ANALYSIS OF MAMMALIAN COMMUNITIES FROM THE LATE EOCENE AND OLIGOCENE OF SOUTHERN FRANCE

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SOMMAIRE

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Key-words : MAMMALIAN COMMUNITIES, LATE EOCENE, OLIGOCENE, QUERCY, SOUTHERN FRANCE.
Mots-clés : COMMUNAUTÉS MAMMALIENNES, ÉOCÈNE SUPÉRIEUR, OLIGOCÈNE, QUERCY, FRANCE.

Palaeovertebrata, Montpellier, 16 (4) : 191-212, 14 fig.
(Reçu le 5 Juillet 1986, accepté le 5 Septembre 1986, publié le 15 Décembre 1986)

ABSTRACT

Valverde's cenogram method is used to analyse mammalian communities from the late Eocene to late Oligocene of southern France, mainly from the "Phosphorites du Quercy". Cenogram analysis involves plotting the size of each component species in a fauna on a semilog diagram in rank order, permitting fossil faunas to be compared with Recent ones. The configurations of Recent communities serve as models for establishing the general environmental characteristics of fossil mammalian faunas. This method of analysis applied to faunal sequence can reveal major and sudden ecological perturbations. The paleobiogeographical event (i.e. the mammalian immigration wave) at the Eocene-Oligocene Boundary in western Europe, known as the «Grande Coupure», is here shown to represent a drastic and sudden ecological change : late Eocene tropical environments in Europe deteriorated rapidly turning to subdesert or desert environments at the beginning of the Oligocene.

RÉSUMÉ

La méthode des cénogrammes de Valverde est utilisée pour l'analyse des communautés mammaliennes de l'Eocène supérieur à l'Oligocène supérieur du Sud de la France, principalement des Phosphorites du Quercy. Un cénogramme est construit en portant sur un diagramme le poids des espèces d'une communauté classées dans un ordre de taille décroissant. Cette analyse permet de comparer des faunes fossiles et actuelles. La configuration de communautés actuelles sert de modèle pour établir les caractéristiques générales de l'environnement des faunes mammaliennes fossiles. Cette méthode d'analyse appliquée à des séquences fauniques permet de révéler des perturbations écologiques majeures et soudaines. L'événement paléobiogéographique correspondant à la vague d'immigration de mammifères à la transition Eocène-Oligocène en Europe occidentale («Grande Coupure») est corrélée à un changement écologique drastique : les milieux de l'Eocène supérieur, de type tropical, se détériorent rapidement au début de l'Oligocène pour laisser place à des milieux de type sub-désertique à désertique.

INTRODUCTION

"Since the major component of the environment of most species consists of other species in the ecosystem, it follows that we need a theory of ecosystems in which the component species are evolving by natural selection. Such a theory is hard to formulate : the data needed to test it will be, primarily, the data of paleontology." (Maynard Smith 1982 : 128). A theory is here proposed for mammalian communities. A method of analysis of mammalian faunas is elaborated, taking into account the body size of the different mammalian species in a local fauna. It is applied to some Recent, mainly African, faunas and to fossil faunas of the middle and late Paleogene of southern France.

Body size plays a prominent role in the adaptation of an animal to its environment. Natural selection acts on the body size of animals in the evolution of species primarily because of its ecological importance (Peters 1983). Body size also influences the number of species to be found in a given area (e.g. MacArthur and Wilson 1967, Van Valen 1973b, Diamond 1975, Flessa 1975) and the probability of extinction of a given species in habitat islands (Diamond 1984).

The analysis of species diversity and the configuration of mammalian communities, as well as their succession during geological time, allows one to clarify the influence of major ecological changes in the evolution of mammalian communities.

METHODS

PRINCIPLES

Many biological and ecological attributes of species are related to body size (e.g. life and pregnancy durations, population densities, home ranges, predation relationships; see for instance Einsenberg 1981 and Peters 1983). Thus, meaningful analysis of a fauna can be made in terms of the body size of its species components. Some biological and paleontological studies have already been made employing the body size parameter, either for particular groups (e.g. Fleagle 1978), partial faunas (e.g. Charles-Dominique *et al.* 1981, Emmons *et al.* 1983) or complete faunas (e.g. Valverde 1964, 1967, Andrews *et al.* 1979). These studies usually associate body size with some interpretative criterion such as diet, locomotor type or position in a trophic chain. These criteria are difficult to apprehend on the basis of fossil material, and they are necessarily usually inferred indirectly and are therefore subjective.

Several authors have shown the relationship between tooth dimensions and body size in mammals (see, for example, Gould 1975, Creighton 1980, Gingerich *et al.* 1982). The strong correlation between body weight and tooth crown area permits calculations of weight on the basis of crown area (both expressed in natural logarithms). Thus, the average body weight of a fossil species can be estimated from tooth crown area.

In the following analysis, the species are grouped into three sets : the small-sized group with a body weight less than 500 g, the medium-sized set between 500 g and 8 kg, and the large-sized category more than 8 kg. The thresholds of 500 g and 8 kg are empirically determined by the study of modern faunas (see below).

BODY WEIGHT-TOOTH AREA CORRELATION

The first step in the analysis was to estimate the degree of correlation and the regression parameters for tooth size and body size in different groups of Recent mammals, using standard least-squares regression. The tooth selected for this study is M/1 which is generally considered to be the least variable in mammals (Gingerich 1974). Nevertheless, this minimal variability of M/1 is not an absolute rule for all groups (see, for example, Gingerich and Ryan 1979).

Sexual dimorphism was not taken into account in the analysis of Recent mammals; the mean size was calculated for entire tooth sample for each species. Similarly the body weight used corresponds to a mean for all specimens (males and females). Data on primates are from Gingerich *et al.* (1982). For the other groups, tooth measurements were taken on specimens in the zoological collections of the University of Montpellier II. Body weights were taken from the literature (see below). All computations were made using the natural logarithm of the crown area of M/1 (length × width) and body weight. Method for computation is explained in Gingerich *et al.* (1982) and Gingerich and Smith (1984).

The results obtained (Table 1) show that the correlations between M/1 crown area and body weight are always very high among the various taxonomic groups, but the parameters of the allometric ratio differ among the higher taxa. Some comments on these parameters can be made : it seems that the body weight/tooth area relationship is more closely related to diet than to size classes of species (see also : Gingerich and Smith 1984). Thus, the body weight/tooth crown area correlation is lower when all mammals are grouped into size classes (i.e. small mammals with body weight less than 500 g versus larger ones). But the crown area of M/1 appears to be proportionally smaller for the herbivores (the smallest area is for the primates) than for insectivores and carnivores, the latter having the greatest M/1 area for a given body weight (tooth size here being based on the lower carnassial).

Systematic grouping	N	Correlation coefficient	Slope (a)	Intercept (Ln b)
All mammals	152	0.978	1.827	1.810
Herbivores : rodents, primates, artiodactyls, perissodactyls	83	0.982	1.693	2.694
Insectivores and carnivores : marsupials, Lipotyphla, bats, carnivores	69	0.991	1.739	1.493
Small mammals (<500 g)	58	0.885	1.621	1.786
Large mammals (>500 g)	94	0.940	1.538	3.115
Insectivores (*)	12	0.960	1.654	1.746
Bats (*)	34	0.960	1.289	1.829
Carnivores (*)	23	0.980	1.922	0.709
Primates (*) (data from Gingerich *et al.* 1982)	42	0.966	1.490	3.577
Rodents (*)	19	0.981	1.767	2.172
Artiodactyls + perissodactyls (*)	22	0.954	1.564	3.267

TABLE 1

Correlation coefficients and parameters for predicting body weight from the M/1 crown area in mammals. The computations were made with the natural logarithm of data. The regression equation is $\ln X = a \ln Y + \ln b$, where X is the body weight (in g), Y the crown area (length × width, in mm), a the slope and ln b the intercept. N is the number of species used in the calculations. (*) Parameters used in this study.

