

Time asymmetry in the palaeobiogeographic history of species

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Key-words. – Palaeobiogeography, Species, Origin, Extinction, FAD, LAD, Time.

Abstract. – The difficulties and hindrances of palaeobiogeography and historical biogeography in its long, sterile search for centres of origin or ancestral areas of species, leading some authors to withdraw the centre-of-origin as a non-scientific concept, are here considered as signals and not artefacts for the recognition of patterns in the biogeographic history of lineages. The time-symmetric model, which assumes gradual origination and extinction processes of a species, is here questioned and an alternative time-asymmetric model is proposed. The origination and expansion processes of a species history would be much faster and more unpredictable than the often gradual, long, predictable extinction process marked by previous signals of geographic area contraction. Monitored biological invasions, plankton blooms and episodes of coordinated migrations illustrate the fast expansion of novel species behaving as dissipative structures. The asymmetric biogeographic model is tested through palaeobiogeographic data on Old World mammal species and by the consistent preference of biostratigraphers for species appearance against species extinction as time-marker bioevents. Time-asymmetry is a common phenomenon of nature, indicating that asymmetry could well be a general property of Time itself.

Asymétrie temporelle dans l'histoire paléobiogéographique des espèces

Mots-clés. – Paléobiogéographie, Espèces, Origine, Extinction, FAD, LAD, Temps

Résumé. – Les difficultés et les obstacles de la paléobiogéographie et de la biogéographie historique rencontrés dans la longue et stérile recherche des centres d'origine ou d'« aires ancestrales » des espèces ont amené certains auteurs à abandonner ce concept non-scientifique. Les méthodes qualitatives et quantitatives utilisées pour repérer les aires d'origine des espèces sont confrontées à de sérieuses difficultés du fait des nombreuses hypothèses non vérifiées sur des probabilités ou des directions de dispersion. Aucun centre d'origine d'aucune espèce n'a jamais été documenté, sauf lorsqu'ils ont été rapportés à de très vastes régions (des continents ou des océans entiers). De nombreux auteurs ont renoncé à leur recherche. Ces difficultés sont ici considérées comme un signal, et non pas du bruit de fond, pour reconnaître des « patterns » cohérents dans l'histoire biogéographique des lignées.

On assume couramment que dans l'histoire paléobiogéographique des espèces on doit trouver généralement des processus graduels d'apparition et d'extinction. Ce modèle symétrique dans le temps est ici remis en question et un modèle alternatif, asymétrique dans le temps, est proposé pour l'histoire des espèces. Selon notre modèle, les processus d'apparition et d'expansion des espèces seraient beaucoup plus rapides, courts et imprévisibles que les processus d'extinction, généralement lents, longs et prévisibles parce que précédés graduellement par des signes de diminution progressive par paliers de l'aire de distribution. Des monitorages d'espèces envahissantes, des floraisons instantanées en temps réel du plancton, et des épisodes de migrations coordonnées illustrent la rapidité de l'expansion des espèces qui se comportent comme des structures dissipatives. Le « cycle du taxon » des espèces insulaires *sensu lato*, qui voient leurs aires de distribution se réduire à mesure de leur différenciation, montre aussi la grande vitesse d'apparition de nouvelles espèces et leur lent processus d'extinction. Les espèces insulaires ne sont pas capables d'expansion sur des vastes aires ; les îles ne servent donc pas de centre d'origine ou de source d'espèces qui pourraient se disperser par la suite. Au contraire, elles sont des puits d'espèces qui vont s'éteindre comme prévoit le modèle asymétrique.

Le modèle biogéographique asymétrique est testé sur deux jeux de données : (i) des données paléobiogéographiques d'espèces de mammifères du Vieux Monde qui montrent la rapidité de l'expansion des espèces nouvelles sur des vastes aires, empêchant à la fois de reconstruire leur parcours paléobiogéographique et de connaître leur lieu d'origine. Cette rapidité d'expansion contraste avec l'échelonnement de l'extinction des espèces en déclin, qui permet de suivre leur parcours paléobiogéographique et signaler avec précision leur centre d'extinction; et (ii) des données biostratigraphiques, qui montrent la préférence habituelle des biostratigraphes pour les événements d'apparition des espèces (FADs = *first appearance datum*) pour fixer des limites géochronologiques aussi brèves que possible, au lieu des événements d'extinction (LADs = *last appearance datum*) généralement considérés plus fréquemment diachrones.

Notre modèle asymétrique de l'histoire biogéographique des lignées, déjà détecté par Darwin, rejoint beaucoup d'autres observations. L'asymétrie dans le temps est un phénomène commun dans la nature indiquant que cette asymétrie pourrait être une propriété générale du Temps lui-même.

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INTRODUCTION

Historical biogeography and palaeobiogeography deal with the dynamics of organism and area distributions. In spite of the ever-changing palaeogeography and species geographic ranges, these disciplines try to recognize common biogeographic patterns in the history of areas and species through different methods (panbiogeography, area cladograms, phylogeography, etc.). The search for pattern recognition deals mainly with the biogeographic history of areas, since that of species is considered less prone to regularities, as made up of individual, untestable dispersal events. However, patterns in the biogeographical history of species can be recognized and tested, to what we contribute in this work, using paleobiogeographic data on individual species.

The biogeographic history of species, lineages or clades is generally conceived as starting in a primitive (plesiochoric) area, its centre of origin, then expanding to a new (apochoric) area by dispersal processes. However, the problem of how to locate the biogeographic origin of a species has not yet been resolved [López-Martínez, 2003]. The classical *centre-of-origin* concept, disregarded as non-scientific in the seventies [Croizat *et al.*, 1974], has been replaced by the wider *ancestral area* concept [Bremer, 1992], conceived as the sum of the area occupied by the ancestral populations, minus the area invaded by dispersed populations. Its inference has been approached without success by different qualitative (area with maximum diversity, area of primitive populations, etc.) and quantitative criteria (analytic probabilistic methods, ancestral area analyses; Bremer, 1992; Ronquist, 1994, 1997; Hausdorf, 1998; criticized by Croizat *et al.*, 1974; Ebach, 1999 and Crisp and Cook, 2005). As we will see, none of these approaches gives a reliable answer. The problem of the geographical origin of a lineage cannot solely be resolved with a phylogenetic tree. In fact, a given phylogeny is compatible with any ancestral area, as pointed out by Crisp and Cook [2005].

