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Horizontal Gene Transfer Contributes to the Evolution of Arthropod Herbivory

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Abstract

Within animals, evolutionary transition toward herbivory is severely limited by the hostile characteristics of plants. Arthropods have nonetheless counteracted many nutritional and defensive barriers imposed by plants and are currently considered as the most successful animal herbivores in terrestrial ecosystems. We gather a body of evidence showing that genomes of various plant feeding insects and mites possess genes whose presence can only be explained by horizontal gene transfer (HGT). HGT is the asexual transmission of genetic information between reproductively isolated species. Although HGT is known to have great adaptive significance in prokaryotes, its impact on eukaryotic evolution remains obscure. Here, we show that laterally transferred genes into arthropods underpin many adaptations to phytophagy, including efficient assimilation and detoxification of plant produced metabolites. Horizontally acquired genes and the traits they encode often functionally diversify within arthropod recipients, enabling the colonization of more host plant species and organs. We demonstrate that HGT can drive metazoan evolution by uncovering its prominent role in the adaptations of arthropods to exploit plants.

Key words: arthropods, horizontal gene transfer, herbivory.

Introduction

Plants have evolved a wide and complex set of adaptations to survive the many stressors present in their environment. These include abiotic factors such as drought and nutrition-poor soils, but also herbivore and pathogen attacks. During their evolution, plants have transformed themselves to such a recalcitrant and unfavorable food source that herbivory (or feeding exclusively on plant material) has only evolved in roughly one third of all animal species (Strong et al. 1984). Both the nutritional and defensive qualities of plants are known to limit the evolution of animal herbivory (Awmack and Leather 2002). As many plant species and tissues are characterized by a relatively high carbohydrate content, but low protein and vitamin levels (Mattson 1980; Strong et al. 1984; Awmack and Leather 2002), herbivorous animals need to optimize the assimilation of the limited supply of nutrients in plant tissues. In addition, plants have evolved multi-layered defense strategies that negatively affect the reproductive performance of herbivores. Plant resistance to herbivory can be achieved by physical barriers such as trichomes and waxy cuticles and/or by the production of chemical defenses (Howe and Jander 2008). Defensive phytochemicals, or plant allelochemicals, can repulse and poison herbivores or interfere with the assimilation of plant nutrients inside the herbivore's gut (Whittaker and Feeny 1971).

Nevertheless, arthropods can overcome these nutritional and defensive barriers and various lineages have successfully adapted to a phytophagous lifestyle. The arthropod phylum is now considered to harbor the most successful animal herbivores in terrestrial ecosystems, both in terms of biomass and species diversity (Strong et al. 1984; Labandeira 2002, 2006; Schoonhoven et al. 2006) (fig. 1). Within arthropod–plant interactions, there has been an evolutionary trend for phytophagous arthropods to further specialize to a specific plant family or even species by optimizing the assimilation and detoxification processes (Bernays and Graham, 1988; Schoonhoven et al. 2006). Using next-generation sequencing-based methods, many studies are currently investigating the genomic and genetic innovations that are associated with these evolutionary transitions to arthropod herbivory and further host plant

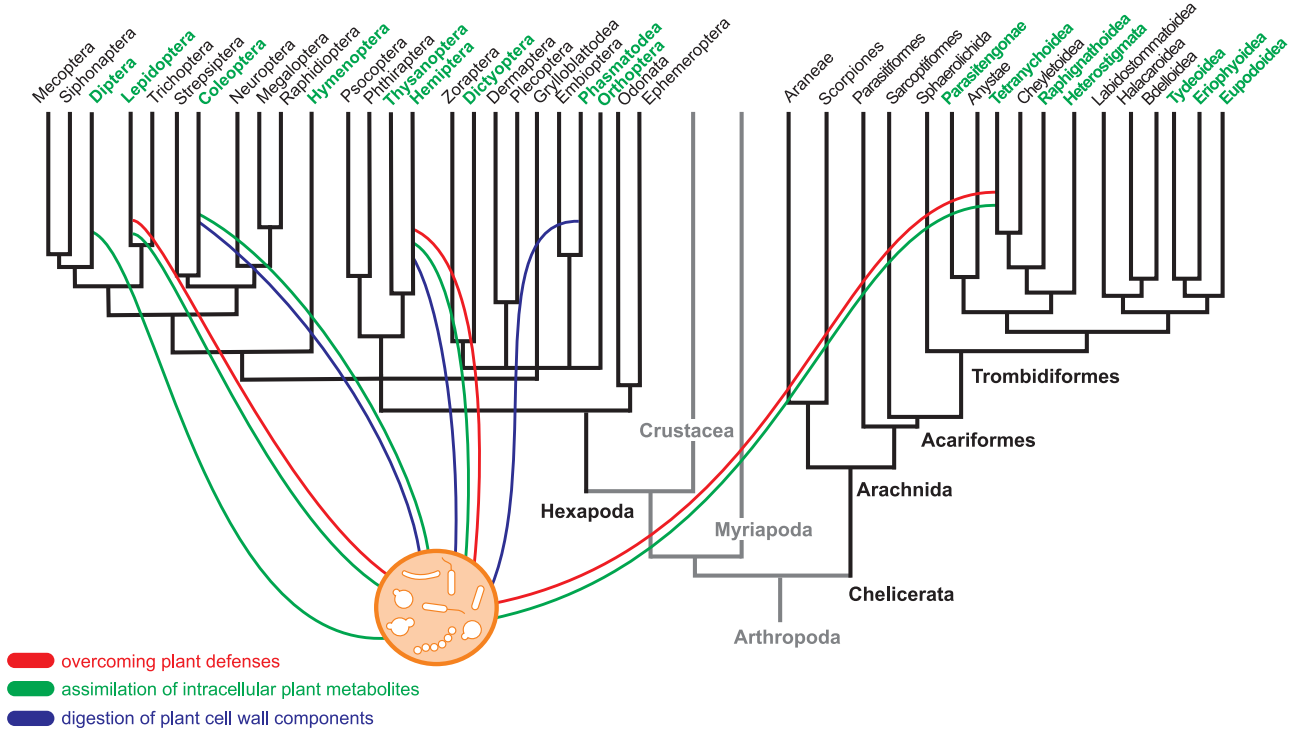

Fig. 1.—Arthropod phylogenetic tree showing documented HGT events in phytophagous chelicerate and hexapod lineages. The names of the clades harboring herbivores are depicted in green. Horizontally transferred genes coding for traits involved in plant cell wall digestion, intracellular plant metabolite assimilation, and overcoming plant defenses are depicted in blue, green, and red lines, respectively. Detailed lists of the methodologies that identified the HGT events, the nature of the horizontally transferred genes and donor and recipient species can be found in table 1.

specializations. Of the identified arthropod genes that code for enzymes with a clear selective advantage to the phytophagous lifestyle, a subset has been identified with two unusual properties: high similarity to microbial genes, and absence in the majority of other lineages within the Arthropoda phylum. This unusual phylogenetic distribution has often prompted the conclusion that these functional genes were introduced to the arthropod genome by the process of horizontal gene transfer (HGT), defined as the nonsexual transmission of genetic material across species boundaries (Kidwell 1993; Li and Graur 1991). This entails that in contrast to the classical evolutionary model where new genes arise by duplication of pre-existing ancestral genes followed by mutation and then gradual selection for novel functions, HGT suddenly introduces new genes that had already been subjected to natural selection in a nonrelated species. Such inferences of HGT in animal genomes are often met with high skepticism, as the mechanisms of HGT are only well documented within the prokaryotic domain of life. HGT is accepted to be widespread and prevalent among prokaryotes and acknowledged as a major force in their adaptive evolution (Koonin et al. 2001; Springael and Top 2004; Pal et al. 2005). An additional argument against HGT in animal genomes is that eukaryotic biology presents too many barriers to HGT. Before a mobile functional genetic element can be stably introduced in an animal genome, it has to enter the nucleus within the isolated germ cell line, and needs to be adjusted to the transcription machinery of the recipient species. Despite these evolutionary barriers, an increasing number of apparently horizontally transferred genes are being reported in arthropod herbivores. Moreover, many of these unique genes, while still coding for functionally active enzymes after the HGT event, additionally show signs of functional diversification. Here, we discuss the different criteria that are used to establish that arthropod herbivores are the recipients of functional foreign genetic information. We furthermore argue for an evolutionary trend in arthropods where HGT facilitates adapting to the nutritive and defensive barriers of plants, and we argue that HGT has played a substantial role in the ecological success of arthropod herbivory within several lineages.