CENOGRAMS

Valverde (1964, 1967), in a study of a Recent vertebrate community from southern Spain, proposed a method for analysing the relationship between the size of predators and their prey. He concluded that amphibians, reptiles and mammals are trophically grouped into "microcommunities", each of which is structured and practically independent of the others. Valverde also studied the size of mammals in a "mastocenosis" (i.e. a mammalian microcommunity). He constructed a "cenogramic curve" or "cenogram" for a mammalian community, plotting the body size of each mammal (using head-body length) on the Y-axis and the rank order of their size on the X-axis. The species were divided into three groups on the basis of trophic criteria : entomophagous, phytophagous, and predators. Valverde thus connects predators with their prey, showing that species that are potential prey are generally either large or small, whereas the predators are usually intermediate in size.

Valverde's method is here extended to fossils, using the estimated average body weight. Ancient faunas are analysed not only to clarify possible trophic relationships among the taxa, but also to understand their general structure (Legendre and Sudre 1984).

FAUNAL DATA

Recent faunas, mainly from Africa, were studied and used for comparisons with fossils communities. Faunal lists from various Recent localities, with environments ranging from tropical rain forest to desert, are taken from the literature : Aghbolagh, Iranian Kurdistan (Misonne 1959); Doñana, southern Spain (Valverde 1967); High-Ivindo, Gabon (Emmons *et al.* 1983, Duplantier pers. commun.); Kagera Park, Rwanda (Misonne 1965, Verschuren 1965); Algerian northern Sahara (Kowalski pers. commun.); and Rutschuru, Albert Park, Zaire (Frechkop 1938, 1943, Bourlière and Verschuren 1960). Body weight references were either provided in the cited papers or were taken from treatrises (e.g. Eisenberg 1981, Kingdon 1971-1974, Nowak and Paradiso 1983).

The principal fossil localities included in this work are mainly karst fissure-fillings of the "Phosphorites du Quercy" (southern France). Faunal lists were based exclusively on material from new records provided by the excavations started in 1965 by the Laboratories of Paleontology at the Universities of Montpellier II and Paris VI.

The fossil material studied here was collected using excavation on site and screen washing followed by sorting of matrix in the laboratory. The faunas are chronologically homogeneous (Vianey-Liaud 1969, Vianey-Liaud and Legendre 1986). The various vertebrate groups were studied by the following specialists : amphibians, squamates (J.-C. Rage), turtles (F. de Broin), crocodiles (E. Buffetaut), birds (C. Mourer-Chauviré), marsupials, Oligocene insectivores, Eocene creodonts and carnivores (J.-Y. Crochet), Eocene insectivores, bats (B. Sigé), primates (M. Godinot), creodonts (B. Lange-Badré), carnivores, Oligocene perissodactyls (L. de Bonis), Eocene rodents (J.-L. Hartenberger), Oligocene rodents (M. Vianey-Liaud), Eocene and Oligocene artiodactyls (J. Sudre), and Eocene perissodactyls (J.A. Remy).

More than 70 mammal-bearing localities are known to date in the "Phosphorites du Quercy". Their ages range from the late Eocene to the late Oligocene (see Russell

	STAGES		MAMMAL REFERENCE LEVELS	LOCALITIES	
				QUERCY	(SE FRANCE)
			CODERET		
24.5	OLIGOCENE	Stampian	RICKENBACH		
			BONINGEN	Pech du Fraysse, etc.	Cournon *
			MAS DE PAUFFIE	Mas de Pauffié, etc.	
			ANTOINGT	Rigal - Jouet, etc.	
			HEIMERSHEIM	Belgarric	
			LES CHAPELINS	Genebrières 1	
			MONTALBAN	Pech Crabit, etc.	
			VILLEBRAMAR	Mas de Got, etc.	
			HOOGBUTSEL	Aubrelong 1, etc.	
36				• GRANDE COUPURE •	
		Ludian	FROHNSTETTEN		
			MONTMARTRE	Escamps, etc.	
			LA DEBRUGE	Sainte - Néboule, etc.	
	EOCENE		PERRIERE	Perrière, etc.	
			FONS 4	La Bouffie, etc.	
41		Marinesian	GRISOLLES	Le Bretou	
			ROBIAC		Robiac *

et al. 1982). Seven faunas of high diversity were selected for this study, covering all the stated interval of geological time (i.e. the late Eocene to late Oligocene). Two other faunas were also considered in this work, those from Robiac (Gard, southern France) and Cournon (Puy-de-Dôme, central France), because of : (1) their ages (these localities are considered to be contemporary with the oldest and youngest localities from Quercy respectively); (2) their diversity (62 species are listed for Robiac and 40 species are listed for Cournon); and (3) their geographical situation (they are about 200 km away from the Quercy localities) (Figure 1). These faunas from stratified deposits are thus used as a reference and provide a comparison to those of Quercy, which are all obtained from fissure-fillings.

The lists of species were obtained from the faunal evaluation of De Bonis *et al.* (1973) and Crochet *et al.* (1981) for Quercy, Sudre (1969) for Robiac, and Brunet *et al.* (1981) for Cournon. These were supplemented (except for Cournon) with unpublished data based on the collections of the University of Montpellier II as reported by the specialists of the Laboratory of Paleontology. The measurements of the first lower molar, which are used in this work for methodological reasons explained above, were made on the material in the same collections. In rare cases when this tooth was missing in the samples, measurements were extrapolated either from a sample of the same species in contemporaneous localities (or in noncontemporaneous localities when the known dimensions were the same) or from samples of taxonomically and biometrically similar species. The regression parameters used in the estimation of body weight are those marked with an asterisk in Table 1.

Fig. 1. — Position of the localities in the European biochronological time scale. The biochronological positions and the ages are taken from Russell *et al.* (1982). (*) Fluvio-lacustrine deposits; all other deposits are fissure-fillings from the "Phosphorites du Quercy". The localities analysed in this study are underlined.

