

Mammalian faunas as paleotemperature indicators: concordance between oceanic and terrestrial paleontological evidence.

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Received 13 October 1986, 2 March 1987

ABSTRACT: The mean number of species per family in the mammalian faunas of late Paleogene deposits of Quercy (France) was computed for each reference level. The curve obtained for the sequence is compared to a $\delta^{18}\text{O}$ curve obtained from benthic Foraminifera of the Atlantic and Pacific Oceans. The fit of the two curves suggests that continental paleotemperatures may be obtained from the ratio species/families.

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The vertebrate localities of Quercy (Southern France) have yielded faunas which have been the subject of phylogenetic, systematic and paleobiogeographical studies (for references see Vianey-Liaud and Legendre 1986). In addition, a paleoecological analysis of the mammalian communities has been completed (Legendre 1986). A coincidence is here shown between the species/family ratio (S/F index) of these faunas and the isotopic ($\delta^{18}\text{O}$) curve obtained from benthic Foraminifera.

MATERIALS AND METHOD

The vertebrate fossil localities of Quercy (southern France) are situated in an area of approximately 60 km diameter. The duration of the sequence is about 15 MY, from the late Eocene to the late Oligocene. All the collections on which this study is based have been made by expeditions of the Universities of Montpellier and Paris VI, from 1965. Each locality has yielded a homogeneous fauna which can unequivocally be correlated to the biochronological scale of the western European Paleogene (Vianey-Liaud and Legendre 1986). The mammalian faunas in the new collections (80 distinct localities are known up to now) are grouped into 12 standard levels ("niveaux repères") mainly on the basis of rodent biostratigraphy (Hartenberger 1973, Vianey-Liaud 1979, Crochet *et al.* 1981) (Fig. 1).

For this study, lists of species and families were established for each locality based on the most recent studies of the systematics and evolution of the various taxonomic groups. The carnivores were excluded because no recent work has focused on the new material. The lists were based on compilations by De Bonis *et al.* (1973), Crochet *et al.* (1981) and Legendre (1985), to which were added the results of specialized studies of these faunas (Bouvrain *et al.* 1986, Cavaillé *et al.* 1974, Comte 1985, Crochet 1971, 1980, Gèze *et al.* 1978, Godinot 1983, 1984, Hartenberger 1973, Hartenberger and Schmidt-Kittler 1976, Hugueney and Vianey-Liaud 1980, Legendre 1985, Schmidt-Kittler and Vianey-Liaud 1979, Sigé 1974, 1975, 1976, Sigé and Legendre 1983, Sudre 1978, 1984, 1986, Vianey-Liaud 1969, 1972a, 1972b, 1974a, 1974b, 1976, 1979, 1985). They are complemented by unpublished data on material housed in the paleontological collection of the University of Montpellier.

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Evolutionary Theory 8: 77-86 (September, 1987)

The editors thank F.W. Flessa and D.R. Prothero for help in evaluating this paper.

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Faunal lists were established for each reference level by compiling data from all localities referred with certainty to each reference level. In the case of theridomyoid rodents, the sub-families of Hartenberger (1971) were treated as families. When a species (or a family) was not represented in a given level, but present in the two immediately adjacent levels, it was counted as though it were present in this level and included in the faunal list. In contrast, if a lineage (or a family) was missing in two successive levels, it was considered to be really absent from the Quercy area, and was therefore not counted in the faunal elements of these levels. This is based on the fact that the number of localities per level and the quality of their fossil records are high. Therefore, the possibility of introducing a bias from taphonomic or sorting reasons appears to be low, and the absence is more realistically to be interpreted as representing a local disappearance from the relatively restricted area comprising Quercy. For example, the rodent family Ischyromyidae is known from the levels represented by Le Bretou and Escamps but has never been found in the intermediate levels of Aubrelong 2, Perrière and Gousnat (comprising more than 20 discrete faunas): the hypothesis postulated here is that during this period the geographic range of the family did not include the Quercy area. The same approach was adopted for species - and family - level calculations. For this reason, the "species" employed in my calculations are understood to be specific lineages and are not based on their names, i.e. their taxonomic status.

