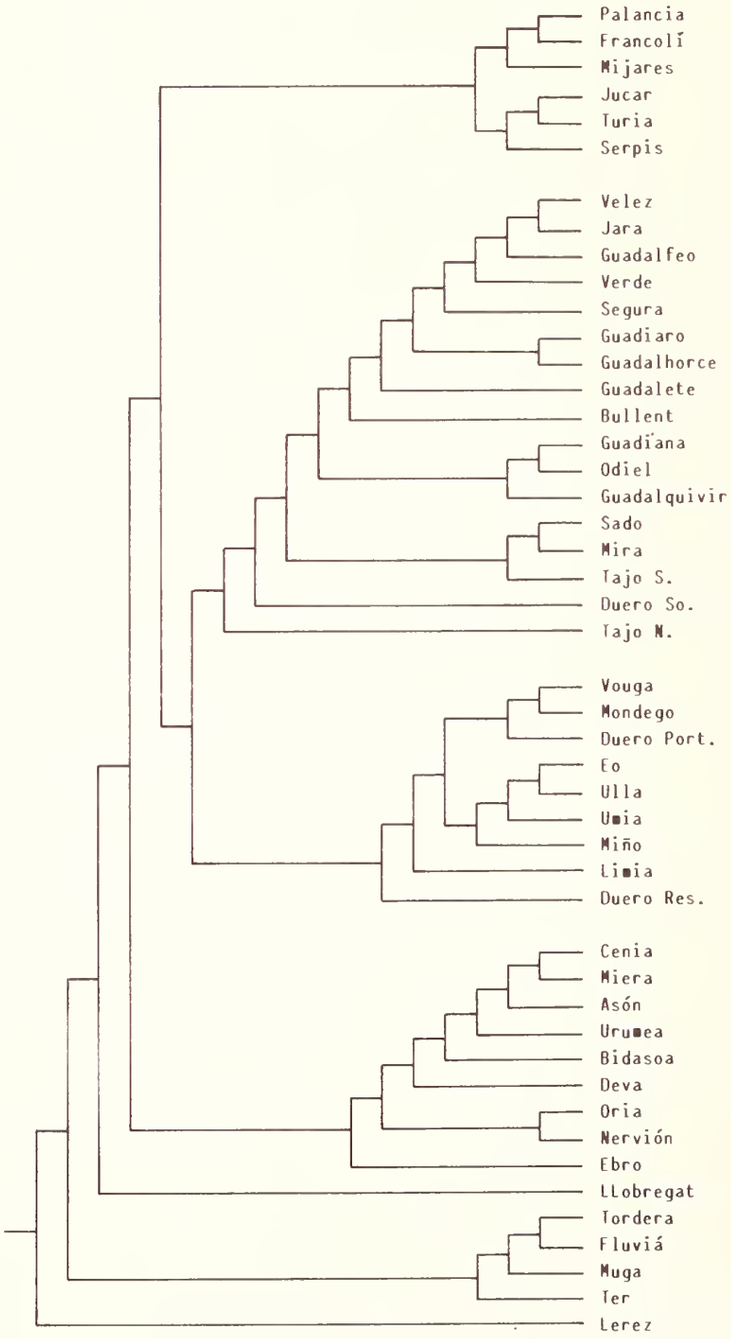

Fig. 4: Dollo clustering for real distributions.

Areas transformed by apochoric reduction (fig. 3)

There were three major regions:

1. Fluvial basins of Catalonia, the Cantabrian watershed and the Ebro.

Within this region, two subregions or sectors similar to those described in the previous section were discerned: The Fluvia, Ter and Muga rivers and the rivers of the Cantabrian mountains, the Ebro and the Llobregat and Tordera rivers of Catalonia.

2. Duero, Portuguese basins and the rivers of Galicia.

Two subregions were found in this region: the Duero, Miño and Portuguese basins, and the rest of the Galician basins.