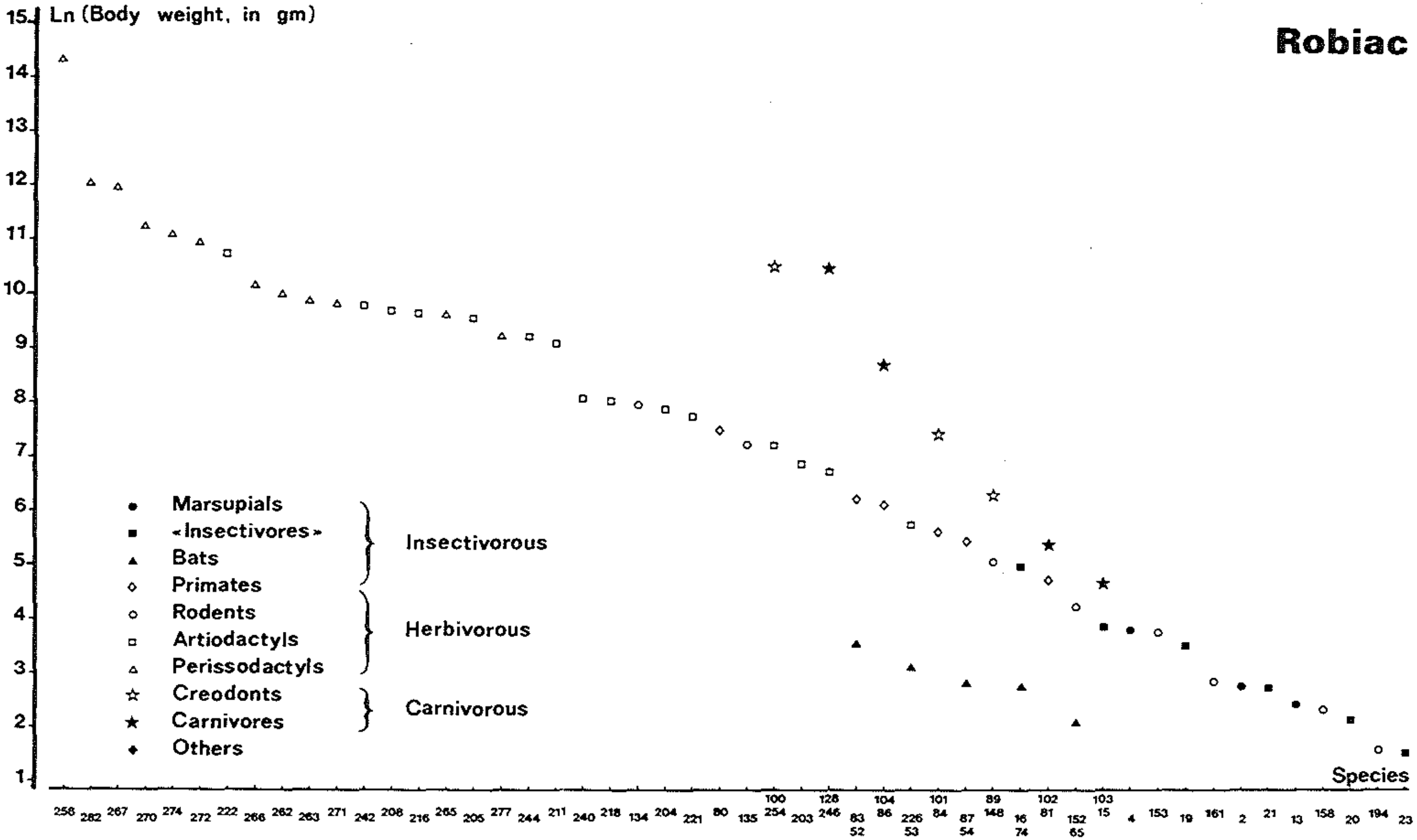

Fig. 2. — Cenogram of fossil fauna from Robiac (South of France). The average body weight (expressed in natural logarithm) of all species is plotted on the Y-axis and the rank of the species in decreasing order of size on the X-axis. The non-predatory mammals are set on a main curve, with the carnivores above and the bats below. Numbers under the abcissa are reference numbers allocated to each species in a master list established for all the localities used in this study (Legendre 1985).

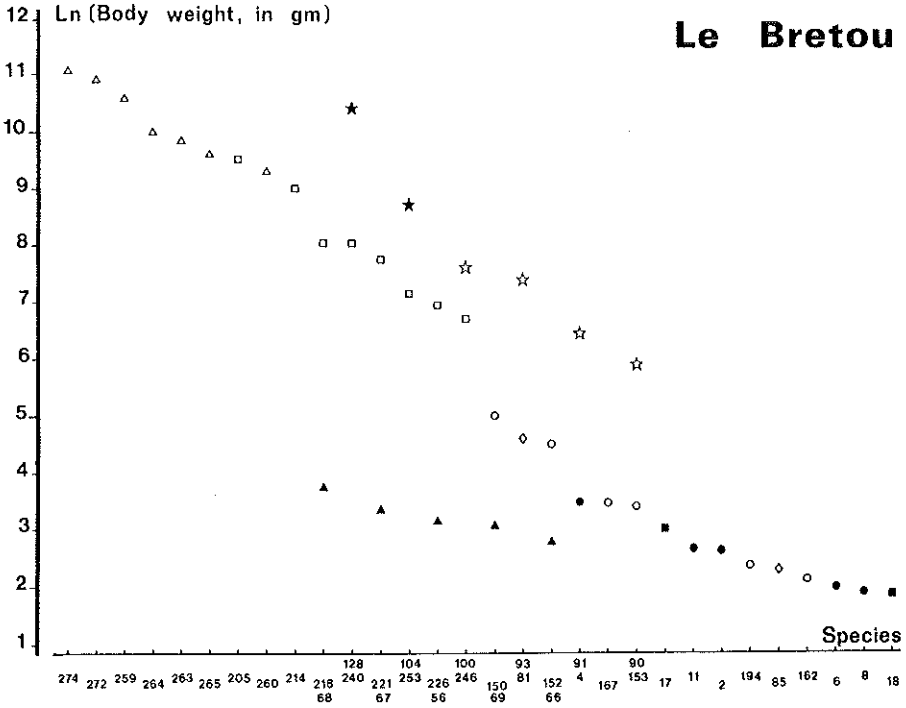

Fig. 3. — Cenogram of fossil fauna from Le Bretou (Quercy, France). Conventions as in Figure 2.

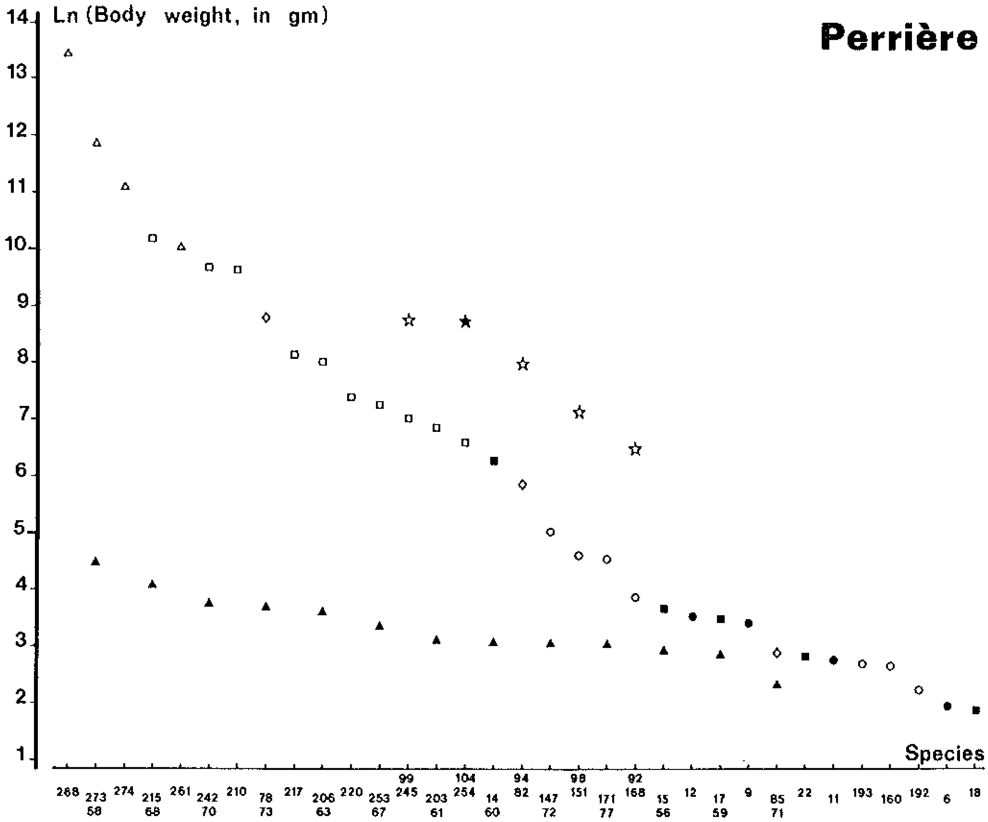

Fig. 4. — Cenogram of fossil fauna from Perrière (Quercy, France). Conventions as in Figure 2.