The biochronological reference levels were then arranged against an absolute time scale based on various synthetic works (Anadon *et al.* 1983, Crochet *et al.* 1984, Russell *et al.* 1982, Pomerol and Premoli-Silva 1986). The absolute age refers to the geochronological time scale given by Cavelier and Pomerol (1983) and Berggren *et al.* (1985). Absolute datings or direct correlations between mammalian biochronological and geochronological time scales are rare for the late

Epoch Stage		Reference level	Quercy
Oligocene	CHATTIAN	RICKENBACH	
		BONINGEN	Pech du Fraysse...
		MAS DE PAUFFIE	Mas de Pauffié...
	STAMPIAN	ANTOINGT	Rigal-Jouet...
		LES CHAPELINS	Belgaric...
		MONTALBAN	Itardies...
		VILLEBRAMAR	Mas de Got...
	LUDIAN	HOOGBUTSEL	Aubrelong 1...
		ESCAMPS	Escamps...
		LA DEBRUGE	Gousnat...
		PERRIERE	Perrière...
		FONS 4	Aubrelong 2...
		GRISOLLES	Le Bretou...
		ROBIAC	
Eocene	MARINES		

Figure 1. Biochronological time scale of the upper Paleogene of Western Europe with the mammalian reference levels and the main localities in the Quercy area.

Eocene and Oligocene of Western Europe. According to the synthesis of Pomerol and Premoli-Silva (1986), the "Grande Coupure", occurring between the reference levels of Escamps and Hoogbutsel, was fixed at about 36 MY. The oldest locality until now reported from the phosphorites of Quercy, Le Bretou, attributed to the late Marinesian, is slightly younger than the reference level of La Livinière 2, which is correlated, on the basis of stratigraphical data, with the NP 17 zone (Anadon *et al.* 1983). Thus Le Bretou is estimated to be 42 MY. The age of the youngest Quercy locality reported until now, Pech du Fraysse, corresponds to the beginning of the late Oligocene, and is therefore estimated at about 28-27 MY. The mean duration between the reference levels is estimated to be 1.3 MY.

The isotopic ($\delta^{18}\text{O}$) curve is that furnished by Miller and Fairbanks (1985). It corresponds to a mean of data obtained from the Cenozoic benthic foraminiferal $\delta^{18}\text{O}$ in the Atlantic and Pacific Oceans plotted against absolute age. The $\delta^{18}\text{O}$ curve has been interpreted as a paleotemperature curve within oceans and for estimating continental ice-volume changes (see, for example, Vergnaud-Grazzini 1984, Vergnaud-Grazzini and Saliège 1985, Miller and Fairbanks *in press*). Major changes in sea level (Vail *et al.* 1977) during the Paleogene did not coincide with $\delta^{18}\text{O}$ events. Moreover it seems that paleobiological events cannot be related to relative sea level changes in western Europe (Hartenberger 1986).

RESULTS

A ratio was calculated for each standard level ("niveau repère") with the number of species present (S) being compared to the number of families (F), giving an index (S/F) of intrafamilial species richness per time interval. The S/F index was computed twice, firstly taking into account the Chiroptera, and secondly without this order (Table 1). Curves were then drawn plotting the various values of S/F against the absolute time scale (Figs. 3 and 4). The second curve (without Chiroptera) was calculated because of differences in representation of bats in the fossil record; the phosphorites of Quercy are fissure fillings and give a better picture of chiropteran diversity than any known stratified locality (Sigé and Legendre 1983). Thus, the latter curve will permit comparisons with non-fissure-filling sequences.

Table 1. Number of species (S) and families (F) (with/without Chiroptera) and S/F ratio for each reference level in Quercy.

Reference level	S with/without	F with/without	S/F with/without
Pech du Fraysse	44 / 40	24 / 20	1.83 / 2.00
Mas de Pauffié	27 / 24	18 / 15	1.50 / 1.60
Rigal Jouet	34 / 31	22 / 19	1.55 / 1.63
Belgaric	31 / 28	21 / 18	1.48 / 1.56
Pech Crabit	46 / 39	27 / 23	1.70 / 1.70
Mas de Got	43 / 31	23 / 18	1.87 / 1.72
Aubrelong 1	43 / 32	24 / 19	1.79 / 1.68
Escamps	60 / 47	26 / 21	2.31 / 2.24
Gousnat	61 / 48	26 / 21	2.35 / 2.29
Perrière	66 / 49	27 / 21	2.44 / 2.33
Aubrelong 2	55 / 43	24 / 19	2.29 / 2.26
Le Bretou	53 / 46	21 / 19	2.52 / 2.42

