

Review

Genetic exchange and the origin of adaptations: prokaryotes to primates

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Data supporting the occurrence of adaptive trait transfer (i.e. the transfer of genes and thus the phenotype of an adaptive trait through viral recombination, lateral gene transfer or introgressive hybridization) are provided in this review. Specifically, we discuss examples of lateral gene transfer and introgressive hybridization that have resulted in the transfer or de novo origin of adaptations. The evolutionary clades in which this process has been identified include all types of organisms. However, we restrict our discussion to bacteria, fungi, plants and animals. Each of these examples reflects the same consequence, namely that the transfer of genetic material, through whatever mechanism, may result in adaptive evolution. In particular, each of the events discussed has been inferred to impact adaptations to novel environmental settings in the recipient lineage.

Keywords: introgressive hybridization; horizontal transfer; adaptation

1. INTRODUCTION

The role of introgressive hybridization or introgression (i.e. the transfer of genetic material between hybridizing taxa through backcrossing; Anderson & Hubricht 1938) in the evolutionary history of sexually reproducing organisms has gained much attention over the past decade and a half (e.g. Grant & Grant 1992; Arnold 1997, 2006; Mallet 2005). Of particular interest, and the subject of this review, are the potential effects from the introduction of ‘foreign’ genetic material into a novel (for the introduced material) genetic background. For example, genetic exchange events have been discussed as evolutionary catalysts for the origin of new species (see Arnold (1997, 2006) and Rieseberg (1997) for reviews) and in some cases entire clades (Seehausen 2004).

In this review, we will extend the discussion of genetic exchange to include not only those due to sexual reproduction and thus introgression but also those events that involve lateral gene transfer (i.e. the transfer of genetic material between individuals from two populations, or groups of populations, that are distinguishable on the basis of one or more heritable characters through the processes of transformation, transduction, conjugation or vector-mediated exchange; Arnold 2006). By discussing organisms that do not reproduce sexually, it is possible to illustrate the taxonomic breadth of similar effects from genetic transfer *sensu lato*. The observation of such widespread common effects reflects why the tree-of-life metaphor is now argued to be a less predictive hypothesis for biological evolution (e.g. Doolittle & Bapteste 2007). Indeed, we have argued for the adoption of a new metaphor, that of a web of life (Arnold & Larson

2004; Arnold 2006). Given the extent of genetic exchange that has occurred during the evolution of all clades of organisms, the web-of-life metaphor appears to be a more accurate descriptor of evolutionary pattern and process.

Though we will broaden the discussion to include organisms as diverse as bacteria and mammals, we will limit our review to examples consistent with a single evolutionary outcome—that of adaptive trait transfer (i.e. the transfer of genes and thus the phenotype of an adaptive trait through viral recombination, lateral gene transfer or introgressive hybridization; Arnold 2006). Our rationale for choosing to discuss only adaptive trait transfer reflects (i) our detection of this process in species under investigation by our group and (ii) the relatively recent increase in the number of examples that reflect this process. We do not intend to suggest that this is necessarily the most common outcome of natural hybridization, viral recombination or lateral gene transfer, though for certain clades it might well be. In addition, each of the examples given will benefit from further experimental manipulations or comparative analyses to provide a more rigorous test of the adaptive trait transfer hypothesis. Yet, the biological diversity reflected by these examples (Arnold 2006), and the inference of this process by such a wide array of researchers applying diverse approaches provides compelling evidence for adaptive trait transfer. Furthermore, the evolutionary effects that may be realized by the transfer of loci underlying adaptations are of profound importance. These include: (i) an increase in the ecological amplitude of the recipient lineage, (ii) the origin of novel adaptations in the recipient lineage, (iii) the evolution of hybrid taxa with a novel array of adaptations, and (iv) the adaptive radiation of entire taxonomic assemblages (see Anderson (1949), Arnold (1997, 2006) and Seehausen (2004) for reviews).

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One contribution of 16 to a Theme Issue ‘Hybridization in animals: extent, processes and evolutionary impact’.

2. BACTERIAL SPECIES

(a) *Lactobacillus salivarius*

It is common to consider the evolutionary effects from lateral gene transfer among bacterial species from the viewpoint of species harmful to humans. This bias does not reflect a lack of transfer events involving bacterial species that provide benefits to their human (or other) hosts. It seems instead to reflect the understandable focus of research on control issues involving pathogens. However, in the present discussion, we will focus on two non-pathogenic bacterial examples, *Lactobacillus salivarius* (the topic of this section) and lactic acid bacterial species (discussed in §2*b*). These two examples illustrate the observation that beneficial bacterial taxa also possess genomic signatures indicative of gene transfer events during their evolution. Significantly, the species in these clades reflect the occurrence of adaptive trait transfers.

