

Originations: Land and Sea Compared

Gunther J. Eble

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Originations: Land and Sea Compared

Origines: Comparaisons Terre-Mer

Gunther J. Eble

Department of Paleobiology
National Museum of Natural History
Smithsonian Institution
MRC-121, Washington, DC 20560
USA

and

Santa Fe Institute
1399 Hyde Park Road,
Santa Fe, NM 87501
USA

e-mail: ebleg@nmnh.si.edu, eble@santafe.edu

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Abstract. The dynamics of origination in the fossil record of three marine groups (molluscs, echinoderms and fishes) and three terrestrial groups (mammals, insects and plants) is analyzed in this paper. Four hypotheses are tested: (1) secular decline in lineage origination; (2) secular decline in evolutionary innovation; (3) diversity dependence of lineage origination; (4) self-organized criticality of lineage origination. A decline in lineage origination and in the production of major innovations is present in all groups, suggesting controls that transcend the land-sea distinction. The relationship between diversity and origination appears to be strong in the sea and weak on land, a difference that might imply environment-specific controls. Mixed support for a logistic dynamics of origination is found. Finally, no general support for a self-organized critical behaviour of origination is found, with the predictions appearing to hold robustly only in insects and pteridophytes/gymnosperms.

Résumé. La dynamique d'apparitions des lignages et des innovations évolutives dans l'histoire fossile de trois groupes marins (mollusques, échinodermes, et poissons) et de trois groupes terrestres (mammifères, insectes et plantes) est analysée en cet article. Quatre hypothèses sont examinées: (1) déclin sur le long terme des apparitions de lignages; (2) déclin sur le long terme d'innovations évolutives; (3) dépendance en diversité des apparitions de lignages; (4) criticalité auto-organisée. On observe un déclin des apparitions de lignages et de la production d'innovations évolutives dans tous les groupes, ce qui suggère des règles d'apparition qui dépassent la distinction terre-mer. Le rapport entre diversité et apparitions semble être forte en mer et faible sur terre, une différence qui suggère des règles déterminées par l'environnement. Une dynamique logistique des apparitions n'est pas omniprésente. Enfin, l'hypothèse d'un comportement critique auto-organisé des apparitions de lignages ne peut être confirmé de manière générale. Les prédictions semblent être satisfaites seulement chez les insectes et les ptéridophytes/gymnospermes.

INTRODUCTION

Comparative studies of diversification in the fossil record hold our best hope of gaining insight into its dynamics through time, but most studies to date have focused either on extinction or on diversity. Yet origination is the ultimate source of diversity, and a useful proxy for the assessment of evolutionary flexibility and evolutionary radiations. This contribution explores the fossil record of origination on land and in the sea. Because there are demonstrable diversity differences between land and sea, with more documented species on land but many more phyla in the sea (May 1994), a focus on origination might make more explicit the causes for such differences. In contrast, similarities can suggest general processes or mechanisms of origination.

The extent to which marine and terrestrial environments themselves impart different evolutionary pathways to organic form and diversity is still an open issue. First, are ecological properties such as food web structure, productivity, biogeography, environmental heterogeneity, and stress susceptibility unique to each major realm (Cohen 1994; May 1994; Rapoport 1994; Roughgarden et al. 1994)? How do these properties translate into macroevolutionary time scales? Second, how group-specific are evolutionary patterns in each realm? Valentine et al. (1991a), for example, suggested that differences in longevity and extinction dynamics between plants and animals (both terrestrial and marine) relate to different levels of structural complexity and to different environmental preferences. It is also generally assumed that particular apomorphies (e.g., related to dispersal and mate recognition) may underlie highly idiosyncratic diversity dynamics in particular groups, by directly affecting origination and extinction rates. Third, are there regularities in diversification that transcend environmental context and taxonomic membership? Origination data potentially bear a relationship to all of these issues.

One approach to land-sea comparisons is to combine marine and terrestrial records across groups (e.g., Benton 1995, 1997; Solé et al. 1997). This is appropriate when the interest is in a synthetic, global signal. Alternatively, one might be interested in decomposing such a signal, by considering regularities and contingencies apparent in individual groups. One advantage of this approach is that it allows evaluation of the possibility that conflicting signals may exist among different groups. This is the approach taken here.

In this paper, three main groups are studied in each major environment. Molluscs, echinoderms and fishes are considered in the marine realm, and insects, mammals and plants (tracheophytes only, with angiosperms analyzed separately) are

treated in the terrestrial realm. Patterns at the level of lineages and at the level of putative major innovations are derived. Aside from overall comparisons of the patterns across individual groups, several hypotheses are tested to assess possible controls on the origination process: (1) secular decline in the intensity of lineage origination; (2) secular decline in the intensity of innovation; (3) diversity dependence of origination; and (4) self-organized criticality. These hypotheses reflect much of the current debate concerning the causes of diversification.

MATERIALS AND METHODS

Choice of taxa. The rationale for choosing the particular set of taxa studied was not arbitrary. The groups were chosen because they tend to maximize phylogenetic breadth; they account for a considerable proportion of the respective records on land and sea; they correspond to well-circumscribed Baupläne; they have particularly extensive fossil records that, with the exception of mammals, cover a large portion of the Phanerozoic; and they all have a sufficiently large number of orders to allow meaningful estimates of changes in the production of major innovations (see below). This latter requirement is particularly stringent: although groups like bryozoans, brachiopods, trilobites and reptiles all have good and extensive fossil records, these groups would make comparability difficult in this study because of their relatively small number of orders.

Data and data sources. The data correspond to compilations from global synoptic compendia of stratigraphic ranges, including the Compendium of Fossil Marine Animal Families (Sepkoski 1992 and pers. comm.), Sepkoski's unpublished generic database (Sepkoski, pers. comm.), the Fossil Record 2 (Benton 1993), and the Compendium of Fossil Insect Families (Labandeira 1994). Data on first appearances of angiosperm organ types were taken from Friis and Crepet (1987). The original data were culled to minimize taxonomic and sampling biases, with removal of single-stage, *incertae sedis*, problematic and poor preservation taxa.