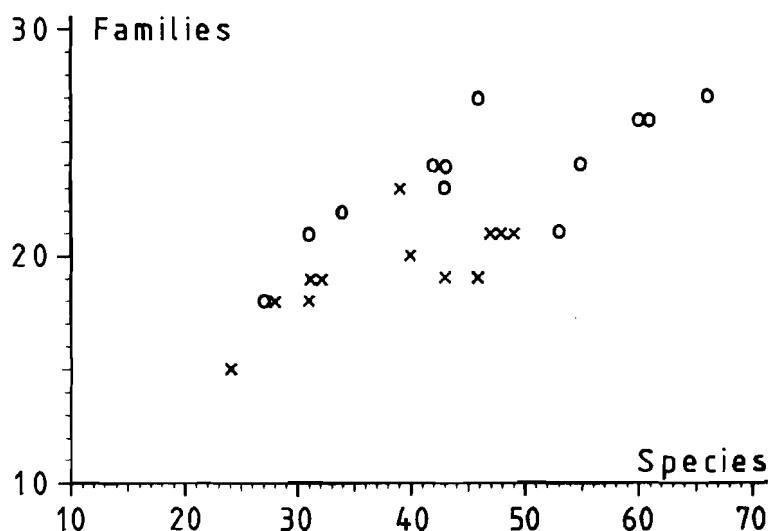


Figure 2. Number of families plotted against number of species for all mammal levels in Quercy. o: with Chiroptera; x: without chiroptera.

The species/family ratio depends mainly on species diversity (Jablonski and Flessa 1986), but changes in family number also influence it (Table 1 and Figure 2).

Figures 3 and 4 show that the curves obtained from the S/F index fit extremely well with the $\delta^{18}\text{O}$ isotopic curve, indicating close concordance between the evolution of paleotemperatures in the oceans and the fluctuation of the intra-familial species-richness index obtained from the mammals in a mid-latitude continental environment.

On the basis of this similarity, it is here suggested that the S/F index of mammals reflects paleotemperatures in terrestrial environments. This hypothesis can be tested by sequences taken from other time periods and geographical areas. For a valid test, however, the compilation of species and families should be restricted to rather small areas with chronologically continuous sequences of fossil localities. This restriction is in order to avoid taphonomic differences or faunal changes due to regional effects. For example, too great geographical areas or time gaps could alter or conceal taxonomic diversity, thereby biasing the results.

If the S/F ratio remains the same for a given $\delta^{18}\text{O}$, it should be possible to calibrate the S/F index against temperatures. This point can also be verified by comparison with extant faunas, where the parameters (numbers of species and families, and temperatures) are known, but it would be necessary to apply correction factors in order to make the fossil and extant data compatible. Some examples of the S/F index for modern faunas are given in table 2.

The sharpness of the curves constructed with the S/F index obtained from fossil mammals depends on the length of the time interval which is recognized in a sequence. The fluctuations observed in Quercy are those occurring for intervals averaging 1.3 MY. Evidence for more short-lived fluctuations needs a finer time interval, i.e. finer paleotemperature fluctuations can be seen only with smaller time intervals between reference levels.

Interest in the correspondence between the intrafamilial species richness (S/F) index and the $\delta^{18}\text{O}$ data is twofold. Firstly, it may provide a method for reconstructing past continental climates. Until now this kind of data has never been available directly for terrestrial environments and has always been inferred indirectly. Secondly, it may be possible to use the S/F curves for correlation between marine and continental sequences. Major faunal fluctuations which can be