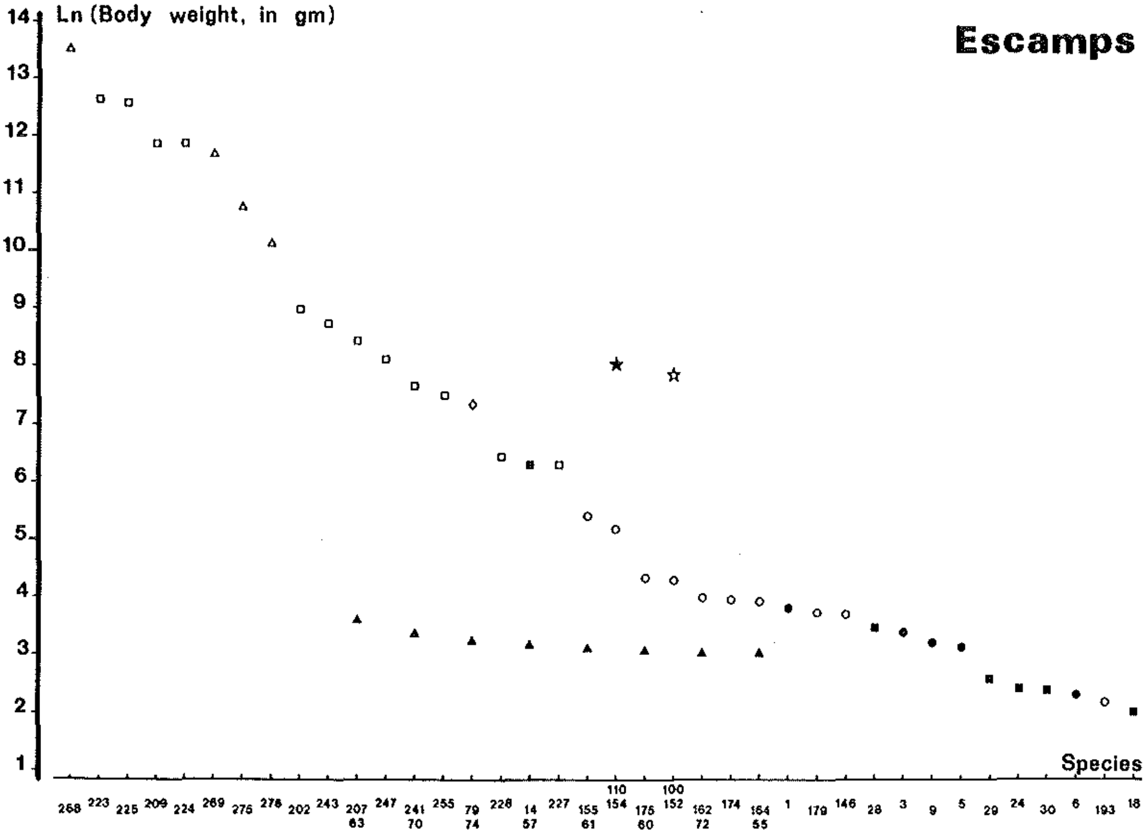

Fig. 5. — Cenogram of fossil fauna from Escamps (Quercy, France). Conventions as in Figure 2.

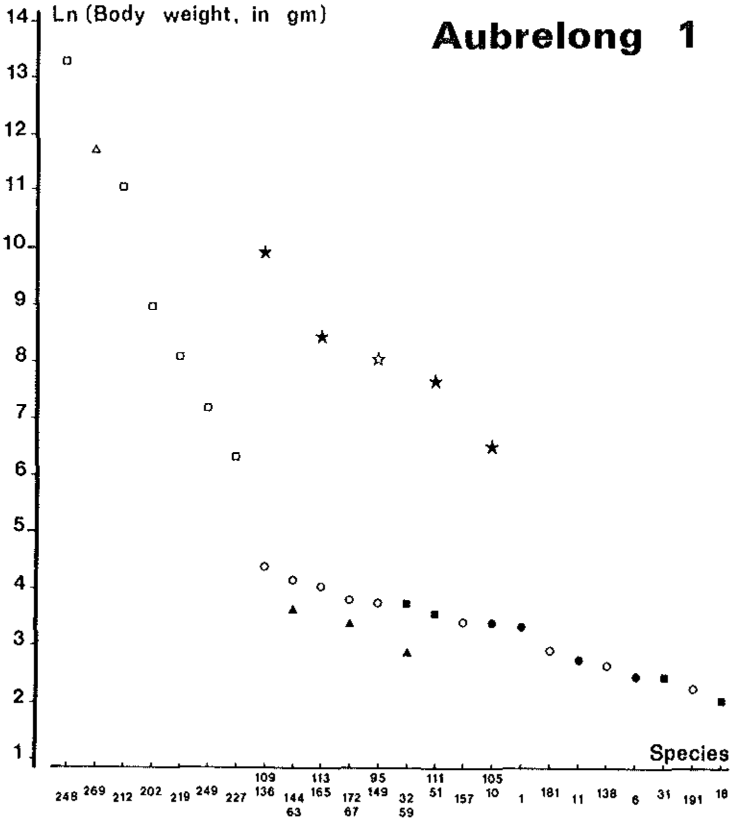

Fig. 6. — Cenogram of fossil fauna from Aubrelong 1 Quercy, France). Conventions as in Figure 2.

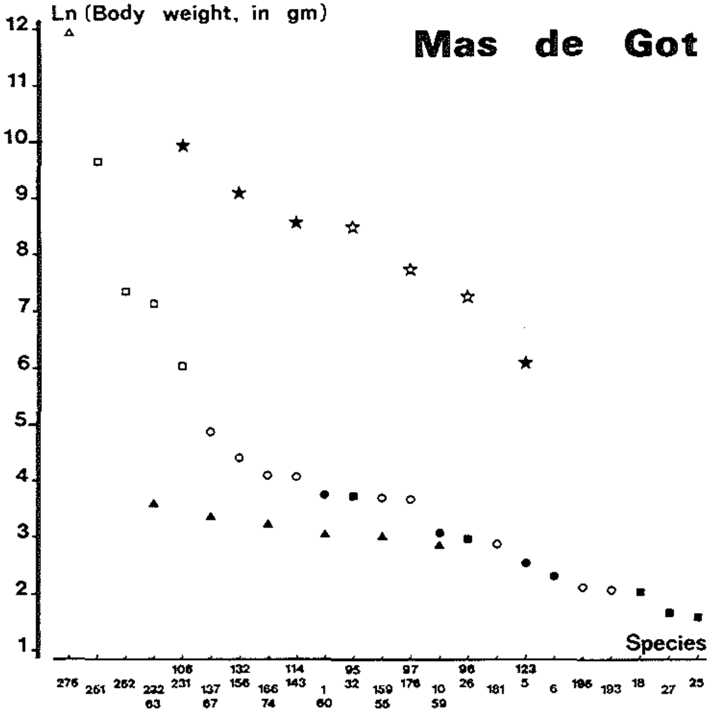

Fig. 7. — Cenogram of fossil fauna from Mas de Got (Quercy, France). Conventions as in Figure 2.

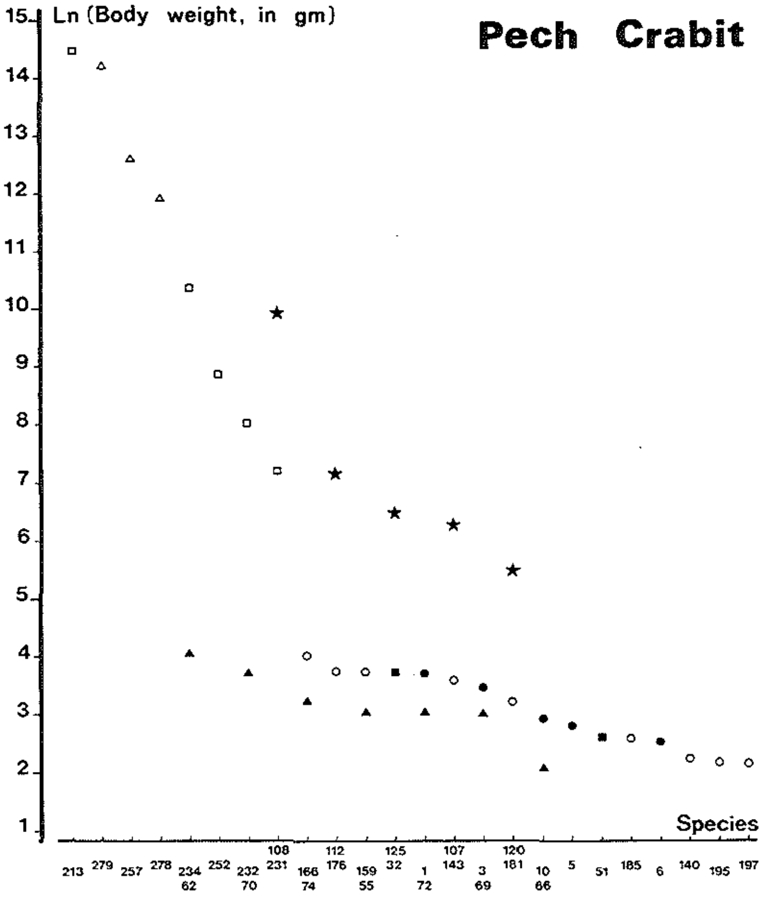

Fig. 8. — Cenogram of fossil fauna from Pech Crabit (Quercy, France). Conventions as in Figure 2.