Detecting HGT by Its Phylogenetic Signatures

The direct observation of an individual HGT event that occurred in the distant past is physically impossible. Therefore, putative HGT events must be inferred from currently available data, and the hypothesis that a specific HGT event has

occurred can only be tested by probabilistic methods. As HGT presents an unusually high degree of sequence similarity between the distantly related donor and recipient species for the gene of interest, studies employ methodologies that analyze different properties of the nucleotide and/or amino acid sequence to test the HGT hypothesis.

Molecular phylogenetics is the study of the evolutionary history and relationships of genes across organisms by using molecular data such as nucleotide and amino acid sequences. A phylogenetic analysis generates a phylogenetic tree which is characterized by a certain branching pattern or topology. This topology mirrors the courses of inheritance of the genes of interest over evolutionary time. The reliability of these topologies can be inferred by various computational techniques that estimate the confidence level of each internal bifurcation. By creating a consensus tree of numerous individual gene trees (often on a genome-wide level), a species tree can be produced where the actual speciation events are mapped. Molecular phylogenetic methods are the gold standard in arthropod studies and suggest an HGT when the gene of interest is grouped with homologues of nonrelated species by strongly statistically supported branches (for instance with at least 60% bootstrap support) (Efron et al. 1996) (fig. 2). In order to be reliable, these phylogenetic incongruence methods require: (1) a well-established species phylogeny which is needed as a reference topology and (2) an expansive set of closely and step-wise more distantly related homologous genes in order to avoid sampling bias. For many arthropod studies, both requirements can be met as a significant part of the arthropod phylogenomic tree is well mapped and keeps improving due to the increasing number of sequenced arthropod genomes and transcriptomes (Regier et al. 2010; Wheat and Wahlberg 2013; Misof et al. 2014). These genomic sequences simultaneously offer an unbiased set of orthologues spanning both short taxonomic distances (often within the same genus) and large ones (between different subphyla). In order to be convincing as a general methodology, phylogenetic incongruence methods must also be able to reject the HGT hypothesis under appropriate conditions. For instance, using this extensive sequence dataset, phylogenetic analysis finally concluded that a much-debated putative horizontally transferred gene in termites is instead much more likely to be a typical vertically transmitted gene, present in various other arthropod lineages (Lo et al. 2011). A potential shortcoming of this type of test is that the putative horizontally transferred gene and the set of available homologues may not contain a strong enough phylogenetic signal (for instance due to short sequence lengths). Alignments of such sequence sets typically lead to various poorly supported branches in phylogenetic reconstructions. When faced with nonoptimal tree support values at critical bipartitions, studies often combine multiple phylogenetic methods to minimize the chances of an erroneous identification of an HGT event in arthropods (Wybouw et al. 2012; Husnik et al. 2013; Pauchet and Heckel 2013).

Doubts about the identification of an HGT event by phylogenetics often arise due to a misunderstanding of the ancestral distribution of the gene of interest. To address this problem, it is useful to divide phylogenetic reconstructions into three major scenarios, based on the occurrence of the gene of interest across all lineages of the tree of life. First, HGT can convey a completely novel gene to arthropods which is normally absent in their entire phylogenetic lineage (fig. 2*B*, left tree). Here, the simple presence of the gene in an arthropod genome already strongly favors HGT, and HGT cannot be ruled out even if the donor clade cannot be identified by suboptimal phylogenetic support. Clear-cut examples of completely novel genes in plant feeding arthropods include genes that code for carotenoid cyclases/synthases, chorismate mutase (CM), and cyanase (Grbic et al. 2011; Novakova and Moran 2012; Wybouw et al. 2012; Sloan et al. 2014). In the second scenario, the arthropod species already harbors a related homologue to the potential laterally transferred gene (fig. 2*B*, middle tree). Here, HGT is inferred when the candidate transferred and the other paralogue(s) show strongly divergent evolutionary histories. Spider mites of the Tetranychidae family (Arthropoda: Chelicerata) and lepidopterans (Arthropoda: Hexapoda) possess a universal arthropod cystathionine β-synthase (*CBS*) gene and a unique cysteine synthase (or β-cyanoalanine synthase) (*CAS*) gene, part of the same β-substituted alanine synthase gene family, but with the latter normally restricted to bacterial and plant species. Wybouw et al. (2014) showed phylogenetically that the mite and lepidopteran CAS enzymes clustered together with bacterial and plant enzymes, while their CBS enzymes were embedded with high probability in a eukaryotic group of enzymes. In a third scenario (fig. 2*B*, right tree), the close ancestral homologue to the transmitted gene is lost in the recipient species. Here, HGT is identified when the homologues of species related to the recipient exhibit distinct evolutionary histories compared with the gene of interest. For instance, Ahn et al. (2014) suggested by a phylogenetic reconstruction that an ancestral chelicerate lost the arthropod UDP-glycosyltransferase (*UGT*) gene(s) and that tetranychid mites later horizontally received novel *UGT*s, clearly different from the vertically transmitted arthropod UGT sequences. Independent of the ancestral distribution, as gene duplications, differential gene losses and evolutionary convergence can also result in a phylogenetic reconstruction where distant species lineages cluster together, the likelihood of an HGT event versus alternative scenarios should always be weighed (Ku et al. 2015).

Detecting HGT by Other Probabilistic Methods

To maximize the likelihood of correctly identifying an HGT event, studies can incorporate additional, independent probabilistic methods before concluding that a gene arose by HGT. Many of these approaches take advantage of the high