The securest way to approach the reconstruction of biogeographic histories and ancestral areas is the fossil record. Although scarce or absent for most recent taxa, fossil documents are abundant enough for many groups of organisms, which would allow reconstructing individual biogeographic histories and inferring common patterns. There is however, a rarity of palaeontological studies conclusively documenting the geographical origin of a lineage, which is worthy to be examined. Data from the fossil record and from the biosphere are applied in this work to the problem of the ancestral area inference, aiming to recognize possible common patterns in the biogeographic histories of lineages.

FAILURE OF METHODS FOR INFERRING ORIGINAL AREAS

The classical (biblical) conception of species biogeographic history, through a local origin and dispersal, has been formulated by Cuvier [1798]:

“It seems that in the beginning, each animal and even plant species did not exist but in a particular region, from where it spread according to the capabilities given by its configuration. Even now, several of them seem to have been limited around these centres of origin, by the seas when they

cannot swim or fly, or by temperatures they cannot support, or by mountains they cannot cross over...”

Croizat [1960] found this explicit idea in the literature at the end of XVth century, when Spanish clerics were asking themselves as to what was the centre of origin of the Native Americans for they concluded that they were immigrants from another continent (confirmed by modern anthropologists). The centre-of-origin concept was further reinforced in the evolutionary theory by Darwin [1859 p. 352]:

“Undoubtedly there are many cases of extreme difficulty in understanding how the same species could possibly have migrated from some one point to the several distant and isolated points, where now found. Nevertheless, the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects it, rejects the vera causa of ordinary generation with subsequent migration, and calls in the agency of a miracle.”

However, in spite of many studies since then, it has not yet been possible to document unambiguously the biogeographic origin of any species. Carlton [1996] even proposed the term “cryptogenic” (of unknown origin) for the high number of species that cannot be identified as native or invader in a region. Only insular species (*sensu lato*) have clear geographic origins in their restricted geographic area; but unless they would disperse away from their island (of which there are not examples, see below) [López-Martínez, 2003], insular endemic species just occupy a small geographic area and do not show the alleged biogeography of local origin and expansion. On the contrary, the history of insular lineages shows the ‘taxon cycle’ model of differentiation through contraction of their geographic area [Wilson, 1961; Ricklefs and Cox, 1972; Ricklefs and Bermingham, 2002; see below].

Inferring the biogeographic origin by application of different criteria results in satisfactory answers in some particular cases (e.g., domestic plants); however, there is no general criterion or analytic method to infer the original area of a species. This was the main reason Croizat *et al.* [1974] rejected the centre-of-origin as inapplicable and a non-scientific concept. The process of organism dispersal (area expansion over a geographic barrier) was also discarded as unverifiable, because of its accidental and individual nature, and many biogeographers focussed then in searching for vicariant area patterns instead of organism dispersal histories [Nelson and Rosen, 1981; Humphries, 2002]. However, the fever for the search of the centre of origin concept did not diminish. The search for individual biogeographic histories has now extended the restrained *centre-of-origin* concept to a wider *ancestral-area* concept (a larger area, e.g., a whole continent that could even be larger than the descents’ area) [Bremer, 1992]. Qualitative and quantitative procedures are used to infer the original area of lineages.

Qualitative approaches

Three main criteria are generally used for inferring the centre-of-origin / ancestral area of a lineage: 1) area with maximum diversity, 2) area with primitive populations, and 3) area with the oldest fossil.

1) The maximum diversity centre as the centre-of-origin / ancestral area of a lineage is one of the most widespread

criterion in biogeography, particularly in phylogeography and population genetic studies (“gene centre theory”) [see for instance Avise, 2000; Chowdhury and Slinkard, 2000; Wikler and Gordon, 2000; Schoch *et al.*, 2001; Hagen *et al.*, 2002; Andronov *et al.*, 2003; etc.]. The rationale behind this criterion is that a lineage would accumulate its maximum molecular, genetic, morphological or taxonomic diversity in the area where it settled longer. This criterion implies first, a permanent settlement of the taxon in its original area; second, a sympatric model of speciation; and third, an accumulation of the successive, modified populations in the ancestral area, instead of dispersal. These assumptions are not supported by data, on the contrary: the allopatric model is more frequently assumed (*i.e.*, speciation in an isolated small area and dispersal away from the primitive area). In fact, genetic and morphological polymorphisms seem to be directly related to environmental heterogeneity, not to settlement duration [Van Valen, 1965; McDonald and Ayala, 1974; Doadrio *et al.*, 1996]. Moreover, the low speciation rates inferred for areas bearing high biological diversity [Weir and Schluter, 2007] strongly suggest that species do not often originate in these areas. This criterion is however widely used, even in face of many contradictory evidences (such as the existence of more than one centre; or the discrepancy between a centre richer in species and another richer in polymorphism) [see Sáiz, 1973, p. 290; Hengeveld, 1989, p. 95].

2) Another widespread criterion identifies the original area with that where the taxon shows the most primitive characters. This criterion is based on Hennig’s progression rule [Hennig, 1966], stating that populations / taxa with more primitive traits would settle around their original area, while derived populations would disperse away of it. Hennig’s rule is the opposite of Darlington’s (assumed by Simpson, Willis, etc.), which states that primitive taxa would be rejected to marginal areas by new derived taxa that would keep the original area. In fact, both rules are equally possible and not particularly supported by data [Platnick, 1981; Morrone and Crisci, 1995]. Ironically, Darlington’s rule is more compatible with criterion 1, which invalidates it for locating the ancestral area of the lineage.

3) The third commonest criterion to locate the original area of a lineage is the area with the oldest fossil remains. The palaeontological criterion for identifying ancestral areas is limited by the biases of preservation and accessibility of fossil remains, but can be applied when the fossil record of a lineage is representative. Authors usually apply this palaeontological criterion by combining it with Hennig’s rule [e.g., Rubidge and Sidor, 2001]: ancestral areas would have the oldest fossils with the most primitive features.