Levels of analysis. Lineages were approximated by genera for molluscs, echinoderms and fishes, and by families for insects, plants and mammals. While this difference would likely affect detailed comparisons, the analyses concentrated on general, secular patterns, which have been shown to be recoverable with both family and genus-level data (Sepkoski 1997). The use of families and genera as proxies for lineages is justifiable because of the increased reliability of stratigraphic ranges and the ability to better track underlying patterns when sampling is poor (Raup and Boyajian 1988; Sepkoski and Kendrick 1993). The issue of non-monophyly (see Smith and

Patterson 1988; Sepkoski and Kendrick 1993) disappears in the case of origination because the first appearance of any group (monophyletic, paraphyletic or polyphyletic) corresponds to a single event, of equivalent status across taxa (see Smith 1994).

Orders were used as proxies for putative major innovations in all groups, except in angiosperms. Orders are usually considered to be good indicators of morphological distinctness (see Jablonski and Bottjer 1990a; Valentine et al. 1991b; DiMichele and Bateman 1996). Also, ordinal diversity patterns seem to be decoupled from the similarity exhibited by lower levels (Jablonski and Bottjer 1990a,b,c; 1991; Bambach and Sepkoski 1992). In addition, recent disparity studies have documented a good agreement between ordinal dynamics and disparity dynamics (Foote 1996; Eble 1998a, submitted). Thus, orders will here be taken to be good indicators of macroevolutionary innovation. In angiosperms, the match between ordinal status and morphological distinctness is poorly understood and, accordingly, major angiosperm innovations were here approximated by flower and fruit types.

Scope of analyses and analytical approach. Time series of origination were produced for the entire history of each of the groups considered. Stratigraphic resolution is mostly at the stage level, with some lumping of intervals depending on the original source. The time scale used is that of Harland et al. (1990), with updates, and the Recent is excluded from the analyses. Because each group is to a certain extent subject to its own taxonomic, taphonomic and sampling biases, only relative comparisons are carried out. The goal here is not to determine whether absolute origination, say, in insects was more intense than in molluscs at any given interval, but to assess if the relative timing and magnitude of origination differs. This comparative approach does not eliminate the potential overprint of biases that might affect the time series of individual groups, but it does allow statistical generalizations.

Proportional metrics of origination are used in the analyses of decline in origination intensity and of self-organized criticality. They account for the relative propensity to produce new taxa, i.e., the number of opportunities for origination at any given interval relative to a source pool. Proportional lineage origination is the number of originations divided by diversity. In the case of ordinal origination, the relevant denominator is the number of lineage originations, the actual experiments in evolutionary innovation. This produces an "innovation per lineage ratio", which is used here. The analysis of diversity dependence of origination (see Sepkoski 1978, 1991) must rely on time-normalized metrics (total rate and per-taxon rate), which are biased by interval length (Gilinsky 1991; Foote 1994; Sepkoski and Koch 1996). Bias is more pronounced for per-taxon rates (Gilinsky 1991; Foote 1994), which are

also problematic when compared to diversity because of induced negative correlations (Sepkoski 1978). Thus, total origination rates will be used to study diversity dependence. Finally, estimates of error for each interval are not presented because the focus is on long-term patterns and not on smaller-scale fluctuations. Such focus also diminishes the impact of inherent limitations of the record, such as the overprint of Lagerstätten, the unevenness of collection effort per interval, and taphonomic differences between land and sea.

Hypotheses of Origination

(1) Secular decline in lineage origination. A secular decline in origination intensity has been documented for marine invertebrate families (Van Valen and Maiorana 1985; Sepkoski 1993; Foote 1994), marine invertebrate genera (Sepkoski 1998), for marine invertebrate families within higher taxa at and below the class level (Van Valen and Maiorana 1985; Gilinsky and Bambach 1987), for terrestrial tetrapod families (Benton 1985), and for plant genera and species (Knoll et al. 1984; Niklas 1997). The pattern as such is robust, and a number of explanations have been advanced (see Sepkoski 1998). However, it has never been evaluated for molluscs, echinoderms and fishes as a whole (see Van Valen and Maiorana 1985 for major subgroups), and individual terrestrial groups have received limited attention. Both ecological (Van Valen 1973, 1985; Van Valen and Maiorana 1985; Maurer 1989; Sepkoski 1998) and developmental (Gilinsky and Bambach 1987; Eble 1998b) explanations for the decline would be weakened if terrestrial groups did not show it. In this study, Spearman rank correlation is used to assess the presence and strength of the pattern.

(2) Secular decline in evolutionary innovation. The decline in the production of major innovations through time has been extensively documented (Knoll et al. 1984; Erwin et al. 1987; Valentine et al. 1991b; DiMichele and Bateman 1996; Eble 1998b), and a variety of explanations advanced to account for it (see Erwin et al. 1987; Valentine and Erwin 1987; Gould 1989; Kauffman 1993; Erwin 1994; Valentine 1995; DiMichele and Bateman 1996; Valentine et al. 1996; Conway Morris 1998; Eble 1998b). Most studies have dealt with marine invertebrates as a whole. The pattern is very strong, and indicates pervasive differential flexibility through time. Still, its documentation in individual groups over long periods of time has been wanting (but see Jacobs 1990; DiMichele and Bateman 1996), and its presence in them, while commonly acknowledged on qualitative grounds, has hardly been assessed statistically with origination data. As with lineage origination, Spearman rank correlation is used here.

(3) Diversity dependence of origination. When total origination rates are plotted against diversity, the expectation in a logistic system is that of a parabola (Sepkoski 1978, 1991; origination increases with increasing diversity at first, and then decreases as crowding becomes more severe). If there was no significant relationship between total origination and diversity or if, say, a quadratic function did not significantly improve explanation over a linear function, a claim for diversity dependence of origination (in the sense of declining rates with increasing diversity) would not be supported. This would **not** mean that diversity itself does not obey a logistic system, since logistic-like diversity curves will always be produced whenever the underlying functions for origination and extinction rates intersect (Sepkoski 1978). But it would suggest that factors other than crowding and ecological interference might be involved in the origination process, even if declines in proportional origination through time were present. In this paper, an exploratory statistical treatment of the relationship between origination and diversity was carried out by (1) calculating the significance of the relationship with Spearman rank correlation, and by (2) assessing whether a quadratic fit (implying a logistic system) significantly improves explanation over a linear one (with one less parameter). An *F*-test is used for this purpose.