The genus *Lactobacillus* contains numerous species that provide their hosts 'probiotic properties' (i.e. '...upon ingestion, they confer a range of benefits on the host...'; Claesson *et al.* 2006). Like other members of this genus, *L. salivarius* is beneficial to its hosts. For example, this species has been shown to weaken the effects of both colitis and arthritis in mice (McCarthy *et al.* 2003; Sheil *et al.* 2004). Furthermore, it produces a bacteriocin ('bacteriocins are loosely defined as biologically active protein moieties with a bacteriocidal mode of action'; Riley & Wertz 2002) that acts against harmful Gram-positive bacteria including some *Staphylococcus* species (Flynn *et al.* 2002; Claesson *et al.* 2006).

Evidence for the adaptive transfer of genes into *L. salivarius* comes from the description of its 2.13 megabase (Mb) genome. In particular, Claesson *et al.* (2006) found that this genome consisted of four replicons: a 1.83 Mb circular chromosome, a 242 kb megaplasmid and two smaller plasmids (20.4 and 44 kb, respectively). The detection of the megaplasmid reflects the first characterization of this type of genomic component in intestinal lactobacilli, and Claesson *et al.* (2006) suggested that the megaplasmid itself resulted from a horizontal gene transfer event that conferred adaptations to the host *L. salivarius*. Several observations provide evidence for adaptive consequences resulting from the lateral transfer of components into the megaplasmid and from the incorporation of the megaplasmid replicon into *L. salivarius*. Characteristics of the megaplasmid, which are well-known signatures for horizontal transfers (see Ochman *et al.* (2000) for a review), include the presence of a high proportion of transposable elements and skewed G–C ratios in some genes (Claesson *et al.* 2006). However, most germane to the present discussion is the observation that the megaplasmid, '...although apparently dispensable for viability...confers on the strain a large number of contingency metabolic capabilities and traits directly related to GI tract survival or competitiveness' (Claesson *et al.* 2006). This conclusion highlights the adaptive trait transfer event caused by the incorporation of this genomic element into *L. salivarius*. Intriguingly, one of the adaptive traits conferred by this transferred genome is the ability to produce a bacteriocin (Flynn *et al.* 2002; Claesson *et al.* 2006). Thus, the adaptive trait transfer that benefits

L. salivarius has also resulted in one of the probiotic characteristics that benefits this bacterial species' hosts, including humans.

(b) *Lactic acid bacteria*

Makarova *et al.* (2006) define lactic acid bacteria (LAB) as '...microaerophilic, Gram-positive organisms that ferment hexose sugars to produce primarily lactic acid'. These authors also point out that the use of LAB by humans dates back to the dawn of agricultural systems and that at present they (i) provide the key bioconversions in the fermentation of dairy, meat and vegetable products and (ii) are crucial for the production of, for example, wine, coffee and silage (Makarova *et al.* 2006). These species are naturally associated with plant and milk environments as well as mucosal environments (e.g. small intestine) of animal hosts.

Like all other bacterial species (Ochman 2005), the predominant pattern of genome evolution in the LAB is the progressive loss of genes (Makarova *et al.* 2006). However, also like other bacterial lineages (Jordan *et al.* 2001), these species possess numerous horizontally acquired gene products (Makarova *et al.* 2006). Furthermore, analyses of the transferred elements indicate the presence of adaptive trait transfer. In particular, selective pressures generated by the nutrient-rich environments encountered by LABs appear to have favoured the acquisition of many peptidases. In addition, Makarova *et al.* (2006) provided an example involving the acquisition of the glycolytic enzyme, enolase. Though all bacterial species contain one copy of this gene, the lactobacilli possess two. The second copy of this gene was apparently acquired through horizontal gene transfer from another bacterial lineage (Makarova *et al.* 2006).

An additional signature of adaptive trait transfers in the lactobacilli involves the relative rate at which genes are either lost or gained (Makarova *et al.* 2006). The number of genes lost along lineages was strongly correlated with the length of the lineages. By contrast, the number of gene gain events was not correlated with the phylogenetic branch length. This observation led Makarova *et al.* (2006) to conclude that purifying selection was probably responsible for the genome reduction events, but that positive selection (i.e. for the acquisition of new adaptations) was a possible cause of the unequal rate of addition of new genes.