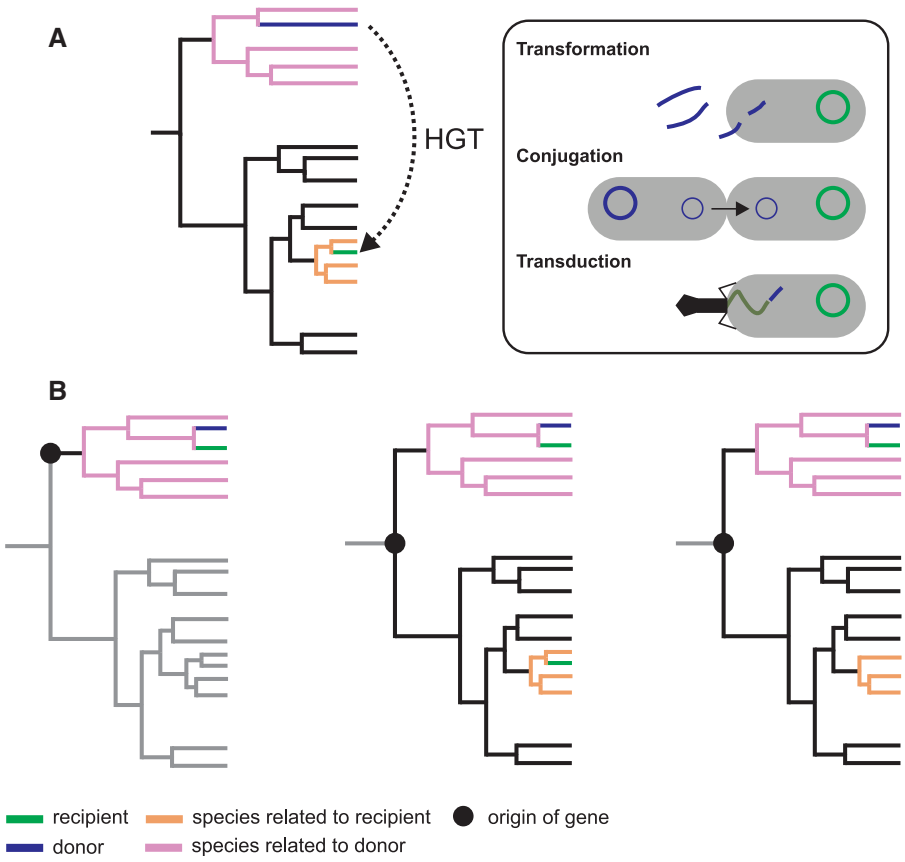

Fig. 2.—(*A*) Left: A species tree where the bifurcations represent speciation events. Species trees are based on the sequence information of multiple genes (often genome-wide; phylogenomic trees) and depict how species are related. Here, horizontal transfer of a single gene is not expected to change the phylogenomic tree. Right: the three known mechanisms of HGT in prokaryotes; transformation (direct uptake of foreign DNA), conjugation (plasmid-mediated uptake) and transduction (virus-mediated uptake). (*B*) Phylogenetic analysis of a gene of interest can detect an HGT event by showing that a particular species is embedded within a group of distantly related organisms. The implanted species and the surrounding clade are then considered to be the recipient species and donor clade of the transferred gene, respectively. Three scenarios are depicted of how HGT can distort the phylogenetic reconstruction of a single gene. These scenarios are characterized by a certain ancestral gene distribution across the tree of life. Left: The gene is originally restricted to a certain phylogenetic clade, distantly related to the recipient species. As the horizontally transferred gene does not have related homologues within the clade harboring the recipient species, it is unique to the recipient. Middle: The gene is present in all lineages, but a gene copy from a distant species supplements an existing innate homologue in the recipient genome. Right: Here, a foreign gene replaces the original homologue in the recipient genome through HGT. In each case however, the possibility of alternative scenarios to an HGT event should always be considered (for instance, differential gene loss across the tree of life).

number of sequenced genomes across the tree of life. After phylogenetic analysis, one approach analyzes the codon content of the entire genome of the recipient and putative donor species. As phylogenetic reconstruction usually does not uncover the exact donor species, the genomes of a broader group of species are included in the codon content analysis. Based on the theory that the codon usage pattern of all coding sequences within a certain genome is similar and that this genomic signature varies between species (Lawrence and Ochman 1997), a horizontally transferred gene candidate can be confirmed by detecting a different codon content compared with the rest of the recipient genome. However, this methodology should always be used in combination with a phylogenetic analysis as it has several imperfections. First, a true HGT event can be overlooked if the nonrelated donor and recipient species have similar genomic codon contents. Second, even if the donor and recipient genomes are characterized by distinctly different codon contents, the hypothesis of an ancient HGT can still be rejected. Once a gene is laterally incorporated, it is subjected to the same mutational processes as the rest of the recipient's genome and will, over time, homogenize its codon content with its genomic surroundings, in a process called amelioration (Lawrence and Ochman 1997). Indeed, in arthropods and other animals, laterally acquired genes often exhibit nondistinguishable codon contents from those of ancestral, innate

genes (Danchin et al. 2010; Wybouw et al. 2014). Therefore, this methodology only gives further support when the HGT was very recent and when the reproductively isolated species have distinctly different genomic codon signatures. More and more HGT cases with an arthropod recipient are being examined with this technique, in addition to the standard phylogenetic analysis (Sun et al. 2013; Wybouw et al. 2014; van Ohlen et al. 2016).

Using the plethora of sequenced genomes, families of orthologues can be systemically classified (Tatusov et al. 1997; Li et al. 2003). These comparative genomics techniques allow for a new approach to examine the HGT hypothesis: the analysis of the phyletic pattern within a certain orthologue family. The phyletic pattern is the occurrence or absence of species within these defined clusters of orthologues. For instance, when a fungal lineage is detected within an otherwise exclusively bacterial protein family, an HGT event can be inferred. This methodology has confirmed multiple HGT events to microorganisms (Koonin et al. 2001). After a BLASTP search of a proteome under investigation against a large species curated sequence database, Clarke's phylogenetic discordance test identifies horizontally transferred genes that exhibit statistically significantly different similarity patterns compared with the median similarity pattern shown by the proteome (Clarke et al. 2002).These and other methodologies are not yet well established in arthropod studies but show great potential for future studies, despite the fact that each technique is not without its potential limitations (Koonin et al. 2001; Ragan 2001; Lawrence and Ochman 2002).

Incorporation of a Microbial Gene in the Arthropod Genome

The first nucleotide and amino acid sequences of horizontally transferred genes in plant feeding arthropods were mainly uncovered by transcriptomic and proteomic studies (Pauchet et al. 2008, 2009, 2010b; Kirsch et al. 2012). Although phylogenetic procedures strongly pointed toward an HGT scenario with an arthropod recipient, skeptical reviewers claimed that these genes and the enzymes they encode had such unusual phylogenetic distributions because they originated from associated free-living or symbiotic microorganisms and were not part of the arthropod genome. Indeed, arthropods often host large bacterial communities in various organs, including their digestive tract (Buchner 1965; Watanabe and Tokuda 2010). Even though these genes exhibit strong sequence similarity to bacterial genes, they often possess typical eukaryotic characteristics, strongly disfavoring the contamination hypothesis and supportive of an HGT event. These gene attributes include eukaryotic signal peptides, polyadenylation tails and spliceosomal introns (Acuna et al. 2012; Ahn et al. 2014; Luan et al. 2015). In addition, genomics now provide a growing body of evidence showing that these bacterial genes are physically incorporated into arthropod genomes (table 1). For instance, after identifying potential laterally transferred genes coding for xylanases in a midgut transcriptome of the mustard leaf beetle (*Phaedon cochleariae*), Pauchet and Heckel (2013) screened a genomic DNA fosmid library to prove that two laterally transferred xylanase genes reside in the beetle genome and are neighbored by insect-derived transposable elements (TEs). Using next-generation sequencing technology, multiple genomic studies of various arthropod lineages show that horizontally transferred genes are present on large genomic scaffolds, where they are flanked by typical arthropod genes (Grbic et al. 2011; Husnik et al. 2013; Vega et al. 2015; Zhao et al. 2015). As genome assemblies can have imperfect computational sequence filters (Baker 2012), an apparent lateral acquisition can be an artifact due to the presence and incorrect concatenation of contaminating bacterial sequences with other reads from the shotgun library (Koutsovoulos et al. 2016). If a Bacterial Artificial Chromosome library is available, this possibility can be ruled out (Pauchet et al. 2014b). Potential genome assembly artifacts can also be ruled out by validating the genomic sequence through PCR amplifications which often include geographically distinct arthropod populations. After identifying a horizontally transferred gene, encoding for a mannanase, in the genome of the coffee berry borer beetle (*Hypothenemus hampei*), Acuna et al. (2012) showed that the transferred gene is incorporated at the same genomic location in *H. hampei* populations spanning Asia, Africa, and America. The genomic location of the horizontally transferred *CAS* gene in the spider mite species *Tetranychus urticae* was confirmed by PCR amplification and shown to be identical in strains sampled from different regions worldwide (Wybouw et al. 2014). If speciation in the recipient group occurred after the HGT event, the genomic region bracketing the laterally acquired gene can also be analyzed in all descendent species. The genomic region bracketing the *CAS* gene exhibits clear synteny between *T. urticae* and a closely related mite species, *Tetranychus evansi*. Such approach was also followed by Wheeler et al. (2013), who uncovered a single, ancient horizontal transfer of a glycosyl hydrolase (GH) family 31 gene from bacteria to the ancestor to all modern lepidopterans by demonstrating microsynteny neighboring the laterally transferred gene in different lepidopteran genomes.

