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Lessons from parasitic flatworms about evolution and historical biogeography of their vertebrate hosts

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Abstract

Cophylogenetic studies investigate the evolutionary trends within host-parasite associations. Examination of the different levels of fidelity between host and parasite phylogenies provides a powerful tool to inspect patterns and processes of parasite diversification over host evolution and geological times. Within the phylum Platyhelminthes, the monogeneans are mainly fish parasites. The Polystomatidae, however, are known from the sarcopterygian Australian lungfish and tetrapods such as amphibians, freshwater turtles, and the African hippopotamus. Cophylogenetic and biogeographic vicariance analyses, supplemented by molecular calibrations, showed that the Polystomatidae may track the evolutionary history of the first aquatic tetrapods in the Palaeozoic age. Evolutionary lines of the major polystome lineages would also be intimately related to the evolution of their hosts over hundreds of millions years. Since the Mesozoic, evolution of polystomes would have been shaped mainly by plate tectonics during the break-up of Gondwanaland and subsequent dispersal of ancestral neobatrachian host lineages. Therefore the Polystomatidae could serve as a novel model to improve cophylogenetic tools and to inspect a suite of questions about the evolution of vertebrate hosts. ***To cite this article: O. Verneau et al., C. R. Biologies 332 (2009).***

Résumé

Contributions des plathelminthes parasites à l'histoire évolutive et biogéographique de leurs hôtes vertébrés. Les études de cophylogénie recherchent les tendances évolutives qui gouvernent les associations hôte-parasite. L'examen des différents niveaux de fidélité entre les phylogénies hôte et parasite fournit un outil puissant pour inspecter les caractéristiques et les processus de diversification des parasites au cours de l'évolution de leurs hôtes et des temps géologiques. Au sein du Phylum des Plathelminthes, les monogènes sont principalement des parasites de poissons. Les Polystomatidae, cependant, sont connus chez le dipneuste australien et certains tétrapodes, à savoir les amphibiens, les tortues d'eau douce et l'hippopotame africain. Des analyses de cophylogénie et de vicariance biogéographique complétées par des calibrations moléculaires ont montré que les Polystomatidae suivraient l'histoire évolutive des premiers tétrapodes aquatiques depuis le Paléozoïque. Les lignes évolutives des grandes lignées de polystomes seraient aussi intimement liées à l'évolution des hôtes sur des centaines de millions d'années. Depuis le Mésozoïque, l'évolution des polystomes aurait été façonnée principalement par la tectonique des plaques, suite au démantèlement du Gondwana,

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et par les événements de dispersion des lignées ancestrales de Neobatrachia. Par conséquent, les Polystomatidae pourraient servir de nouveau modèle pour améliorer les outils cophylogénétiques et répondre à une suite de questions sur l'évolution des hôtes vertébrés. ***Pour citer cet article : O. Verneau et al., C. R. Biologies 332 (2009).***

Keywords: Cophylogeny; Biogeographic vicariance; Vertebrates; Platyhelminthes; Monogenea; Polystomatidae

Mots-clés : Cophylogénie ; Biogéographie vicariante ; Vertébrés ; Plathelminthes ; Monogènes ; Polystomatidae

1. The cophylogeny: A fundamental approach for investigating evolutionary trends within host-parasite associations

Evolutionary biology is a multidisciplinary approach that seeks to unveil the patterns and processes that shape the phenotypic and genetic diversity. Although organisms may be studied at different levels of their biology, they can also be investigated at different scales of time, with macro evolution involving the largest scales and micro evolution the smallest. Species have evolved through a combination of different processes to fit their changing environments. Many authors are interested in exploring all the features that influence evolution of species, but also how they interact with closely associated non-related species. In specific cases, such as in host-parasite systems, the environment for both interacting species is part of the other living species. Coevolution is a term that was first defined by Ehrlich and Raven [1] to describe changes in one species that may result from evolutionary changes in another one and vice-versa, thus reflecting coadaptation within closely interacting species. For Brooks and McLennan [2], the primary definition of coevolution was too restrictive because it only referred to cases of reciprocal adaptive changes between ecologically interacting species. They gave a broader definition that encompassed coadaptation, for the degree of mutual modification, and cospeciation for the degree of mutual phylogenetic association. Within a systematic framework, phylogenies are very useful for investigating evolution of interacting species, particularly within host-parasite associations. Because cospeciation has been further used in a narrower sense to design synchronous host-parasite divergences [3], this approach is now referred as cophylogeny [4] and has an explicit terminology to account for concordances and conflicts between systematic of hosts and their parasites [5]. Examination of the different levels of fidelity between host and parasite branching patterns thus provides a powerful tool to inspect patterns and processes of parasite diversification over host evolution and geological times.

With the advance of molecular techniques [6–8] and cophylogenetic tools (reviewed in [9]), it is now possible to compare host and parasite distance trees and to explore all kind of evolutionary events that account for parasite evolution. Four main categories of events have been recognised [5] (Fig. 1). Firstly, cospeciation illustrates analogous cladogenetic events within hosts and their associated parasites. Divergences within an ancestral host and its parasite are synchronous over geological times even if host speciation does not necessary entail parasite speciation. However, hosts and their parasites may experience codivergence due to the same causal process, as it is exemplified in biogeographic vicariance where two populations of the same species may diverge after being isolated following the emergence of a geographical barrier. Secondly, duplication refers to parasite speciation within ancestral host without host speciation. Consequently, two or several

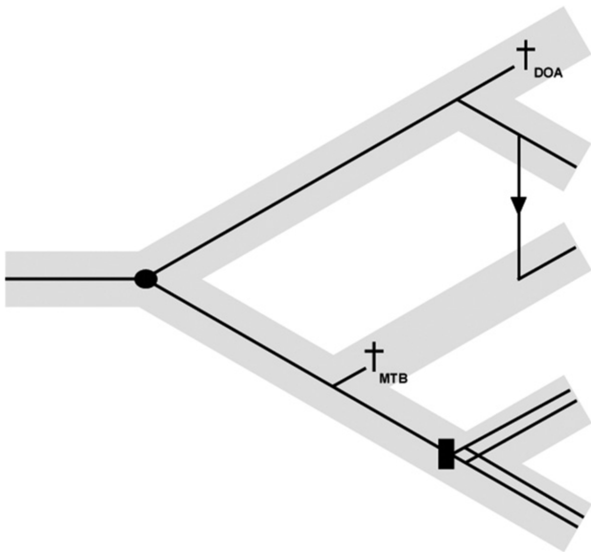

Fig. 1. Evolutionary events describing the processes of parasite diversification. The grey and black narrow lines correspond respectively to host and parasite relationships. The black circle refers to cospeciation, the black rectangle to duplication, the arrow to host-switching and crosses to extinction (MTB means "Missing the boat" and DOA "Drowning on Arrival" [5]).