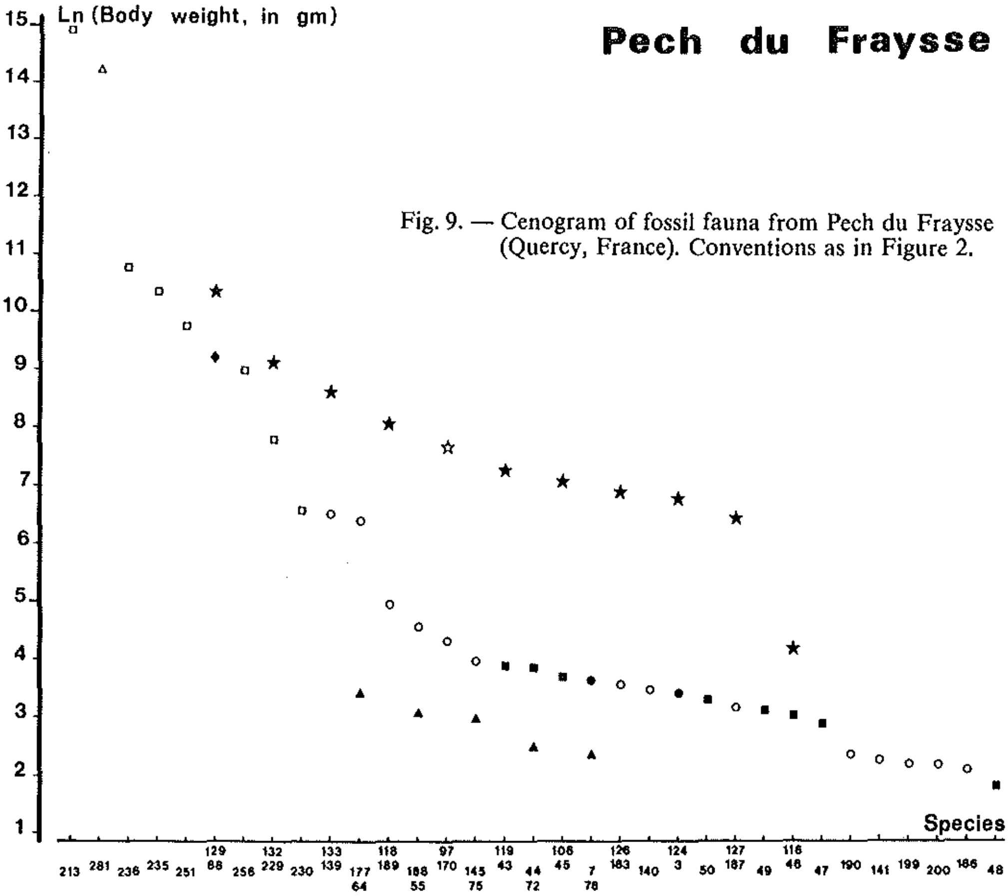

Fig. 9. — Cenogram of fossil fauna from Pech du Fraysse (Quercy, France). Conventions as in Figure 2.

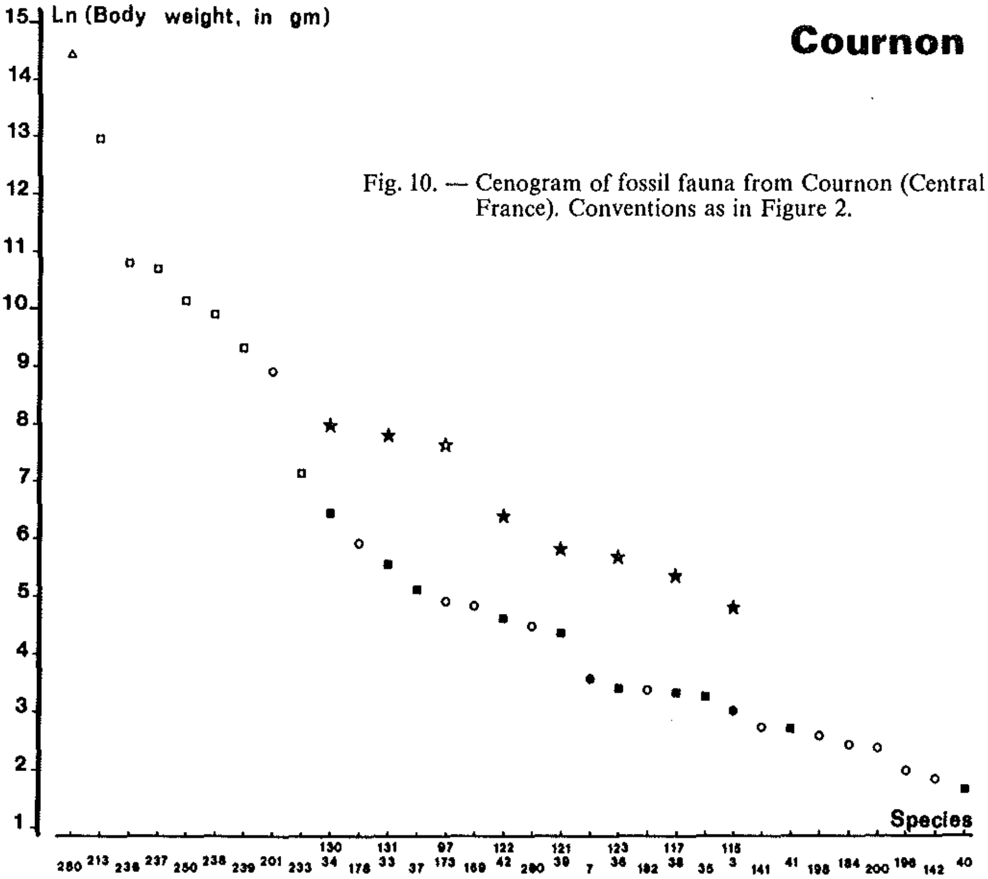

Fig. 10. — Cenogram of fossil fauna from Cournon (Central France). Conventions as in Figure 2.

RESULTS

Cenograms were constructed for the various fossil faunas considered in this work. They are here plotted on a main curve in decreasing size order for the species subject to predation. The carnivores are set above this curve, and the bats below (Figs 2-10).

The regression line of body weight of the rank of the species defines these cenograms. Their slope reflects the number of species in the body weight interval considered : a gentle slope points to a great number of species in the body weight interval, whereas a pronounced slope indicates a smaller number of taxa. It is applied to the main curve, but not to the predatory and flying mammals (Figs 11-13).

RECENT FAUNAS

Recent faunas representing diverse environmental types are examined here : intertropical forest (High-Ivindo Valley, Gabon), wooded savannah (Kagera Park, Rwanda) or savannah (Rutschuru, Zaire), desert (Aghbolagh, Iranian Kurdistan; Berber area, Algeria) and Mediterranean area (Doñana, Spain). It seems that faunas from forest or wooded savannah in tropical environments provide curves in which the slope for small and largest size remains the same : the species are almost homogeneously distributed (Fig. 11 a-c). The distribution is continuous in closed environment (Fig. 11 a) whereas a gap in medium-body weight (500 g - 8000 g) seems to appear in more open environments (Fig. 11 b-c). A change of slope can be in samples from more arid environments, where it is very pronounced between small and large species, the latter being rare. This phenomenon, which is quite noticeable in savannah environments (Fig. 11 c), is more marked in desert environments (Fig. 11 d-e). In the arid Mediterranean areas, the entire fauna is impoverished, giving more pronounced slopes (Fig. 11 f).