HGT and the Evolution of Arthropod Herbivory

Recent comparative studies show a high prevalence of HGT in arthropod lineages, relative to other animal clades (Hotopp et al. 2007; Hotopp 2011; Ramulu et al. 2012), which raises the question of how these genes and the traits they encode shape arthropod evolution. In this review, we will gather strong indications that HGT from microbial species enhanced the enzymatic repertoire of phytophagous arthropods, which in turn seems to have facilitated adaptations toward herbivory

Table 1

A List of Horizontally Transferred Genes into Plant Feeding Arthropods that Underpin Adaptations to Phytophagy

Gene Name	Donor	Recipient (Order)	Validation	Reference	C
Digestion of plant cell wall components					
Cellulase/xylanase (GH5, sub2)	Bacteroidetes	Lamiinae (Coleoptera)	ML, BI, G, F	Danchin et al. (2010) and Pauchet et al. (2014a)	*
Mannanase (GH5, sub8)	*Bacillus*	*H. hampei* (Coleoptera)	ML, MP, G, F	Acuna et al. (2012) and Vega et al. (2015)	
Xylanase (GH10)	*Streptomyces*	*H. hampei* (Coleoptera)	ML, G, F	Padilla-Hurtado et al. (2012) and Vega et al. (2015)	
Xylanase (GH11)	γ-Proteobacteria	*P. cochleariae* (Coleoptera)	ML, BI, NJ, G, F	Pauchet and Heckel (2013)	
Polygalacturonase (GH28)	Pezizomycotina	Phytophaga (Coleoptera)	ML, BI, G, F	Kirsch et al. (2014), Shen et al. (1996), and Shen et al. (2003)	*
	Ascomycota	Lamiinae (Coleoptera)	ML, BI, G, F	Kirsch et al. (2014) and Pauchet et al. (2014a)	*
		Mirinae (Hemiptera)	ML, BI, F	Celorio-Mancera et al. (2008) and Hull et al. (2013) and Kirsch et al. (2014)	*
	Bacteroidetes	Bruchinae (Coleoptera)	ML, BI, G	Kirsch et al. (2014)	*
	γ-Proteobacteria	Verophasmatodea (Phasmatodea)	ML, BI, MP, G	Shelomi et al. (2014)	*
Cellulase (GH45)	Fungi	Phytophaga (Coleoptera)	ML, G, F	Pauchet et al. (2014a)	*
Pectin methylesterase (CE8)	Bacteria	Curculionoidea (Coleoptera)	ML, BI, MP, G, F	Evangelista et al. (2015), Kirsch et al. (2016), Pauchet et al. (2010a), Shen et al. (1999, 2005)	
Assimilation of intracellular plant metabolites					
Carbohydrate assimilation					
Glycosyl hydrolase (GH31)	*Enterococcus*	Lepidoptera (Lepidoptera)	ML, BI, NJ, G	Li et al. (2011), Sun et al. (2013), and Wheeler et al. (2013)	
β-fructofuranosidase (GH32)	Bacteria	Lepidoptera (Lepidoptera)	ML, BI, NJ, G, F	Daimon et al. (2008), Li et al. (2011), Sun et al. (2013), and Zhu et al. (2011)	*
	Bacteria	*A. planipennis* (Coleoptera)	ML, G	Zhao et al. (2014)	*
	Bacteria	Curculionidae (Coleoptera)	ML, G, F	Keeling et al. (2013) and Pedezzi et al. (2014)	*
	Bacteria	*M. destructor* (Diptera)	G	Zhao et al. (2015)	*
	Bacteria	Tetranychidae (Trombidiformes)	ML, G	Bajda et al. (2015) and Grbic et al. (2011)	*
Amino acid assimilation					
Argininosuccinate lyase	Enterobacteriales	*B. tabaci* (Hemiptera)	ML, BI, G	Luan et al. (2015)	
	Carsonella	Psylloidea (Hemiptera)	ML, G	Sloan et al. (2014)	
Argininosuccinate synthase	Enterobacteriales	*B. tabaci* (Hemiptera)	ML, BI, G	Luan et al. (2015)	
CM	Enterobacteriales	Aleyrodinae (Hemiptera)	ML, BI, G	Luan et al. (2015)	*
	Bacteria	Psylloidea (Hemiptera)	ML, G	Sloan et al. (2014)	*
Cyanase	Plants	Tetranychidae (Trombidiformes)	ML, G, F	Bajda et al. (2015), Grbic et al. (2011), and Wybouw et al. (2012)	*

(continued)

Table 1 Continued

Gene Name	Donor	Recipient (Order)	Validation	Reference	C
Cysteine synthase	Methylobacteria	Lepidoptera (Lepidoptera)	ML, BI, NJ, G	Li et al. (2011), Sun et al. (2013), Van Ohlen et al. (2016), and Wybouw et al. (2014)	*
	Methylobacteria	Tetranychidae (Trombidiformes)	ML, G, F	Bajda et al. (2015) and Wybouw et al. (2014)	*
	γ-Proteobacteria	*P. citri* (Hemiptera)	ML, BI, G	Husnik et al. (2013)	*
Diaminopimelate epimerase	Enterobacteriales	*B. tabaci* (Hemiptera)	ML, BI, G	Luan et al. (2015)	
	α-Proteobacteria	*P. citri* (Hemiptera)	ML, BI, G	Husnik et al. (2013)	
Diaminopimelate decarboxylase	Planctomycetes	*B. tabaci* (Hemiptera)	ML, BI, G	Luan et al. (2015)	
	α-Proteobacteria	*P. citri* (Hemiptera)	ML, BI, G	Husnik et al. (2013)	
4-Hydroxy-tetrahydrodipicolinate reductase	Rickettsiales	*B. tabaci* (Hemiptera)	ML, BI, G	Luan et al. (2015)	
Kynureninase	*L. grayi* bacteria	Lepidoptera (Lepidoptera)	ML, BI, NJ, G, F	Meng et al. (2009), Li et al. (2011), Sun et al. (2013), and Zhu et al. (2011)	
methionine synthase	Bacteria	Tetranychidae (Trombidiformes)	ML, G	Bajda et al. (2015) and Grbic et al. (2011)	
N-methyltryptophan oxidase	Bacteria	*B. mori* (Lepidoptera)	ML, BI, NJ, G	Li et al. (2011), Sun et al. (2013), and Zhu et al. (2011)	
Tryptophan 2-monooxygenase	Proteobacteria	*P. citri* (Hemiptera)	ML, BI, G	Husnik et al. (2013)	*
Vitamin assimilation					
Adenosylmethionine transaminase	Bacteria	Aleyrodinae (Hemiptera)	ML, BI, G	Luan et al. (2015)	
	α-Proteobacteria	*P. citri* (Hemiptera)	ML, BI, G	Husnik et al. (2013)	
Biotin synthase	Rickettsiales	Aleyrodinae (Hemiptera)	ML, BI, G	Luan et al. (2015)	
	α-Proteobacteria	*P. citri* (Hemiptera)	ML, BI, G	Husnik et al. (2013)	
Dethiobiotin synthase	α-Proteobacteria	*P. citri* (Hemiptera)	ML, BI, G	Husnik et al. (2013)	
GTP cyclohydrolase	γ-Proteobacteria	*P. citri* (Hemiptera)	ML, BI, G	Husnik et al. (2013)	
Riboflavin synthase	Bacteria	Psylloidea (Hemiptera)	ML, G	Sloan et al. (2014)	
Fused deaminase/reductase	α-Proteobacteria	*P. citri* (Hemiptera)	ML, BI, G	Husnik et al. (2013)	
Carotenoid assimilation					
Carotenoid desaturase	Mucoromycotina	Aphididae (Hemiptera)	ML, BI, G, F	Moran and Jarvik (2010) and Novakova and Moran (2012)	
		Adelgidae (Hemiptera)	ML, BI	Novakova and Moran (2012)	
	Zygomycota	Tetranychidae (Trombidiformes)	ML, BI, G	Altincicek et al. (2011), Bajda et al. (2015), and Grbic et al. (2011)	
	Mucorales	Cecidomyiidae (Diptera)	ML, BI, G	Cobbs et al. (2013)	
Fused carotenoid cyclase/synthase	Fungi	Macrosiphini (Hemiptera)	ML, G	Moran and Jarvik (2010)	
	Zygomycota	Tetranychidae (Trombidiformes)	ML, BI, G	Altincicek et al. (2012), Bajda et al. (2015), and Grbic et al. (2011)	
	Mucorales	Cecidomyiidae (Diptera)	ML, BI, G	Cobbs et al. (2013)	

