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An Ecological Classification of European *Drosophila* Species

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Summary. The associations shown between species of *Drosophila* collected in three European countries are analysed using a clustering method. The resulting dendrograms are combined to give a plan of associations shown by all three surveys. These general groupings are interpreted in the light of what is known about *Drosophila* breeding sites.

One ecological group, the fungal breeding species are examined in detail and their pattern of geographical associations investigated. The three most abundant species in collections, *D. transversa, D. phalerata* and *D. cameraria* appear to replace one another in a north-south direction in western Europe. It is suggested that ecologically marginal areas may be defined using the frequency of a species within its ecological group.

Introduction

It has been said that, "to do science is to search for repeated patterns, not simply to accumulate facts" (MacArthur, 1972). The present paper examines collection data from three European *Drosophila* surveys and attempts to uncover any underlying pattern of species associations.

The surveys were carried out in the Catalan region of Spain (Monclús, 1964), the Netherlands (Sobels et al., 1954) and southern England (Dyson-Hudson, 1954). The collected flies were attracted to fermented fruit; in the Spanish and English collections this was banana. The results of the latter survey have never been published and they are therefore summarised in Table 1. The present author is indebted to Dr. Dyson-Hudson for allowing him to publish and use these results.

Methods

In each set of collection data, the associations between the species were examined by calculating product moment correlation coefficients (r) between all pairs of species. However not all species

Table 1. The collection data of Dyson-Hudson. The percentages in brackets next to each major habitat indicate the frequency of each among the 175 collection sites. 0 = less than 0.5%; – = not present

	Numbers	% of each species in major habitats						
		Deciduous woodlands (22%)	Coniferous woodlands (15%)	Unclassified woodlands (23%)	Gardens and orchards (15%)	Farms (6%)	Indoors and markets (3%)	Open habitats (15%)
deflexa	1,496	46	26	23	3	0	–	1
rufifrons	4	–	–	75	25	–	–	–
melanogaster	1,222	5	0	4	73	10	3	5
subobscura	20,692	16	19	21	16	5	5	18
obscura	6,110	28	26	27	12	4	0	3
subsilvestris	381	46	29	24	1	0	–	0
ambigua	190	33	7	–	47	6	1	5
tristis	1,175	24	15	42	5	3	0	11
helvetica	271	57	2	11	3	27	–	–
kuntzei	475	16	27	48	1	1	–	7
limbata	8	38	12	–	50	–	–	–
phalerata	1,523	20	17	50	7	–	–	6
transversa	64	72	3	12	–	1	–	12
confusa	17	–	35	47	6	–	–	12
histrio	56	21	32	21	11	5	–	9
cameraria	218	8	41	40	4	2	–	5
immigrans	18	35	–	26	6	33	–	–
littoralis	9	–	–	100	–	–	–	–
funebris	893	10	3	8	16	55	2	6
hydei	49	–	4	7	85	4	–	–
busckii	184	2	2	8	9	72	–	7
andalusiaca	1							
Total	35,056	20	19	23	16	6	3	12

were used in the analysis. Species were considered rare if they numbered less than one per collection (e.g. for the Dyson-Hudson data there were 175 collections and therefore all species with less than 175 specimens are called rare) and excluded from the analysis because an excessive number of zero's can produce a spurious positive correlation. The correlation matrix was calculated not from the original raw data but from their standardised scores (Sokal and Sneath, 1963). The data in each of the three correlation matrices was then subjected to a cluster analysis (the weighted variable-group method) using Spearman's sums of variables method for recomputing the correlation coefficients (Sokal and Sneath, 1963). The resulting dendrograms are shown in Figure 1.