However, no conclusive fossil documents have unambiguously shown the ancestral area of any lineage. The general opinion now among palaeontologists gives no credit to this research, which raged among North and South American palaeontologists at the beginning of the XX century (e.g., Matthew vs. Ameghino). The recent case of the oldest fossil hominids, discovered in Central Africa several thousand kilometres away from its second oldest findings in East Africa, illustrates this modern opinion:

“If the origins of hominids occurred rapidly, followed by rapid area extension, as seems likely, it may be as futile to seek a specific and localized place of origin for hominids as it is for any other group” [Brunet et al., 1995].

These authors do not discuss the claimed African origin for hominids, agreed by the combined evidence of the three criteria; however, the hominid fossil record being extremely poor, the existence of a wider or different ancestral area cannot be discarded.

The statement by Brunet *et al.* [1995] does not reject the existence of a local centre of origin of a species, but rejects the possibilities of identifying it because the rapid geographic expansion of new lineages (as stated by Eldredge and Gould’ punctuated evolutionary model).

The failures of the qualitative approaches for inferring centres of origin / ancestral areas, lead authors to search for new analytical tools in order to decipher the palaeobiogeographic history of biological lineages.

Quantitative approaches

Analytic approaches to the ancestral area problem based on phylogenetic trees are also widely used, although subjected to severe criticisms. The more widespread methods are those of Bremer [1992; ancestral area analysis], Ronquist [1994, 1997; Fitch optimisation; DIVA] and Hausdorf [1998; weighted ancestral area analysis]. They identify as an ancestral area of a lineage, part of or the sum of the descendant’s geographic area; a larger ancestral area cannot be identified by these methods. The results heavily depend of the complete sampling of the lineage, including areas of extinct populations (often overlooked in biogeographic analyses) [Lieberman, 2003].

All these methods are based in Hennig’s *rule* (an unguaranteed assumption; see above), and consider basal-branching taxa supposedly corresponding to ancestral taxa, whose geographic area is assumed as part or all the ancestral area of a clade [see for instance Repetur *et al.*, 1997; Mathee *et al.*, 2004; Díaz-Gómez and Lobo, 2006]. As demonstrated by Platnick [1981], Ebach [1999] and Crisp and Cook [2005], the major failures of these method are: (i) dispersal processes have no rules; (ii) length of branches in a phylogenetic tree does not correlate with time of differentiation; and (iii) in case of paralogy (areas with more than one taxon of the same clade, or a taxon in more than one area), the analyses would indicate as ancestral area the more repeated one, which may on the contrary be an apochoric area subject to recurrent dispersal events [see Ladiges, 2006]. Thus, a phylogenetic hypothesis is not sufficient ground for tracing back the biogeographic history of the species and reconstructing their original area.

Ree *et al.* [2005] propose a probabilistic method to simulate the biogeographic history of a lineage using phylogenetic and palaeogeographic timing data, assuming heredity by daughter species of part or all the ancestral area and modelling constant parameters of dispersal and extinction rates; they can then measure the likelihood of some alternative scenarios. However, the number of possible scenarios is far too large to be tested by this procedure [Humphries, 2002].

When possible, authors usually contrast their analytical biogeographic results on modern species with the fossil record, as the best constraint for historical hypotheses. *“The ideal materials from which to estimate the ages of lineages and their presence in particular places are abundant fossils”* [Renner, 2005]. However, even if the quality of the fossil record is improving, not a *single* case has yet been

documented for the existence of a centre of origin of a lineage. All we can do at present is to point to large oceans or continents as possible ancestral areas for some lineages, but this hypothesis cannot be guaranteed. The fossil record has not yet allowed an unambiguous identification of the centre of origin of any species, even in the well-represented, best-preserved groups (marine skeletonized animals). In fact, the more fossil documents that are gathered for a particular lineage, the more diffuse its hypothetical centre of origin becomes. The sentence of Olson [1971] seems perfectly valid today: “*What is commonly seen in the fossil record seems to suggest that evolution always occurred somewhere else*” [Olson, 1971, p. 738]. Particularly in cladogenetic radiation events, the region where descendants appear lacks possible ancestors for most of the new lineages. As stated by Rozhnov [2007, p. 307] “*When it is possible to define a probable ancestor, it appears that ancestors and descendants lived in different regions during formation of new taxa*”.

This general “lack of data” in the fossil record for documenting the local palaeobiogeographic origins of lineages has been considered a signal supporting the punctuated equilibrium model [see the above statement by Brunet *et al.*, 1995]. The rapid expansion of new species of phytoplankton, foraminifers, brachiopods, molluscs, graptolites, echinoderms and mammals, where the fossil data are abundant, makes them good time-markers in biostratigraphy but impedes the identification of the biogeographic origin of lineages. The reason why it can be so deserves detailed examination.

Alternative models for the biogeographic history of lineages

The renewal by phylogeographers of inferences on dispersal processes across huge distances [see De Queiroz, 2005] has particularly refuelled the search for centres of origin. As stated by Martín Piera and Sanmartín [1999]:

“...it is highly improbable that a new taxon appears at the same time along the whole area of the ancestor, by simultaneous and parallel evolution. On the contrary, it will appear in an area where conditions would be particularly favourable to it, from where it would expand its geographic area according to the favourable environmental conditions and/or the own dynamics of the Earth’s crust”.

This view has been called the monotypic concept of species origin (as opposed to the polytypic or multiregional concept of the origin of a new species across the whole ancestor’s area) [Hedges, 1985]. As proposed by Jenkins [1994], most authors searching for the centre of origin of a lineage share a unique model for lineage’s biogeographic histories (fig. 1A). According to this model, a new species starts as a small population in an area (its centre of origin), then it gradually disperses and expands its geographic area, finally the lineage’s area suffers a gradual contraction followed by its extinction when its last local small population disappears. We called this model the symmetric model of the biogeographic history of lineages because of its time-symmetry [López-Martínez, 2003]. It agrees with Darwin’s view [1859, chapter 10]: On the geological succession of organic beings: on the slow and successive appearance of new species “...the general rule being a gradual increase in

number, till the group reaches its maximum, and then, sooner or later, it gradually decreases.”