(continued)

Table 1 Continued

Gene Name	Donor	Recipient (Order)	Validation	Reference	C
Overcoming plant defenses					
CAS	Methylobacteria	Lepidoptera (Lepidoptera)	ML, BI, NJ, G, F	Li et al. (2011), Sun et al. (2013), Van Ohlen et al. (2016), and Wybouw et al. (2014)	*
	Methylobacteria	Tetranychidae (Trombidiformes)	ML, G, F	Bajda et al. (2015) and Wybouw et al. (2014)	*
	γ-Proteobacteria	*P. citri* (Hemiptera)	ML, BI, G	Husnik et al. (2013)	*
CM	Enterobacteriales	Aleyrodinae (Hemiptera)	ML, BI, G	Luan et al. (2015)	*
	Bacteria	Psylloidea (Hemiptera)	ML, G	Sloan et al. (2014)	
Cyanase	Plants	Tetranychidae (Trombidiformes)	ML, G, F	Bajda et al. (2015), Grbic et al. (2011), and Wybouw et al. (2012)	*
β-fructofuranosidase	Bacteria	*B. mori* (Lepidoptera)	ML, BI, NJ, G, F	Daimon et al. (2008), Li et al. (2011), Sun et al. (2013), and Zhu et al. (2011)	*
Intradiol ring-cleaving dioxygenase	Fungi	Tetranychidae (Trombidiformes)	ML, G	Bajda et al. (2015), Dermauw et al. (2013), and Grbic et al. (2011)	*
Kynureninase	*L. grayi* bacteria	Lepidoptera (Lepidoptera)	ML, BI, NJ, G, F	Meng et al. (2009), Li et al. (2011), Sun et al. (2013), and Zhu et al. (2011)	
UDP-glycosyltransferase	Bacteria	Tetranychidae (Trombidiformes)	ML, G	Ahn et al. (2014) and Bajda et al. (2015)	*

Techniques used to examine each HGT event are listed in the Validation column. The phylogenetic methodologies are abbreviated as ML: Maximum Likelihood analysis of protein sequences, BI: Bayesian Inference, NJ: Neighbor-Joining and MP: Maximum Parsimony. Further analysis include; G: proof of physical incorporation into the arthropod genome and F: enzyme product is functional. An asterisk within column 'C' indicates whether a similar gene has been independently horizontally transferred to a phytophagous species within the Fungi, Oomycota, and Nematoda lineage.

and novel host plants. Here, the horizontally transferred genes are categorized based on how their enzyme products interact with the nutritional and defensive barriers of plants. The categories discussed are: (1) penetration and digestion of plant cell walls, (2) assimilation of plant nutrients, and (3) overcoming plant defenses (table 1).

Penetration and Digestion of Plant Cell Walls

Various networks of complex composite fibers form the plant cell wall and cuticle and enclose all cells of land plant species. These plant structures are central to the biology of all terrestrial plants as they provide the necessary structural integrity and mechanical support for living on land. In some plant species, these composite fibers form a thick rigid layer (for instance in woody plants), and pose a barrier for arthropods aiming to feed on plant nutrients (Carpita and Gibeaut 1993; Whetten and Sederoff 1995; Heredia 2003; Sorensen et al. 2010). These complex matrices are mainly built from polysaccharides and constitute the largest reservoir of organic carbon on earth. As all animals, arthropods have an inherently inadequate battery of enzymes that are able to cleave these recalcitrant cell wall polysaccharides and access their stored energy. Some specialized phytophagous arthropods, like wood-feeding termites, have extensively proliferated a gene family of ancestral animal cellulases to enzymatically cleave certain cell wall components (Watanabe and Tokuda 2010), while other arthropods seem to solely rely on microbial symbionts in their gut (Breznak 1982). Microorganisms are able to convert the complex fibers of the plant cell wall into simple oligo- and monosaccharides by producing unique plant cell wall degrading enzymes (PCWDEs). These microbial PCWDEs are able to digest the rigid plant cell wall constituents in the digestive tract and release their stored energy, benefiting both the microorganisms and their arthropod hosts. Most of the PCWDEs belong to various GH families that hydrolyze glycosidic bonds either by a single or double displacement mechanism. GHs are delineated into specific families and subfamilies through the curated Carbohydrate-Active database of enzymes involved in carbohydrate metabolism (Cantarel et al. 2009). Although GH families are found across the whole tree of life, most GH families coding for PCWDEs are restricted to bacterial and fungal species (Rye and Withers 2000; Gilbert 2010).

Within the insect orders of the Coleoptera, Phasmatodea, and Hemiptera (fig. 1), studies have indicated that genes coding for PCWDEs have been laterally transferred to insect genomes enabling the host to degrade the complex cell wall polysaccharides themselves. Within Coleoptera, the most diverse monophyletic clade of herbivorous beetles is the Phytophaga group (harboring ~80% of all plant feeding beetles) and contains the superfamilies Chrysomeloidea and Curculionoidea (Farrell 1998; Marvaldi et al. 2009) (fig. 3).

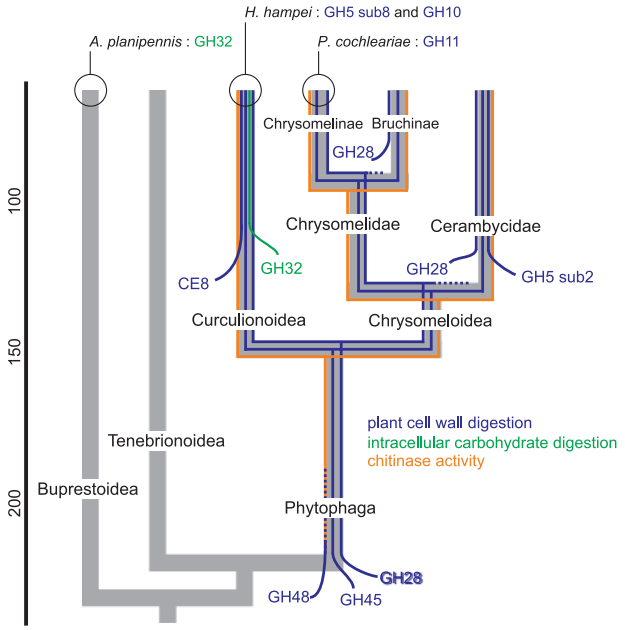

Fig. 3.—Coleopteran phylogenetic tree focusing on the Phytophaga lineage, which harbors the majority of all phytophagous beetles. Horizontal transfer of genes coding for enzymes that digest plant cell wall components and intracellular carbohydrates and chitinases are depicted in blue, green, and orange, respectively. Recent, apparent species-specific HGT events are depicted by circles and the name of the recipient species. Dated phylogenetic relationships are scaled in MYA and based on different sources (Farrell 1998; Marvaldi et al. 2009).