Results and Discussion

Species Association Patterns

There are a number of significant groupings (at the 1% level) which appear to make ecological sense. For instance in the English collections *D. busckii* and *D. funebris* are both recorded as domestic species having been bred from

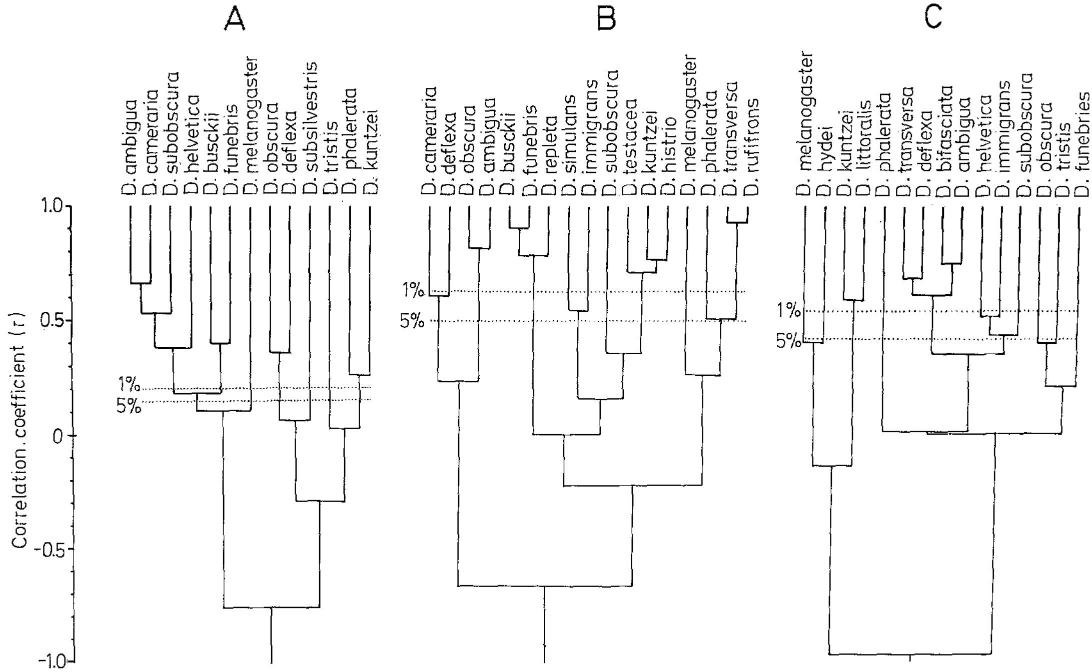


Fig. 1 A–C. Dendrograms resulting from the initial cluster analysis on the three European *Drosophila* surveys. **A** Southern England, **B** Catalonia, and **C** Holland

decaying material (Shorrocks, 1972). *Drosophila obscura* and *D. deflexa* are woodland species both recorded from sap fluxes (Gordon, 1942; Frydenberg, 1956) and *D. phalerata* and *D. kuntzei*, woodland species also, bred from fungi (Shorrocks, 1972; Shorrocks and Wood, 1973). In the Spanish collections *D. obscura* and *D. ambigua* are both wild species, the latter being also recorded breeding in sap fluxes (Prevosti, 1959); *D. busckii, D. funebris* and *D. repleta* are all domestic species; *D. testacea, D. kuntzei* and *D. histrio* are all woodland species breeding in fungi (Shorrocks, 1972; Shorrocks and Wood, 1973).

It would be interesting to see if there are significant associations of species irrespective of the mode of collection, the year of the survey or the geographical location within Europe. In order to investigate this the three cluster analyses were combined in the following way. Firstly, the eight species of *Drosophila* present in all three sets of data were analysed. Their inter-correlations from the original matrices were combined to give a value of X^2 using the expression:

$$X_q^2 = \Sigma[z^2(n\text{-}3)],$$

where q is the number of replicates (3), n is the number of data pairs that produce the original r and

$$Z = \tfrac{1}{2}\log_e\left(\frac{1+r}{1-r}\right)$$

(Fisher, 1948).

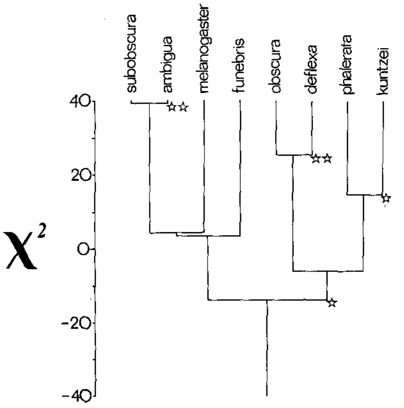


Fig. 2. Dendrogram resulting from a combination of the three surveys shown in Figure 1

Table 2. Association between *D. ambigua* and *D. obscura/D. subobscura* for the Dyson-Hudson (DH) collections in Southern England and the Monclùs (M) collections in the Catalan region of Spain