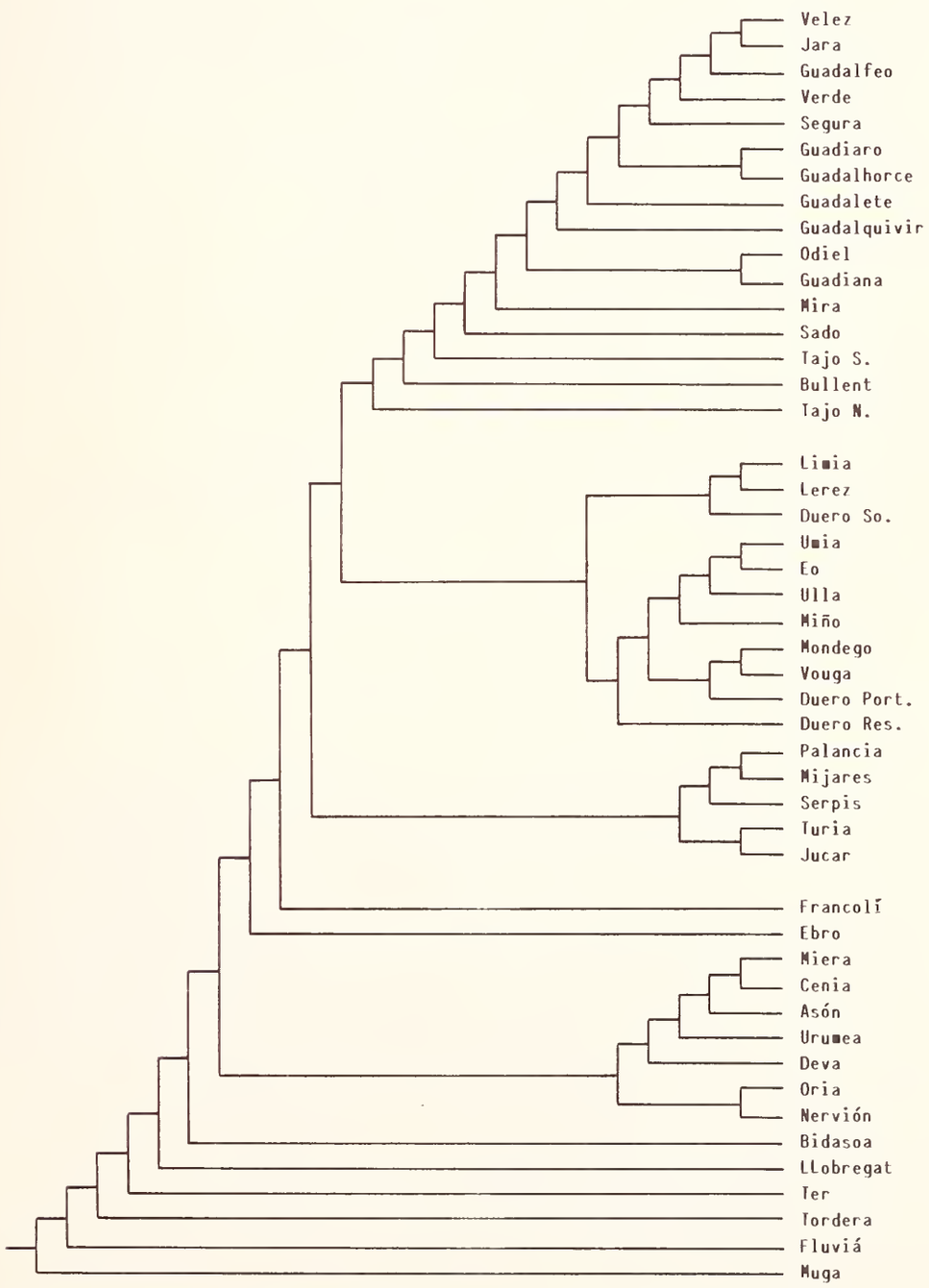

Fig. 5: Dollo clustering for distributions modified by apochoric reduction.

3. Fluvial basins not clearly classified. Three sectors were designated:
   a) Odiel, Guadiana, Guadalquivir, Mira and Guadalete basins.
   b) Tajo, Sado and levantine basins. In this sector, the area of the Tajo and Sado was separated from the rest.
c) Guadiaro, Guadalhorce and Segura river basins.

Dollo parsimony method

For modern taxa distributions (fig. 4)

Using this method, five main regions were determined:

1. Northern Catalonian fluvial basins.
2. Basins of the Ebro, Cantabrian watershed and the Cenia.
3. Levantine basins.
4. The Galician and Duero basins, except for the south-western and Portuguese sections. In figure 4, the Galician basins are apparently grouped closer to each other.
5. Basins of the south and southwestern Iberian Peninsula and the southwestern section of the Duero.

Three areas were differentiated within this large group:

   a) The rivers of south and south-eastern Spain.
   b) Guadalquivir, Guadiana and Odiel rivers.
   c) Rivers of the left bank of the Tajo, Sado and Mira.

Areas transformed by apochoric reduction (fig. 5)

The following regions were differentiated:

1. Basins of the south and south-west Iberian Peninsula.
2. The basins of the Duero, rivers of Galicia and Portuguese basins.
3. Levantine basins.
4. Ebro River basin.
5. Cantabrian watershed basins.

Wagner parsimony method

For modern taxa distributions (fig. 6)

As can be seen in the figure, two main groups were differentiated:

1. The basins of the Ebro, Cantabrian watershed Cenia and Catalonian rivers.

Within this group, the Catalonian rivers were more closely related to each other. The rivers of Catalonia seem to have been united throughout their history, except for the Francolí linked to the Palancia. As indicated by the other methods, this relation seems to be the result of recent faunistic dispersions in the Francolí basin.

2. The second major faunistic group was formed by the remaining hydrographic basins. In this group, the following subgroups were made:
   a) Basins of south-eastern Spain.
   b) Galician river basins and the Vouga.
   c) Duero, Limia and Mondego basins.
   d) Tajo and Guadiana basins.
   e) Levantine basins.
   f) Basins of southern Spain.

Areas transformed by apochoric reduction (fig. 7)

Two main regions were differentiated:

1. The Ebro, Cantabrian watershed and Catalonian basins. The Ebro basin was the first to separate in this group.
2. In the second region there are two large subgroups:
   a) The Tajo, Mira, Sado, Duero, Galician basins and the Portuguese basins.
   b) Basins of the Levant and southern Spain.

Subgroup a contained three perfectly differentiated areas: The Tajo, Sado and Mira basins; close to these, the Duero and Portuguese basins; and an area formed by the Galician confluences.

Subgroup b had two areas: The basins of southern Spain and the Levantine basins.