3. FUNGAL SPECIES

(a) *Ophiostoma novo-ulmi*

Unlike bacterial taxa, the process of introgressive hybridization, rather than horizontal gene exchange, is the basis of genetic transfer between fungal lineages. However, regardless of the mode of transfer, the acquisition of novel genes by the recipient fungal form has, in some cases, resulted in the transfer or de novo origin of adaptations (see Arnold (2006) for references). A clear example is provided by the plant pathogen *Ophiostoma* (Brasier 2001).

Brasier & Kirk (2001) recognized two subspecies of the causal agent of the Dutch elm disease pandemic, the ascomycete fungus *Ophiostoma novo-ulmi*. The fungal

variants *Ophiostoma novo-ulmi novo-ulmi* and *Ophiostoma novo-ulmi americana* were originally designated as Eurasian and North American isolates, respectively. It was hypothesized that two separate hybrid subspeciation events had resulted in the two lineages (Brasier & Kirk 2001). Specifically, Brasier & Kirk (2001) suggested that subsequent to a Eurasian point of origin, *O. novo-ulmi* hybridized with *Ophiostoma ulmi*, resulting in the European subspecies and that the introduction of *O. novo-ulmi* into North America in the 1940s was followed by its hybridization with the North American *O. ulmi*, giving rise to *O. n.-u. americana*. The detection of diagnostic differences between the two subspecies that were shared with either the Eurasian or North American forms of *O. ulmi* provided support for this hypothesis (Brasier & Kirk 2001).

Subsequent to their formation, *O. n.-u. novo-ulmi* and *O. n.-u. americana* have been brought into contact in Europe. This contact has resulted in introgression between these two subspecies (Brasier 2001; Brasier & Kirk 2001). Though the recombinant forms demonstrated intermediate phenotypes relative to their parents, they were found to be just as pathogenic (Brasier 2001; Brasier & Kirk 2001). Brasier (2001) hypothesized that 'From such a mélange of recombinants, natural selection may in the future favour... a new race or subspecies of the pathogen'. Brasier's (2001) hypothesis has indeed been supported by subsequent observations. In particular, the conclusions drawn by Paoletti *et al.* (2006) are of most significance for the present discussion. These authors argued that the introgression of the *MAT-1* and *vic* loci reflected a '...rapid adaptation of invasive organisms to a new environment' (Paoletti *et al.* 2006). Specifically, the transfer of these loci allowed the recipient lineages to reproduce sexually, thereby providing an escape mechanism from the viral infections that would otherwise be perpetuated through the clonal fungal lineages (Paoletti *et al.* 2006).

4. PLANT SPECIES

(a) Louisiana irises

Edgar Anderson (using data from Riley 1938) began his classic book, *Introgressive hybridization*, with a discussion of the morphological variation found in naturally occurring parental and hybrid populations of the plants known as Louisiana irises. He used these data to describe the process of introgressive hybridization. In a publication from a year earlier, Anderson (1948) also used these species to highlight the catalytic effect of human-mediated habitat disturbances on rates of hybridization and introgression. In both of these publications, Anderson stressed the exemplary nature of the Louisiana irises in defining the results of introgressive hybridization. In particular, Anderson (1949, p. 62) stressed repeatedly 'A trickle of genes so slight as to be without any practical taxonomic result might still be many times more important than mutation...'

Recent analyses of both natural and experimental hybrid populations of Louisiana irises have supported the conclusions of Anderson (1948, 1949). For example, Cornman *et al.* (2004) determined both the

spatial distribution of naturally occurring hybrid clones and the paternal contribution to the hybrid genotypes. Their detection of spatial genetic structuring and the recruitment of only a subset of the possible hybrid genotypes supported the hypothesis that certain hybrid genotypes possessed a higher fitness due to acquired adaptations (Cornman *et al.* 2004). These authors also hypothesized a role for differential selection that favoured or disfavoured different hybrids in '...the establishment of recombinant lineages that are more fit than the parental types in some habitats' (Cornman *et al.* 2004).

Like the analysis of Cornman *et al.* (2004), linkage and quantitative trait locus (QTL) mapping experiments involving the Louisiana irises species, *Iris fulva* and *Iris brevicaulis* have supported the hypothesis of adaptive trait transfer and origin. First, a study by Bouck *et al.* (2005) detected genomic regions (in reciprocal backcross (BC₁) individuals) characterized by significantly lower- or higher-than-expected levels of introgression. In the context of adaptive trait transfer, the detection of regions with significantly increased frequencies of introgression suggests that gene transfer led to positive selection reflected by the increased survivorship of these genotypes.