(4) Self-organized criticality. Self-organized criticality (SOC) is one rendition of the potential importance of self-organization in nature. The idea involves a particular explanation for the skewed curves so commonly found in frequency distributions of natural events. The distributions of earthquakes, floods, market prices, solar flares, traffic jams and forest fires, among other phenomena, display a few large events and many small ones. It has been suggested that both large and small events follow the same scale-free functional relationships, with no characteristic or average size. SOC theory interprets such behaviour as implying an internal dynamics in which a system with a high degree of connectivity organizes itself into a critical state (Bak et al. 1987; Bak and Paczuski 1995; Bak 1996). Self-organization here refers to the spontaneous generation of pattern with little or no external control. Criticality refers to a state of a system where all components may affect each other -- hence the characterization of SOC behaviour in terms of "interaction-dominated threshold systems" (Jensen 1998). As in a sandpile that grows through addition of small grains of sand, when a critical point is reached avalanches of all sizes may result. Mechanistically, disturbances would lead to unpredictable disruptions of connectivity patterns, frequently with localized consequences, but occasionally spreading through the system. SOC theory predicts that the distributions of events should follow a

power law, taking a linear form in a log-log plot with a slope (scaling exponent) in the vicinity of negative 1.

Recently, it has been argued that extinctions also conform to the predictions of self-organized criticality theory (Kauffman 1993, 1995; Bak 1996; Bak and Paczuski 1995; Solé and Bascompte 1996). In a comprehensive analysis of the fossil record, including separate analyses of marine and terrestrial realms, this claim also has been made by Solé et al. (1997), who argued that not only extinction but also origination on land and sea follows a scale-independent pattern consistent with self-organized criticality. These authors hypothesize internal biotic dynamics as a likely explanation.

The procedure used in this paper to test the predictions of self-organized criticality theory involves (1) construction of frequency distributions of proportional lineage origination for each of the groups studied; (2) calculation of the slope of a power law fit (a linear function) to the frequency data in log-log space; and (3) assessment of whether an alternative fit (a quadratic fit was chosen for simplicity) significantly improves explanation. An *F*-test was also used here.

RESULTS AND DISCUSSION

Lineage origination. The time series of proportional lineage origination for all six groups considered are shown in Fig. 1. Angiosperms are presented separately in Fig. 2 because the angiosperm record lacks resolution and is subject to a number of limitations that make it hardly comparable to the record of pteridophytes and gymnosperms (see Collinson et al. 1993). However, the fact that here only angiosperm families erected from macrofossils are used places the analyses in the context of roughly equivalent levels of morphological complexity. For fishes and mammals, initial lags at very low diversity (and origination) were removed (an initial history of low diversity would not demand special explanation because of stochasticity, and thus lag removal is justifiable on statistical grounds; see Sepkoski 1991).

In all groups, there is a significant decline in origination (but notice the marginal significance in fishes). The first point in each original time series is artificially high (see Gilinsky and Bambach 1987), and was excluded. Such uniform decrease in evolutionary activity is impressive given the widely differing environments, ecological roles, morphological themes and temporal scales involved. It supports claims for an inherent temporal asymmetry in evolution (Gilinsky and Bambach 1987; Gould et al. 1987), and points to the involvement of evolutionary factors that are robust to the contingencies of life on land and in the sea. Diversity