Independent genomic approaches and in-depth phylogenetic analysis provide proof that genes of various microbial GH families have been laterally transferred to phytophagan beetle genomes at various time points during their evolution. Moreover, some laterally acquired genes subsequently duplicated and diversified in a lineage-specific manner, while others were lost and replaced by other, more recently laterally acquired *GH* genes (Shen et al. 2003; Kirsch et al. 2012, 2014; Eyun et al. 2014; ; Pauchet et al. 2014b; Vega et al. 2015) (fig. 3). There is a growing multi-layered body of evidence that clearly indicates that these transferred genes code for functional PCWDE and were of adaptive significance to phytophagan beetles. First, transcriptomic and proteomic studies show that transcription and translation of these foreign genes is concentrated in the mid- and hindgut, where the digestion takes place (Pauchet et al. 2009, 2014a; Kirsch et al. 2012, 2014; Pauchet and Heckel 2013;Scully et al. 2013). Second, *in vitro* functional expression assays unambiguously prove that these *GH* genes continue to code for functionally active enzymes that cleave cell wall constituents (Shen et al. 1996; Padilla-Hurtado et al. 2012; Pauchet and Heckel 2013; Kirsch et al. 2014; Pauchet et al. 2014a). By the horizontal transfer of new types of *GH* genes, beetle recipients gained new metabolic capabilities which in turn likely facilitated the

colonization of novel plant tissues and species. For instance, cerambycid beetles are wood-feeders and can metabolize xylan, a polysaccharide abundantly present in woody plant tissues, by the enzymes coded by horizontally acquired subfamily 2 genes of the extremely diverse GH5 family (Pauchet et al. 2014a) (fig. 3). Enzyme kinetics also show that post-transfer gene duplications have led to functional diversification, potentially further expanding the host plant range of the beetles (Sugimura et al. 2003; Lee et al. 2005; Pauchet and Heckel 2013; Xia et al. 2013; Kirsch et al. 2014, 2016; Pauchet et al. 2014a). Such functional diversification is shown by microbial *GH48* genes, which no longer code for PCWDEs with cellobiosidase activity, but have been co-opted by the beetles to serve as chitinases (Fujita et al. 2006; Sukharnikov et al. 2012) (fig. 3).

In addition to Coleoptera, *GH28* genes, which code for polygalacturonases (fig. 3), were also laterally transferred into the Phasmatodea and Hemiptera lineages and were subsequently duplicated within their genomes (Allen and Mertens 2008; Celorio-Mancera et al. 2008; Shelomi et al. 2014) (fig. 1). In contrast to the recurrent and ongoing HGT events in Coleoptera, phylogenetic analysis indicates a single ancient HGT event within Phasmatodea. Although no GH28 enzyme has been functionally characterized in this insect lineage yet, the genes are also expressed in the gut and show differential transcript levels along the phasmid digestive tract, strongly indicative of a role in digestive physiology (Shelomi et al. 2014). Whereas Phasmatodea and Coleoptera disrupt plant tissue by chewing, hemipteran insects pierce plant tissue using highly specialized stylet-like mouthparts. Within Hemiptera, the distribution of laterally acquired polygalacturonase genes seems to be limited to species of the Mirinae, a subfamily within the large and diverse Miridae family (Allen and Mertens 2008; Celorio-Mancera et al. 2008; Hull et al. 2013; Shelomi et al. 2014). These mirid insects digest plant material extra-orally by secreting enzymatically active saliva through their stylet into the host (Miles and Taylor 1994). In line with the *in plantae* digestion of this macerate-and-flush feeding strategy, polygalacturonase genes in mirid plant bugs are expressed in the salivary glands whereupon the protein products are secreted into the plant (Celorio-Mancera et al. 2008).

In addition to their stalks and leaves, plants also accumulate huge amounts of complex cell wall carbohydrates in their seeds (Buckeridge et al. 2000). Many arthropods feed exclusively on seeds and show HGT-mediated adaptations to fully utilize the seed's high carbohydrate content. Homogalacturonan and xylogalacturonan are highly methylated polysaccharides that serve as a backbone in the complex pectin network and can be abundantly present in seeds (Zandleven et al. 2006). Methylation of the polysaccharide backbone typically inhibits the pectin cleaving activity of polygalacturonase enzymes, including those that are produced by weevils (Coleoptera: Curculionoidea) after an HGT event from fungi (fig. 3). Rice weevil, a seed specialist, is however able to demethylate pectin through an independent horizontal transmission of bacterial genes of the carbohydrate esterase family 8 (Shen et al. 1999, 2005; Pauchet et al. 2010a; Kirsch et al. 2016). These genes code for functional pectin methylesterases that remove the methyl-groups of both homogalacturonan and xylogalacturonan. The two independently horizontally acquired pectin methylesterase and polygalacturonase families are shown to act synergistically in the rice weevil's degradation of plant pectin (Kirsch et al. 2016). Bacterial pectin methylesterase genes have been transferred to an ancestral species within the Curculionoidea superfamily and could serve a similar function in other descendent weevil species (Pauchet et al. 2010a; Evangelista et al. 2015; Kirsch et al. 2016).

Seeds of the coffee plant consist of 60% of recalcitrant polymeric carbohydrates of which galactomannan is the major storage product (Bradbury and Halliday 1990). Within the *Hypothenemus* genus (Coleoptera: Curculionoidea), *H. hampei* is a specialist and, in contrast to its close relatives, can complete a full life cycle when feeding exclusively on coffee beans. In search for the responsible digestive enzymes, Acuna et al. (2012) discovered a very recent horizontal transfer of a bacterial mannanase gene. The recombinant mannanase enzyme exhibits endo-β-mannanase activity and is able to metabolize galactomannan extracted from coffee beans, suggesting that this HGT promoted the transition of the specialist *H. hampei* to its current seed diet (fig. 3).

In conclusion, various phytopathogenic and symbiont microbial species provide a source of genetic diversity that allows arthropod lineages to quickly adapt to recalcitrant plant cell wall components.

Assimilation of Intracellular Plant Nutrients

Carbohydrate Metabolism

In addition to a polysaccharide-enriched extracellular cell wall, plants are also characterized by a high intracellular carbohydrate content (Mattson 1980; Strong et al. 1984). For herbivores, these high intracellular carbohydrate levels represent a substantial amount of potential energy. Indeed, early studies indicate that leaf-feeding caterpillars harvest this energy by a dual α- and β-glycosidase activity in their midgut, which breaks disaccharides down into monosaccharides (Santos and Terra 1986; Sumida et al. 1994). As only microbial organisms express β-fructofuranosidases (or also called invertases or β-glucosidases) that are able to catalyze β-glucosidase reactions, it was long postulated that the observed dual activity in the lepidopteran midgut was a combined product of the insect and its midgut microflora. The insect host benefits from its microflora, as α- and β-glycosidases only hydrolyze terminal α- and β-linked glucosyl residues, respectively, and differ in substrate specificities (Terra and Ferreira 1994).

However, more recent studies started to indicate that these digestive enzymes might be expressed by the insects themselves and not by associated symbionts (Carneiro et al. 2004; Pauchet et al. 2008). The study of Daimon et al. (2008) shows that a *Bombyx mori* gene of the GH32 family codes for a functional β-fructofuranosidase and claims that this is acquired by an HGT from a bacterial donor. Further phylogenetic analysis and genome mining shows that close homologues of the *B. mori GH32* gene are present in all lepidopteran genomes sequenced so far, suggestive of a single ancient HGT about 145-200 MYA (Li et al. 2011; Zhu et al. 2011; Sun et al. 2013). In addition, current comparative genomic studies across the Arthropoda also uncovered the presence of β-fructofuranosidase genes in the genomes of beetles belonging to the Curculionoidea and Buprestoidea superfamilies, the dipteran *Mayetolia destructor* and in the chelicerate spider mite *T. urticae*, suggestive of multiple, independent HGT events (Grbic et al. 2011; Keeling et al. 2013; Sun et al. 2013; Pedezzi et al. 2014; Zhao et al. 2014, 2015) (figs. 1 and 3 and table 1). The alternative evolutionary scenario explaining the presence of β-fructofuranosidase genes in the genomes of these phytophagous arthropods and their absence in all other sequenced arthropod genomes so far is that a gene copy was present in an arthropod ancestor and subsequently lost in all individual lineages across the whole arthropod phylogenetic tree (fig. 1). For now, this is a far less parsimonious scenario due to the extremely high prevalence of gene loss that would be required. Moreover, phylogenetic analysis strongly suggests independent horizontal transfers of the β-fructofuranosidase genes from different bacterial donor species to the diverse phytophagous lineages (Keeling et al. 2013; Pedezzi et al. 2014; Zhao et al. 2014). As within Lepidoptera, the transferred gene into the Curculionoidea superfamily still codes for a functional β-fructofuranosidase (Pedezzi et al. 2014).