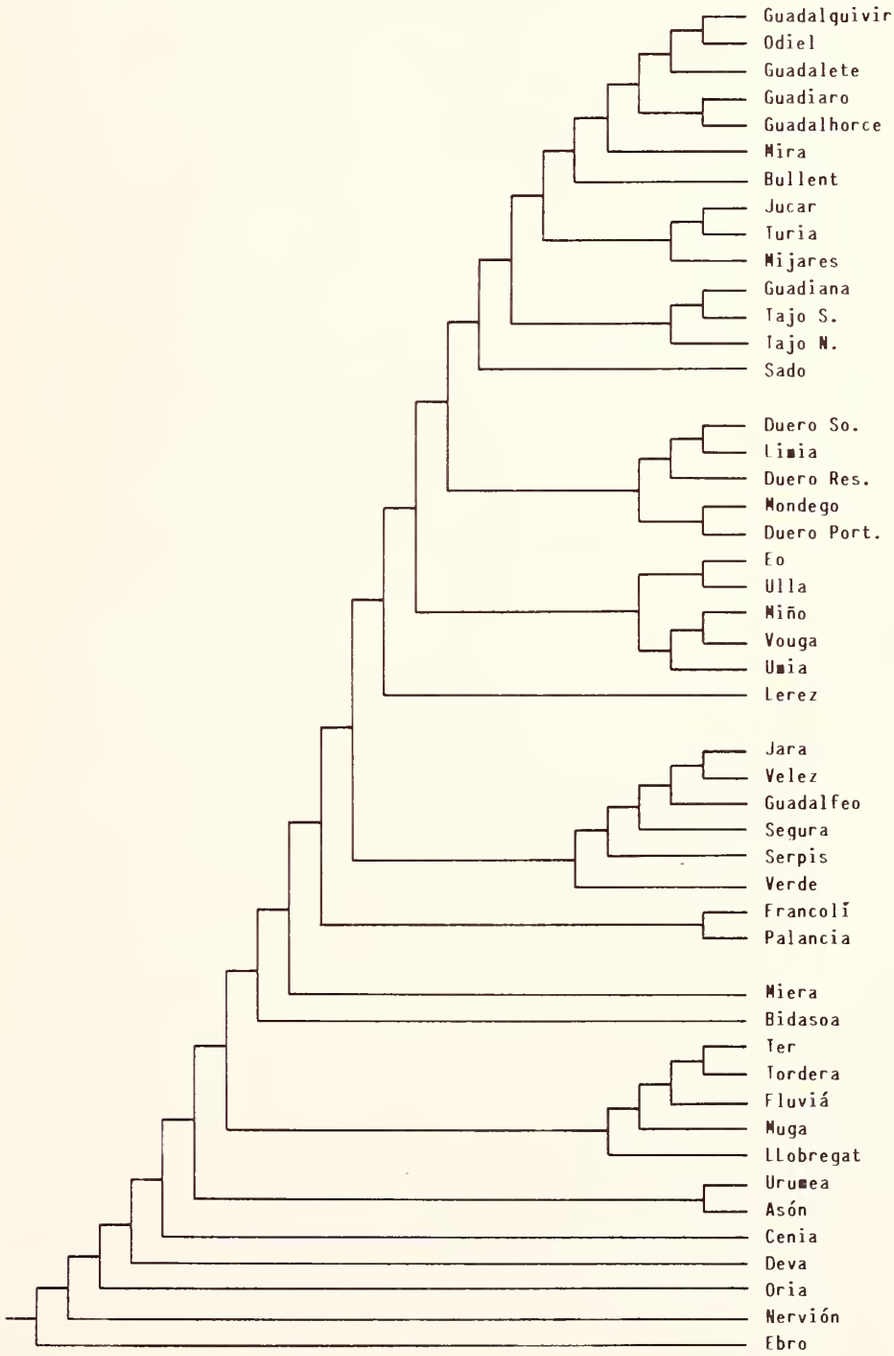

Fig. 6: Wagner clustering for real distributions.