Consistent with the above inference, Martin *et al.* (2005) defined QTLs (figure 1) associated with the phenotype of long-term survivorship in the same greenhouse environment used by Bouck *et al.* (2005). Though the plants were watered regularly, the greenhouse environment reflected a water-limited setting for some of the Louisiana irises genotypes. *Iris brevicaulis* is often found in drier, greenhouse-like, natural environments. By contrast, natural populations of *I. fulva* most often occur in water-saturated soils (Viosca 1935; Cruzan & Arnold 1993; Johnston *et al.* 2001). One prediction from the habitat associations observed in the natural populations of *I. brevicaulis* and *I. fulva* is that alleles from the former should increase survivorship in the, relatively dry, greenhouse environment. The predicted patterns of mortality were indeed found between the two backcross (BC₁) hybrid classes, with *I. fulva* backcrosses demonstrating twice the frequency of mortality as *I. brevicaulis* backcross plants. In addition, a QTL analysis detected four genomic regions in the *I. fulva* hybrids that were significantly associated with survivorship (figure 1; Martin *et al.* 2005). As expected, introgressed *I. brevicaulis* DNA increased survivorship at three of the four QTLs. However, the fourth QTL indicated that introgression of *I. brevicaulis* alleles was associated with decreased survivorship. For this latter locus, the presence of two copies of the *I. fulva* genomic region increased survivorship (Martin *et al.* 2005). Though not predicted, this result indicates the adaptive potential arising from the combination of genomic elements from different evolutionary lineages (Arnold 1997, 2006).

Based on their data, Martin *et al.* (2005) constructed the following hypothesis: 'The present findings have important implications for the evolutionary dynamics of naturally occurring hybrid zones. Regions of the genome that increase survivorship when in a heterozygous (i.e. hybrid) state should have an increased likelihood of passing across species boundaries,