Vrba and DeGusta [2004] partially tested this model against the fossil record, using fossil data of African large mammals, to verify if biogeographical histories of species did really start in smaller areas (fewer fossil localities) than in subsequent intervals (more fossil localities) when they expanded their geographic area. They do not test the gradual extinction end of lineages because they take it for granted [Vrba and DeGusta, 2004, p. 286]. They conclude the validity of its prediction, of fewer fossil localities at the beginning of lineage’ histories (first 0.5 m.y.), reaching a long-term equilibrium by about 1 m.y. after origin (2.33 m.y. average time span of these lineages, 14.8 m.y. maximum).

However, these authors did not study the size of the geographic area during the period of the species record. Instead, the number of fossil localities was used as a proxy for the magnitude of the geographic area. Consequently, they could not conclude about geographic size increase but just on abundance increase: “...The question of precisely how small the average large mammal species is at origin cannot be resolved by the proxy we used. Our results are probably as compatible with the minuscule founder populations envisioned by Carson (1982) as with extensive populations in large separated geographic areas.” [Vrba, 2005; 159].

Jenkins [1992, 1994] focused his research on the end of biogeohistories, to test the predicted gradual pattern of the final extinction after geographic contraction of a species’ area. He verified the validity of this part of the model, by using the record of several well-documented planktonic foraminifer species from the Pacific Ocean along the Cenozoic. He could clearly verify the slow, gradual contraction of the geographic area of most extinct lineages before their final extinction (*Globigerinoides obliquus*, *G. dehiscens*, *G. altispira*, *G. decoraperta*). This author assessed the predictability of the extinctions in general, and particularly in some extant foraminifera species (*G. quadrilobatus*, *G. trilobus*), showing a similar palaeobiogeographic history of continuous and gradual contraction of their geographic area. Conservation biologists have also been able to make predictions about the extinction fate of modern threatened

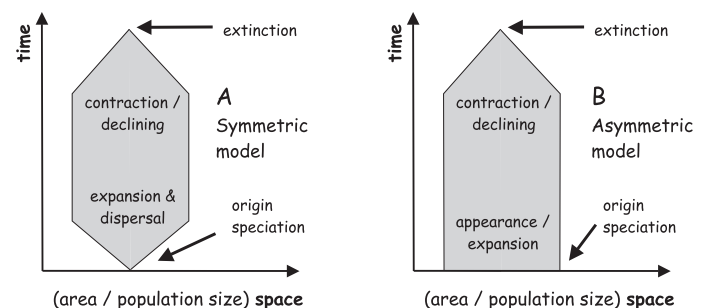


FIG. 1. – Alternative models for the biogeographic history of a lineage. A: symmetric model [from Jenkins, 1994], and B: asymmetric model [from López-Martínez, 2003]. Both models highly simplify the geographic area changes during the long-term equilibrium of the established lineage.

FIG. 1. – Modèles alternatifs pour l’histoire biogéographique d’une lignée. A : modèle symétrique [d’après Jenkins, 1994] ; B : modèle asymétrique [d’après López-Martínez, 2003]. Ces deux modèles simplifient considérablement les changements d’aire géographique pendant l’équilibre à long terme de la lignée.

species [Charlesworth and Charlesworth, 1987; Frankham, 1995; Jiménez *et al.*, 1994; Newman and Pilson, 1997]. A positive feedback affects the declining, small fragmented populations of threatened species by reducing their variability through inbreeding, leading them gradually to their fatal extinction [Lynch *et al.*, 1995; Saccheri *et al.*, 1998; Nieminen *et al.*, 2001]. The extinction process of individual lineages can be very long, as suggested by the existence of a great number of very rare species in nature (lognormal distributions rule), and by inferences of rather long survival of small populations in refuges (*Lazarus* taxa, ghost lineages, bottleneck effects, etc.). Abundant documented cases of recent extinctions show how the geographic area reduces gradually, until a local centre-of-extinction can be accurately signaled (see CREO database).

Thus, apart from particular global events (mass-extinctions), the extinction process of individual lineages generally appears as a gradual decline, in the fossil record and the biosphere as well. It starts by a decrease of the distribution area, often followed by fragmentation and severe contraction, until the local extinction of the last population. This general pattern has been documented in such a way that predictions can be made for the extinction of a lineage based on its biogeographic history.

Therefore, palaeontological and neontological data on biogeographic histories do not support both extremes of the symmetric model. The local biogeographic origin of lineages is rarely well documented, both in the fossil record and the biosphere, to the point that palaeontologists consider this pursuit a hopeless task. In contrast, the end of lineages can in many cases be rather well reconstructed from the fossil record, to the point that palaeontologists consider the extinction as predictable. The rich information on the extinction processes of lineages contrasts with the lack of documents about their origins and areas where new species could have originated.

Origination (speciation) is thus supposed to be a rapid and elusive process (unobservable in the biosphere) [see Reif, 2004]. New species behave as dissipative structures: (i) appearance of a new species is a singular phenomenon, not predictable by our theoretical evolutionary models; speciation is unpredictable in spite of a general tendency towards the increase of diversity; (ii) the expansion of the geographic area is a very rapid process, as documented by rapid coordinated migrations after barrier disappearance [geo-dispersals *sensu* Liebermann and Eldredge, 1996 *vide* Liebermann, 2003], by invasive species and plagues, and by the “blooms” of plankton species. These phenomena are what are expected from irreversible thermodynamic processes [Prigogine, 1979].

Thus, the gradual end of lineages appears much better documented than their claimed gradual beginning. This challenges the symmetric model of biogeographic history of lineages and calls for an alternative model, asymmetric in time [López-Martínez, 2003; fig. 1B]. Instead of symmetric gradual processes of expansion and extinction, the asymmetric model proposes a time-asymmetric biogeographic history of lineages, contrasting the sudden appearance of the new species across its geographic area and its gradual disappearance.