Species pair	Correlation coefficient	
ambigua/obscura	DH -0.5711	$P<0.001$
	M $+0.8243$	$P<0.001$
ambigua/subobscura	DH $+0.4480$	$P<0.001$
	M -0.2163	$P>0.05$

The result is shown in Figure 2. At the 1% level of significance, these eight widely distributed species form a number of associations even though data have been combined from several sources. *D. obscura* and *D. deflexa* remain together as woodland species recorded from sap fluxes and *D. phalerata* and *D. kuntzei* remain together as woodland species recorded from fungi. These four woodland species are negatively associated with the four other 'domestic' species. Interestingly enough, the four species recorded from 'domestic' habitats do not form a positive group; only *D. subobscura* and *D. ambigua* are positively associated.

Although these eight species do appear to form natural groupings when all the data are combined it is sensible to check that there are no major internal inconsistencies between the original correlation coefficients for the three surveys. There appear to be no major contradictions between the combined correlations except for *D. ambigua*, so that the associations of Figure 2 are generally true of all three surveys. The anomalous results for *D. ambigua* are shown in Table 2. They suggest that while Figure 2 is a true reflection of the situation in central Europe (Netherlands and southern England) it may not be so for Spain. In Catalonia *D. ambigua* is significantly associated with *D. obscura* whilst showing a negative correlation with *D. subobscura*. This is interesting since Basden (1954) suggests that the late appearance of *D. ambigua* in the year, coupled with its high frequency in man-made habitats indicates that it is not a native species

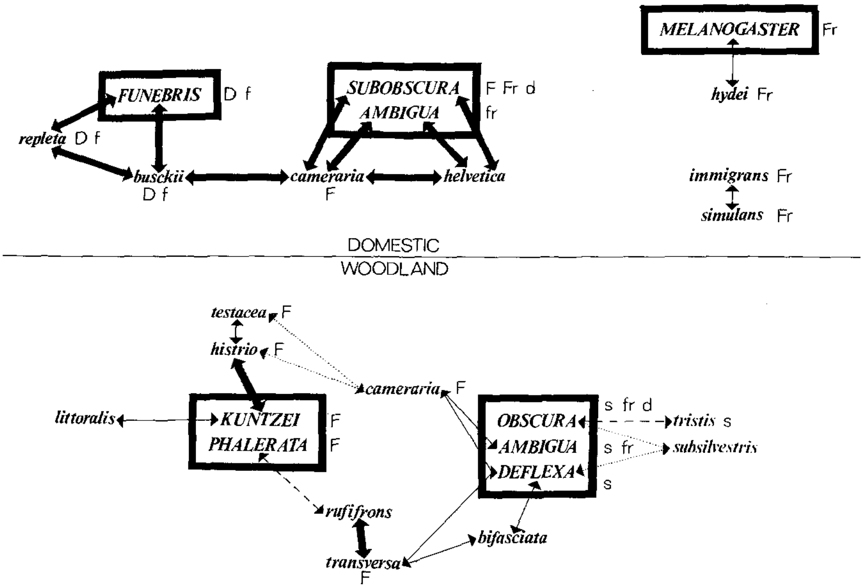


Fig. 3. Associations between the *Drosophila* species present in the three surveys. — sig. at the 0.1% level, —— sig. at 1%, ---- sig. at 5%, and ····· sig. at 10%

in Britain. In fact as already noted it has been recorded breeding in sap fluxes in Spain and is a typical wild species (Monclús, 1964) rather like *D. obscura*. Because of this dual association, *D. ambigua* appears twice in Figure 3 where all the species associations are depicted. With *D. subobscura* it reflects the situation of central Europe where it is not a truly wild species, whilst with *D. obscura* and *D. deflexa* it reflects the situation in Spain where it is apparently a wild species.

The situation described in Figure 3 is produced by using the eight species, already discussed, as focal points around which all the remaining species present in the cluster analyses are grouped. All significant associations are shown and the degree of significance is indicated by the type of line connecting two species. Once again, one species, *D. cameraria* appears to have different associations in Spain and central Europe, although in both collections it is strongly associated with *D. ambigua*.