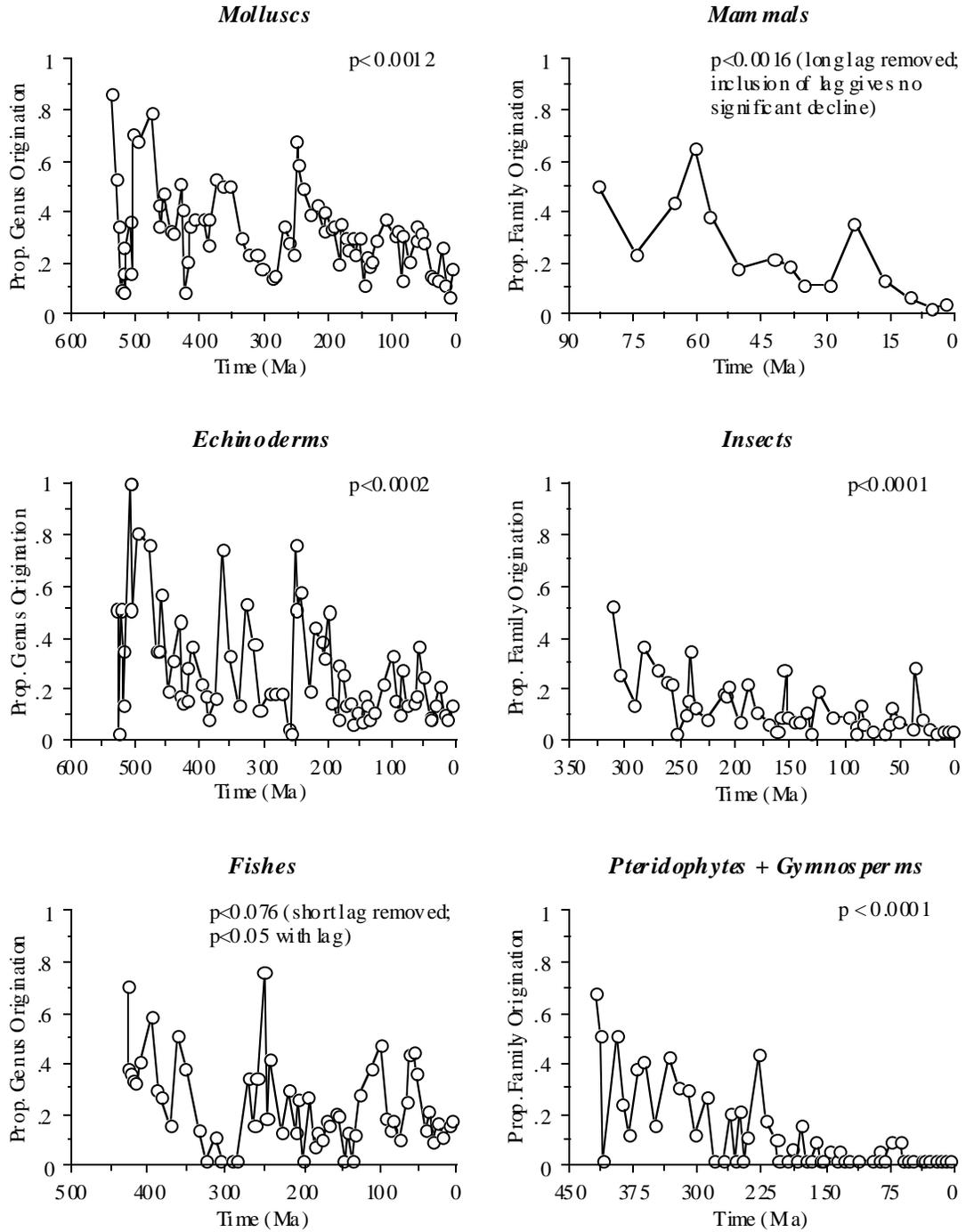


Figure 1. Time series of proportional lineage origination. P-values for Spearman's rank correlation are given. *Série chronologique des apparitions proportionnelles de lignages. Les valeurs de signification statistique pour la corrélation de Spearman sont données.*

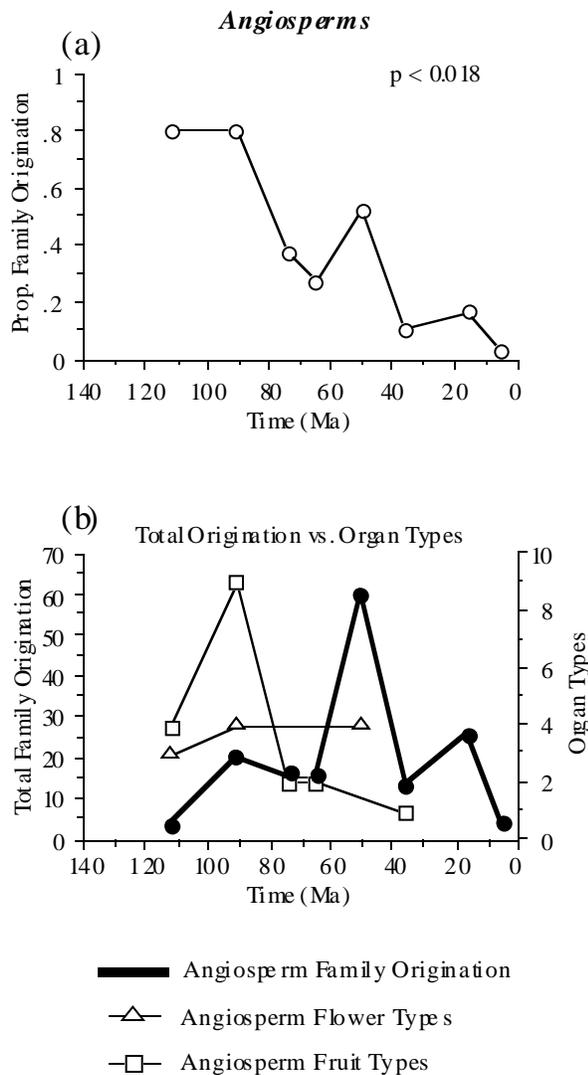


Figure 2. Time series of angiosperm proportional lineage origination (a) and major innovations (b). In (b), total number of lineage originations is also presented for comparison. Spearman's p-value is given in (a). *Série chronologique des apparitions proportionnelles de lignages (a) et d'innovations évolutives (b) pour les angiospermes. En (b), le nombre total des apparitions de lignages est présentée aussi. Le valeur de signification statistique pour la corrélation de Spearman est donné en (a).*

dependence would not seem to be consistently present (see below), such that intrinsic factors, like evolvability (understood as the potential to produce variation) in its ecological or developmental dimensions, may be more at issue than interactive dynamics. Sorting among higher taxa with different characteristic rates of origination and extinction, an explanation advanced by Gilinsky (1994) and Sepkoski (1998) for the decline in origination intensity of marine invertebrates as a whole, might

conceivably also account for part of the pattern within the groups here studied. This is a possibility worth exploring (see also Miller 1998), even though the proximate causes of characteristic rates of origination would still demand explanation in ecological or developmental terms.

Sepkoski (1998) described in detail the decline in proportional origination for marine invertebrates as a whole, and modelled the trend as the combination of two decays, one for the Paleozoic and one for the post-Paleozoic. In the present study, this appears also to hold in approximate form in all groups that have Paleozoic and post-Paleozoic histories (Fig. 1). With variable lags (see Erwin 1996), the rebound from the end-Permian mass extinction seems to have entailed a temporary intensification in origination. This has been commonly attributed to recolonization of vacant niches through selection and adaptation. Another possibility is that the disruption of characteristic population structures and population sizes brought about by the stresses associated with mass extinction may have enhanced the opportunities for geographical isolation, population subdivision, and evolution through genetic drift.

Major innovations. Fig. 3 displays the temporal profile for the order/lineage ratio in each group, with angiosperms illustrated in Fig. 2. The first point in each original time series was removed, except for molluscs (strictly speaking, only the appearance of an equal number of lineages and orders at the inception of a group would generate an artificially high order/lineage ratio). As with lineage origination, a significant decline is apparent in all groups, although the decline is less continuous and in some cases more irregular than in Fig. 1. The decline is clear even after lag removal in fishes and mammals. Statistics are not presented for angiosperms because of the limited number of data points; lineage origination is contrasted separately with flower and fruit type origination instead, and a marked reduction in relative terms is clear in both cases. This uniform decline in evolutionary flexibility is predicted by synthetic analyses of the marine record (Erwin et al. 1987; Eble 1998b). Although there is spikiness in some groups (a result of the smaller number of lineage originations and thus higher stochasticity), the fact that as a tendency the decline seems to hold in individual groups on both land and sea strengthens the claim, and suggests that long-term controls on evolutionary flexibility may transcend environmental context. As with lineage origination, this temporal asymmetry is suggestive of fundamental inhomogeneities in evolvability through time.