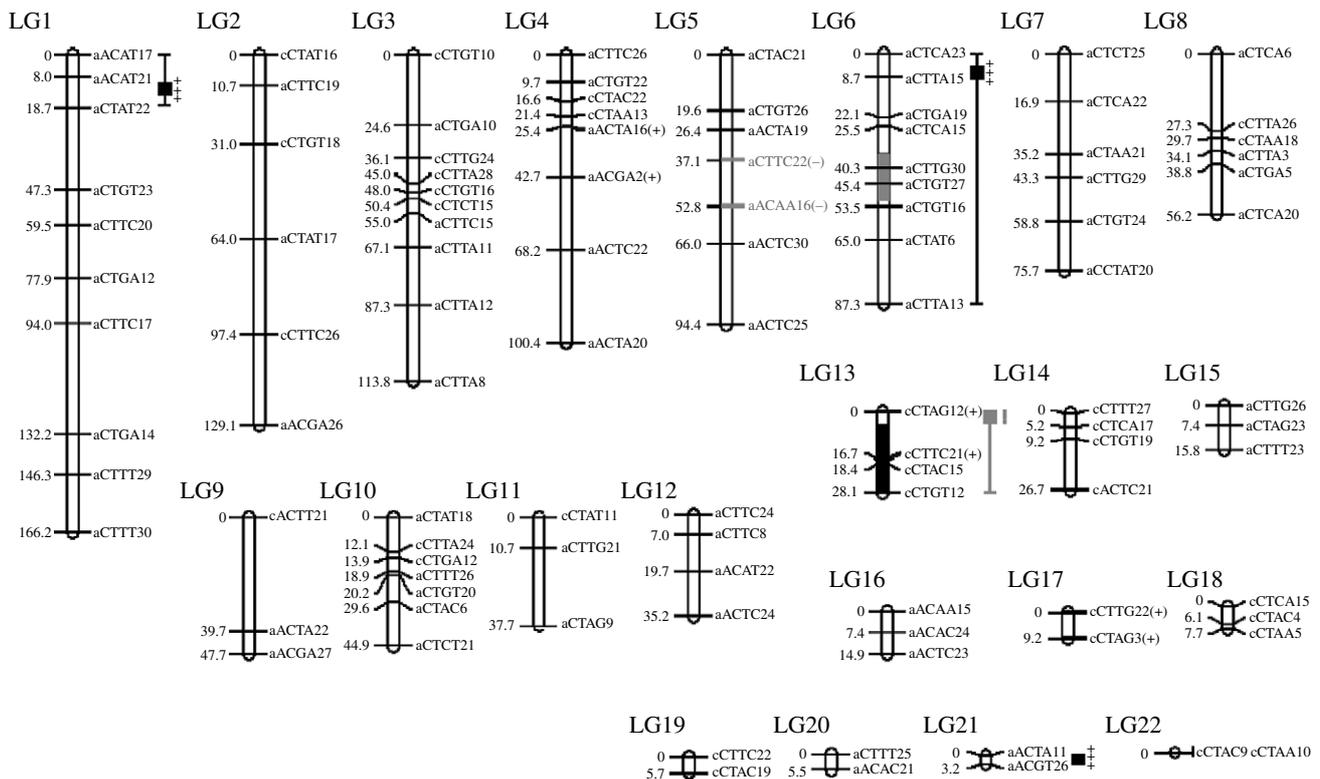


Figure 1. Linkage map of dominant *I. brevicaulis* iris retroelements (IRRE) retrotransposon display markers (Kentner *et al.* 2003; Bouck *et al.* 2005) segregating in the F₁ hybrid used to produce backcross hybrids towards *I. fulva*. Significant QTL for survival in greenhouse conditions are denoted (with 2-LOD CIs—LOD scores a distribution of distances from genetic markers estimated from recombination frequencies; CIs are the confidence intervals around these estimates) to the right of the marker names (Martin *et al.* 2005). Black or stippled bars (2-LOD CIs) denote QTLs for survival under natural conditions (Martin *et al.* 2006). Stippled bars represent regions where introgressed (hybrid/heterozygous) regions are favoured, while black bars represent regions where recurrent (parental/homozygous) regions are favoured.

whereas those that decrease survivorship will be less likely to introgress'. A subsequent study (Martin *et al.* 2006), involving the transplantation of the same genotypes used in the analysis of survivorship under greenhouse conditions into natural settings, supported this hypothesis. This latter study also determined the genetic architecture, via QTL analyses, of survivorship. However, unlike the relatively dry greenhouse setting of the first two experiments, these same genotypes were exposed to a prolonged (lasting more than three months) flooding event. Under such a regime, it was predicted that alleles from the wet-adapted *I. fulva* species should positively affect survivorship. In general, the observed patterns of survivorship agreed with this prediction: (i) *I. fulva* individuals survived at significantly higher frequencies than *I. brevicaulis* plants, (ii) *I. fulva* backcross genotypes had a significantly higher frequency of survivorship than the reciprocal backcross genotypes towards *I. brevicaulis*, (iii) the frequency of survivorship of the *I. brevicaulis* backcross hybrids was increased by the presence of introgressed *I. fulva* alleles, and (iv) survivorship in the *I. fulva* backcross hybrids was affected by two epistatically interacting QTL of opposite effects (Martin *et al.* 2006). It should also be pointed out that the two QTLs that affected survivorship in the *I. fulva* BC₁ hybrids were on two of the linkage groups that contained QTLs that impacted survivorship in the dry greenhouse environment. However, the effects of the QTLs under the two different environments were found to be in

opposite directions. Specifically, the introgressed QTLs lowered survivorship in the dry habitat, while in the flooded environment the introgression of QTLs on these same linkage groups increased survivorship (Martin *et al.* 2006).

More recent analyses of natural and experimental Louisiana iris hybrid populations provide support for Anderson's (1949) conclusion that introgression has affected the evolutionary trajectory of this species complex. In general, these findings '...demonstrate the potential for adaptive trait introgression between these...species and may help to explain patterns of genetic variation observed in naturally occurring hybrid zones' (Martin *et al.* 2006).

5. ANIMAL SPECIES

(a) *Heliconius*

Species belonging to the butterfly genus *Heliconius* provide striking examples of Müllerian mimicry (mimicry between taxa that are unpalatable to predators; see Jiggins *et al.* (2001) for references). In addition to acting as a warning colour-mediated defence mechanism, the variation in wing markings also affects mate choice thus leading to elevated levels of assortative reproduction (e.g. Jiggins *et al.* 1997, 2001). Notwithstanding the limitations that divergent wing patterns place on interspecific hybridization, there are now numerous datasets that confirm the role of introgressive hybridization in the evolution of *Heliconius* and other butterfly genera that display Müllerian mimicry

(e.g. Jiggins *et al.* 2006; Kronforst *et al.* 2006; Mavárez *et al.* 2006). For example, Jiggins *et al.* (2006) used a species-level phylogenetic approach for the genus *Ithomia* to test for cladogenesis due to colour pattern change. In general, their results supported this hypothesis. However, they also found signatures of divergence accompanied by gene flow. In particular, the phylogenetically most closely related species were determined to be those that were either sympatric or parapatric. One explanation for this phylogenetic signal was ‘...divergence driven by ecological change with ongoing gene flow...’ (Jiggins *et al.* 2006). Like *Ithomia*, *Heliconius* provides excellent examples of divergence accompanied by introgression. Furthermore, because hybrid derivatives demonstrate novel wing patterning, and thus novel adaptations to their ecological settings (i.e. predators), their evolution reflects the process of introgressive hybridization-driven adaptive evolution.