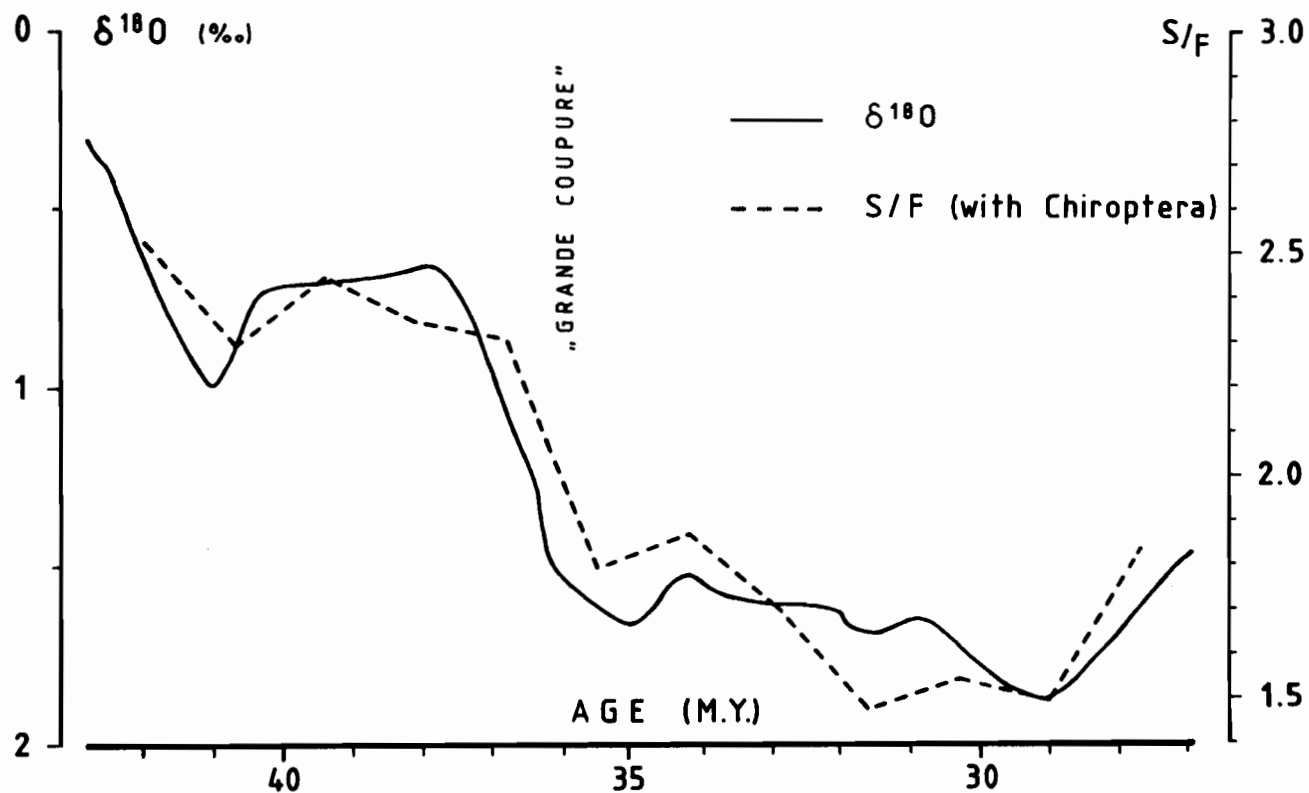


Figure 3. Oceanic $\delta^{18}\text{O}$ curve (after Miller and Fairbanks 1985) and S/F curve obtained for Quercy. The carnivores are not included in the calculations of the S/F index (see text for explanations).