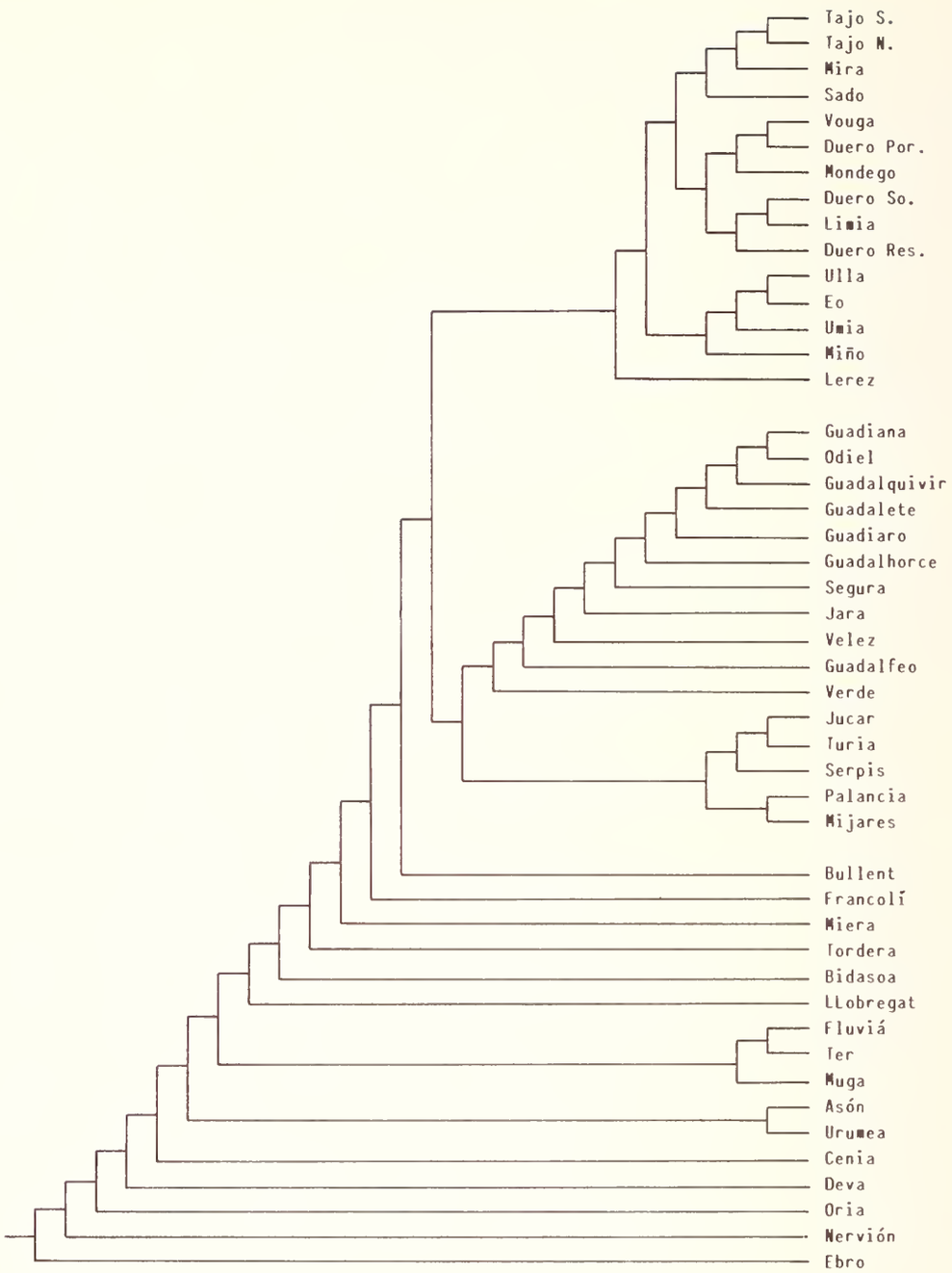

Fig. 7: Wagner clustering for distributions modified by apochoric reduction.

Discussion and conclusions

Several different methods, derived from valid premises, were used in order to determine biogeographic areas. Although the results would be expected to differ in each case, they were found to be congruous, especially in the delimitation of general areas. This is explained as due to the system noise produced by establishing areas on the basis of overall similarities, independent of biogeographic suppositions.

All the methods used (Camin-Sokal parsimony, Dollo and Wagner) concurred in defining two large regions (see fig. 8).