The asymmetric biogeographic model is supported by examples of rapid geographic expansion and slow extinction

processes documented in modern species: (i) invasive species with extremely rapid biogeographic dynamics [Mooney and Cleland, 2001; D’Antonio and Kark, 2002]; (ii) expansion “blooms” of plankton species, monitored by satellite in real time and verified as instantaneous (*Emiliania huxleyi*) [Brown, 1998]; and (iii) rapid colonization processes following a linear function with time, indicating intrinsic regulatory factors [Kooijman, 1993; Lewis and Pacala, 2000], are examples of the sudden appearance and expansion of novelties.

The ‘taxon cycle’ model of island species is another example of time-asymmetric biogeographic histories in modern species [Wilson, 1961; Ricklefs and Cox, 1972]. Islands *sensu lato* (restricted geographic areas, such as caves, lakes, etc., distant from main geographic areas) are active areas of origination of new species, which differentiate from colonialist populations coming from a source area. Insular species show a ‘taxon cycle’ history, independent of external factors or phylogeny, which develops by contraction of the geographic area as the differentiation progresses, until the extinction occurs in its final smallest area [Ricklefs and Bermingham, 2002]. The ‘taxon cycle’ model can also be applied to species differentiation history in continuous areas [García-París *et al.*, 2000].

Instead of centres-of-origin, islands thus show a rapid origin and a slow end of new species, exactly what is predicted by the asymmetric model. Islands do not act as centres of origin for expanding, widespread species. There are not to our knowledge examples of insular species which have successfully expanded to colonize other areas, either as a true dispersal over geographic barriers or as a common area expansion profiting from favorable geographic connections. Mainland species easily spread on islands, but the opposite, even led by anthropic agents, does not occur. A counter-example, the Corsican mouflon successfully introduced and spreading in Europe, is in fact not a native Corsican species but a continental European one [López-Martínez, 2003]. As a rule, insular new species do not disperse away to enlarge their geographic area. On the contrary, islands become sinks for new endemic species that seem unable to expand from their small geographic area and disperse to the main area [López-Martínez, 2003].

In the following paragraphs, we will focus on palaeontological documents supporting the asymmetric model of biogeographic history of lineages. Fossils are the best reference for documenting historical processes and for providing constraints to test evolutionary hypotheses. The fossil record has been the base of important controversies around the geographic origin of lineages, since having the oldest fossil of a lineage is considered an important contribution for an author and a region. However, as the palaeontological knowledge increases and the fossil record of a lineage is better known, the location of its ancestral area becomes fuz-zier.

DOCUMENTING TIME-ASYMMETRY IN PALAEOBIOGEOGRAPHIC HISTORIES

The rich source of data contained in the fossil record is being gathered and tested to show regularities and temporal coincidences, as a way to decipher the history of life on

Earth. As the fossil database improves, successive documents should allow for a refinement of the palaeobiogeographic histories of organism lineages. In the following, we will focus on two lines of evidence supporting the asymmetric model of biogeographic history of lineages: (1) documented species' biogeohistories, mainly using mammal lineages because of the particular research field of the author, and (2) asymmetry in the use of first and last species' appearance data in biostratigraphic scales.

Palaeobiogeographic history of species

Biogeographic histories of particular lineages can be gathered from the bibliography, although they have been rarely compiled in reliable databases because of the complexity and scattered nature of palaeontological data. Individual palaeontologists are however able to confidently illustrate the history of the best-documented lineages for the cases of which they have direct knowledge. We present just some examples chosen from the abundant record on Old World mammals, to illustrate how fossil data can be trusted for reliably documenting the biogeographic history of some lineages.

Near the beginning of the Oligocene (about –34 Ma), a large number of mammalian orders and families suddenly appeared in Europe: felids, bears, rhinoceroses, lagomorphs, two families of insectivores, five families of rodents (squirrels, beavers, hamsters, etc.), where this remarkable bioevent is known as “Large Rupture” [“Grande Coupure”, see López and Thaler, 1974]. The origin of all these immigrants in Europe was assigned to Asia, the major regression of this period favoring a land connection between both continents. However, later progress in the fossil studies in Asia further demonstrate that a similar rupture, named “Mongolian Revolution” occurred almost simultaneously there, with the sudden appearance of new rhinos, carnivores, rodents, etc. [Meng and McKenna, 1998]. The radiation was thus much more expansive, covering Europe and Asia at the same time, and no plausible origins can now be guessed for the newcomers.

The case of the *Dorcatherium* lineage (Artiodactyla, Tragulidae) has been considered by Van der Made *et al.* [2006] to represent a common pattern of gradual reduction of geographic area before extinction. The centre of origin of this ruminant is as obscure as that of the origin of ruminant mammals, or that of the Artiodactyla in general (which show a fast, widespread radiation in the whole northern hemisphere 55 million years ago from unknown origin). *Dorcatherium* appeared in early Miocene times (around –16.5 Ma, MN4) in the Old World across a huge geographic area, from Namibia to East Africa, Arabia, Europe, India, Pakistan, Thailand and China. During 13 million years, it developed about 12 species. Its area gradually contracted during late Miocene, and the lineage extinguished first in SW Europe (at –8 Ma, MN11), then in eastern Europe (at –6 Ma, MN13) and finally in Pakistan (at –4 Ma, Pliocene). Modern tragulids from Southeast Asia, India and Africa belong to different genera. The biogeohistory of *Dorcatherium* is typical of many common cases, which show a similar, asymmetric model in their palaeobiogeographic history.

The case of the *Prolagus* lineage (Lagomorpha, Ochotonidae) is directly known from the author's studies. The

palaeobiogeographic history of this small European pika has been summarized by Lopez-Martinez [2001] (fig. 2). Its beginnings are related to its European ancestor *Piezodus*, from which it differs in heterochronic dental features (more complex and rootless cheek teeth). Transitional populations between both genera are found in MN2 (between –22 and –21 Ma) in different European localities, from the Iberian Peninsula to North and Central Europe, thus a particular centre of origin for *Prolagus* cannot be clearly inferred. During the Miocene, the lineage increases its diversity (up to 2 genera and 11 species) and maintains a large European geographic area. At the Mio-Pliocene transition, it invades North Africa and Caucasus and during Plio-Pleistocene times, its populations become increasingly differentiated, fragmented and isolated. Its history ends in the islands of Corsica and Sardinia in the Holocene, where the last surviving population from the small Tavolara Island was contemporaneous of the people of the Middle Ages.