Given these observations, some empirical rules can be established for the analysis of the cenograms :

1. a gap in the medium-sized species should indicate an open environment whereas a more continuous distribution of the species should suggest a more closed one;
2. the slope for the large mammals reflects the degree of aridity of their environment : the more pronounced the slope, the more arid is the environment;
3. the slope observed for the small-sized species could be an index of minimal temperatures : in more temperate conditions, there are fewer small species than found in tropical conditions.

FAUNAS FROM THE LATE EOCENE TO LATE OLIGOCENE

The size range for the analysed fossil faunas is considerable : the body weights of species range from several grams to more than 100 kilograms. The number of predators tends to be somewhat biased : for some faunas (Perrière, Escamps), they seem to be under-represented, especially for the small sizes; for the other faunas, the predators are reresented by the size observed in Recent faunas studied here (from 100 g to 100 kg or so).

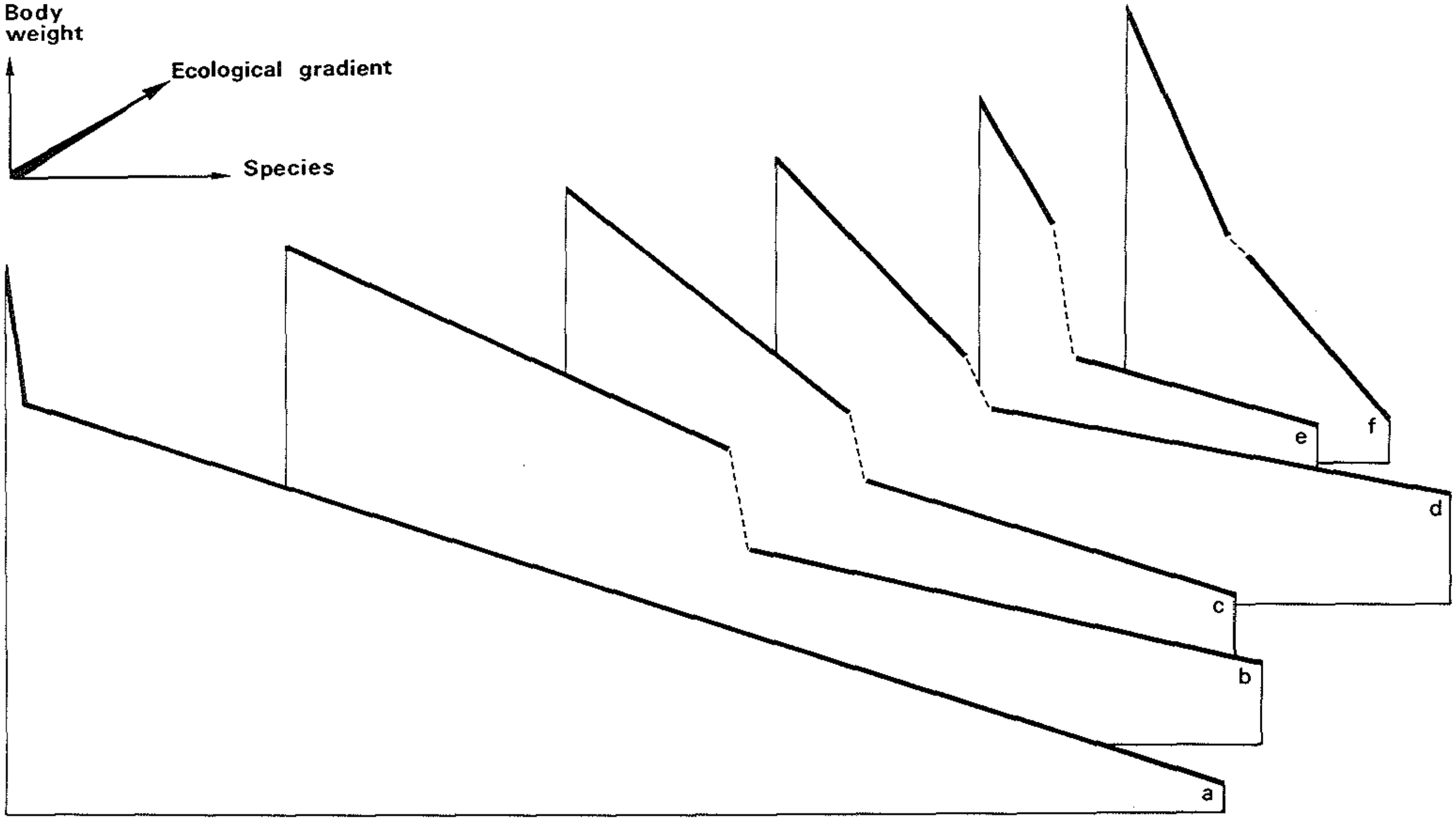

Fig. 11. — Cenograms of modern faunas. A regression line of body weight versus species if drawn for the main curve of cenograms. a - High Ivindo (Gabon) : tropical rainforest environment; b - Kagera Park (Rwanda) : tropical wooded savannah; c - Rutshuru (Zaire) : tropical savannah; d - Algerian Northern Sahara (Algeria) : predesert; e - Aghbolagh (Iran) : desert; f - Doñana (Spain) : Mediterranean arid zone. From left to right, the ecological gradient is humid and wooded to arid and open environements. A gap in medium-sized species occurs in open environment type (b to e); large-sized species are less abundant in arid zones (d to f); in higher latitudes, the entire fauna is impoverished (f).

The composition of faunas, as observed in the cenograms, seems to be generally consistent and cannot result from the way that the local faunas accumulated. The configuration of the Eocene mammalian communities at Robiac (Fig. 13 a) and the Oligocene mammalian communities at Cournon (Fig. 13 b) (both of which are fluvio-lacustrine deposits) fits with those from the Quercy (fissure-fillings).

The regular and similar shape of the cenogramic curves of fossil faunas leads to two important conclusions :

1. The diversity of the faunas appears to be nearly complete regarding the breadth of the faunal spectrum represented.
2. Possible specific gaps in faunas cannot be to size filtering during the formation of the fossil assemblage or due to the method of exploitation of the fossil deposits.

Thus, when a fossil fauna has a large diversity (i.e., at least 30 species), studies must consider limits of the size spectrum so that any gaps in size and even lack of some taxonomic groups may be considered to be consistent with biological or ecological reality for this fauna. Therefore, interpretations need not be restricted by the alleged deficiencies in the composition of the faunas. Arguments based on the completeness and the potential reality of a fossil animal community are valuable because of what they provide for debates on evolution; in contrast, *a priori* rejection of the biological reality of fossil assemblages automatically condemns them as worthless to paleontology.

DISCUSSION

COMPARISONS BETWEEN FOSSIL AND RECENT FAUNAS

The cenograms of fossil faunas (Figs 12-13) show that the slopes are relatively constant for the small sizes (<500 g). This distribution is to be found for the whole period considered. The slopes observed for the larger species (>500 g) are more variable, but the curves can be divided into two major groups : the oldest faunas (Figs 12 a-c, 13 a) have a greater number of taxa than the youngest ones (Figs 12 d-g, 13 b). This characteristic, which appears to be constant in the nine faunas studied, cannot be due to fossilization bias. A major paleobiogeographical event, the so-called "Grande Coupure" of Stehlin (1909), occurs in Europe between these two modal faunal types; extinctions and immigrations determine the faunal turnover at the "Grande Coupure" and introduce a drastic change in faunal configuration.