In all sequenced lepidopteran genomes, horizontally transferred genes of a bacterial origin have been identified that code for enzymes classified as GHs of the 31 family. Although these genes are not yet functionally characterized, *GH31* genes often code for enzymes that cleave oligosaccharides (Cantarel et al. 2009; Sun et al. 2013; Wheeler et al. 2013).

These studies suggest that horizontally transferred genes from various sources offer selective advantages to phytophagous arthropods by enabling them to fully harvest the carbohydrate-rich compositions of plant tissue (table 1).

Amino Acid, Vitamin, and Carotenoid Metabolism

Compared with animals, bacteria and fungi exhibit an extremely high diversity of biosynthetic metabolic networks. This rich enzymatic repertoire enables microorganisms to uniquely synthesize certain compounds, some of which have been defined as vitamins (Karlin et al. 2001; LeBlanc et al. 2011). Arthropod herbivores again have taken advantage of the microbial metabolic richness and harbor horizontally transferred genes that code for enzymes with key roles in *de novo* nutrient synthesis. Both the functional replacement of pre-existing metabolic traits as well as the acquisition of completely new ones by HGT have occurred in phytophagous arthropod lineages (Meng et al. 2009; Moran and Jarvik 2010; Grbic et al. 2011; Sun et al. 2013; Luan et al. 2015). For instance, carotenoid biosynthesis genes detected in dipteran, hemipteran, and tetranychid genomes, but nowhere else in the animal kingdom, all have a high similarity to fungal homologues, leading multiple studies to conclude that these were laterally acquired from fungal donors. These genes have been proven to still code for functional enzymes and likely offer phytophagous arthropods the unique ability to endogenously produce carotenoids, which are conjugated isoprenoid molecules (Moran and Jarvik 2010; Grbic et al. 2011; Altincicek et al. 2012; Novakova and Moran 2012; Bryon et al. 2013; Cobbs et al. 2013).

Relative to other plant tissues, phloem, which translocates photosynthate, is especially low in essential amino acids and vitamins (Sandstrom and Pettersson 1994; Sandstrom and Moran 1999). Hemipteran insects are nonetheless able to feed exclusively on phloem sap. At first glance, HGT would not seem to be required, as hemipterans supplement their phloem diet with nutrients by engaging in intimate symbiotic associations with bacteria. Hemipterans form an organ, the bacteriome, where bacteria are sequestered into specialized host cells called bacteriocytes (Buchner 1965). This symbiosis benefits both insect and endosymbiont, since the bacteria receive a steady flow of nutrients and in return provide the sap-feeding hemipteran host with essential amino acids and vitamins. After the original bacterial inoculation of the bacteriome organ, these symbiotic bacteria go through extreme population bottlenecking, facilitating the fixation of non-functional mutations by genetic drift and resulting in progressive genomic decay. As the bacterial genome deteriorates, the symbionts become more and more dependent on the metabolism of their insect hosts, mirroring the evolution of organelles (Mccutcheon and Moran 2012). Gene losses in vitamin, amino acid and other synthetic pathways unique to bacteria have been observed, endangering the persistence of the mutualistic symbiosis as the insect host does not produce the necessary battery of enzymes. By sequencing the genomes of different hemipteran insects, a convergent evolutionary trend emerged in that independent HGT events from other, free-living bacteria to the insect genome counteract the genomic deterioration of unique bacterial pathways within the endosymbionts (Husnik et al. 2013; Sloan et al. 2014; Luan et al. 2015). For instance, both the citrus mealybug and silverleaf whitefly possess multiple horizontally acquired genes that function within the microbial lysine synthesis pathway (Luan et al. 2015). Genome analysis of various hemipteran hosts and their symbionts revealed that several gene losses within the

bacterial biosynthesis pathways of the vitamins biotin and riboflavin have been compensated by multiple, independent HGT events to the host (table 1) (Husnik et al. 2013; Sloan et al. 2014; Luan et al. 2015). The transcription of these foreign genes is often concentrated in the bacteriocytes where the enzyme products can readily interact with the intermediate substrates within the bacterial synthetic pathways (Husnik et al. 2013; Sloan et al. 2014; Luan et al. 2015).

Overcoming Plant Defenses

In response to the selection pressure of herbivore attacks, plants have developed numerous anti-herbivore physical and chemical defenses. Plant toxins and their mode of action vary widely across the plant kingdom (Whittaker and Feeny 1971; Howe and Jander 2008), and HGT events have been implicated in arthropod adaptations to some of them.

Mulberry plants defend themselves by accumulating alkaloid compounds in their foliar latex layer. These alkaloids deter herbivores from feeding by strongly inhibiting their α-glycosidase activity. Functional characterization of the *B. mori* β-fructofuranosidase, coded by the horizontally transferred *GH32* gene, showed that the enzyme is not only active but also insensitive to these inhibitory alkaloids. Therefore, Daimon et al. (2008) claimed that after HGT to an ancestor and subsequent natural selection, *B. mori* was able to specialize on mulberry plants by co-opting this carbohydrate metabolizing enzyme in its defenses.

Cyanogenic plants release poisonous cyanide from nontoxic precursor compounds upon herbivore attack (Zagrobelny et al. 2008). Like plants, bacteria are also able to biosynthesize cyanide and both prevent auto-toxicity by producing a CAS enzyme. CAS efficiently detoxifies cyanide by incorporating it into cysteine, hereby releasing the amino acid derivative β-cyanoalanine (Miller and Conn 1980; Ebbs 2004). In contrast, animals have less efficient cyanide detoxification pathways, making cyanide an effective allelochemical (Beesley et al. 1985; Zagrobelny et al. 2008). In-depth phylogenetic analysis from different studies indicates that at different times in arthropod evolution, spider mites and Lepidoptera independently acquired genes related to characterized *CAS* genes from a common bacterial clade often associated with the phyllosphere. Functional characterization of both mite and lepidopteran recombinant CAS enzymes shows that they convert toxic cyanide rapidly into β-cyanoalanine (Wybouw et al. 2014; Van Ohlen et al. 2016). Furthermore, it is shown in caterpillars that CAS activity is widespread and inducible upon exposure to dietary cyanide (Witthohn and Naumann, 1987; Meyers and Ahmad 1991; Stauber et al. 2012). By endogenously producing this cyanide detoxifying enzyme, some Lepidoptera could not only colonize a whole new range of host plants, but also develop their own cyanogenic defenses to deter predators (Witthohn and Naumann 1987; Zagrobelny et al. 2008). These studies provide strong evidence that these two arthropod lineages co-opted this bacterial gene to serve in their xenobiotic metabolism with significant ecological consequences.

In addition to a *CAS* gene, spider mites also laterally acquired a gene that codes for a functional cyanase enzyme. As cyanase metabolizes noxious cyanate, a common oxidation product of cyanide, into nontoxic products, it may represent a second, alternative route of cyanide detoxification in phytophagous spider mites. Indeed, cyanase gene-expression was induced in mites feeding on cyanogenic bean, compared to an acyanogenic bean cultivar. However, transcription analysis across a wider range of host plants led Wybouw et al. (2012) to conclude that it may also serve other biological functions (such as regulation of amino acid metabolism).

Aromatic ring structures are commonly found in plant toxins and give these compounds an exceptionally high stability due to their resonance structure. Phytopathogenic fungi nevertheless metabolize complex catecholic metabolites, such as procyanidins, by secreting intradiol ring-cleaving dioxygenases. This family of dioxygenases, restricted to microorganisms, catalyze the oxygenolytic fission of aromatic structures between adjacent hydroxyl groups (Vaillancourt et al. 2006; Roopesh et al. 2010, 2012; Yang et al. 2012). An intradiol ring-cleaving dioxygenase has been horizontally transferred into the plant feeding Tetranychidae mite family with secreted fungal enzymes as its closest homologues. Here, the dioxygenase gene duplicated and currently forms multigene families in descendent mite species (for instance, the *T. urticae* genome harbors 17 intradiol dioxygenase genes). Previous studies uncovered a high transcriptional response of this unique gene family to various chemical stresses, including host plants and acaricides (Grbic et al. 2011; Dermauw et al. 2013; Bajda et al. 2015; Van Leeuwen and Dermauw 2016). Although this dioxygenase gene family awaits functional characterization, current data strongly suggest that mites use these laterally acquired genes in their detoxification pathways.

