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Review article Foreign DNA acquisition by invertebrate genomes

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ABSTRACT

Recent studies have highlighted that the accidental acquisition of DNA from other species by invertebrate genomes is much more common than originally thought. The transferred DNAs are of bacterial or eukaryote origin and in both cases the receiver species may end up utilising the transferred genes for its own benefit. Frequent contact with prokaryotic DNA from symbiotic endocellular bacteria may predispose invertebrates to incorporate this genetic material into their genomes. Increasing evidence also points to viruses as major players in transferring genes and mobile elements between the species they infect. Unexpectedly a gene flux between Hymenoptera and Lepidoptera mediated by endogenous viruses of parasitic wasps has been recently unravelled, suggesting we are probably just seeing the tip of the iceberg concerning horizontal gene transfers in invertebrates. In the context of insect for feed and food, if the new technology of insect genome editing (such as Crisper/Cas9) were used to modify the genome of reared insects it is important to take into account the risk that an introduced gene can be transferred. More generally, although insects are traditionally consumed in Asia and Africa, knowledge on insect rearing at an industrial scale.

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1. Introduction

Far from being set in stone, genomes often look upon close examination somewhat like an odd assortment of sequences

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forming the gene pool of particular species. Indeed, in addition to functional genes, genomes contain a high proportion of viruses or remnants of genetic parasites, as well as DNA possibly originating from other species. It is now very well known that gene exchanges are common between bacteria (Ochman et al., 2000). In unicellular eukaryotes gene transfers are also relatively common (Andersson, 2005). These organisms feed through phagocytosis of bacteria and other microorganisms leading to frequent contact with prokaryotic DNA, which may predispose them to incorporate this genetic material into their genomes (Doolittle, 1998). By contrast,



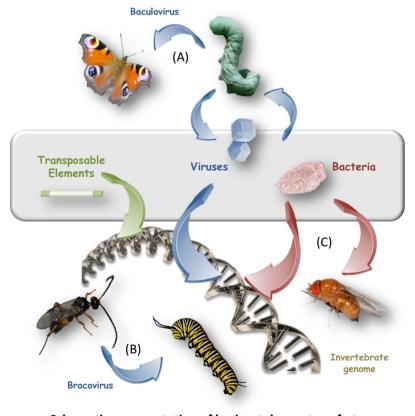




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multicellular organisms are generally thought to evolve mainly through vertical transmission by reproduction (either sexual or asexual) of existing genetic information. However evidence that horizontal gene transfer (HGT) occurs in these organisms is rapidly accumulating (Boto, 2014; Crisp et al., 2015; Keeling and Palmer, 2008; Syvanen, 2012) (Table 1 and Fig. 1), HGT being defined as the accidental acquisition of DNA from another species independently of reproduction and regardless of the evolutionary distance between the two species. To the exception of some species such as rotifers that have massively acquired genes from non-metazoan sources due to their peculiar way of life (Eyres et al., 2015), the majority of reported events of HGT between metazoans concern selfish DNA transposable elements (TEs), DNA sequences capable of excising or copying themselves from one genomic locus to integrate into another locus, generally within the same genome. From time to time these elements enter a new genome where they can spread until their expansion becomes regulated by the new host (Ronsseray et al., 1989). However genes conferring a function have also been acquired by HGT by both vertebrates and invertebrates (Crisp et al., 2015). Several initial reports that attracted much attention concerning HGT in humans could not be confirmed upon closer examination (Crisp et al., 2015), thus casting some doubt on the real extent of HGTs. Indeed contamination of DNA samples or low quality genome assembly can easily result in apparent HGT. Experimental confirmation that can be obtained by sequencing junctions between the insertion and the analysed genome is the most convincing way to confirm that HGT actually occurred. Conversely, filters are often applied to raw data before genome computational assembly to avoid incorporation of foreign DNA, which might impair the identification of genuine HGT events and thus lead to an underestimation of their frequency (Dunning Hotopp et al., 2007).

Genome sequencing has also revealed that DNA acquisition by an invertebrate genome can encompass a large part of a bacterial genome, probably because the intimacy of the relationships with some endosymbiotic bacteria favours DNA exchange. For example, numerous insect and nematode genomes contain sequences originating from the endocellular bacteria Wolbachia widespread in arthropod populations (Dunning Hotopp et al., 2007). Last but not least, remnants of virtually all virus families, so called endogenous viral elements (EVEs), can also be found in invertebrate genomes (Feschotte and Gilbert, 2012; Katzourakis and Gifford, 2010). Virus genomes can integrate into host genomes during their life cycle, like retroviruses, but many EVEs derive from viruses displaying no DNA stage, such as RNA viruses (see Invertebrate RNA virus diversity review in this issue, Ryabov, 2017) or from DNA viruses that are not reported to mediate their integration (see in this issue, Williams et al. 2017 and Thijssen and Bergoin for Invertebrate large DNA viruses and small DNA viruses, respectively). In fact it appears that all kinds of viruses may end up in genomes, however the mechanisms involved are generally unknown (Feschotte and Gilbert, 2012; Katzourakis and Gifford, 2010). EVEs are most often



Schematic representation of horizontal gene transferts targeting invertebrate genomes

Fig. 1. Invertebrate genomes have received DNA sequences of foreign origin such as transposable elements (TE) and viruses, the remnants of which constitute one of their major components. Invertebrate genomes may also contain prokaryote genes or large fragments of bacterial chromosomes. Viruses play a pivotal role in the sequence exchange of genes and TEs between species. For example baculoviruses pick up genes from the lepidopteran species they infect and can transfer genes or TEs to other species belonging to their host range (A). The endogenous bracovirus associated with parasitoid wasps acquires genes from the wasp genome that are later transferred to different lepidopteran species (B). Intracellular bacteria of the genus *Wolbachia* infecting germ cells are the source of large fragments of prokaryotic DNA found in many invertebrate genomes (C). Some of the sequences transferred are passively transmitted, while genes of prokaryotic or eukaryotic origin are sometimes utilised by the receiver organism for its own benefit.

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