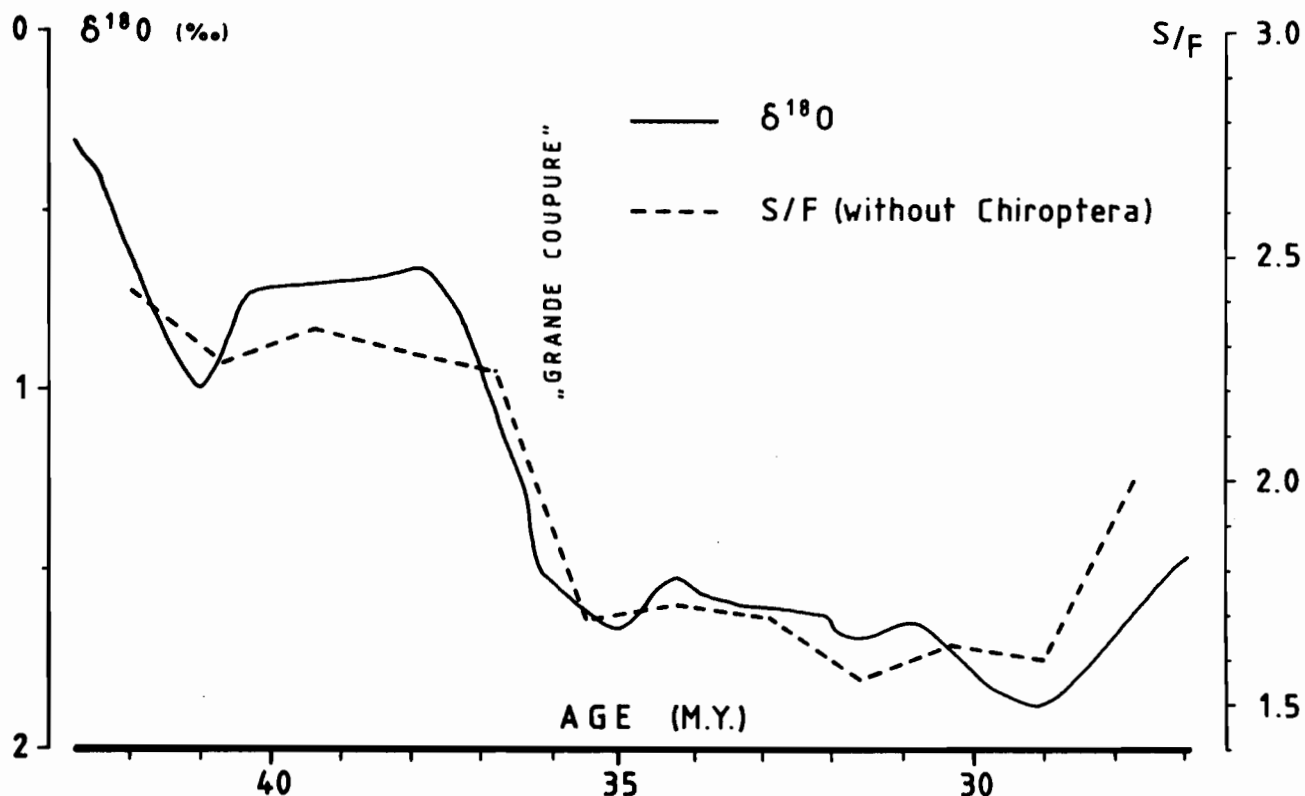


Figure 4. Same as figure 3, but the S/F index was computed after omitting the Chiroptera.

Table 2. S/F index (with and without Chiroptera) of some modern faunas (Carnivora are excluded), with indications concerning their environments and mean annual temperature.

Locality	Environment	Annual mean temperature*	S/F index	
			with Chiroptera	without Chiroptera
Makokou, Gabon, Africa (1)	Equatorial rain forest	27°	3.93	3.81
Rwindi-Rutshuru plain, Zaire, Africa (2)	Tropical, savanna	23.6°	2.70	2.71
Gabirol, Rwanda, Africa (3)	Tropical, savanna	20.6°	-	2.47
Berber region, Algeria, Africa (4)	Arid, steppe-desert	22°	2.91	2.51
Aghbolagh, Iran, Asia (5)	Arid, desert	17°	-	1.82
Donana, Spain, Europe (6)	Mediterranean arid steppe	17°	-	1.50
Rio Cenepa drainage, Peru, S. America (7)	Tropical, forest	22.5°	3.31	2.94
Rio Santiago basin, Peru, S. America (7)	Tropical, forest	22°	2.63	2.69

* When not otherwise available, data were taken from Walter and Lieth 1960-67.

Source of Data: (1) Dubost 1978, Emmons *et al.* 1983; Duplantier pers. comm.; (2) Frechkop 1938, 1943, Bourlière and Verschuren 1960; (3) Misonne 1965, Verschuren 1965; (4) Kowalski pers. comm.; (5) Misonne 1959; (6) Valverde 1967; (7) Patton *et al.* 1982.

identified on the basis of the S/F index are hypothesized to be due to continental paleotemperature changes. In turn these fluctuations can be correlated with the isotopic ($\delta^{18}O$) curve fluctuations which are due to marine paleotemperature changes, because it is suggested that important changes in oceanic temperatures will result in major atmospheric climatic changes, and hence changes in terrestrial conditions.

It must be emphasized here that the S/F index does not depend on the turnover in fauna, i.e. it is not directly affected by extinction or origination of taxa. If species and families become extinct, the species/family ratio can remain the same. It is affected only when differential extinction or origination occurs between species and families (see for example: Simberloff 1974, Sepkoski 1984).

Explanations about the underlying cause of the correlation between the intrafamilial species-richness index within mammals and paleotemperature curves remain speculative for the moment and are under study. In this respect it should be noted that species richness of modern faunas is affected by latitude (Fisher 1960, Stehli 1968), i.e. by temperatures and climates, but little is known of latitudinal effects at the family level. However, when temperatures are high, as in the tropics, there usually exist ecological conditions which are more suitable for mammals, and then more niches. In the tropics species are often more specialized and exhibit a greater tolerance for niche overlap (Klopfer and MacArthur 1961): they are therefore more numerous as a result of adaptive radiation. In contrast, in environments with lower temperatures, such as occur in

the high latitudes, species tend to be ubiquitous, with a lower niche overlap, and are thus not so diversified within each group. Therefore, explanations for the coincidences between S/F and O curves should be based on both ecological and evolutionary evidence.

ACKNOWLEDGMENTS

The author is especially indebted to Martin Pickford: many of the ideas which form the basis of this paper, as well as suggestions and discussions on this subject, are due to him. He has also criticized and improved the English manuscript. Leigh Van Valen is thanked for correcting the English of the final draft. The study has benefited from comments by Norbert Schmidt-Kittler, Bernard Sigé, Monique Vianey-Liaud, Louis de Bonis, Karl W. Flessa and Donald R. Prothero. This work is supported by a fellowship of the Alexander von Humboldt-Stiftung and by a grant (A.T.P. "Evolution") from the C.N.R.S.