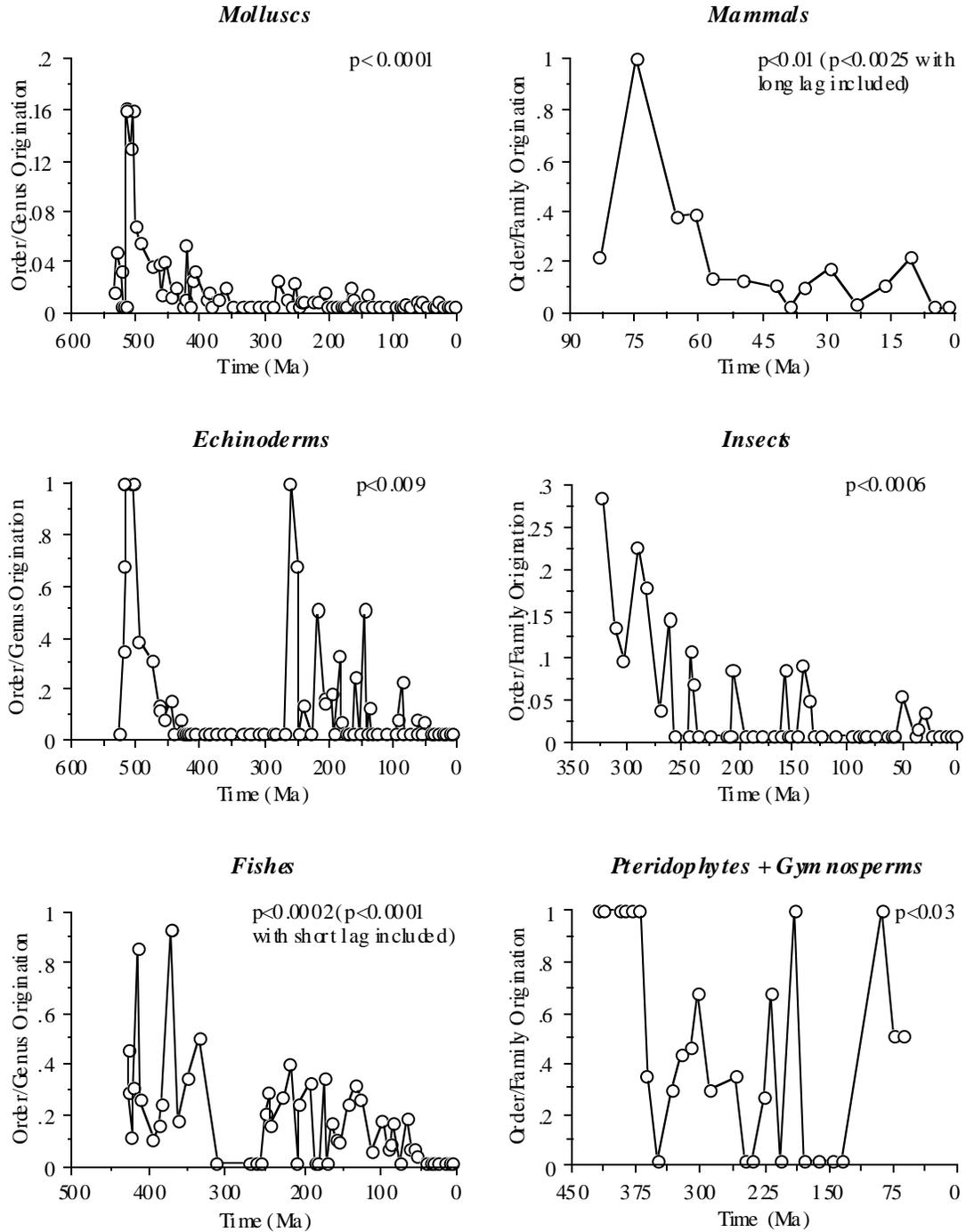


Figure 3. Time series of order/lineage ratio. P-values for Spearman's rank correlation are given. For fishes and mammals a second p-value is given. *Série chronologique du rapport ordre/lignage. Les valeurs de signification statistique pour la corrélation de Spearman sont données. Pour les mammifères et poissons une seconde valeur est donnée.*

With the exception of echinoderms, there is no clear two-stepped decline in connection with the recovery from the end-Permian mass extinction, contrary to what is seen with lineage origination. This implies that different processes, or different manifestations of processes, may have affected lineages vis-à-vis major innovations. Guild structure might be involved, since a smaller number of guilds relative to a possible total was available in the Triassic than in earlier times (Bambach 1983, 1985). But since there **were** guilds available, and the average number of classes per guild and of guilds per class was not at a maximum (Bambach 1983, 1985), it is doubtful that ecological opportunity (or lack thereof) alone was responsible for the whole pattern at the level of orders. It is possible instead that the building up of historical constraints through time, with developmental entrenchment restricting the production of variation, had an important effect (Erwin et al. 1987; DiMichele and Bateman 1996; Eble 1998b). This explanation is consistent with the generality of the pattern in individual groups and on land and sea. Even so, guild occupation studies in marine orders and in terrestrial groups in general are still lacking (but see Labandeira and Sepkoski 1993; Labandeira 1997; DiMichele et al. in press). They could throw further light into the ecological controls of evolutionary flexibility.

Origination and diversity. Total origination rate is contrasted with diversity in Fig. 4. The evidence for diversity dependence of origination is mixed. All three marine groups show a significant relationship between total origination rate and diversity, but in echinoderms a quadratic fit does not significantly improve explanation over a linear fit (F -test). Molluscs and fishes, in contrast, conform to a logistic system with a quadratic fit better accounting for the data once the Pliocene-Pleistocene is removed ($F=11.29$ and $p<0.005$ in molluscs and $F=16.32$ and $p<0.001$ in fishes). While this discrepancy does not disprove a logistic behavior for marine diversity as a whole (nor for echinoderm diversity in isolation), it suggests a dynamics for origination that is at least partially independent from crowding and ecological opportunity. Of course, the histories of each group have not run their full course, which might eventually reveal or conceal crowding effects.