If we compare these cenograms to those obtained from Recent biota, the curves of mammalian faunas preceding the "Grande Coupure" (Figs 12 a-c and 13 a) have the same shape as those observed in the intertropical environments of Africa (Fig. 11 a-c). We can find faunal types comparable to those of the Oligocene (Figs 12 d-g and 13 b) only in the biotopes for the desert environments (Fig. 11 d-e); thus late Eocene environments from Quercy could be of tropical forest or savannah type, and those of the Oligocene of desert or predesert type. This assessment seems to be consistent with geological data (Astruc 1979, Muratet *et al.* 1985). Results from investigation in other disciplines (like taphonomy, palynology, paleobotany) in the Quercy area may test the validity of this conclusion.

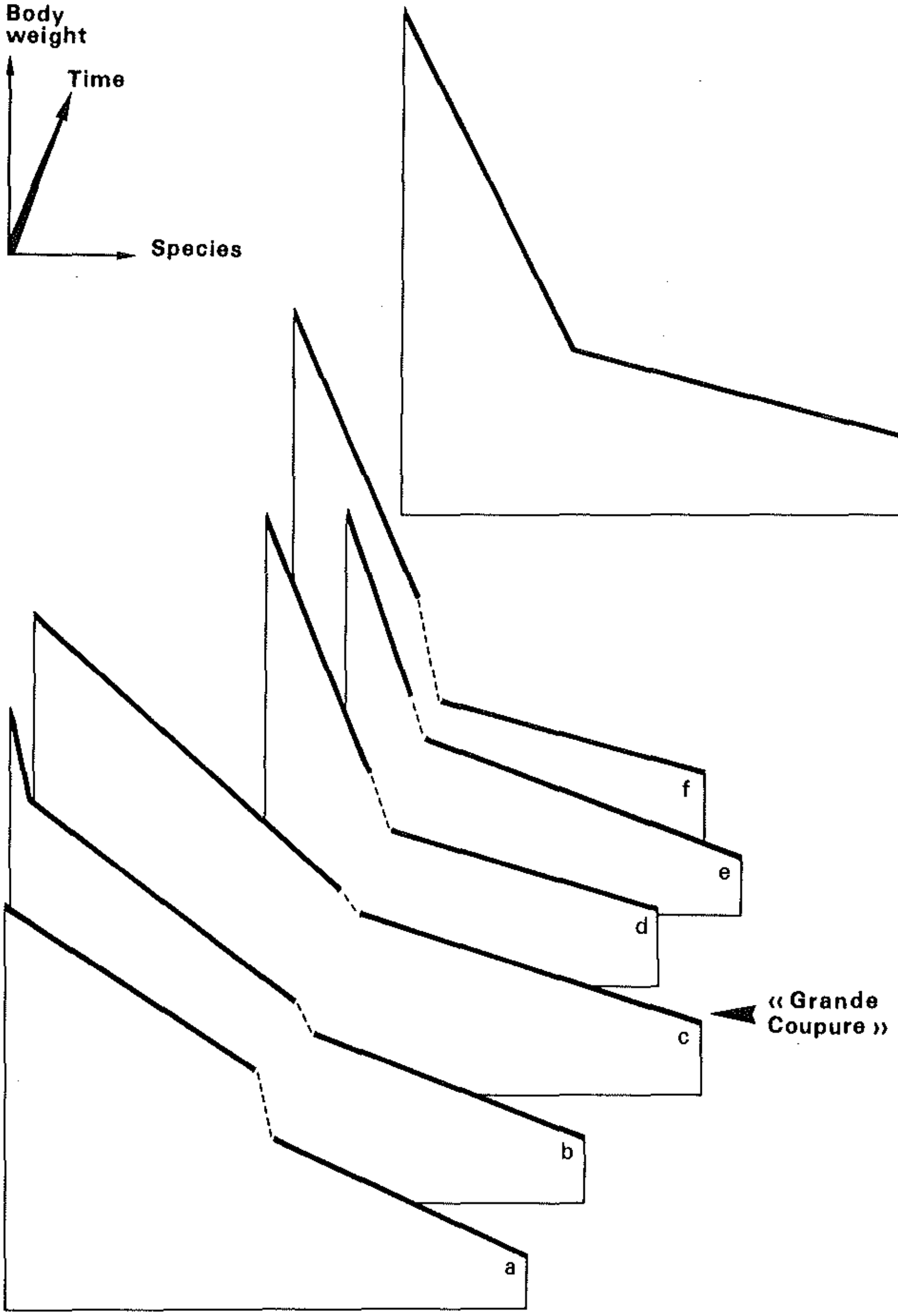

Fig. 12. — Cenograms of the fossil faunas from the "Phosphorites du Quercy". a - Le Bretou ; b - Perrière ; c - Escamps ; d - Aubrelong 1 ; e - Mas de Got ; f - Pech Crabit ; g - Pech du Fraysse. Before the "Grande Coupure" (a-c), the cenograms are similar to those obtained in tropical rainforest or savannah environments (Fig. 11 a-c), whereas after the "Grande Coupure" (d-g), they are comparable to those of desert zones (Fig. 11 d-e).

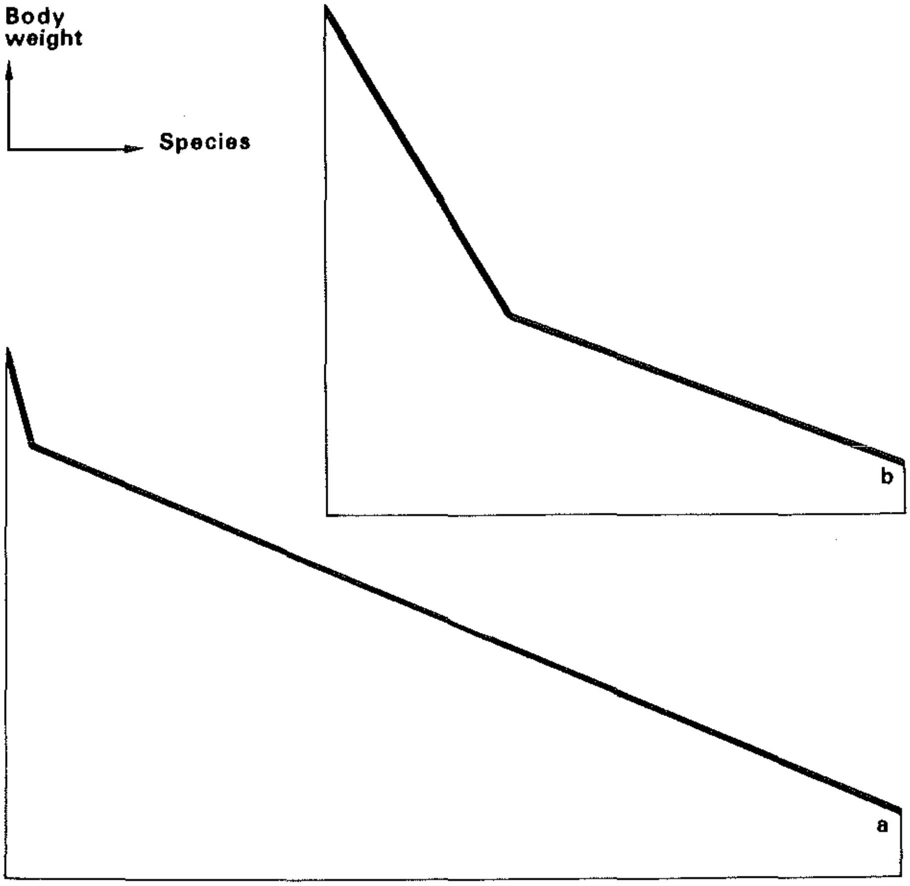

Fig. 13. — Cenograms of two fossil faunas from fluvio-lacustrine deposits. a - Robiac (penicontemporaneous with the locality of Le Bretou, Quercy); b - Cournon (contemporaneous with that of Pech du Fraysse, Quercy). The cenogram of Robiac (a) is similar to that of tropical rainforest environment (Fig. 11a) and agrees in general climatic conditions to faunas from the "Phosphorites du Quercy" before the "Grande Coupure" (Fig. 12 a-c). The diagram of Cournon (b) is the same as that of Pech du Fraysse (Fig. 12 g) and is like that of Recent predesert zones (Fig. 11 d).