As well as detoxifying, some arthropod herbivores also suppress toxin production to avoid the negative effects on their reproductive performance. Such manipulation of plant physiology by arthropods (and other herbivores) is achieved by secreting salivary compounds into the plant where these interfere with plant pathways (Kant et al. 2015; Zhao et al. 2015; Villarroel et al. 2016). Aromatic allelochemicals (including flavonoids) are produced by enzymes of the conserved shikimate pathway, restricted to plants and bacteria (Herrmann 1995). Specifically, the aromatic toxins are derived from chorismate, the end product of the shikimate pathway (Strack 1997). CM is a key branch-point enzyme that converts chorismate to prephenate (Romero et al. 1995). In plant parasitic nematodes, it has been proposed that by horizontal transfer of a *CM* gene, nematodes are able to modulate the plant shikimate pathway to their own benefit (Lambert et al. 1999; Vanholme et al. 2009; Haegeman et al. 2011). The discovery of a horizontally transferred *CM* gene in multiple

hemipteran lineages now raises the question whether it serves a similar function there (Husnik et al. 2013; Luan et al. 2015) (table 1).

These examples show that arthropods have evolved various counter adaptations to their host plants' defenses by hijacking pre-evolved genes from bacteria and fungi, some of which share the same metabolic pathways as plants.

Parallel Roles for HGT in Other Eukaryotic Linages

Moreover, a role of HGT in the evolutionary transition towards exploiting plants, whether by herbivory or a phytopathogenic strategy, has also been suggested in three other eukaryotic lineages, namely Fungi, Oomycota (Heterokontophyta) and the animal phylum of Nematoda. The genomic innovations due to HGT have shaped the penetration, assimilation and detoxification pathways of plant tissue independently and in parallel within these phylogenetically diverse plant parasites (Danchin et al. 2010; Haegeman et al. 2011; Soanes and Richards 2014). Comparing these studies with the data reviewed here, it is apparent that a significant number of genes coding for enzymes with identical catalytic properties were horizontally transferred to these highly divergent lineages where they play similar roles in the herbivorous lifestyle (table 1). For instance, laterally acquired PCWDEs and β-fructofuranosidases are also found in a wide range of plant parasitic nematodes and are responsible for the digestion of recalcitrant plant cell wall components and host-derived sucrose, respectively (Danchin et al. 2010, 2016). Moreover, horizontally transferred genes have a tendency to duplicate and form novel multi-gene families across the four lineages, strongly indicative of functional diversification (Danchin et al. 2010; Dermauw et al. 2013; Ahn et al. 2014; Kirsch et al. 2014).

The strong parallel role of HGT in the evolution of plant exploitation across different eukaryotic linages indicates that the genomes of non-related microorganisms already adapted to living on and from plants provide a great adaptive potential for eukaryotes trying to colonize the same niche.

Potential Mechanisms of HGT to Arthropod Herbivores

Because HGT to a eukaryotic recipient has only been detected after the fact, the exact mechanisms of the transfer remain elusive. HGT must be a multi-step process whereby a genetic element is excised from a donor genome, transmitted and introduced into a reproductively isolated recipient genome. Multiple facets of eukaryotic biology seem to lower the likelihood of successfully completing this multi-step process. First, before genetic information can be integrated and expressed in a eukaryotic genome, it first has to pass through the selective double membrane of the nucleus. Second, if it concerns a bacterial donor, the mobile genetic element needs to be expressed by a functionally appropriate promoter and adjusted to the eukaryotic transcription machinery (polyadenylation, codon compositions, and binding site modifications). Last, in multicellular eukaryotes, a new laterally acquired genetic element can only be transmitted to the following generation if it is incorporated within the isolated germ cell line. Arthropods have widespread and intimate relationships with bacterial communities which consist of free-living bacterial species and/or of symbiotic bacteria that permanently reside within certain arthropod organs (Buchner 1965; Hotopp et al. 2007; Hotopp 2011; Li et al. 2011). Even the reproductive tissues of arthropods are commonly infected with intracellular endosymbiotic bacteria. Some endosymbionts are extremely closely associated with germ line tissues as they are able to interfere with the reproductive processes of their arthropod hosts in order to increase their vertical transmission to the next generation (Stouthamer et al. 1999; Hotopp et al. 2007; Hotopp, 2011). Although the barriers of HGT to a eukaryote are high, the close proximity of dense and complex bacterial populations around and within arthropods at least facilitates HGT to the germ cell line.

In prokaryotes, HGT is known to operate through three mechanisms, namely (1) transformation—the direct uptake of exogenous DNA, (2) conjugation—the plasmid-mediated uptake of foreign DNA through cell-to-cell contact, and (3) transduction—the virus-mediated uptake of foreign DNA (fig. 2A). Studies have found that some laterally transferred genes in animal recipients are linked to genomic regions enriched in TEs (Acuna et al. 2012; Paganini et al. 2012; Flot et al. 2013; Pauchet and Heckel 2013; Gasmi et al. 2015). TEs are mobile and can jump within and between genomes. Other genes close to these TEs could potentially hitchhike on such a transposition event between close physical interacting organisms (through endosymbiosis, husbandry, parasitism, predatorism or other forms of contact). Moreover, studies indicate that viruses can act as a shuttle for TE-mediated HGT (Liu et al. 2010; Gilbert et al. 2014; Gasmi et al. 2015). For instance, parasitoid wasps inject bracoviral particles into their lepidopteran hosts to aid in the development of their offspring. Genome analysis revealed that wasp genes have been stably incorporated into lepidopteran species through the bracoviral integration mechanism (Gasmi et al. 2015). As viruses can act as gene transfer agents, the donor and recipient species do not necessarily have to be in direct physical contact, further increasing the potential source of alien genetic information (Houck et al. 1991; Dimmock et al. 2007; Liu et al. 2010; Gilbert et al. 2014; Gasmi et al. 2015). Extracellular vesicles, such as exosomes, could also be a potential route of gene transfer into eukaryotic species. These vesicles function in intercellular communication and are produced by organisms throughout the domains of life. They contain various compounds, including DNA and RNA molecules. Notably, within bacteria, genetic information is known to be transferred not

only between the cells of the same organism but also across species boundaries (Yaron et al. 2000; Mashburn-Warren and Whiteley 2006).

Concluding Remarks

Arthropods show great adaptability toward the biochemical challenges posed by herbivory. Various independent techniques show that a plethora of horizontally transferred genes are embedded within the genomes of phytophagous insects and mites. Functional characterization shows that these genes code for active enzymes and are co-opted by the arthropod recipient to serve in their detoxification and assimilation pathways of plant compounds. Beetles from the Phytophaga clade exhibit a complex evolutionary sequence of multiple lateral acquisitions and subsequent duplication and loss events of genes that code for active PCWDEs. This acquired metabolic repertoire enabled them to specialize to various new plant organs, including seeds and wooden tissue. More studies are however needed to fully map the intricate evolutionary history of various phytophagan-specific PCWDE families, such as hemicellulases and pectate lyases. Insects of the Hemiptera order independently integrated various microbial genes in their genome of which the enzyme products seem to play a role in their endosymbiont-mediated assimilation of plant metabolites. Future studies should be directed towards functionally expressing these genes and gaining additional evidence for their function in the symbiotic relationship. Within the Hexapoda subphylum, numerous sequenced genomes and transcriptomes have allowed for a greater understanding of how HGT facilitates insect herbivory. The exact role of HGT across the other subphyla (Myriapoda, Crustacea, and Chelicerata) largely remains to be discovered when more sequence data will become available (fig. 1). However, the first sequenced genome of a plant feeding mite revealed an unusually high number of horizontally transferred genes, strongly indicating that HGT might be a driving force shaping many unique and unprecedented metabolic capabilities within Chelicerata.

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