The major division of the species shown in Figure 3 occurs because of a spatial separation of the two major habitats available for European *Drosophila*-woodlands of various kinds and domestic sites such as farms, gardens and orchards. This separation of species is quite obvious even from Table 1 and has been recognised by *Drosophila* workers for many years. The cause of the smaller groups of associated species is not so obvious. Both Carson (1971) and Shorrocks (1975) have suggested that it is the larval breeding sites that are the focal point of *Drosophila* ecology; it is here that ecological specialisation has been most apparent. A systematic search through European records of breeding sites (Table 3) has provided the information which has been added to Figure 3 and as a result a second pattern emerges. The species within several

Table 3. Literature sources used for the data on presumed major breeding sites included in Figure 3

Fungi			
D. phalerata	Basden (1954), Burla and Bächli (1968), Shorrocks and Wood (1973), Shorrocks and Charlesworth (in prep.)		
D. transversa			
D. cameraria			
D. testacea			
D. kuntzei			
D. histrio			
Sap and fruit			
D. deflexa	Frydenberg (1956)		Basden (1954)
D. tristis			
D. obscura	Gordon (1942)	Begon (1975)	
D. ambigua	Prevosti (1959)		
Decaying material and fungi			
D. funebris	Basden (1954), Shorrocks and Wood (1973)		
D. busckii			
D. repleta			
Fruit			
D. melanogaster	Basden (1954)		
D. hydei			
D. immigrans			
D. simulans			
Fruit and fungi			
D. subobscura	Begon (1975), Shorrocks and Charlesworth (in prep.)		

of the groups appear to have similar larval food niches. Within the woodland species there is a fungal group and a sap group, the latter also utilizing fermenting fruit. The characteristics of the larval niche appear to influence strongly the distribution and associations of the adults. There could be several reasons for this. Firstly, the spatial distribution of adults may simply follow the spatial distribution of breeding sites, with flies being attracted primarily to either fungi or sap and secondarily to banana bait. Flies may be attracted locally within a wood to groups of fungi or to exuding sap; alternatively certain woods may contain many fungi and others many sap flows. An example of this kind of close association between adult fly and breeding site has been demonstrated quite nicely by Richardson and Johnson (1975) in Hawaiian *Drosophila*. It would be interesting to know if European species show similar habitat selection.

A second possibility is that sap flows and fungi show seasonal separation, so that the two woodland groups of Figure 3 reflect a seasonal grouping. At the present time there is no information on this point.

A third possibility is that the bait used to make these collections, although constant in the sense of always being banana, was variable in its microbial composition. Any differences in yeasts or bacteria may well favour the attraction of either fungal or sap/fruit breeding species.

Perhaps the important point is that this separation of *Drosophila* into a fungal breeding group and a sap/fruit breeding group may represent a rather fundamental ecological division that should be investigated further. In the laboratory, *D. phalerata* females prefer decaying fungi to fresh fungi (Shorrocks et al., in prep.) and in Japan, *D. testacea* has been bred from decaying leaves (Kimura, 1976). This suggests that the fundamental ecological division in these flies is between those that utilize decaying substrates as breeding sites and those that use substrates undergoing alcoholic fermentation. The same division appears among the domestic species also.

This parallel between the 'domestic' species and woodland species is interesting, since the former group are often referred to as unspecialised and broad-niched in their larval food requirements (Carson, 1965). Unfortunately this kind of statement is usually based upon the range of food items used rather than their frequency of utilisation. Detailed quantitative collections of 'domestic' breeding sites will probably reveal a degree of specialisation in this group also.