Kronforst *et al.* (2006) used 657 AFLP markers (a method for generating anonymous genetic markers via polymerase chain reaction) and the sequence variation at 1 mitochondrial and 14 nuclear loci to test for introgression among *Heliconius cydno*, *Heliconius pachinus* and *Heliconius melpomene*. The patterns of variation revealed by this analysis indicated the occurrence of contemporary and historical introgressive hybridization (Kronforst *et al.* 2006). Significantly, Kronforst *et al.* (2006) also suggested that *H. pachinus*’ demonstration of a wing pattern with components typical of the other two species studied might reflect a hybrid origin for *H. pachinus*. This conclusion is, however, not restricted to *H. pachinus*. Mavárez *et al.* (2006) also documented the evolution of a novel wing pattern adaptation, and thus the origin of the hybrid species, *Heliconius heurippa*.

The detection of novel hybrid wing patterning and molecular genetic variation indicating both ancient and recent introgression lends ‘...support to the hypothesis that phenotypic diversification in the genus *Heliconius* has been fuelled by introgressive hybridization...’ (Kronforst *et al.* 2006). This conclusion is likely to be true as well for other clades marked by Müllerian mimicry (e.g. Jiggins *et al.* 2006).

(b) *Manacus*

Birds provide some of the clearest, and best documented, zoological examples of the evolutionary role of introgressive hybridization (see Grant & Grant (1992) and Arnold (1997, 2006) for references). Indeed, the most well-characterized avian example, and one that includes evidence for adaptive trait transfer, the Darwin’s finches, is discussed elsewhere in this volume (Grant & Grant 2008). However, the genus *Manacus* also provides an illustration of not only the effect of introgressive hybridization but also the process of adaptive trait transfer.

Manacus candei (white-collared manakin) and *Manacus vitellinus* (golden-collared manakin) form a hybrid zone, the centre of which is proximal to Rio Robalo in the Panamanian province of Bocas del Toro (Parsons *et al.* 1993; Stein & Uy 2006). Within this hybrid zone, morphological and genetic characters diagnostic for the two species demonstrate significantly different patterns of changeover. In particular, the patterns are typified by

non-coincident, clinal changeover for nuclear and mitochondrial molecular markers relative to the male plumage characteristics (Parsons *et al.* 1993; Brumfield *et al.* 2001). Importantly, the male plumage traits of the golden-collared species were found to have introgressed into populations of the white-collared phenotype approximately 50 km further than other morphological traits and the DNA markers (Brumfield *et al.* 2001).

Parsons *et al.* (1993) and Brumfield *et al.* (2001) hypothesized that introgression of the male plumage characteristics from the golden- into the white-collared species reflected a selective advantage for males carrying these traits. Furthermore, Parsons *et al.* (1993) argued that this advantage was most likely due to highly skewed male mating success at the lek sites of *Manacus*. Support for the hypothesis of sexual selection-driven introgression of the golden-collared traits has come from two studies of behaviour and/or mating success for the two species and their hybrids (McDonald *et al.* 2001; Stein & Uy 2006). The study conducted by McDonald *et al.* (2001) involved an analysis of male behaviour demonstrated by three classes of *Manacus*: (i) white collared, (ii) golden collared, and (iii) ‘lemon collared’. These classes contained *M. candei*, *M. vitellinus* and natural hybrid genotypes, respectively. McDonald *et al.* (2001) hypothesized that higher levels of aggressiveness by the golden- and lemon-collared males, relative to the white-collared form, might be an important contributor to sexual selection-derived introgression. In support of this hypothesis, the golden and lemon males demonstrated a significantly higher attack frequency on taxidermy-mounted specimens. In addition, males belonging to the hybrid (i.e. lemon) class produced more vocalizations than either of the parental classes (McDonald *et al.* 2001).