The case of the Mediterranean vole lineage (*Microtus brecciansis* – *M. cabrerai*) has been also directly studied by us [Cabrera *et al.*, 1983]. This lineage belongs to the Pleistocene radiation of rootless-toothed voles in the Holarctic. The presence of this lineage in southwestern Europe from the Middle Pleistocene to present times can be rather accurately tracked, because histories that are more recent often have a better record. A possible ancestor of the Mediterranean vole lineage (*Microtus (Iberomys) huescarensis*) appears in the early Pleistocene in the Iberian Peninsula. The anagenetic *Iberomys* lineage is formed by the widespread species *Microtus (I.) brecciansis* from the Iberocitane province during the Middle Pleistocene, and its descendant the extant *Microtus (I.) cabrerai*, which gradually reduced its geographic area from the late Pleistocene to recent times (fig. 3). After being the dominant vole in southwestern Europe until Neolithic times, the lineage is today threatened with population reduction and dispersion into small, isolated areas, which will lead to its extinction in a gradual and fatal way.

The different examples of palaeobiogeographic histories of mammalian lineages presented here only touch a very small part of the whole theme and they have been used because of their particular fit to the asymmetric model which we have proposed. As and when additional well-documented cases are compiled in the future, a more complete picture will emerge of what we consider a probable common pattern of the biogeographic history of species.

In the next paragraph, we propose a new approach to test the two alternative biogeographic models above, namely the symmetry or asymmetry in the use of species appearance and extinction events in biostratigraphy.

Bioevents in biostratigraphic scales

Biostratigraphic scales, widely used in geology, are at the base of stratigraphic correlations and support the whole chronostratigraphic time scale, calibrated in particular sections by different procedures (palaeomagnetic or geochemical events, geochronometric isotopic analyses, counting astronomical cycles, etc.). Biostratigraphic scales are based on particular fossils, mainly microfossils (charophytes, coccoliths, conodonts, diatoms, foraminifera, organic-walled microfossils, ostracods, radiolarians) but also macrofossils (ammonoids, graptolites, mammals, rudists) from widespread and turnover-prone groups of organisms. After refinements of the

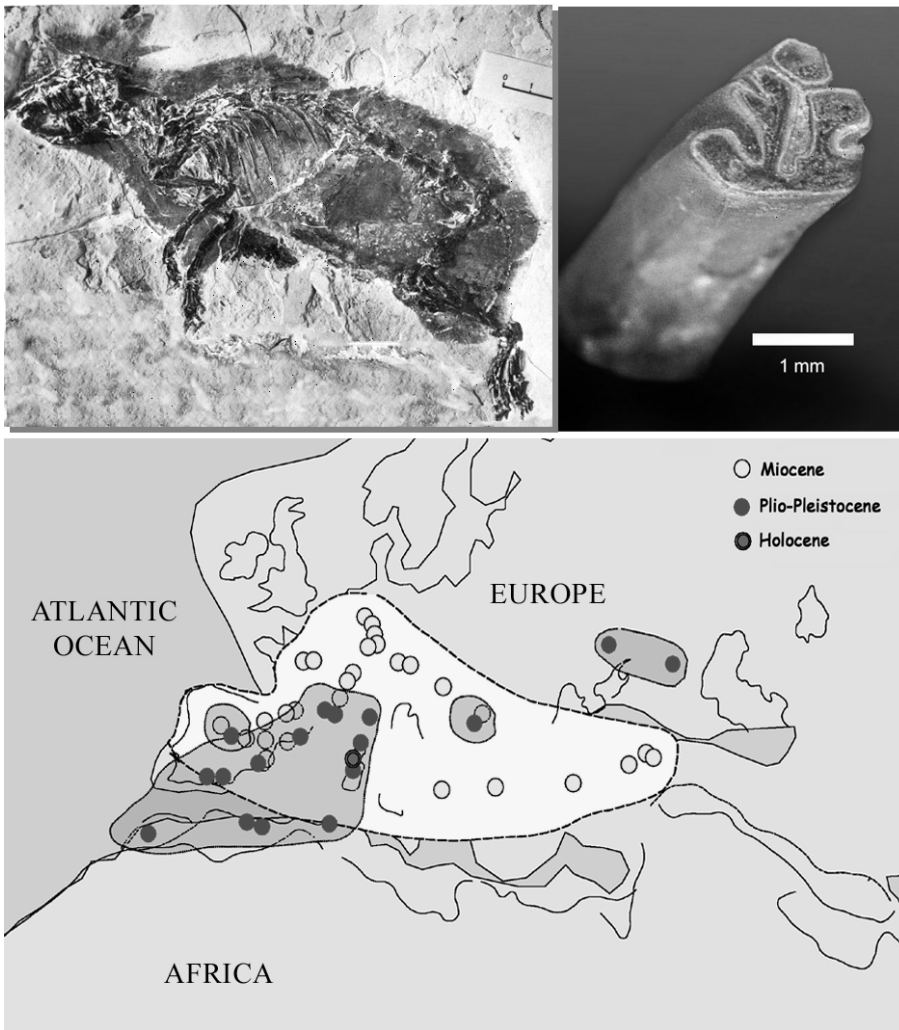


FIG. 2. – Palaeobiogeographic history of *Prolagus* lineage (Mammalia, Ochotonidae) along 20 million years before extinction in Middle Age. Palaeogeographic map from Rögl [1998]. Data from López-Martínez [2001].

FIG. 2. – Histoire paléobiogéographique de la lignée de *Prolagus* (Mammalia, Ochotonidae) pendant 20 millions d'années et avant l'extinction au Moyen-Age. Carte paléogéographique d'après Rögl [1998]. Données d'après Lopez-Martínez [2001].

various methods for biozonation, biostratigraphic scales are now mainly defined on the significant presence or absence of marker species.