1. The basins of the Ebro River, Cantabrian watershed (Bidasoa, Urumea, Oria,

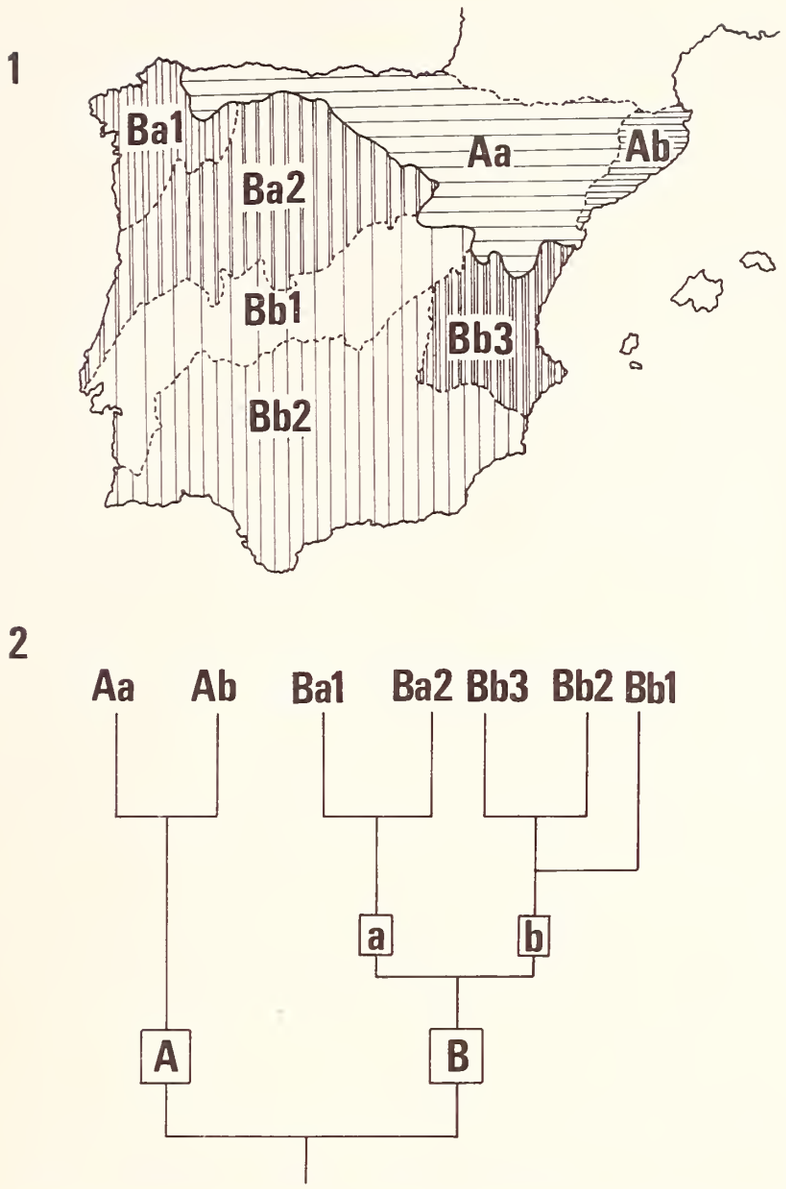

Fig. 8: 1. Biogeographical areas in the Iberian Peninsula on the basis of freshwater fish distributions.

2. Hypothetical relationships among the different areas. A = Northern Iberian region, Aa = Ebro-Cantabrian sector, Ab = Catalonian sector. B = Southern Iberian region, Ba = Galician-Portuguese sector, Ba1 = Galician subsector, Bb2 = Portuguese subsector, Bb = southern sector, Bb1 = Central subsector, Bb2 = Andalusian subsector, Bb3 = Mediterranean subsector.

Deva, Lastras, Nervión, Asón, Miera, Nansa, Pas, Deva-Cares, Sella, Narcea and Navia), Catalonia (Muga, Ter, Fluviá, Tordera, Llobregat and Francolí) and the Cenia. We denominated this area as the northern Iberian region.

Within the northern Iberian region, the results obtained with the different methods varied. According to the Wagner method, the Ebro river basin was the first to separate from the other hydrographic basins. However, with the Camin-Sokal and Dollo methods, the Catalonian river basins separated before the Ebro and Cantabrian basins, which conserved their relations longer. As such, the union between the Ebro and Cantabrian basins was considered most probable (the Ebro-Cantabrian

relations having lasted longer than those of the Ebro-Catalonian sector) (see fig. 8).

The Cenia river basin was classified by the Camin-Sokal method as independent, undoubtedly because only one species was present in its waters, making it almost impossible to establish biogeographic relations.

When true distributions were considered by the Dollo and Wagner methods, the Francolí basin was classified as being very near the Levantine areas. When apochoric regions were reduced, it was classified among the Catalonian basins. This basin probably underwent a faunistic exchange with more southern basins after a preliminary isolation.

2. The second large region (southern Iberian region) included the other hydrographic basins in the Iberian Peninsula (see fig. 8). Within this region, all the methods discerned two subgroups or sectors: on the one hand, the Galician basins (Eo, Ulla, Umia, Masma, Oro, Sor, Eume, Donas, Miño, Lerez, Limia, Cave and Ave) and the Duero, Vouga and Mondego basins (Galician-Portuguese sector), and on the other, the basins of the southern Iberian Peninsula (Mira, Odiel, Guadalete, Jara, Barbate, Guadiaro, Guadalhorce, Guadalfeo, Verde, Segura, Serpis, Guadiana, and Guadalquivir) and Levant (Mijares, Palancia, Turia, Júcar and Bullent) (southern sector). This subgroup included the Tajo and Sado Basins (Central subsector) according to most of the criteria used. However, with the Wagner method for plesiochories and the Camin-Sokal method for true distributions, the Tajo and Sado rivers were grouped close to the Duero and Galician basins.

In the first subgroup, there are two prominent faunistic areas: the Duero, Cave, Ave, Vouga, Mondego and Limia basins (Portuguese subsector) and the Miño, Umia, Ulla, Eo and Lerez basins (Galician subsector). The Lerez basin appears in different areas because of the paucity of its fauna.

The different subdivisions of the Duero were close to each other in every case, historically disqualifying the diversion of the river in sections. Only the Dollo method for true distributions disclosed a relation between the so-called southeastern stretch of the Duero river with the Tajo. It is possible that after these rivers separated, there were captures or colonizations from the Tajo towards this section of the Duero.

The second subgroup (southern sector) had three well- defined areas. The area most distantly related to the other two was that formed by the Tajo and Sado basins (central subsector). The sections into which the Tajo was divided evidenced a close relationship in all the analyses, which eliminates the historical justification for this division. Another area grouped the levantine basins (Palancia, Mijares, Júcar, Turia and Serpis) (Mediterranean subsector). Of these, the Júcar and Turia rivers were consistently more closely united to each other than other hydrographic basins. The Serpis basin did not appear in this area when Dollo and Wagner methods for real distributions were applied.

The third area is formed by the basins of the southern Iberian Peninsula (Mira, Guadiana, Odiel, Guadalquivir, Guadalete, Jara, Barbate, Guadiaro, Guadalhorce, Vélez, Guadalfeo, Segura and Verde) (Andalusian subsector). Within this sector, the Guadiana, Odiel and Guadalquivir basins seem to be more closely related to each other than to the rest. The results of the division of the Iberian Peninsula into seven areas is depicted in the fig. 8.

Contrasted hypotheses

The hypothesis for establishing biogeographic areas that we have developed here can be contrasted with freshwater fish phylogeny and paleogeographic knowledge of the Iberian Peninsula.