Like McDonald *et al.* (2001), Stein & Uy (2006) investigated the possible role of male–male interactions as a catalyst for the adaptive trait introgression of male plumage characteristics from *M. vitellinus* into *M. candei*. Stein & Uy (2006) also tested for the role played by female mate choice. In contrast to McDonald *et al.* (2001), Stein & Uy (2006) found that the two classes demonstrated equivalent aggressiveness and ‘...held comparable positions within leks’ (Stein & Uy 2006). Furthermore, the golden and white males had equivalent courtship visits from females. Yet, the golden class had significantly more matings. Overall, Stein & Uy’s (2006) observations supported a role for sexual selection-driven adaptive trait transfer between the two manakin species. However, their data led them to conclude that male–male interactions were not the major process determining the introgression of male plumage traits. Instead, they concluded rather that sexual selection provided by female mate choice was the primary causal factor. Relevant to the present context, their findings also provided ‘...evidence for hybrid zones as an important source for attractive and adaptive display traits’ (Stein & Uy 2006).

(c) *Ficedula*

The collared and pied flycatchers (*Ficedula albicollis* and *Ficedula hypoleuca*, respectively) reflect our second exemplar of the potential for adaptive trait transfer

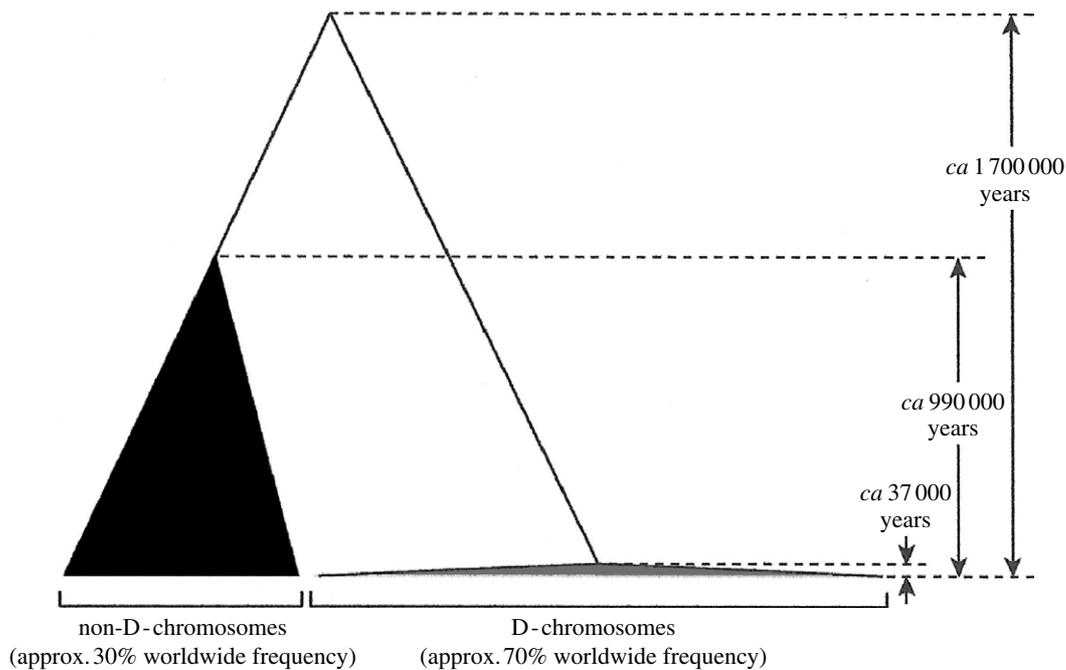


Figure 2. Genealogical representation of coalescent times for D- and non-D-haplogroup alleles of the *microcephalin* gene (two different groups of closely related haplotypes at this locus; Evans *et al.* 2006). The extremely recent coalescence time for the D-haplogroup alleles, and their ancient divergence from the non-D-haplogroup alleles, supports the hypothesis of introgression of the D-alleles from an archaic *Homo* lineage into *H. sapiens* ca 37 000 yr BP (Evans *et al.* 2006).

between avian taxa. Though these species have primarily been used as a model system for studying reproductive isolation and biological speciation (e.g. Sætre *et al.* 2001), natural hybrid zones characterized by introgression have been detected (Tegelström & Gelter 1990; Sætre *et al.* 2001, 2003). Furthermore, introgression between these species has resulted in mosaic hybrid genomes characterized by introgressed and non-introgressed regions. For example, Sætre *et al.* (2003) observed restricted transfer of sex chromosome loci, but ‘...rather extensive introgression and recombination of autosomal genes’.