A more detailed investigation of the taxonomic composition of fossil faunas shows that rodents become proportionally more important in diversity relative to ungulates after the "Grande Coupure" (Fig. 14). An evolutionary transfer of trophic functions (among the herbivorous types in this case) might have occurred at this period between higher taxa in the Eocene and Oligocene ecosystems of Quercy : rodents may have partly replaced ungulates among herbivores.

The so called Terminal Eocene Event ("Grande Coupure") appears to be worldwide. It is observed in mammalian faunas (Hartenberger 1973, 1983, Prothero 1985, Vianey-Liaud 1979, 1985) as well as in plants (Wolfe 1978), pollen (Gorin 1975, Bessedik 1983, Hubbard and Boulter 1983), and marine records (for a review see Cavelier 1979, Corliss *et al.* 1984). Various authors generally agree that the event

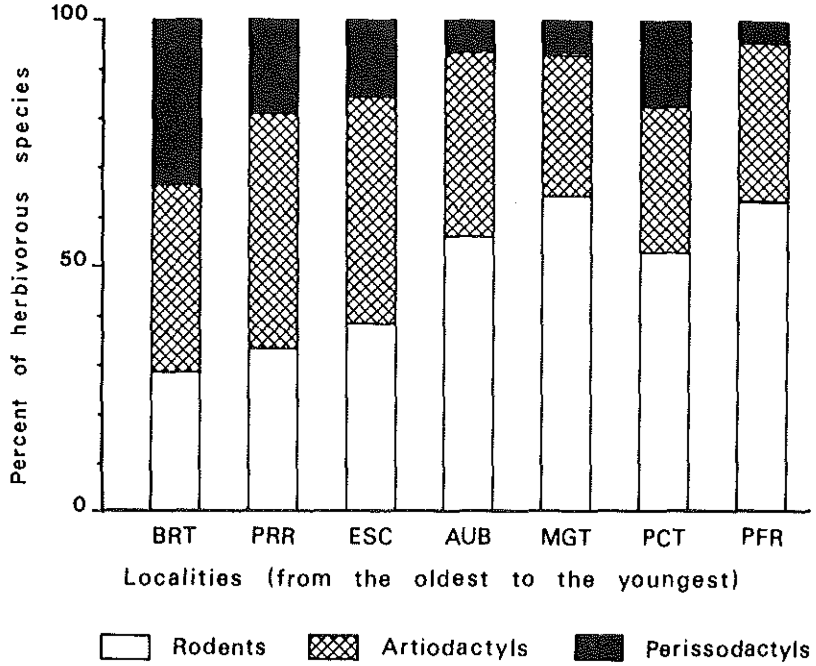

Fig. 14. — Relative proportion of the number of species of ungulates (Artiodactyla + Perissodactyla) with respect to that of rodents in the faunas from the "Phosphorites du Quercy". AUB : Aubrelong 1; BRT : Le Bretou; ESC : Escamps; MGT : Mas de Got; PCT : Pech Crabit; PFR : Pech du Fraysse; PRR : Perrière. After the "Grande Coupure", which occurs between the localities of Escamps and Aubrelong 1, rodent species are more numerous than ungulates.

seems more to be a progressive turnover in species and morphological modifications within lineages, associated with climatic cooling, than a catastrophic event. The paleogeographic change occurring with the connection of Europe to Asia in consequence to the closing of the Turgai Straits (Pomerol 1973) explains the arrival of new taxa in terrestrial European faunas at the beginning of the Oligocene (Lopez and Thaler 1975, Heissig 1979, McKenna 1983), but these newcomers do not reach Europe at the same time (Schmidt-Kittler and Vianey-Liaud 1975), and some immigrants precede this wave (Sigé 1976, Sudre 1978, Sigé and Vianey-Liaud 1979). It is here shown that an important ecological modification must be invoked for the drastic change in the configuration of mammalian communities, even though this was not revealed so clearly before. The biogeographical event occurring among mammals in Western Europe at the Eocene-Oligocene Boundary coincides with a sudden ecological change due ultimately to climate alteration.

EVOLUTIONARY MODES OF THE COMMUNITIES

When drastic ecological changes occur, communities are modified in their configuration, as the shape of the cenograms shows. *In situ* phyletic evolution, as well as extinction and immigration of species, leads to change in both species composition and community structure (Fowler and MacMahon 1982, Futuyama and Slatkin 1983). Local extinction and immigration tend to promote the fitness of a community to its environment. But each component species does not reach its ecological optimum because of continuous environmental perturbations; when major or minor additional perturbations extend beyond the threshold of evolutionary capacity of a species, it becomes extinct (Van Valen 1973 a). Thus, these extinctions, which occur continually but sporadically, may not discriminate minor from major ecological changes. However, the study of cenogram sequences can easily distinguish a drastic habitat perturbation from less significant ones.

We reach the following conclusion : species interact with their environment and therefore adapt themselves continuously, more or less quickly, to it, or disappear, independently of the importance of the ecological change. Conversely, the community reacts to major and sudden changes but not to less important fluctuations in the ecosystems. This study provides an example of this statement at the Eocene-Oligocene Boundary : whereas the evolution of mammal lineages and of the species turnover in the successive faunas do not indicate any clearly catastrophic event (as expounded above), the cenogram analysis reveals a major ecological change.

CONCLUSION

The first result of this study is to provide an empirical model for mammalian communities. It thus contributes to elaboration of a theory of ecosystems as proposed by Maynard Smith (1982), Stenseth and Maynard Smith (1984) and Damuth (1985). The method of analysis (i.e. the use of cenogramic curves) shows that mammalian communities seem to be structured : make-up of mammalian faunas should be governed by environmental criteria and one of its important expressions is the mean body weight of each component species.

A tentative typology of cenograms of extant faunas is made. The analysis of cenograms permits one to infer some general aspects of the physical environment of fossil communities. The assumption of ecological actualism which is used in this case can be tested by independent data, taken for example from the fields of geology, taphonomy, and palynology.

On another level, some conclusions were reached concerning what can be inferred from the configuration of successive fossil mammalian communities : in the absence of strong environmental perturbations, the structure of the fauna remains stable, but modification of the shape of cenogramic curves reveals the occurrence of a major ecological change together with a notion of its rate of change.

These different aspects were illustrated by the study of several fossil faunas from the "Phosphorites du Quercy" which cover an interval of Paleogene time of about 15 ma duration. In this way, a drastic ecological change is shown to occur at the Eocene-Oligocene Boundary, at least in southwestern Europe : following conditions similar to those of the Recent intertropical environment, desertification caused the establishment of faunal types similar to those observed in Recent times only in desert or subdesert zones.

This general approach should contribute to developing a methodological link between paleontological and neontological models in research on evolution, especially mammalian evolution. Indeed, if an accurate basis for comparison with Recent fossil faunas could be found, the search for an ecological equivalent of the species of ancient communities would be easier and the reconstruction of its life environment more surely established. Then many hypotheses relating to evolutionary modes would be easier to test which fossil data.

ACKNOWLEDGEMENTS

I wish to thank B. Sigé for many helpful discussions during the development of this research. L. Thaler, J.-L. Hartenberger, M. Vianey-Liaud, Ph. D. Gingerich, R.D. Prothero, J.J. Sepkoski, M. Pickford, J. Damuth and an anonymous reviewer read early drafts of the manuscript and made several suggestions for its improvement. I am indebted to all researchers of the Laboratory of Paleontology of the University of Montpellier II, who enabled me to work on the "Phosphorites du Quercy" and the fossil material they collected and studied for many years. Photographic reproductions of figures are by J. Martin.

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