LITERATURE CITED

- Anadon, P., M. Feist, J.-L. Hartenberger, C. Müller and J. de Villalta-Comella. 1983. Un exemple de corrélation biostratigraphique entre échelles marines et continentales dans l'Eocène: la coupe de Pontils (bassin de l'Ebre, Espagne). *Bull. Soc. géol. Fr.* 25: 747-755.
- Berggren, W.A., D.V. Kent, J.J. Flynn and J.A. Van Couvering. 1985. Cenozoic geochronology. *Geol. Soc. Amer. Bull.* 96: 1407-1418.
- Bonis, L. de, J.-Y. Crochet, J.-C. Rage, R. Sigé, J. Sudre and M. Vianey-Liaud. 1973. Nouvelles faunes de vertébrés oligocènes des phosphorites du Quercy. *Bull. natn. Hist. nat.* (3), *Sci. Terre* 28, 174: 105-113.
- Bourlière, F., and J. Verschuren. 1960. Exploration du Parc national Albert. Mission F. Bourlière et J. Verschuren. Fasc. 1: introduction à l'écologie des ongulés du Parc national Albert. Institut des Parcs nationaux du Congo, Bruxelles: 1-158.
- Bouvrain, G., D. Geraads and J. Sudre 1986. Révision taxonomique de quelques ruminants oligocènes des phosphorites du Quercy. *C.R. Acad. Sci. Paris, Sér.* 2, 302(2): 101-104.
- Cavaillé, A., B. Gèze, L. de Bonis, B. Sigé, J. Sudre, L. Ginsburg, M. Brunet, J.-Y. Crochet, J.A. Remy, J.-L. Hartenberger, M. Vianey-Liaud, N. Lopez, L. Thaler and J.-C. Rage. 1974. Table ronde sur les phosphorites du Quercy. *Palaeovertebrata* 6(1-4): 1-303.
- Cavelier, C., and C. Pomerol. 1983. Echelle de corrélation stratigraphique du Paléogène. Stratotypes, étages standards, biozones, chimiozones et anomalies magnétiques. *Géologie de la France* (3): 261-262.
- Comte, B. 1985. Eléments nouveaux sur les genres *Eucricetodon* et *Pseudocricetodon* (*Eucricetodontinae*, *Rodentia*, *Mammalia*) de l'Oligocène d'Europe occidentale. *Palaeovertebrata* 15: 1-69.
- Crochet, J.-Y. 1971. Les vertébrés de l'Oligocène supérieur de Pech du Fraysse, poche à phosphate du Quercy (commune de Saint-Projet, Tarn-et-Garonne). *C.R. somm. Soc. géol. Fr.* (6): 316-317.
- . 1980. Les marsupiaux du Tertiaire d'Europe. Ed. Singer-Polignac, Paris: 279 p.
- , J.-L. Hartenberger, J.-C. Rage, J.A. Remy, B. Sigé, J. Sudre and M. Vianey-Liaud. 1981. Les nouvelles faunes de vertébrés antérieures à la "Grande Coupure" découvertes dans les phosphorites du Quercy. *Bull. Mus. natn. Hist. nat.*, 4ème Sér., C (3): 245-266.
- , ----, M. Hugueney, M. Godinot, S. Legendre, J.A. Remy, B. Sigé, J. Sudre and M. Vianey-Liaud. 1984. Mammifères. In: Chapitre Paléogène (C. Cavelier, coord.), pp. 392-396, Synthèse géologique du Sud-Est de la France. Mém.