Correlation of local biostratigraphic scales established global standard biochronozones bounded by global appearance and extinction bioevents and named by marker species. Biostratigraphers choose marker species by their coherence in order and sequence of appearance and extinction events in different geological sections. The first and last appearance of the marker species, respectively coded as FAD (first appearance *datum* – time of origination) and LAD (last appearance *datum* – time of extinction) in databases, are inferred from the correlation respectively of FO (first occurrence) and LO (last occurrence) of the marker species recorded in different biostratigraphic sections. The appearance of new species in local successions is usually considered as a migratory event (dispersal of an immigrant) or as a phylogenetic event when the new species can be related to a plausible ancestor in the area (although the ancestor-descendant relationships are unguaranteed). Some LADs coincide with the FADs of the replacing putative descendants, and thus they do not indicate extinction but a pseudo-extinction of a chronospecies (successive members of an anagenetic lineage).

Marker species are chosen among those showing particularly rapid expansion and extinction events and more cosmopolitan areas. However, the dimension of the distribution area of a species at its FAD is always limited and can subsequently change. At any moment of a lineage's history, migratory events could happen that will change the geographic area of a species and produce its diachronous appearance out of its former distribution area.

FADs and LADs of marker species at global scale can be quasi-synchronous, as verified by independent calibration and dating [Simmons *et al.*, 1997; Sadler, 2004]. The widespread use of these phenomena in defining geological time boundaries indicates that appearance and disappearance of species in the fossil record are extremely rapid events in relation to the long periods of lineage stability (e.g., 30 million years average duration of foraminifera species). In fact, if expansion or extinction of species were long, gradual processes, it would impede the widespread use of standard biochronozones for geological dating.

In spite of the usual systematic and taphonomic problems, there are a high number of well-documented marker species across geologic time showing well-tested successional order of FADs and LADs bioevents covering a wide geographic area. If species would obey the symmetric model, then the number of FADs must approximately be similar to

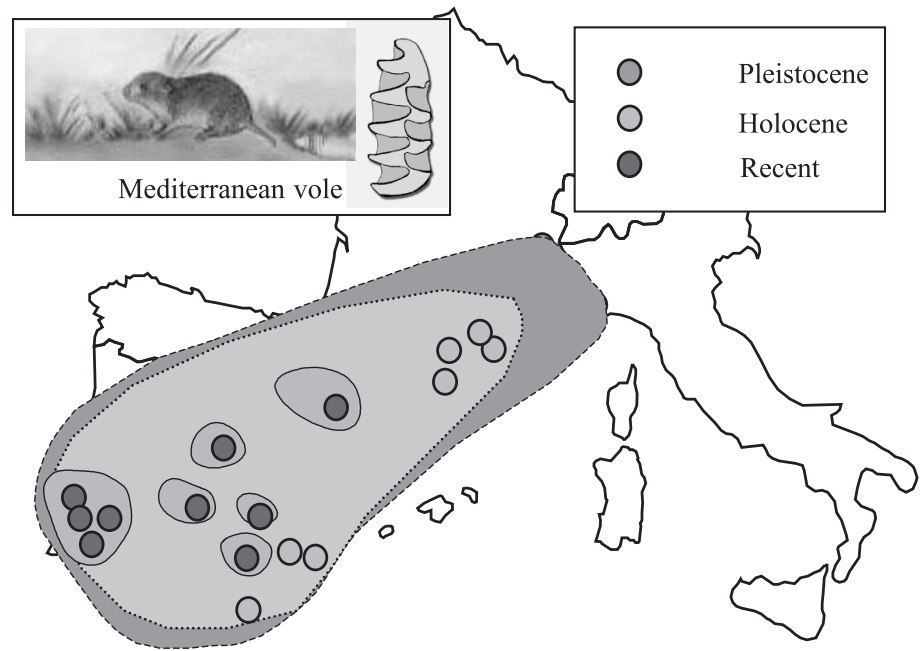


FIG. 3. – Paleobiogeographic distribution of the Mediterranean vole lineage *Microtus brecciensis* (middle Pleistocene) and *Microtus cabreræ* (upper Pleistocene-recent). From Cabrera *et al.* [1983] and López-Martínez [2003].

FIG. 3. – Distribution paléobiogéographique de la lignée méditerranéenne d'arvicolidés *Microtus brecciensis* (Pleistocène moyen) et *Microtus cabreræ* (Pleistocène supérieur-Actuel). D'après Cabrera *et al.* [1983] et López-Martínez [2003].

the number of LADs. If conversely the asymmetric model predominates, FADs events must surpass LADs events. A third model with reverse asymmetry (gradual appearance and sudden extinction) would produce LADs > FADs but it has never been postulated.

The predictions of both alternative palaeobiogeographic models can thus be verified using Graciansky *et al.* [1998] database, a compilation of global Mesozoic and Cenozoic biochronozones covering a period of 248 million years. Our quantitative results concern only microfossils (see below for macrofossils). Independent counting of 2,398 total FADs and LADs across the Mesozoic (Triassic, Jurassic and Cretaceous) and Cenozoic shows a dominance of FADs (total percent 57%) over LADs (see table I and fig. 4). There is thus a constant difference between the two ends of lineages in the adopted stance preferred by biostratigraphers in their studies of microfossils. This difference is even larger in favour of the appearance events, as the pseudo-extinction cases have not been taken into account and have thus been included in the extinction events (see above). Although the Chi square test needs 60%-40% (or larger) differences to show statistical significance, the consistent advantage of FADs over LADs in all periods appears to vindicate the biostratigraphical preference for appearance events (i.e. more rapid) over the relatively more gradual extinction events.

TABLE I. – Percent of biochronologic events based on first appearance (FAD) or last appearance (LAD) of microfossil species in different geological periods (n = 2,398 total data)

TABLE I. – Pourcentage d'événements biochronologiques basés sur les premières apparitions (FAD) ou les dernières apparitions (LAD) d'espèces microfossiles à différentes périodes géologiques (n= 2398 données totales).