Phylogeny

The phylogenetic relations of the Iberian continental ichthyofauna are unknown, except for the genus *Barbus* (Doadrio, 1984). The evolution of this genus is represented in the cladogram in fig. 9. Unfortunately, as can be observed in fig. 9, in the Iberian Peninsula, the species of the genus *Barbus* constitute a polyphyletic group, in the sense of Farris (1974) and Platnick (1977), precluding elaboration of a single area cladogram. In the present case, cladograms can only be made of two areas, which as Platnick and Nelson (1978) have demonstrated, is inadequate.

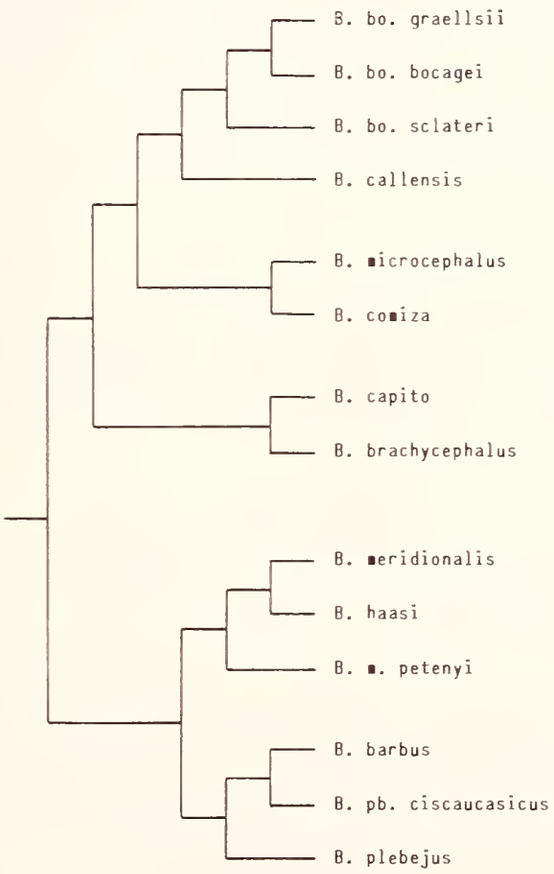

Fig. 9: Phylogeny of the genus *Barbus* (Doadrio, 1984).

Paleogeography

The geological origin of the fluvial basins is not known in detail, except in concrete cases like the Júcar basin (Garcia Abbad, 1975, Perez Gonzalez, 1981).

Generally speaking, Spanish fluvial basins in their present form date from the Quaternary. Prior to this epoch, large endorrheic basins occupied the entire Iberian Peninsula. The most recent basins are the southern ones because the Andalusian

region was submerged until the lower Miocene (Rögl & Steininger, 1983). Separation of the modern Tajo and Duero basins must have taken place in the Oligocene (Garzon et al., 1983) with the formation of the Central System. The basins of the Ebro, Catalonia and Cantabria must have also become independent in the Oligocene with the formation of the Iberian System.

The paleogeographic data therefore seem to coincide completely with our separation of areas, but various taxa studied are of more recent origin than the Oligocene, such as the genus *Barbus* (Doadrio, 1984). It is improbable that the three subspecies of *Barbus bocagei* Steind., 1865, the two subspecies of *Chondrostoma polylepis* Steind., 1865, and the two subspecies of *Chondrostoma toxostoma* Vallot, 1856 separated before the Miocene.

It can be assumed that the isolation of these areas was practically complete and that random relationships have been established in more recent epochs. It is difficult to imagine that this would have occurred by means of fluvial captures, since only certain groups have colonized new areas. In fact, recently known fluvial captures, such as those of the Alberche and the Júcar (Júcar, Guadiana) (Perez Gonzalez, 1980) do not seem to have influenced freshwater fish distribution. Nonetheless, some rivers present characteristic fauna of other fluvial basins, such as the Huebra (Duero-Tajo), Lozoya (Tajo-Duero) and Jalón (Ebro-Tajo). This may have resulted from either fluvial captures (although this has not been geologically proved) or unknown systems of dispersion.

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References

Arevalo, C. (1929): La vida en las aguas dulces. — Barcelona.
Blondel, J. (1979): Biogéographie et Ecologie. — Paris.
Croizat, L. (1958): Panbiogeography. — Caracas.
—, G. Nelson & D. E. Rosen (1974): Centers of origin and related concepts. — Syst. Zool., 23 (2): 265—287.
Doadrio, I. (1981): Primeros datos sobre la distribución de *Cobitis calderoni* Bacescu, 1961 (Pisces, Cobitidae) en la Península Ibérica. — Doñana Acta Vertebrata, 8: 291—293.
— (1984): Relaciones filogenéticas y biogeográficas de los barbos (*Barbus*, Cyprinidae) de la Península Ibérica y aportes corológicos y biogeográficos a su ictiofauna continental. — Madrid.
—, B. Elvira, C. R. Vigal & J. Lobon-Cervia (1980): Nuevas citas de la "Loina" *Chondrostoma* (*Machaerocheilus*) *toxostoma arrigonis* Steind. (Pisces, Cyprinidae) en España. — Doñana Acta Vertebrata, 7 (1): 97—99.
Farris, J. S. (1974): Formal definitions of paraphyly and polyphyly. — Syst. Zool. 23: 548—554.
Garcia-Abbad, F. J. (1975): Estudio Geológico de la región del Pantano de Alarcón (Cuenca). — Madrid.
Garzón-Heydt, M. G., J. Pedraza Gilsanz & A. G. Ubanell (1983): Los modelos evolutivos del relieve del Sistema Central Ibérico (Sectores de Gredos y Guadarrama). — Rev. R. Acad. Cienc. Fis. y Natur. Madrid, 86 (2): 475—496.
Illies, J. ed. (1978): Limnofauna Europaea. — Stuttgart.
Lozano Rey, L. (1952): Los peces fluviales de España. — Madrid.