- mammal community in amazonian Peru: knowledge and Utilization patterns among the Aguaruna Jivaro. In: Mammalian biology in South America (M.A. Mares and H.H. Genoways, eds.). Spec. Publ. Pymatuning Lab. Ecol. 6: 111-128.
- Pomerol, C., and I. Premoli-Silva (Eds). 1986. Terminal Eocene events. Elsevier Science Publ., Amsterdam.
- Russell, D.E., J.-L. Hartenberger, C. Pomerol, S. Sen, N. Schmidt-Kittler and M. Vianey-Liaud. 1982. Mammals and stratigraphy: the Paleogene of Europe. *Palaeovertebrata*, Mém. extra.: 1-77.
- Schmidt-Kittler, N., and M. Vianey-Liaud. 1979. Evolution des Aplodontidae oligocènes européens. *Palaeovertebrata* 9: 33-82.
- Sepkoski, J.J., Jr. 1984. A kinetic model of phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10: 246-267.
- Sigé, B. 1974. Insectivores et chiroptères de l'Eocène supérieur et Oligocène inférieur d'Europe occidentale. Article de Synthèse. Thèse. A.O. 10537, Montpellier. 85 p. (Unpublished).
- . 1975. Insectivores primitifs de l'Eocène supérieur et Oligocène inférieur d'Europe occidentale: apatemyidés et leptictidés. Coll. intern. C.N.R.S. 218: 653-673.
- . 1976. Insectivores primitifs de l'Eocène supérieur et Oligocène inférieur d'Europe occidentale. Nyctithériidés. Mém. Mus. natn. Hist. nat., C, Sci. Terre 34: 1-140.
- and S. Legendre. 1983. L'histoire du peuplement de chiroptères du bassin méditerranéen: l'apport comparé des remplissages karstiques et des dépôts fluvio-lacustres. Mém. Biospéol. 10: 209-225.
- Simberloff, D.S. 1974. Permo-triassic extinctions: effects of area on biotic equilibrium. *J. Geol.* 82: 267-274.
- Stehli, F.G. 1968. Taxonomic diversity gradients in pole location: the Recent model. In: *Evolution and environment* (E.T. Drake, ed.), pp. 163-227. Yale Univ. press, New Haven, London.
- Stehlin, H.G. 1909. Remarques sur les faunules de mammifères des couches éocènes et oligocène du Bassin de Paris. *Bull. Soc. géol. Fr.* 9: 488-520.
- Sudre, J. 1978. Les artiodactyles de l'Eocène moyen et supérieur d'Europe occidentale: systématique et évolution. Mém. et trav. E.P.H.E., Inst. Montpellier 7: 1-229.
- . 1984. *Cryptomeryx* Schlosser, 1886, tragulidé de l'Oligocène d'Europe; relations du genre et considérations sur l'origine des ruminants. *palaeovertebrata* 14(1): 1-31.
- . 1986. Le genre *Bachitherium* Filhol, 1882 (Mammalia, Artiodactyla): diversité spécifique, phylogénie, extension chronologique. *C.R. Acad. Sci. Paris, Sér. 2*, 303 (8): 749-754.
- Vail, P.R., R.M. Mitchum and S. Thompson. 1977. Seismic stratigraphy and global changes of sea level, parts 3 and 4. *AAPG Mem.* 26: 63-97.
- Valverde, J.A. 1967. Estructura de una comunidad de vertebrados terrestres. *Monografías de la Estacion biologica de Donana* (1): 1-219.
- Vergnaud-Grazzini, C. 1984. Major Cenezoic climatic changes: the stable isotope record of marine carbonates in the World ocean - A review. *Paléobiologie continentale*, Montpellier 14(2): 433-473.
- and J.F. Saliège. 1985. Les événements isotopiques en milieu océanique à la transition Eocène-Oligocène dans le Pacifique et l'Atlantique; paléocirculations profondes en Atlantique sud. *Bull. Soc. géol. Fr.*, (8), 1(3): 441-455.
- Verschuren, J. 1965. Exploration du Parc national de la Kagera. 2ème série. Fasc. 1(1): Contribution à l'écologie des grands mammifères. Institut des Parcs Nationaux du Congo et du Rwanda, Bruxelles: 3-62.
- Vianey-Liaud, M. 1969. Rongeurs de l'Oligocène moyen provenant de nouvelles fouilles dans les Phosphorites du Quercy. *Palaeovertebrata* 2(5): 209-239.