	FAD	LAD
Cenozoic	55,75	44,25
Cretaceous	58,8	41,2
Jurassic	56,28	43,72
Triassic	54,87	45,13

Differences between FADs and LADs of marker species in biostratigraphic scales based on macrofossils (ammonites, graptolites, mammals, etc.) are generally larger than those based on microfossils. Extinction events are usually rejected as bad time markers by biostratigraphers using macrofossils because of their more frequent recognition as generally diachronous: "As has been known for a long time, first occurrences (appearances) of species tend to be more nearly isochronous (less diachronous) over great distances than last occurrences (disappearances). Biozones are, therefore, commonly defined by the regional appearance of the guide fossil" [Westermann, 2001, p. 188]. As an example of this preference, the widely used "Interval zones" are solely based on FADs events, and most "Assemblage zones" are mainly based in nearly simultaneous FADs of associated taxa.

The asymmetric use of FADs and LADs bioevents in biostratigraphy, where the fossil documents and studies are particularly numerous, constitutes an independent test of the asymmetry of the species biogeographic history. Biostratigraphers need not adhere to a particular evolutionary model to do their work. They just apply to their species successions the best time-markers that they can find. They recognize in their more and more refined, high-resolution correlations, the rapid appearance of new species in widespread areas as a common phenomenon of practical use. Conversely, the end of lineages is less used for this purpose, because it seems highly diachronous in many cases. This election indicates the favour of biostratigraphers for the asymmetric biogeographic model.

CONCLUSIONS

The time asymmetry of species' biogeographic histories between rapid origination and slow extinction of lineages [López-Martínez, 2003], challenges the common conception of symmetric, gradual beginnings and ends of species' history. As documented by the fossil record, palaeobiogeographic appearance and expansion of species and lineages

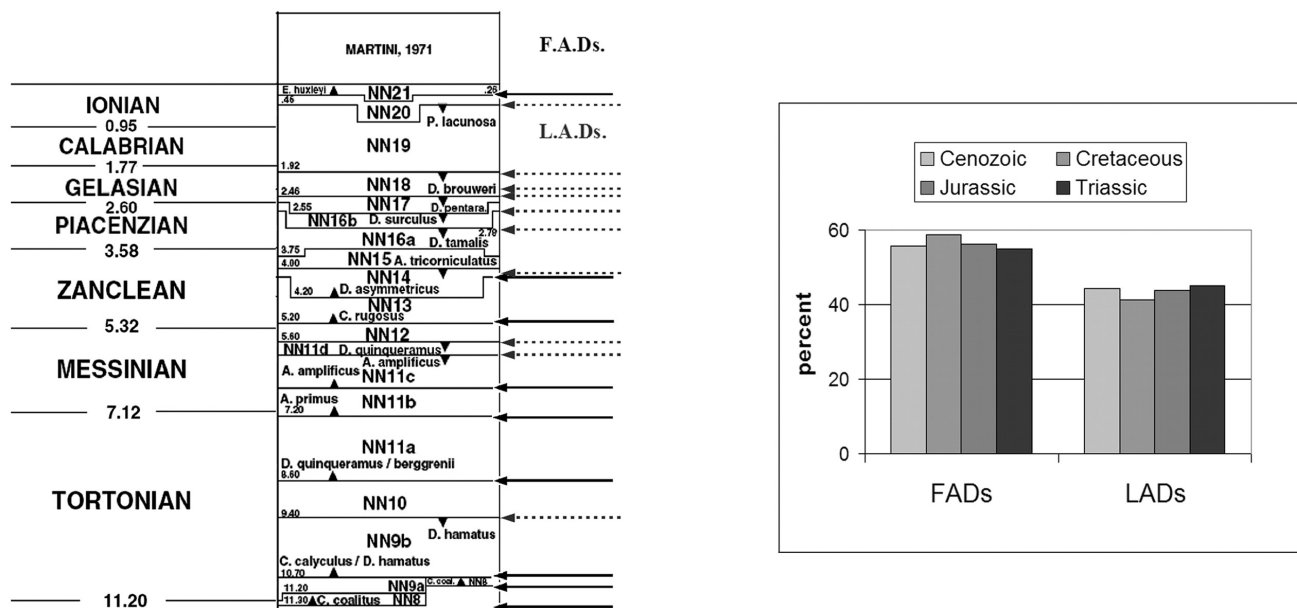


FIG. 4. – Asymmetry in the use of FADs and LADs of microfossil species used as biochronological time markers for three geological periods (2,398 total counts; data from Graciansky *et al.* [1998])

FIG. 4. – Asymétrie dans l'usage des premières apparitions (FADs) et dernières apparitions (LADs) d'espèces microfossiles utilisées comme marqueurs chronologiques à trois périodes géologiques (2 398 comptages, données de Graciansky *et al.* [1998]).

can be extremely rapid, as is the case with dissipative structures in physics, and this phenomenon (postulated by the punctuated evolutionary model) is widely used by biostratigraphers in building geological time scales (FADs events). Conversely, the extinction processes (LADs events) are less prone to synchronicity and are often discarded as time markers in biostratigraphy. Apart from mass-extinction events, the extinction processes in many cases shows a gradual pattern of biogeographic contraction, fragmentation and isolation that allows predicting the fatal end of a given species.

The asymmetric model of biogeographic histories seems less compatible with modern conceptions of evolutionary theory than the current symmetric model, but reliable fossil data must be incorporated in that same theory, as was already noted by Darwin [1859]: “*There is reason to believe that the (complete) extinction of the species of a group (of a whole group of species) is generally a slower process than their production*”. Darwin [1859, chapter 11: On the geological succession of organic beings; on extinction].

The proverbial “incompleteness” or “imperfection” of the fossil record cannot be responsible for this time asymmetry noted in palaeobiogeographic studies of individual lineages, since it cannot be less representative for the beginning than for the end of lineages. On the contrary, as in other cases, the fossil record shows a relevant evolutionary pattern, where many species show a rapid origin and expansion *versus* a slow decline and contraction.

This asymmetric timing of biogeographic histories points to and subsumes a deep physical asymmetry in states of non-equilibrium in nature, observed in symmetry-breaking dissipative structures in general, and even in the pattern of Time itself [Penrose, 2005].

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