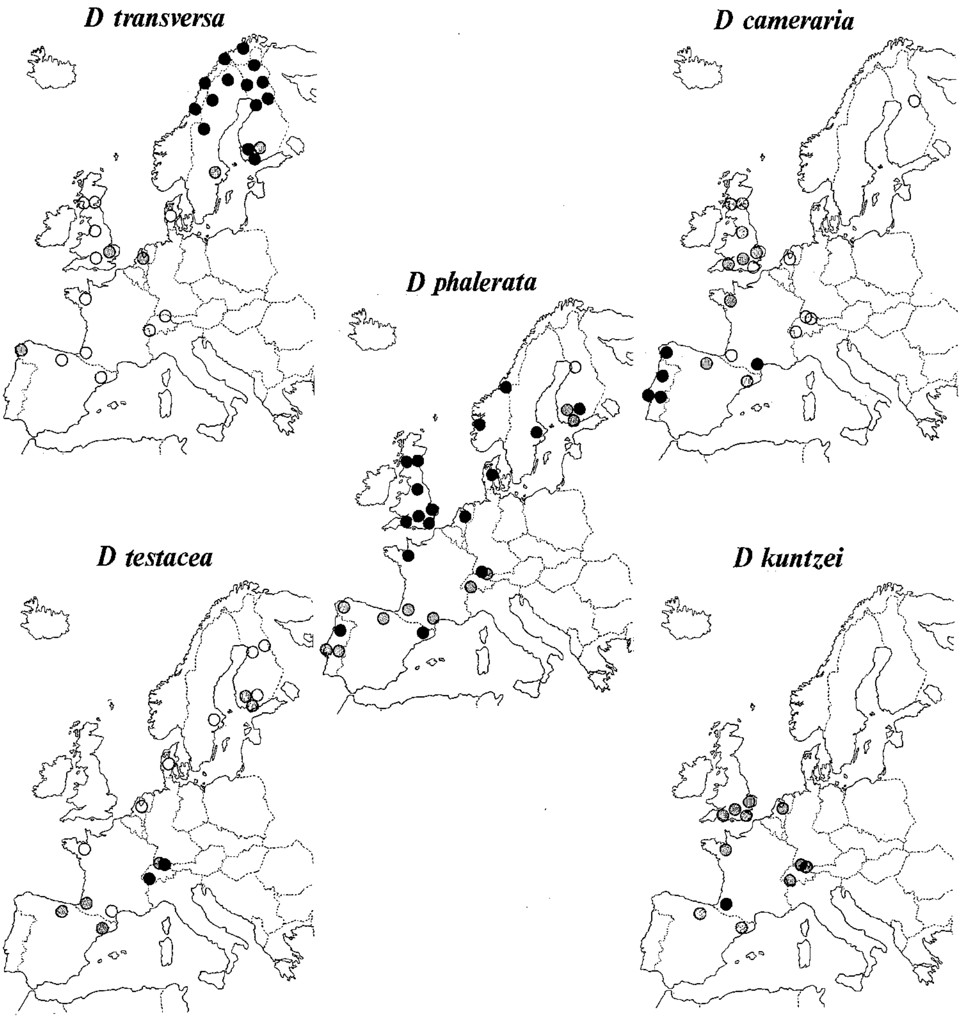
Geographical Patterns

In the search for patterns in the distribution of European *Drosophila*, the frequency of any species in a collection has usually been expressed as a proportion of the total *Drosophila* caught (Hadorn et al., 1952). It would seem more profitable however to examine the change in frequency within an ecological group and this has been done for the fungal breeding species (*D. phalerata, D. transversa, D. cameraria, D. testacea, D. kuntzei, D. confusa, D. histrio* and *D. limbata*) using the sources listed in Table 4. At every collection location each species is recorded as a proportion of the total numbers of fungal species caught.

Disbribution maps of the five most common fungal species are shown in Figure 4. Three species appear to replace each other in a regular way from northern to southern Europe. *Drosophila cameraria* has an Iberian distribution

Table 4. Sources used for the European collection data shown in Figures 4 and 5

Finland, Norway, Sweden	Basden and Harnden (1955), Gahne (1959), Lakovaara, Muona and Lumme, pers. comm.
Denmark	Frydenberg (1956)
Holland	Sobels et al. (1954)
Switzerland	Burla (1950), Bächli (1972a, b, 1973, 1974)
Scotland	Basden (1954)
England	Dyson-Hudson (1954), Shorrocks and Charlesworth (in prep.)
France	Hadorn et al. (1952)
Spain	Hadorn et al. (1952), Monclús (1964), Fontdevela (pers. comm.)
Portugal	Hadorn et al. (1952), Pite (1972)
Canary Isles	Monclús (pers. comm.)