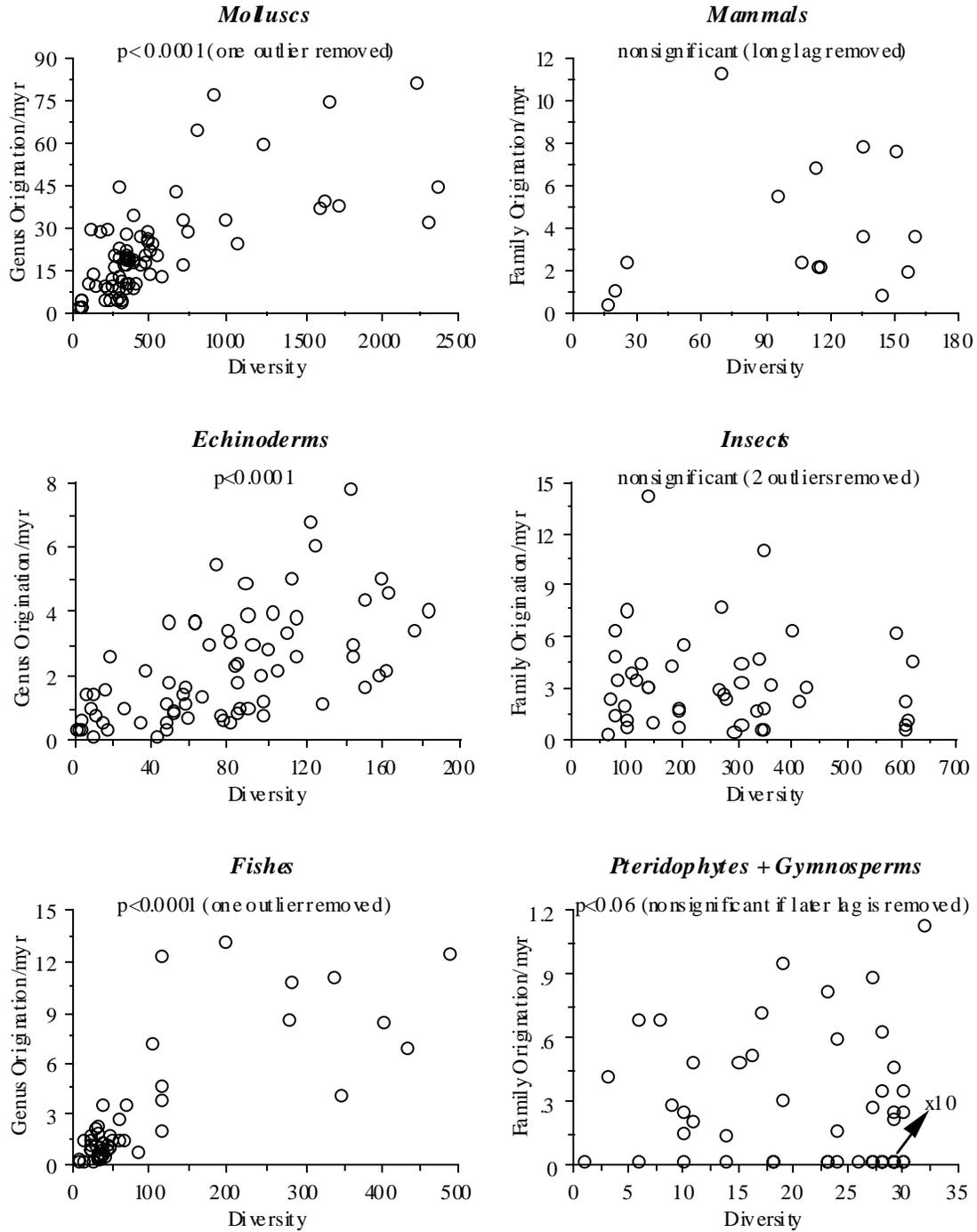


Figure 4. Analysis of diversity dependence of total origination rate. P-values for Spearman's rank correlation are given. See text for additional explanation. *Analyse de la dépendance en diversité du taux total d'apparitions de lignages. Les valeurs de signification statistique pour la corrélation de Spearman sont données. Voir le texte pour explication supplémentaire.*

On land, the patterns are somewhat more idiosyncratic. Mammals show no significant relationship between total origination and diversity if the long lag at low diversity is excluded. If the long lag is included, a significant relationship accrues and a quadratic fit is marginally better than a linear one. Logistic diversity dependence was also suggested by Alroy (1996) for post-Paleocene North American mammals, although in this case per-taxon rates were used. Insects, in turn, show very clearly a nonsignificant relationship between total origination and diversity. Pteridophytes/gymnosperms (the angiosperm record is too limited) show a significant relationship, in fact slightly negative, when all data are included, but the data are equally well explained by linear and quadratic fits. If the rather long Cenozoic “lag” with no origination is removed, on the grounds that the system is no longer dynamic, the relationship becomes nonsignificant.

Although this general discordance between land and sea may be a product of inherent differences in the quality of the record, it is possible that differences in ecological homogeneity (Cohen 1994; May 1994; Roughgarden et al. 1994), geographical and population structure (Rapoport 1994; May 1994), and environmental unpredictability (Cohen 1994; May 1994) between terrestrial and marine realms were implicated on short-term controls on origination. Whatever the causes, the present comparisons indicate that origination responses to diversity on land and in the sea may be fundamentally different. This prediction deserves additional testing.

Self-organized criticality. Frequency distributions for proportional lineage origination are presented on the left-hand side of Figs. 5 (marine groups) and 6 (terrestrial groups; angiosperms not considered). In all cases, the distributions are skewed, with a smaller proportion of intervals displaying substantial origination. In order to test the predictions of SOC theory, the data are replotted on the right-hand side in log-log form, the slope of the linear fit (power law) depicted, and linear and quadratic functions fit to the data.

