C. R. Palevol 10 (2011) 335–340

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

Paléontologie générale, systématique et évolution (Mécanismes évolutifs, microévolution)

Quand l'évolution parle à la biologie fondamentale

When evolution talks to fundamental biology

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INFO ARTICLE

Historique de l'article :
Reçu le 2 décembre 2010
Accepté après révision 7 février 2011
Disponible sur internet le 20 avril 2011

Rédigé à l'invitation du Comité éditorial

Mots clés :
Évolution
Protéases
Brassage d'exons
Transposon
Transfert horizontal
Fluidité du génome

RÉSUMÉ

Les travaux d'histologie osseuse d'Armand de Ricqlès et, plus généralement, de nombreux résultats d'anatomie comparée, trouvent tout leur sens dans le cadre de la théorie de l'évolution. Il en est de même en génomique et en biologie moléculaire. Différents exemples montrent que la fluidité du génome n'est pas assurée par les mêmes processus chez les eucaryotes et chez les procaryotes. Dans un taxon, les transposons jouent un rôle capital, tandis que dans l'autre, les transferts horizontaux se révèlent essentiels. Ces dynamiques sont nécessaires pour comprendre les bases de l'évolution des génomes, autant d'un point de vue fondamental qu'appliqué.

Keywords:
Evolution
Proteases
Exon shuffling
Transposon
Horizontal transfer
Fluidity of the genome

ABSTRACT

Like many results in comparative anatomy, the works on bone histology led by Armand de Ricqlès have found their whole sense within the framework of the theory of evolution. It seems to be the same thing in genomics and molecular biology. However, some examples show that the fluidity of genomes is not realized by the same processes in eukaryotes and in prokaryotes. In the first taxon, transposons play a fundamental role, since in the other case horizontal gene transfers are essential. These dynamics seem to be necessary for understanding the bases of genomic evolution both from fundamental and applied points of view.

Abridged English version

All the work carried out in bone histology by Armand de Ricqlès has always been interpreted within a comparative framework. But who says comparative biology says evolution, and who says evolution says history. This illustrates Theodosius Dobzhansky's famous maxim (Dobzhansky, 1973): "*Nothing in biology makes sense except in the light of evolution*". As it happens, this sentence becomes even more interesting if one adds another one, from Jean Perrin, in which he tried to sum up the scientific approach (Perrin, 1939): "*Science used to replace complicated visible objects by simple invisible ones*." Obviously, Perrin was thinking about physics, but this also applies to some aspects in biology, such as comparative anatomy or genetics. His-

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1631-0683/$ – see front matter
doi:10.1016/j.crpv.2011.02.005