D transversa

D cameraria

D phalerata

D testacea

D kuntzei

Fig. 4. The distribution maps for the five most abundant fungal-breeding species in Western Europe. *Black circle*, greater than 50% of all fungal species; *shaded circle*, greater than 5% but less than 50%; *open circle*, present but less than 5%

with a northern atlantic extension into France and the British Isles but elsewhere in Europe it is rare. *Drosophila transversa* is the dominant fungal species in northern Scandinavia, becoming rarer in the rest of Western Europe and *D. phalerata* lies between these two species with a central European distribution. Again, the latter species is particularly abundant on the Atlantic edge of its range. *Drosophila testacea* is common in southern Finland and in mountainous areas further south such as the Alps and Pyrenees whilst *D. kuntzei* has a rather restricted central European range. These distributions are plotted in a rather different way in Figure 5. The mean January isotherm taken from Wallen (1970) have been used to divide western Europe into 'temperature zones' into which

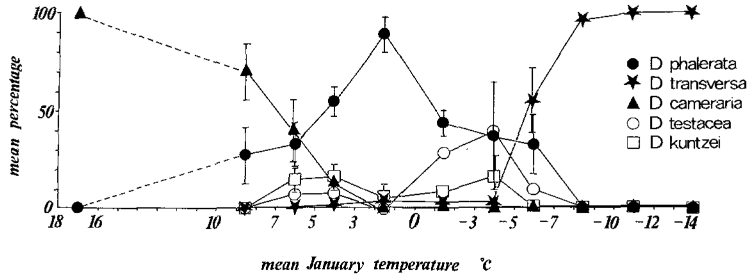


Fig. 5. The mean frequency ± one standard error, of the five abundant species plotted against mean January temp. (°C)

all the collection sites are placed. The mean frequency with its standard error is shown for each species in each climatic zone. The north to south replacement of species is now easily seen.

It is fortunate that extensive *Drosophila* collections have also been made in Japan particularly the northern island of Hokkaido. All eight fungal species discussed here, with the exception of *D. phalerata* and *D. limbata* have been collected there also. *Drosophila transversa* and *D. testacea* appear to be the commonest of these species in Hokkaido (Makino and Takeharu, 1951; Makino et al., 1956, 1958; Takada, 1956; Kaneko and Shima, 1960) although this island is only equivalent in latitude to the Iberian Peninsula. However if we look at the mean January temperature we find it comparable to Switzerland and southern Finland (−3 to −7°C). In Japan therefore these two species occupy a similar climatic zone to their counterparts in western Europe.

It is not of course being suggested that winter temperature is necessarily the causal agent in these *Drosophila* distributions. However in the further investigation of causal mechanisms, winter temperature or some closely associated parameter may well prove a rewarding starting point.

Marginal and Central Populations

Both ecologists and geneticists have for some time made the distinction between marginal and central parts of a species range. For example, Haldane (1956) suggested that in the optimal centre, a species will exist close to its density dependent limit. In the less favourable margins however density will increasingly become determined by density-independent factors. Lewontin (1974) suggests that ... "in central populations with predictable, spatially diverse environments, a small number of distinct and diverse physiological and developmental modes will be selected" ... whereas ... "in the highly unstable and unpredictable environment of the margin, quite different genotypes are being selected at different times". Both Mayr (1954) and Wallace (1960) stress the importance of the ecological margins as places where novel genotypes may evolve to extend the geographical range of the species.

In view of such statements we must offer some definition of an ecologically marginal area. It cannot simply be the edge of the species range since if the species is limited by an abrupt geographical border like an ocean then the favourable 'central' area may continue to the edge. Lewontin (1974) suggests that ecologically marginal areas may be defined by looking at ... "average population size and its temporal variation". However, population size may not always decline towards the ecological margins. For example, let us suppose that the average population density for *D. transversa* was 10/m^2 in northern Scandinavia where it is the only fungal species. Let us further suppose that in central Europe its density remains the same but that this ecological group of *Drosophila* increase to a combined density of 100/m^2. On the basis of density alone it might be suggested that both north and central areas were ecologically similar for this species. But in terms of frequency within this ecological group, *D. transversa* has declined from 100 to 10%, suggesting perhaps that it is now ecologically less successful.

Quite obviously we need to know much more about the ecology of *Drosophila* before we can talk confidently about margins and centres. However the kind of information shown in Figure 5 may provide an important starting point for this kind of investigation. Furthermore, if we define as marginal those areas of Figure 5 with frequencies less than 5% then the marginal areas can be very large. They may in fact constitute a major part of the species range.

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