- B.R.G.M. Fr. (125).
- Dubost, G. 1978. Un aperçu sur l'écologie du chevrotain africain Hyemoschus aquaticus Ogilby, artiodactyle tragulidé. *Mammalia* 42: 1-62.
- Emmons, L.H., A. Gautier-Hion and G. Dubost. 1983. Community structure of the frugivorous-folivorous forest mammals of Gabon. *J. Zool., Lond.* 199: 209-222.
- Fischer, A.G. 1960. Latitudinal variations in organic diversity. *Evolution* 14: 64-81.
- Frechkop, S. 1938. Exploration du Parc national Albert. Mission G.F. De Witte (1933-1935). Fasc. 10: mammifères. Institut des Parcs nationaux du Congo Belge, Bruxelles: 1-103.
- . 1943. Exploration du Parc national Albert. Mission S. Frechkop (1937-1938). Fasc. 1: mammifères. Institut des Parcs nationaux du Congo Belge, Bruxelles: 1-186.
- Gèze, B., J.-C. Rage, C. Vergnaud-Grazzini, F. de Broin, E. Buffetaut, C. Mourer-Chauviré, J.-Y. Crochet, B. Sigé, J. Sudre, J.A. Remy, B. Lange-Badré, L. de Bonis, J.-L. Hartenberger and M. Vianey-Liaud. 1978. La poche à phosphate de Sainte-Néboule (Lot) et sa faune de vertébrés du Ludien supérieur. *Palaeovertebrata* 8(2-4): 167-328.
- Godinot, M. 1983. Contribution à l'étude des primates paléogènes d'Europe. Systématique, locomotion. Thèse, Montpellier II. 130 p. (Unpublished).
- . 1984. Un nouveau genre témoignant de la diversité des adapinés (Primates, Adapidae) à l'Eocène terminal. *C.R. Acad. Sci. Paris* 299, Sér. 2, (18): 1291-1296.
- Hartenberger, J.-L. 1971. La systématique des Theridomyoidea. *C.R. Acad. Sci. Paris* 273: 1917-1920.
- . 1973. Etude systématique des Theridomyoidea (Rodentia) de l'Eocène supérieur. *Mém. Soc. géol. Fr., N.S.*, 57 (117): 1-74.
- . 1986. Crises biologiques en milieu continental au cours du Paléogène: exemple des mammifères d'Europe. *Bull. Centres Rech. Explor.-Prod. Elf-Aquitaine*, 10(2): 489-500.
- and N. Schmidt-Kittler. 1976. un nouveau genre de Theridomyoidea (Mammalia, Rodentia) dans les phosphorites du Quercy. *Mitt. Bayer. Staatsslg. Paläont. hist. Geol., München* 16: 65-69.
- Jablonski, D., and K.W. Flessa. 1986. The taxonomic structure of shallow-water marine faunas: implications for Phanerozoic extinctions. *Malacologia* 27: 43-66.
- Hugueney, M., and M. Vianey-Liaud. 1980. Origine et évolution des Dipodidae (Rodentia) paléogènes d'Europe occidentale. *Palaeovertebrata, Mém. jubil. R. Lavocat*: 303-342.
- Klopfer, P.H., and R.H. MacArthur. 1961. On the causes of the tropical species diversity: niche overlap. *Amer. Natur.* 95: 223-226.
- Legendre, S. 1985. Liste révisée des mammifères de quelques riches gisements du Paléogène moyen et supérieur du Sud de la France. *Géologie de la France* 3: 287-292.
- . 1986. Analysis of mammalian communities from the late Eocene and Oligocene of southern France. *Palaeovertebrata* 16(4): 191-212.
- Miller, K.G., and R.G. Fairbanks. 1985. Cainozoic $\delta^{18}\text{O}$ record of climate and sea level. *S. African J. Sci.* 81: 248-249.
- and ----. In press. Cenozoic oxygen isotope records of climate and sea level. *Palaeoceanography*.
- Misonne, X. 1959. Analyse zoogéographique des mammifères de l'Iran. *Mém. Inst. roy. Sci. nat. Belgique*, 2ème Sér., 59: 1-157.
- . 1965. Exploration du Parc national de la Kagera. 2ème Sér. Fasc. 1(3): Rongeurs. Institut des Parcs nationaux du Congo et du Rwanda, Bruxelles: 77-118.
- Patton, J.L., B. Berlin and E.A. Berlin. 1982. Aboriginal perspectives of a

- . 1972a. Contribution à l'étude des cricétidés oligocènes d'Europe occidentale. *Palaeovertebrata* 5(1): 1-44.
- . 1972b. L'évolution du genre Theridomys à l'Oligocène moyen. Intérêt biostratigraphique. *Bull. Mus. natn. Hist. nat.* (3), *Sci. Terre* 18, 98: 295-372.
- . 1974a. Palaeosciurus goti nov. sp., écureuil terrestre de l'Oligocène moyen du Quercy. Données nouvelles sur l'apparition des sciuridés en Europe. *Ann. Paleont. (Vert.)*, Paris 60(1): 103-122.
- . 1974b. Les rongeurs de l'Oligocène inférieur d'Escamps. *Palaeovertebrata* 6(3-4): 197-241.
- . 1976. Les Issiodoromyinae (Rodentia, Theridomyidae) de l'Eocène supérieur à l'Oligocène supérieur en Europe occidentale. *Palaeovertebrata* 7(1-2): 1-115.
- . 1979. L'évolution des rongeurs à l'Oligocène en Europe occidentale. *Palaeontographica*, A, 166: 136-236.
- . 1985. Nouvelle quantification de l'hypsodontie chez les Theridomyidae: l'exemple de Theridomys ludensis nov. sp. *Palaeovertebrata* 15(3): 159-172.
- and S. Legendre. 1986. Les faunes des phosphorites du Quercy: principes méthodologiques en paléontologie des mammifères; homogénéité chronologique des gisements de mammifères fossiles. *Eclogae geol. Helv.* 79: 917-944.
- Walter, H., and H. Lieth. 1960-67. *Klimadiagramm-Weltatlas*. G. Fischer, Jena.