Perez Gonzalez, A. (1981): Neógeno y cuaternario de la Llanura Manchega y sus relaciones con la cuenca del Tajo. — Madrid.
Platnick, N. I. (1976): Concepts of dispersal in historical biogeography. — Syst. Zool. 25 (3): 294—295.
— (1977): Paraphyletic and polyphyletic groups. — Syst. Zool. 26: 195—200.
— & G. J. Nelson (1978): A method of analysis for historical biogeography. — Syst. Zool. 27 (1): 1—16.
Rögl, F. & F. F. Steininger (1983): Vom Zerfall der Tethys zu Mediterran und Paratethys. Die neogene Paläogeographie und Palinspastik des zirkum-mediterranen Raumes. — Ann. Naturhist. Mus. Wien (85) A: 135—163.
Rosen, D. E. (1975): A vicariance model of Caribbean Biogeography. — Syst. Zool. 24 (4): 431—464.
— (1978): Vicariant patterns and historical explanation in biogeography. — Syst. Zool. 27 (2): 159—188.
Sanchiz, B. (1981): Aportes al método de delimitación de regiones en biogeografía histórica. — Memorias del Coloquio sobre Ecología y Biogeografía, Guadalajara 28—31 Marzo, 1979, Madrid: 224—243.

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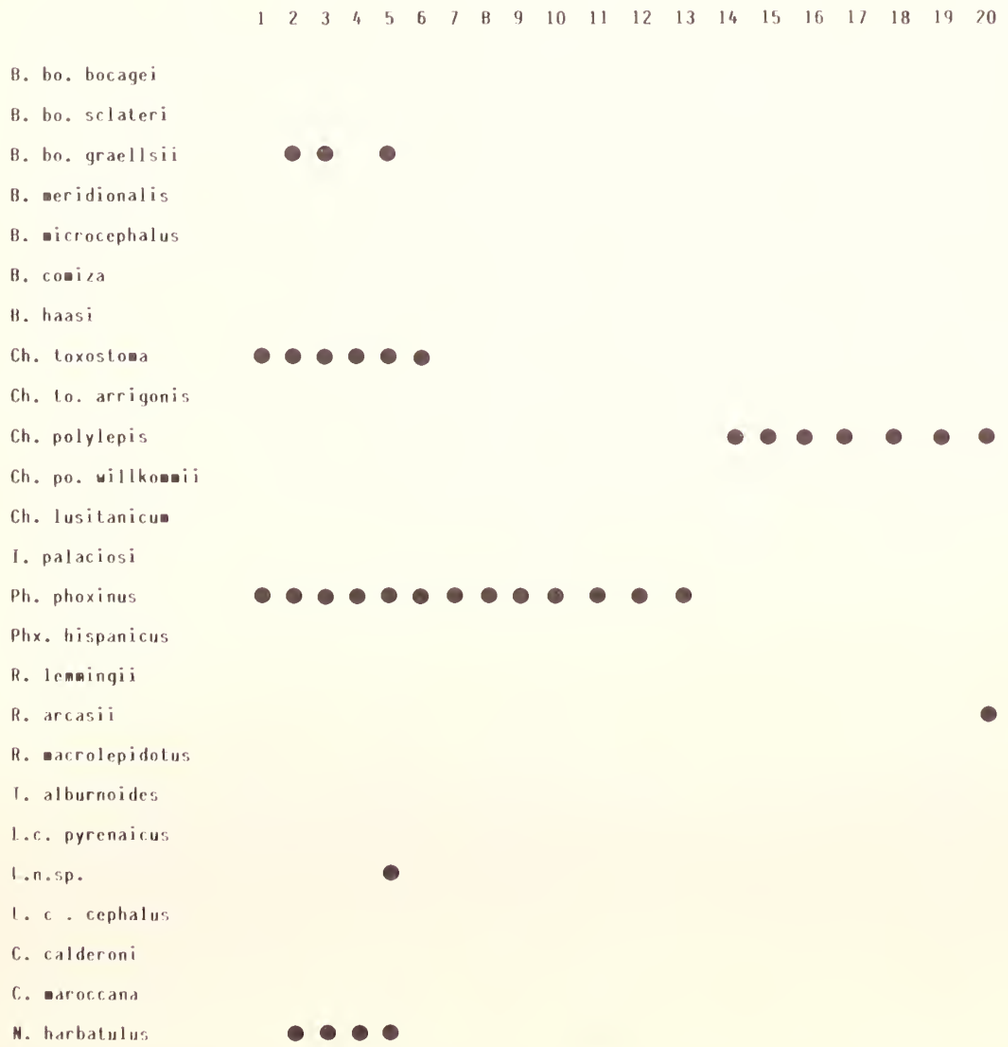
Appendix