As with the other examples described in this review, the elevated frequency of transfer of some loci suggests the action of positive selection. Support for the occurrence of adaptive introgression between *F. albicollis* and *F. hypoleuca* was discovered in an analysis of the frequency of introgression among nine autosomal and four sex chromosome loci (Borge *et al.* 2005). In particular, the *F. hypoleuca* ‘Alasy’ locus allele was found in very high frequencies in *F. albicollis*. Borge *et al.* (2005) hypothesized that this allele was linked to a locus under positive selection when in the hybrid background. Given this, the higher-than-expected frequency of introgression of the pied into the collared flycatcher background would indicate that ‘...the collared flycatcher has inherited an adaptive allelic state from the pied flycatcher through introgressive hybridization...’ (Borge *et al.* 2005).

(d) *Homo*

It would seem that one of the more contentious issues concerning human origins concerns whether or not introgressive hybridization occurred between anatomically modern (i.e. *Homo sapiens*) and archaic (e.g. *Homo neanderthalensis* and *Homo erectus*) lineages (Stringer & Andrews 1988; Arnold & Meyer 2006; Evans *et al.*

2006). However, the view that such genetic exchange did not occur seems unsupported given (i) the widespread introgression between contemporary primate taxa (see Jolly (2001) and Arnold & Meyer (2006) for reviews), (ii) the fossil evidence for the spatial and temporal overlap between *H. sapiens* and archaic *Homo* taxa (Stringer & Andrews 1988; Finlayson 2005), and (iii) the genetic variation indicating reticulate evolution within the clade containing *H. sapiens* (e.g. Navarro & Barton 2003; Garrigan *et al.* 2005; Osada & Wu 2005).

In addition to the large body of data supporting the hypothesis that the divergence of *Homo* lineages was accompanied by introgressive hybridization, there is also evidence that some of the genetic exchange events resulted in the transfer/origin of adaptations. One such example comes from the analysis of allelic variation present at the *microcephalin* locus (Evans *et al.* 2006). Patterns of genetic variation at this locus suggested the introgression of anciently derived alleles from an archaic *Homo* taxon (possibly *H. neanderthalensis*) into *H. sapiens* ca 37 000 yr BP (figure 2; Evans *et al.* 2006). The significance of this finding was twofold. First, it is additional evidence of the genetic interaction between archaic and modern forms of *Homo*. Second, it provided evidence of adaptive trait transfer (Evans *et al.* 2006).

The *microcephalin* gene is known to contribute to the regulation of brain size in humans (Jackson *et al.* 2002). In addition, the inference of positive selection acting on this locus, both in the ancestral lineage of humans (Evans *et al.* 2004; Wang & Su 2004) and in the *Homo* lineage as well (Evans *et al.* 2005), suggests its adaptive significance. The pattern indicative of strong positive selection in the *Homo* clade is illustrated in figure 2. In this regard, Evans *et al.* (2006) detected a recent (ca 37 000 yr BP) coalescence age for the D-haplotype alleles (a group of closely related haplotypes at the

microcephalin locus; Evans *et al.* 2006). Yet, these alleles occur at an extremely high frequency and are distributed worldwide (figure 2; Evans *et al.* 2006). The combination of their recent coalescence and high worldwide frequency lead to the conclusion that the D-haplotype alleles have been increased in frequency by positive selection. Evans *et al.* (2006) also concluded that the introduction of these haplotypes into the *H. sapiens* population was via introgressive hybridization with an archaic lineage that had been separated from the lineage leading to modern humans for ca 1.1 Myr (figure 2).

Like each of the examples in §5a–c, the apparent introgression of the *microcephalin* allele from an archaic form into an anatomically modern *Homo* species had the potential to affect adaptive evolution. Indeed, Evans *et al.* (2006) suggested that ‘It is perhaps not surprising then that modern humans...could in theory benefit from adopting some adaptive alleles from the populations they replaced’. Like bacteria, fungi, plants and other animals, the introgression of this key determinant of human brain size supports the hypothesis that adaptive trait transfer has profoundly impacted the evolution of *H. sapiens* as well.

6. CONCLUSIONS

Genetic exchange, involving introgression or lateral exchange, has been a frequent and evolutionary significant factor for all organismic clades (Arnold 1997, 2006). Each genetic transfer event has had the potential to affect the fitness of the recipient individual. When the introduction of the foreign DNA has resulted in an increase in fitness in certain environmental settings, the transfer or de novo origin of an adaptive trait can be inferred. QTL mapping experiments, genome-sequencing projects, experimental determinations of fitness and gene functional assays have identified numerous examples in which horizontal gene transfer or introgressive hybridization has resulted in such adaptive exchanges/origins. Though each of the findings discussed in this review are consistent with the hypothesis of adaptive trait transfer, they will be strengthened by additional experimental and comparative studies. As additional datasets are produced, we expect that the adaptive consequences inferred for the above examples will be identified as a common outcome of genetic exchange.

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