tory or generalization? Heinrich Rickert explained this dilemma by separating natural sciences, which aim at the universal from cultural sciences, which aim at the particular (Rickert, 1997). Following such a classification, biology must be considered as a mix. So, combining Perrin's and Dobzhansky's maxims, we may argue that *complicated visible objects* in biology often can be explicated by a *simple history*. Where Perrin was seeing general laws, since Darwin, biologists study the consequences of evolution. Some classical observations in comparative anatomy illustrate such a topic. But now, it seems essential to find examples in molecular biology, and more precisely in genomics, since biologists must answer the supporters of intelligent design who used to call such structures "irreducibly complex systems", i.e. systems which do not work if one of its components is missing. Such creationists put forward the hypothesis that irreducibly complex systems cannot be built up by the classical mechanisms proposed by evolutionary biology, and that they have been created ex nihilo following an intelligent design (Behe, 1996 ; Padian, 2009). Vertebrate clotting represents such a system that is often quoted. Because of the evident medical applications, it is one of the most studied molecular systems and it has evolved by exon shuffling, an example of Jacob's tinkering of evolution (Jacob, 1977, 1981). The enzymes of blood clotting and fibrinolysis are proteases. Seven of them have been studied by molecular biology in the early 1980s (Patthy, 1985). Four others have been recently added. It has been demonstrated that they are built by protein modules, the histories of which have been reconstructed by molecular phylogeny (Kolkman et Stemmer, 2001 ; Tordai et al., 1999). By combining the molecular phylogenies of these domains, a plausible history of the formation of these genes has been proposed. It has also been demonstrated that their introns contained many repeated sequences and many transposons that promoted mismatches and non-homologous recombinations during meiosis, giving rise to genetic hotspots allowing exon shuffling. So we have an illustration of Perrin's and Dobzhansky's maxims, since: a general mechanism using transposons has been detected; and the gene history has been described. So one wonders how such a gene family could be considered "irreducible" by the supporters of intelligent design. Other facts, like V(D)J recombination in immunology, demonstrate that transposable elements are essential actors in genome evolution. It has been demonstrated that RAG1 and RAG2 enzymes, which together behave as an endonuclease performing this particular recombination, are in fact a transposase (Sadovsky, 2001). Such a system exists in all gnathostomata, and it had been proposed that an ancestor of this phylum had picked up a RAG transposon by horizontal transfer from a prokaryote (Schluter et Marchalonis, 2003). In eukaryota, genetic novelty appears through genomic fluidity, i.e. exon shuffling, gene duplications, polyploidization... It is not the same rule for archaea and bacteria, since gene horizontal transfer seems to be the most frequent evolutionary process (Lopez and Bapteste, 2009). Consequently, evolution of such organisms must not be exclusively by divergent evolution (cladogenesis), but by gene networks, assuming that gene transfers may be performed through multiple vectors, such as plasmids, phages, and integrons (Dagan et al., 2008 ; Halary et al., 2010 ; Kloesges et al., 2010). Therefore, evolutionary processes and phylogenetic histories appear to be very different between Eukaryota and other living beings. Since Darwin, many concepts have evolved: from descent with modification to punctual mutations, and from punctual mutations to tinkering of evolution. The role of transposons in genome fluidity is now quite well understood. Step by step, one discovers that the most complex biological systems are the only result of the trio "mutation/selection/chance", without any project, ruling out creationist argumentation, which appears to be an unscientific point of view. Therefore, biology in its whole is fertilized by breakthroughs in evolution, since the *complex visible* biological objects often may be explained by a *simple* history. It is why, as suggested by Duboule, fundamental biology of the 21st century must strive to improve our understanding of evolutionary mechanisms (Duboule, 2007).

1. Introduction

L'ensemble du travail accompli par Armand de Ricqlès au cours de sa carrière – et en particulier tout ce qui concerne l'histologie osseuse – a pris immédiatement pleinement son sel, parce que ces études étaient réalisées dans un cadre comparatif, celui de l'histologie comparée. Or, qui dit comparatif dit évolutif, qui dit évolutif dit historique. En ce sens, nous avons ici l'illustration de la célèbre maxime de Theodosius Dobzhansky (1973) : « *Rien n'a de sens en biologie, si ce n'est à la lumière de l'évolution* (Nothing in biology makes sense except in the light of evolution) ». En l'occurrence, tout devient encore plus intéressant si on lui adjoint une autre célèbre phrase, celle de Jean Perrin résumant la démarche scientifique (Perrin, 1939) : « *la science remplace du visible compliqué par de l'invisible simple* ». Evidemment, Perrin pensait en tout premier lieu à la physique, qui par des lois – souvent mathématisées, comme celles de la gravitation ou de l'électromagnétisme – résument certaines propriétés de la matière. Certes, en biologie, les lois n'ont pas la même généralité, et le concept de « théorie » n'y a pas le même sens ; par exemple, la théorie cellulaire correspond plus à une constatation – certes capitale – qui n'a pas le même niveau de conceptualisation qu'en physique. Pourtant, si on se rapporte aux bases de l'anatomie comparée, de la génétique ou de la phylogénie, le souhait de généralisation est évident.

2. Biologie et histoire du vivant

Histoire ou généralisation ? Heinrich Rickert avait parfaitement compris l'importance de ce dilemme, en systématisant l'opposition entre « sciences de la nature » et « sciences de la culture », en séparant les sciences qui visent l'universel, de celles qui s'intéressent au particulier (Rickert, 1997) :

> « *Afin d'obtenir deux concepts purement logiques, et ainsi purement formels, [...] j'ai moi-même cherché à formuler ainsi le problème logique fondamental que constitue*