Explaining exceptions to dollo’s law

Explaining exceptions to Dollo’s Law – a review of the concepts of constraint and contingency.

In 1890 Louis Dollo a Belgian palaeontologist, came up with the theory that evolution is irreversible, expanding on the work of Edgar Quinet, a historian who had first pondered this theory (Chopra & Rogers, 2013) . Thus explaining that the constraint of evolution that it is irreversible and if certain traits are lost this effects the contingency of evolution, thus past changes having an effect on the present and future of the species, this could by chance may or may not have an effect on the re-evolution of certain traits. The theory states that evolution is irreversible because of the structures and functions lost in the line of evolution cannot return in the lineages that they were once lost in e. g tails in our monkey like ancestors. This therefore suggests that genes formally required to code for adaptive traits during selection pressures will become non-functional when selection pressure is low or non-existent (Marshall, et al., 1994). The repercussions of this are that any trait coded by these genes will be lost forever and cannot ever occur again in the same lineage according to Dollo’s law (Marshall, et al., 1994). In recent times many papers have been published that have disputed this law. There has been some work done on seeing if the constraints of evolution hinder further adaptation and whether this can either facilitate or hinder the re-emergence of the original/ancestral trait (Yedid et al. 2008). This essay will look at some of the cases where this law potentially does not apply and discuss how relevant Dollo’s law is in biology, and if it is relevant at which point does the law either become to ambiguous or too specific. We will discuss Dollo’s law at two different bases; the Genetic and Morphological.

Under Dollo’s law the genetic basis of this is that if a gene is lost due to natural selection and bred out of a population, the trait coded by the gene is lost and cannot be regained in the same lineage over evolutionary time. A Study to test the genetics of Dollo’s law was tested on the genome coding for the sex combs in *Drosophila bipectinata* and its close relative *Drosophila malerkotliana* (Seher, et al., 2012). The study found that some the genes that code for sex comb may alter the structures dramatically (even in a single inversion) and some that had multiple inversions of the chromosomal structure which had no difference in the sex comb morphology. They then suggested that Dollo’s law should follow molecular pathways rather than just the genes that code for them. This is due to many genes being regulatory genes, which can sometimes when activated; open up many pathways to code for different cellular processes. This can then have an effect in gene expression and therefore a trait previously lost in evolutionary time is now being expressed due to these “ nexus” regulatory genes (Seher, et al., 2012). The can be demonstrated in another experiment where mouse inductive signals that gave rise to stem cells providing teeth, where cultured with graphs of chick oral dermis. The result found that the Chicks oral tissue actually started to form enamel organs and even in some case small malformed teeth (Marshall, et al., 1994). In a review published by Bull & Charnov it says that In relation to irreversibility there are two generalisation from there analysis. 1) “ selection of intermediate phenotypes is critical to evolutionary transitions whenever the two phenotypes are so different that multiple mutations are required to change from one to another” (Bull & Charnov, 1985) , and 2) “ a second principle common to several examples is that the genome may progressively accommodate a character state the

loner it is maintained” (Bull & Charnov, 1985). These two generalities the summary was that irreversible evolution is founded on the dependence of the biological details of the system, with some more general rules that apply at a much less focused level. The constraints with looking at the genetic level are that we are looking literally “ under the microscope” and it is fine picking each detail of gene selection and deletion and applying this to Dollo’s law. But as said before genes can take many pathways due to nexes regulatory genes, so who is to say that a feature i. e. eyes lost in a cave fish (speaking hypothetically) came back in a recent form but using different genes to cause the eye. Is this against Dollo’s law? Or because of the different genetic pathway it is just a natural progression in evolution.

Using morphology as a basis with regards to Dollo’s law it states that any morphological trait that is lost in a lineage cannot ever be re-expressed for example the hind legs in cetaceans. We cannot talk about morphological exceptions to Dollo’s rule without mentioning Atavism. Atavism by definition is a revision/reappearance to an ancestral characteristic previously lost in the evolutionary pathway (Biology-online, 2012). Atavisms arise normally due to a gene recombination or a gene mutation that enables a previous trait to be expressed (Hall, 2010). Hind leg extension in vertebrates has been well documented. In a study by Bejder & Hall, they mention atavisms and the development of limb bud in cetaceans, snakes and legless lizards (Bejder & Hall, 2002). They aren’t as rare as one might think this is due to all these animal species having being evolved from limbed ancestors, and as previously mentioned that genes can code for a multiple of different functions. Atavisms in whales normally occur in the rudiments of the pelvic

girdle, the best case of this has been found in sperm and blue whales. The incident rate of atavisms in adult sperm whales is about 1: 5000 (Bejder & Hall, 2002). In the Individuals found the atavisms skeletal processes are found to be almost complete, even both hind limb have been found in a female humpback whale when normally present is cartilaginous femur (Bejder & Hall, 2002). Because these vestigial limbs actually have no function can these actually be considered against Dollo’s law? Or because that previously forgotten traits are being expressed does that counter Dollo’s law? Another morphological feature that contracts Dollo’s is re-evolution of shell coiling in gastropods (Collin & Cipriani, 2003). The trait was thought to have died out around 10mya but a study has shown that It can be re-evolved using the same genes that gastropods has at that time. There are two hypothesis put forward by this idea; either that genes that signal for shell coiling have a number of function have been kept in there entirety, or that *Trochita* has developed a new pathway to gain the coiling trait completely different to its ancestor (Collin & Cipriani, 2003). There has been evidence to support the second theory due to the coiling being superficially different to other gastropod species (Collin & Cipriani, 2003). Finally an example that is a little closer to home is that there is new evidence of muscle reversions in the primate phylogeny. There have been 220 character state changes that are optimised in the parsimonious 28 of there have been evolutionary reversions, 6 of these have through evolution have contributed to human musculature and 9 of these have directly gone against Dollo’s law (Diogo & Wood, 2012). The one particular case of violating of Dollo’s law for muscle reversion is in the subtribe *hominina* . In this case both the rhomboideus major and rhomboideus minor muscle are found in an ancestral clade. This

was then lost and the Rhomboidus muscles became the more distinct muscle in the *Cercopithecinae* , the ancestral muscle formation then has re-appeared in the *Hominina* there by going against Dollo’s law (Diogo & Wood, 2012). this constant muscle evolution and re evolution causing the muscle to constantly re configure in primate to truly go against Dollo’s law at both eh morphological and genetic level there must be the same genetic pathways and selection pressures present to make this change a selective and adaptive advantage to truly call this change re-evolution.

In summary to this review all of the studies all show great strengths and flaws with the methods and rules abided by in Dollo’s law. Constraints and contingency way heavily on if Dollo’s law is applied, because pathways may be constrained but if they actually help the re evolution of a trait there still may not be a selection pressure for these and this does not apply with the constraints of evolution, there-fore if there is no selection to me it feels like a random mutation with no beneficial attributes to the animal’s evolution. Law I feel is a strong word to use because with law there needs to be the same degree of lenience with this. This is due to papers on the genetic level saying that if the same pathways are used this means that this is against Dollo’s law, but if the same trait appears again but using a different pathway this does not, even if the new trait is a functional advantage. I believe the only way that a species can truly re-evolve traits is that the trait that has been re-evolved needs to be on a functional basis. The functional basis is that under Dollo’s law even if a limb has arisen That limb would need to be functional i. e. have a selection pressure causing this to be an advantage evolutionally.

This is the only way that I can see of being able to out rightly say if something is against Dollo’s law.

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