Tables 1 and 2

Table 1: Real distributions for the different taxa occurring in the Iberian Peninsula. Dots = presence. Basins are: 1 Urumea, 2 Oria, 3 Deva, 4 Lastras, 5 Nervión, 6 Asón, 7 Miera, 8 Pas, 9 Nansa, 10 Cares, 11 Sella, 12 Narcea, 13 Navia, 14 Eo, 15 Masma, 16 Oro, 17 Sor, 18 Eume, 19 Donas, 20 Ulla, 21 Umia, 22 Lerez, 23 Miño, 24 Limia, 25 Cave, 26 Ave, 27 S. O. Duero, 28 Duero, 29 Duero port., 30 Vouga, 31 Mondego, 32 N. Tajo, 33 S. Tajo, 34 Sado, 35 Mira, 36 Guadiana, 37 Odiel, 38 Guadalquivir, 39 Guadalete, 40 Barbate, 41 Guadiaro, Guadalhorce, 42 Jara, 43 Velez, 44 Guadalfeo, 45 Segura, 46 Verde, 47 Serpis, 48 Júcar, 49 Turia, 50 Bullent, 51 Palancia, 52 Mijares, 53 Cenia, 54 Ebro, 55 Bidasoa, 56 Francolí, 57 Llobregat, 58 Tordera, 59 Ter, 60 Fluvia, 61 Muga.



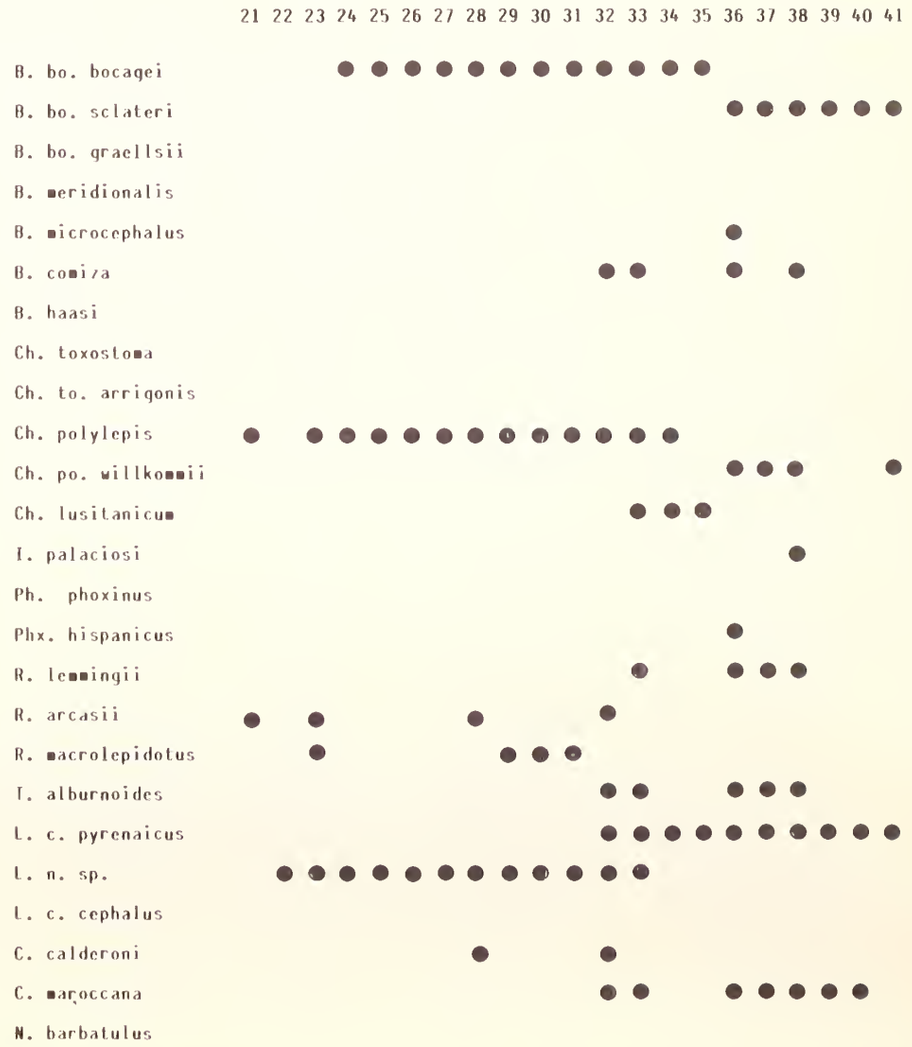


Table 1 (continued).

Table 2: Distributions modified after Sanchiz's (1981) method. Dots = presence. Basins are: 1 Urumea, 2 Oria, 3 Deva, 4 Nervión, 5 Asón, 6 Miera, 7 Eo, 8 Ulla, 9 Umia, 10 Lerez, 11 Miño, 12 Limia, 13 S. O. Duero, 14 Duero, 15 Duero port., 16 Vouga, 17 Mondego, 18 N. Tajo, 19 S. Tajo, 20 Sado, 21 Mira, 22 Guadiana, 23 Odiel, 24 Guadalquivir, 25 Guadalete, 26 Guadiaro, 27 Guadalhorce, 28 Jara, 29 Velez, 30 Guadalfeo, 31 Segura, 32 Verde, 33 Serpis, 34 Júcar, 35 Turia, 36 Bullent, 37 Palancia, 38 Mijares, 39 Cenia, 40 Ebro, 41 Bidasoa, 42 Francolí, 43 Llobregat, 44 Tordera, 45 Ter, 46 Fluviá, 47 Muga.