While recent work suggested that the model should hold for pooled marine and terrestrial families (Solé et al. 1997), origination received less attention than extinction, and alternative model fitting was not attempted. The present frequency distribution analysis does not give general support to a model of self-organized criticality of

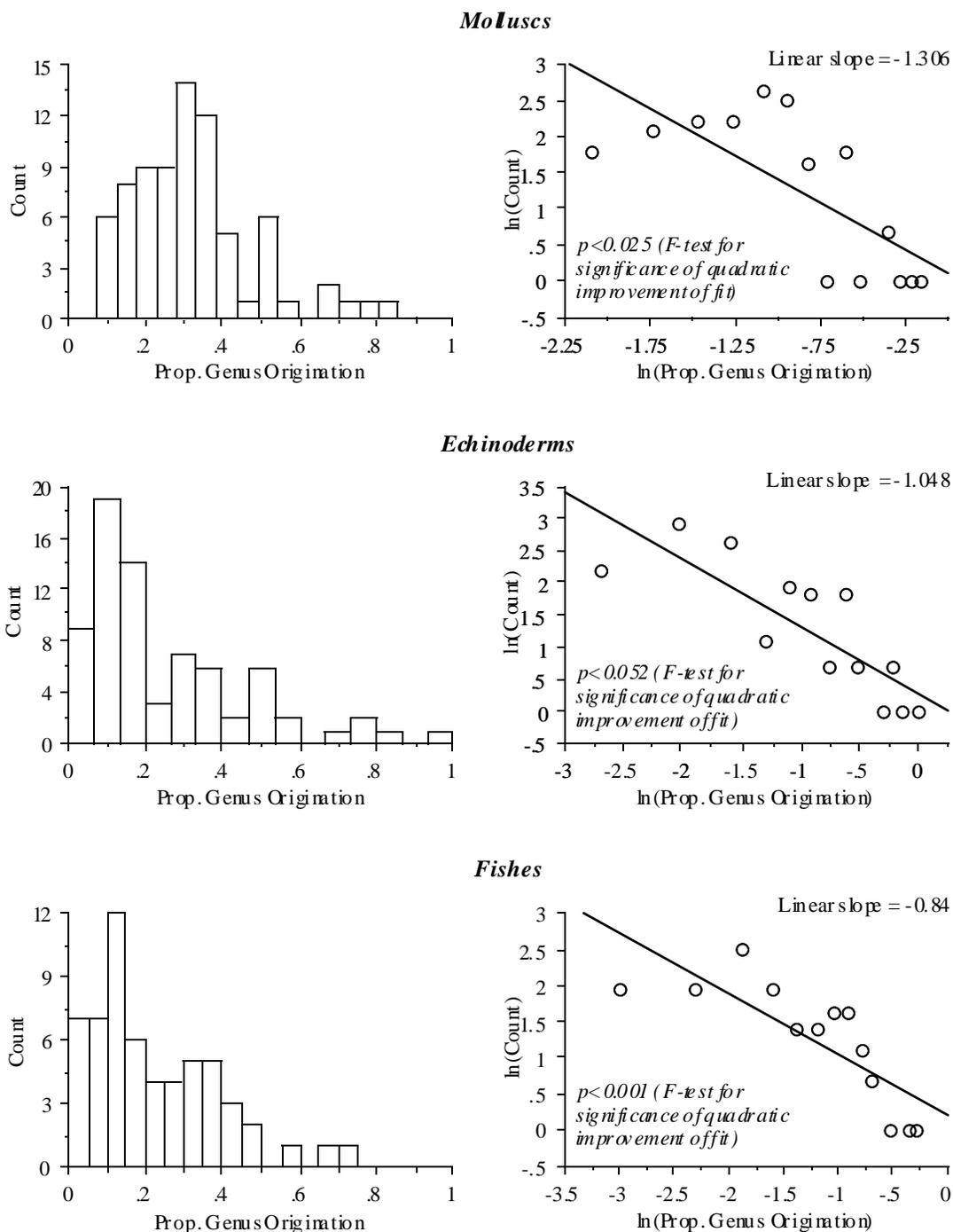


Figure 5. Analysis of self-organized criticality of origination for molluscs, echinoderms and fishes. On the left, the frequency distributions of proportional origination are presented. On the right, linear (power law) and quadratic fits to the data in log-log form are displayed, and the slope of the linear fit is given. See text for further explanation. *Analyse de la criticité auto-organisée d'apparitions pour les mollusques, échinodermes, et poissons. À gauche, les distributions de fréquence des apparitions proportionnelles de lignages sont présentées. À droite, l'adéquation des fonctions linéaire (loi de puissance) et quadratique sont montrées en coordonnées logarithmiques, et l'inclinaison de la fonction linéaire est donnée. Voir le texte pour explication supplémentaire.*

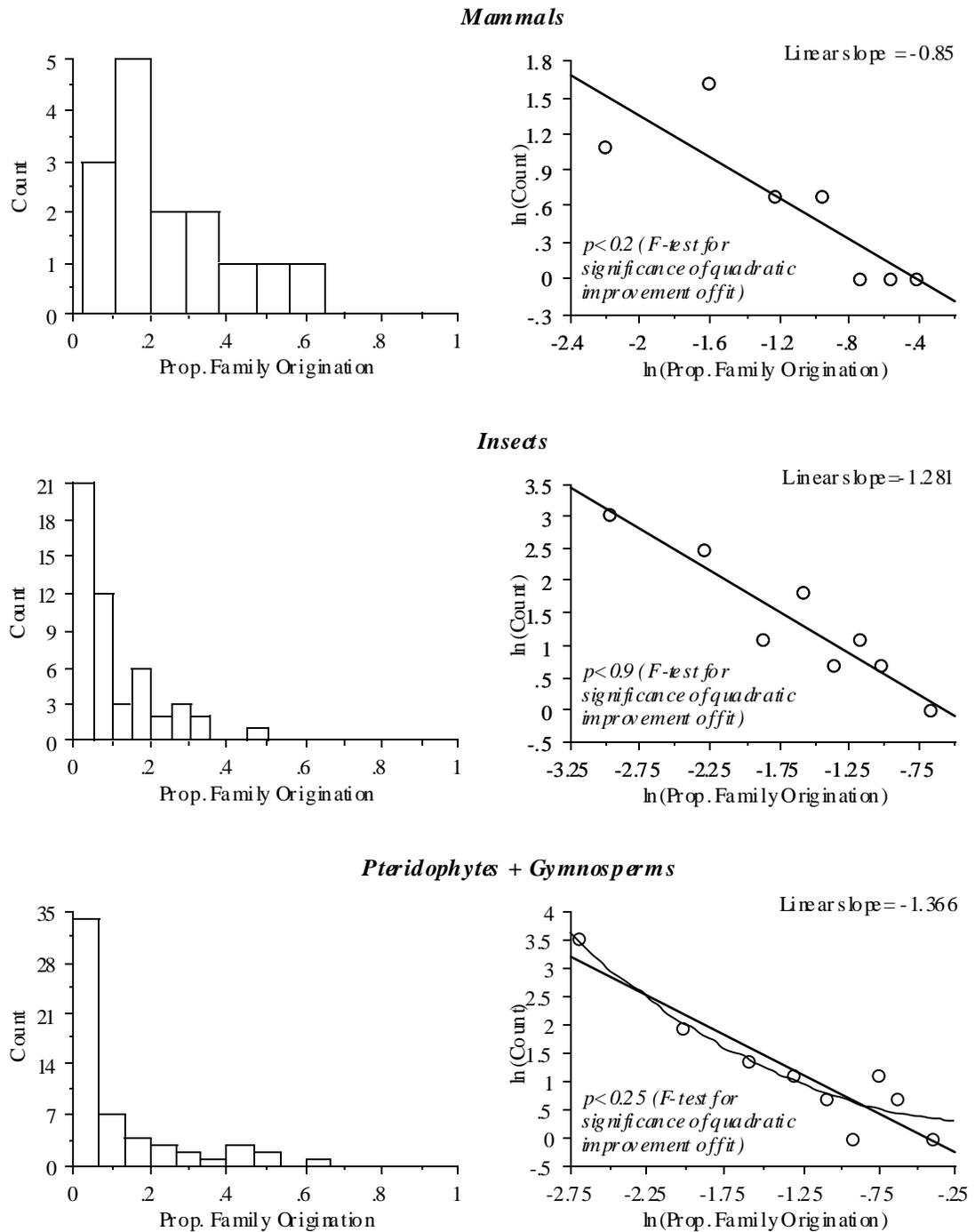


Figure 6. Analysis of self-organized criticality of origination for mammals, insects, and pteridophytes/gymnosperms. See Fig. 5 and text for further explanation. Analyse de la criticité auto-organisée d'apparitions pour les mammifères, insectes, et ptéridophytes/gymnospermes. Voir Fig. 5 et le texte pour explication supplémentaire.

origination. Although the slopes are in general agreement with SOC theory in their restricted departure from -1 (a slope of zero characterizes Gaussian noise and a slope of -2 characterizes random walks -- Halley 1996; Solé and Bascompte 1996), alternative model fitting undermines the generality of SOC for origination. For molluscs ($F=7.58$, $p<0.025$), echinoderms ($F=4.89$, $p<0.052$), and fishes ($F=23.97$, $p<0.001$), a quadratic fit gives a significant improvement over a linear fit. For mammals, although a quadratic fit is not significantly better ($p<0.2$), the small numbers compromise robustness and residual variation (in the same direction as marine groups) suggests that some other model may well provide a better fit -- in fact, an analysis of data from Alroy (1996) indicates that for per-taxon rates log-log linearity does not apply ($F=25.49$, $p<0.001$). Only the distributions of insects and pteridophytes/gymnosperms conform well to a power law, with no significant improvement imparted by a quadratic fit. Thus, of all 6 groups, only one third display patterns that are reasonably suggestive of self-organized criticality.

There are problems with the very predictions of SOC theory, which are consistent with a variety of other explanations (Newman 1996; Kirchner and Weil 1998; Plotnick and Sepkoski 1998; Newman and Eble submitted a,b). Even if these problems are not taken into account (some of them apply to spectral analyses only), it is clear that slopes may not carry much discriminating power and that individual groups show conflicting signals, with alternative functions perhaps better fitting the data. The coarseness of the predictions of SOC theory, and therefore of data analysis, make it difficult to ascertain whether the differences are group-specific or ecological. While the case of insects and pteridophytes/gymnosperms is deserving of further scrutiny (e.g., with consideration of data on levels of interaction or with incorporation of better resolved angiosperm data), it is apparent that a model of self-organized criticality does not uniformly apply to origination on land and sea.

SUMMARY AND CONCLUSIONS

Table 1 presents a summary of results relating to the testing of the four hypotheses of origination addressed in this paper. Given the resolution of the data and the statistics utilized, this summary is best seen as a suggestion of the ways in which concordance and discordance between origination on land and in the sea may be manifested.

Table 1. Summary of results. *Sommaire des résultats.*

Group	Hypotheses			
	Decline in lineage origination?	Decline in innovation	Logistic diversity-dependence	Self-organized criticality?
Molluscs	yes	yes	yes	equivocal
Echinoderms	yes	yes	no	equivocal
Fishes	yes	yes	yes	equivocal
Mammals	yes	yes	no (yes)	equivocal
Insects	yes	yes	no	possibly
Pter./Gymn.	yes	yes	no	possibly
Angiosperms	yes	yes	---	----

A decline in lineage origination and in the frequency of major innovations is consistently present in all groups studied. This is interpreted in terms of an inherent temporal asymmetry in evolvability that is independent of environmental context. For lineages, the rebound from the Permo-Triassic mass extinction imposes a discontinuity to the decline, which appears two-stepped. For major innovations, such a discontinuity is not pervasive. In both cases the involvement of factors other than ecospace occupation seems plausible.

In the sea, origination and diversity are significantly related, and the predictions of a logistic model of diversity dependence of origination are met in molluscs and fishes but not in echinoderms. On land, nonsignificant relationships are present in insects and for the bulk of the history of pteridophytes/gymnosperms and mammals (but not for their full histories). The more idiosyncratic patterns on land might relate to differences between marine and terrestrial ecosystems.

Strong support of self-organized criticality was not found in this study. Insects and pteridophytes/gymnosperms do show a reasonable agreement with the predictions of the model, but in marine groups there is a very poor agreement and in mammals it is equivocal at best. Self-organized criticality of origination, although a plausible phenomenon, is not general.

Much more is known about the dynamics of extinction than of origination. The analyses and hypotheses of origination discussed in this paper represent a step in

the direction of a comprehensive picture of the origination process, and ultimately of a theory of origination that incorporates similarities and differences among groups and environments. While the present comparative analysis of origination patterns on land and sea is not exhaustive, the regularities that emerge are striking. They invite additional studies in order to determine their generality.

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